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COMMENTS ON *"ORNITHOCHEIRUS HILSENSIS"* KOKEN, 1883 – ONE OF THE EARLIEST DINOSAUR DISCOVERIES IN GERMANY

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Abstract

Based on a detailed morphological comparison of the original figures, the lost holotype of *"Ornithocheirus hilsensis"* is identified as the distal part of the proximal pedal phalanx from digit I of a large-sized theropod. The distinctness in the morphology of the distal epiphysis of this element from that present in the manus and in pedal digits II-IV of most theropods may have contributed to the ambiguous interpretation of this specimen in the course of discussion since the 1880s. Features that have been interpreted as indicating pneumaticity – that would support a pterosaur affiliation – can be alternatively explained by taphonomic and diagenetic processes. Aside of this unresolved question, the published information do not indicate the presence of any pterosaur synapomorphies. Although clearly a *nomen dubium, "Ornithocheirus hilsensis"* is a precious record of a large-sized theropod near the Valanginian/Hauterivian boundary of Central Europe. It is furthermore of significance as one of the historically earliest documented remains of a dinosaur from Germany.

Introduction

The relationships of the purported pterosaur taxon *Ornithocheirus hilsensis* Koken, 1883 were controversial from the time of its first description, as it was subsequently interpreted to represent a theropod dinosaur. It was created by Koken (1883) for a bone fragment from the Valanginian-Hauterivian of northern Germany, that he interpreted to represent the distal end of a pterosaur metacarpal. However, following immediately its original publication, Koken's assessment was controversial and it was suggested that the holotype referred to a theropod dinosaur (Meyer, 1884; Williston, 1885, 1886). This interpretation is currently prevailing (*e.g.* Wellnhofer, 1991), although it was never rigorously justified. The arguments by Koken (1883, 1885, 1886) against a theropod origin were never comprehensively invalidated, and as of the 21st century the taxon is still occasionally listed as a potential pterosaur (*e.g.* Barrett *et al.*, 2008). Furthermore, the difficulties of the early investigators to identify unambiguous synapomorphies to support one of the competing systematic assignments are puzzling, and contributed to the long lasting uncertainty about its status. As the specimen is lost, the present contribution understands itself as a rather theoretical approach to the discussion. The present work is based on knowledge about the appendicular osteology of theropod dinosaurs and pterosaurs gathered since the late 19th century, unknown at the time of the first description, opening up new perspectives in its interpretation. In any way the record still holds relevance, as it was found during the early years of vertebrate palaeontology in Germany, and both, pterosaurs as well as dinosaurs, are rarities in the respective stratum and region.

Historical Background

Koch and Dunker (1837: 56) mentioned a *"Theil vom Oberschenkelknochen eines grossen krokodilartigen Thieres",* belonging to a small collection of vertebrate fossils from the "Neocomian" of the Hils mountains (Fig. 1) in the private collection of Friedrich Carl Ludwig Koch. Most of this collection (with the exception of two fish vertebrae) was not illustrated and nothing was described in detail. Koken (1883) restudied it and was able to identify most of Koch and Dunker's material. However, he chose to redescribe solely the purported 'thigh bone of a crocodile-like animal' which he attributed to a pterosaur - *Ornithocheirus hilsensis* - and an isolated crocodyliform tooth, that he included in the hypodigm of his new taxon *Enaliosuchus macrospondylus* Koken, 1883 (see Sachs *et al.*, 2020).

Koken (1883) reassessed the 'thigh bone' as the distal end of a wing metacarpal (digit IV). He based his comparisons largely on descriptions of the diverse assemblage of fragmentary pterosaur remains from the Lower Cretaceous of England (*e.g.* Mantell, 1846; Owen, 1851; Seeley, 1870), emphasizing the distinct morphology of pterosaur wing metacarpals and general similarities to material figured by Owen (1851: pl. 32, figs. 4, 5). Albeit admitting 'differences' to the pterosaur material 'at the first glance', he was nevertheless convinced that "a confusion with the closely related dinosaurs is not possible" (Koken, 1883: 827). His assignment to the genus *Ornithocheirus* Seeley, 1869 was largely based on stratigraphic grounds, as the material of other species then referred to this genus did not include a metacarpal (Seeley, 1869, 1870, 1881).

One year after Koken's original description, his conclusions were challenged by Otto Meyer in an open letter to Wilhelm Dames (Meyer, 1884), who noted that the morphology of the distal articular surface was not similar to that of any pterosaur, and that this bone indeed represented the phalanx of a theropod dinosaur. Koken (1885), in an open letter to Emanuel Kayser, replied that he did not consider the differences to other pterosaur metacarpals important and that the strong pneumaticity of the bone was not supportive for a theropod origin.

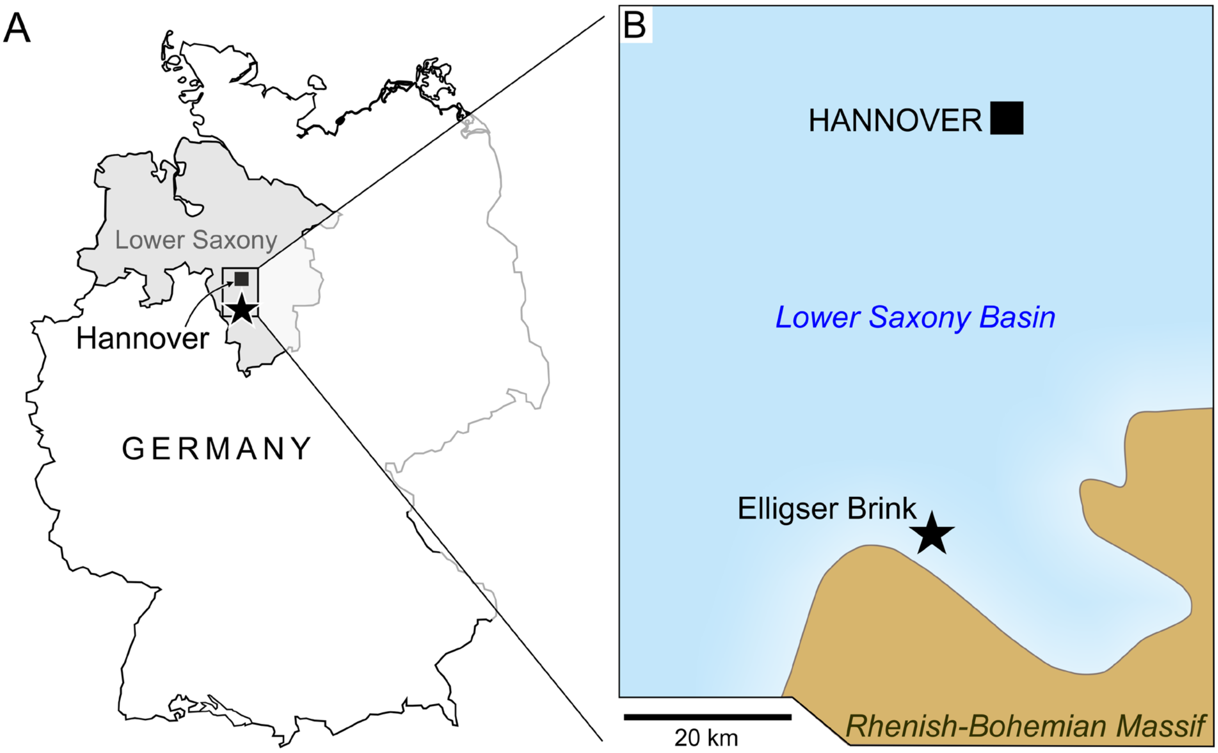
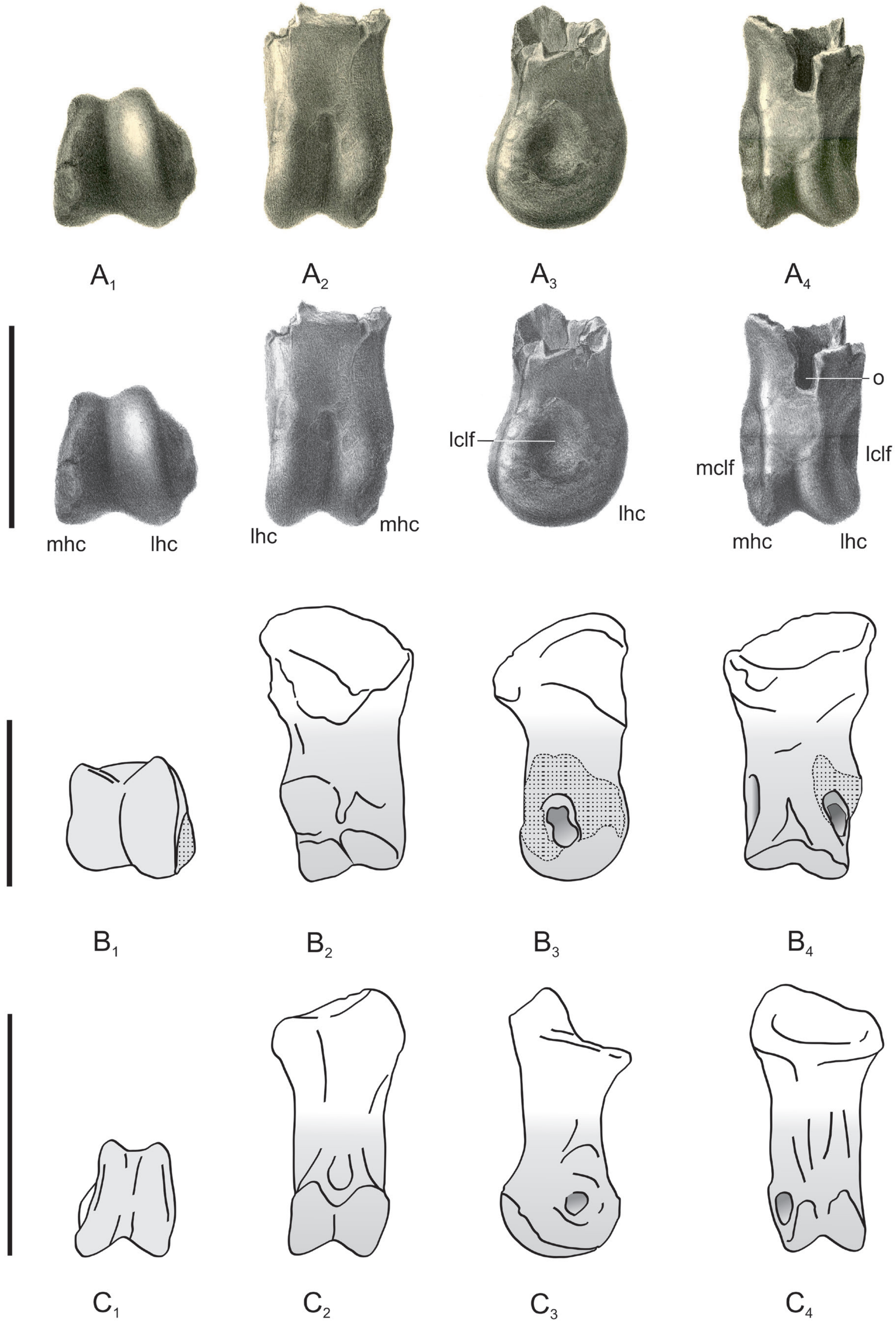


Figure 1. A) Location of the Elligser Brink locality in the Hils mountains (asterisk) of southern Lower Saxony (frame); B) Palaeogeography of southern Lower Saxony during the Hauterivian (after Mutterlose, 1984), indicating the near-shore position of the Elligser Brink.

His view was again challenged by Samuel Williston (1885, 1886), who supported Meyer's arguments in favour of a theropod origin, being firm in his assertion that the specimen was similar to theropod phalanges. Koken (1886) fiercely rebutted the arguments of Williston, denouncing his objections as based on incomplete quotation of his original description and upheld his pterosaur assignment for the specimen. He expanded upon his argument of pneumaticity by suggesting that a slit visible at the broken, proximal end representa a pneumatic foramen. The dispute became quite polemic, highlighting the importance that was given to this matter by the contemporaneous students of the subject (see also the overview by Dames, 1886). However, following the exchange of arguments, not always within the boundaries of courtesy, no conclusion or common agreement was achieved.

In the following century, the specimen was more or less forgotten. Wellnhofer (1978, 1980) listed *O. hilsensis* as a questionable species of *Ornithocheirus* although he noted that it lacked the characteristic grooves anteroventrally to both distal condyles, which are present in all known pterosaurs to allow close folding of the wing finger to the zeugopodium and metacarpal (Wellnhofer, 1978). Later he adopted the view of Meyer (1884) and considered it as belonging to a theropod (Wellnhofer, 1991, 1993) without further discussion. Barrett *et al.* (2008) referred to the fossil as a questionable pterosaur.

▽ *Figure. 2. Right pedal phalanx I-1 of various non-avian theropods. A)* "Ornithocheirus hilsensis" *Koken, 1883, holotype (lost), Valanginian-Hauterivian of Lower Saxony, Germany (from: Koken, 1883: pl. XXIII, figs. 2a-d) top row: unaltered reproduction from the original plate, lower row: explanatory figure; B)* Allosaurus fragilis Marsh, 1877, *Tithonian of the western USA (from Hattori, 2016, inversed from left side, redrawn by the author); C)* Deinonychus antirrhopus Ostrom, 1969, *Aptian-Albian of Montana, USA (from Hattori, 2016, redrawn by the author). A1), B1), C1) in distal views, A2), B2), C2) in flexor views, A3), B3), C3) in lateral views, and A4), B4), C4) in extensor view. Abbreviations: lclf – lateral colateral ligament fossa; lhc – lateral hemicondyle; mclf – medial colateral ligament fossa; mhc – medial hemicondyle: o – opening interpreted by Koken (1886) as pneumatopore. Grey-shaded parts in B) and C) correspond to the preserved part in A); dotted areas indicate damaged bone surface. Scale bars equal 5 cm.*


A1
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B1
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C2
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Systematic palaeontology

Dinosauria Owen, 1842
Theropoda Marsh, 1884

“Ornithocheirus hilsensis” Koken, 1883
(*nomen dubium*)

1837	*“krokodilartiges Thier”*; Koch and Dunker (p. 56 [*fide* Koken, 1883: 824f.])
1883*	*Ornithocheirus hilsensis* nov. sp.; Koken (p. 824, pl. XXIII, fig. 2)
1884	*Ornithocheirus hilsensis* Koken; Meyer (p. 664)
1885	*Ornithocheirus hilsensis* Koken; Koken (p. 214)
1885	*Ornithocheirus hilsensis* Koken; Williston (p. 628)
1886	*Ornithocheirus hilsensis* Koken; Koken (p. 21)
1886	*Ornithocheirus hilsensis* Koken; Williston (p. 282)
1978	*“Ornithocheirus” hilsensis* Koken, 1883; Wellnhofer (p. 58)
1980	*“Ornithocheirus” hilsensis* Koken, 1883; Wellnhofer (p. 110)
1991	*Ornithocheirus hilsensis*; Wellnhofer (p. 117)
1993	*Ornithocheirus hilsensis*; Wellnhofer: (p. 117)
2008	?Pterosauria indet. (=*Ornithocheirus hilsenis* [sic!]); Barrett *et al.* (p. 81)

Material

Holotype and only known specimen: a partial proximal phalanx of right pedal digit I, originally identified as metacarpal IV of a pterosaur (Koken, 1883). Formerly in the collection of Friedrich C.L. Koch, Grünenplan, current repository unknown, possibly lost.

Horizon and locality

‘Elligserbrink-Schicht’ (Koken, 1883), corresponding to the upper Astierien Beds/lower Endemoceras Beds (Burri, 1956), Stadthagen Formation, Minden-Braunschweig Group (Erbacher, *et al.*, 2014), uppermost Valanginian to lowermost Hauterivian (Mutterlose & Bornemann, 2000), Lower Cretaceous. Elligser Brink hill (probably the now abandoned iron ore mine), 0.6 km S of Delligsen, Lower Saxony, northern Germany (Fig. 1, Koken, 1883: 826).

Descriptive Notes

The position of the hallux relative to digits II to IV in the pes of theropods may vary, and potentially depends on the phylogenetic position (Hattori, 2016). Due to this reason, terminologies like ‘dorsal’ vs. ‘ventral’ or ‘plantar’ vs. ‘palmar’ are avoided here for skeletal elements of the hallux. They are replaced by a reference to the ‘flexor’ (comparable to ventral or plantar in digits II to IV) and ‘extensor side’ (comparable to dorsal in digits II to IV), respectively, as these assignments are neutral to the spatial orientation of the hallux.

Without the original specimen it seems problematic to assess its exact affinities. However, the illustration in Koken (1883: pl. XXIII, fig. 2) can be considered reliable. This is based on the fact that the illustrations in this work of other, preserved specimens, are accurate (pers. obs.). This accuracy allows for a synthesis of observations from the figures with the written description of the specimen by Koken (1883) to provide a base for further discussion.

The preserved length was “about” 55 mm. The maximum width and height of the distal epiphysis was 34 and 38 mm respectively (Koken, 1883: 825). Most distinctive is the morphology of the distal articulation surface. This surface encompasses an arc of about 190 degrees between the extensorial and flexorial side of the bone. The hemicondyles are elliptical in lateromedial view. They expand nearly symmetrical into both, the flexorial as well as extensorial directions, but the epiphysis is slightly inclined in extensorial direction. On the flexor side the articulation surface reaches slightly more proximally on the shaft than it does on the extensor side and merges smoothly with the shaft's surface. On the extensor side the articular surface terminates in an axial circular depression, marking the insertion of the digit extensor tendon. The distal condyles are compressed dorsoventrally in lateral aspect. The distal articular surface is asymmetrically subdivided by a deep, v-shaped, fossa trochlearis, resulting in a medial hemicondyle that is distinctly narrower mediolaterally than the lateral hemicondyle, and a strongly ginglymoid joint. Both hemicondyles project distally equally far. The distal articular surface has a trapezoidal outline, being narrower mediolaterally on the extensor side then on the flexor side. Deep colateral ligament fossae are present on the lateral and medial face of the distal epiphysis. They are located in a slightly eccentric position towards the extensor side, and circular in outline with a rugose margin. The distal epiphysis is twisted slightly laterally and towards the extensor side with respect to the shaft's longitudinal axis. The shaft has a trapezoidal cross-section with the a diameter that is widest mediolaterally. The shaft widens mediolaterally towards the broken proximal end.

Discussion

Although recognizable as an archosaurian autopodial element, the specimen exhibited some peculiarities which can explain the heated controversy following its original description. According to Koken (1883, 1885, 1886), two characters were crucial to his interpretation as a pterosaur: (1) a supposed strong pneumaticity, and (2) the 'typical shape' of the distal condyle, that he deemed corresponding to the highly derived morphology in the metacarpal IV of pterosaurs.

Regarding the pneumaticity, the original condition cannot be assessed without the original material. It is possible that the element was pneumatic, as interpreted by Koken. Alternatively it is possible that a more extensive substantia spongiosa was lost to taphonomical or diagenetic effects. It is not uncommon that vertebrate remains from argillaceous strata are affected by degradation from pyritization and subsequent mechanical destruction (Larkin, 2011; pers. obs.). Such effects can act selectively for the delicate spongiose tissue, preserving mostly the substantia compacta. Koken does not state the thickness of the substantia compacta as preserved, but his figure indicates indeed a relatively thin wall enclosing a large central cavity of the bone. The same is true for the narrow, subrectangular incisure in the extensor surface, claimed by Koken (1886) as a pneumatopore. It can easily be interpreted as a post-mortem damage, as the lateral view provided by Koken also shows extensive fracturing of the incomplete proximal end of the bone. These questions cannot be assessed without access to the original specimen. Anyhow, as already Williston (1885) pointed out, hollow autopodial elements commonly occur in theropods (compare *e.g.* White *et al.*, 2012, 2016) and do not preclude an identification as phalanx or even as a weight-bearing phalanx. True pneumaticity (i.e. the presence of a pneumatopore and invasion of the bone by an air sac), however, is not known from distal limb bones in theropods (Benson *et al.*, 2012). Given the morphological considerations below, taphonomic and diagenetic effects are considered more probable to explain the apparent 'thin-walled' condition than to be an indication of true pneumaticity.

Aside of the apparent hollowness, the overall morphology supports an identification as an archosaur phalanx, and the size and lateromedial compression of the distal epiphysis is indicative of a theropod. Anyhow, with regard to the morphology of the distal condyles, the arguments of Koken to reject a theropod affinity can be followed when comparing it to the phalangeal elements of manual digits II and III and pedal digits II to IV of most theropods. In most phalanges of the manus and the pes, the proximodistal axis of the distal condyles is oriented parallel or slightly in flexorial direction in relation to the proximodistal axis of the shaft (*e.g.* Brochu, 2003; Gilmore, 1920; Madsen, 1976; Ostrom, 1969; Currie & Carpenter, 2000; Gishlick & Gauthier, 2007; Galton *et al.*, 2015; Malafaia *et al.*, 2019; White *et al.*, 2012, 2016). Exceptions are some taxa with hyperextensorial digits, including the megaraptorid *Megaraptor namunhuaiquii* Novas, 1998 (manual digit I, Novas *et al.*, 2016), the abelisauroid *Ligabueino andesi* Bonaparte, 1986 (manual digit III?, Agnolin & Chiarelli, 2009), dromaeosaurids (pedal digit II, *e.g.* Ostrom, 1969) and troodontids (pedal digit II; *e.g.* Zanno *et al.*, 2011), in which the distal epiphyses of a least some phalanges are also oriented in extensorial direction.

The holotype of *"Ornithocheirus hilsensis"* differs from most phalangeal elements – manual as well as pedal – by the smooth proximal transition of the hemicondylar ridges into the shaft, forming a gentle curvature. In these, the hemicondylar ridges meet with the shaft proximally steeply, in a rather blunt angle, especially on the flexor side (*e.g.* Brochu, 2003; Gilmore, 1920; Madsen, 1976; Ostrom, 1969; Currie & Carpenter, 2000; Galton *et al.*, 2015; Malafaia *et al.*, 2019; White *et al.*, 2012, 2016). In the manus, extension is limited by a transverse ridge or bulge on the extensional end of the trochlear groove (*e.g.* Galton, 1971; Ostrom, 1969; Gishlick & Gauthier, 2007; White *et al.*, 2012), that appears to be not present in *"O. hilsensis"*. In proximal pedal phalanges of digits II to IV the distal epiphysis is typically much less compressed mediolaterally and wider than high, while this ratio becomes more equal in distal elements (*e.g.* Brochu, 2003; Gilmore, 1920; Madsen, 1976; Ostrom, 1969; Currie & Carpenter, 2000; Gishlick & Gauthier, 2007; Galton *et al.*, 2015; Malafaia *et al.*, 2019; White *et al.*, 2016). The distal articulation surface can be directed in extensional direction in proximal phalanges (to allow increased extension of the proximal foot) but are generally facing in anterior to flexorial direction in the distal elements (*e.g.* Madsen, 1976; Galton *et al.*, 2015; Malafaia *et al.*, 2019; White *et al.*, 2016). Occasionally the penultimate pedal phalanges can show a slight extensorial inclination of the distal articulation surface, articulating with the unguals (e.g. Malafaia et al., 2019: fig. 10, phalanx IV-4). A further exception is the modified distal articular surface to phalanx II-2 in dromaeosaurids that articulate with the raptorial ungual (Ostrom, 1969, Fowler *et al.*, 2011). However, in this case the distal condyle is distinctly wider then high. The epiphysis in pedal phalanges of digits II to IV is generally proximodistally shortened, and higher than long.

The mosaic of characters distinguishes the holotype of *"O. hilsensis"* from typical manual phalanges of digits II and III and pedal phalanges of digits II to IV of theropods. The overall best conformity exists to the phalanges I-1 of the manus and the pes. However, although a "flattened proximoventral extension of the articular condyles" as found typical for theropod manual phalanx I-1 by Gishlick & Gauthier (2007:571f, fig. 2) is also present in the holotype of *"O. hilsensis"*, it differs from most manual elements by the absence of an intercondylar transverse ridge on the extensor side and the presence of equally developed flexorial and extensional expansions of the hemicondyles. In manual phalanges the flexorial expansion of the distal hemicondyles is generally larger than the extensorial one (*e.g.* Madsen, 1976; Gishlick & Gauthier, 2007; Barta *et al.*, 2018; White *et al.*, 2012). The characteristics of the holotype of *"O. hilsensis"* are more congruent with the morphology of pedal phalanx I-1 in some theropods (Hattori, 2016). Pedal phalanx I-1 differs from those of the weight-bearing digits by being more gracile, having a laterally compressed distal articular surface, that is higher than wide, and longer then high. Aside of the gentle transition of the hemicondyles proximally into the shaft, the broad and robust shaft compared to the distal epiphysis, and the expansion of the distal hemicondyles to the extensor side, this identification is supported by the lateral curvature of the distal trochlea. Such a curvature is observed in various theropods, including the allosaurid *Allosaurus fragilis* Marsh, 1877 (weakly to the medial side, Hattori, 2016: fig 3b, 3d), an unnamed carcharodontosaur (weakly to the medial side, Malafaia *et al.*, 2019: fig. 8), the oviraptorid *Citipati osmolskae* Clark *et al.*, 2001 (to the lateral side, Hattori, 2016: fig. 6b, 6d), the dromaeosaurid *Deinonychus antirrhopus* Ostrom, 1969 (to the lateral side, Hattori, 2016: fig. 7b, 7d), and the troodontid *Talos sampsoni* Zanno *et al.*, 2011 (to the lateral side, Hattori, 2016: fig. 10b, 10d, compare also Zanno *et al.*, 2011). No curvature is observable in the basal tetanuran *Poekilopleuron bucklandii* Eudes-Deslongchamps, 1838 (Eudes-Deslongchamps, 1838; pl. 8, fig. 8, compare also Allain & Chure, 2002) and in the tyrannosaurid *Tarbosaurus bataar* (Maleev, 1955) (Hattori, 2016: Fig. 4b, 4d). A lateral curvature is supportive to a slight pronation of the ungual phalanx during flexion that contributes to the grasping function of the foot as reconstructed by Fowler *et al.* (2011). The known distribution of this character may provoke the question whether such a weak pronation during flexion of ungual I is a diagnostic trait in non-avian maniraptorans in general. However, due to data deficiency, such a decision appears premature. In the holotype of *"O. hilsensis"* the morphology of the distal condyle as well as the presence of colateral ligament fossae are not in accordance to the characteristics of a pterosaur metacarpal IV (*e.g.* Wellnhofer, 1978), and is therefore identified unequivocally as phalanx I-1 of a theropod.

Hattori (2016) described the hallux of several theropod clades in detail and demonstrated a considerable diversity of morphologies of phalanx I-1 across them although they share basic characteristics as outlined above. *"O. hilsensis"* shows some similarities with the allosaurid *Allosaurus fragilis* Marsh, 1877 (Fig. 2B) in the relative posterodorsal and posteroventral extent of the distal articular surface, hemicondylar asymmetry, and mid-shaft proportion, as well as overall size. It differs, however, in the extensorial expansion of the distal epiphysis, the symmetrical distal extension of the hemicondyles, the circular shape of the colateral ligament fossae, and the lateral curvature of the distal trochlea. In these characteristics it compares more closely to the dromaeosaurid *Deinonychus antirrhopus* Ostrom, 1969 (see Hattori, 2016, Fig. 2C). A good conformity exists also to phalanx I-1 of an unnamed carcharodontosaurian from the Upper Jurassic of Spain (Malafaia *et al.*, 2019). This mosaic of characters – in conjunction with a lack of information for the morphology of phalanx I-1 across many theropod taxa – indicates that a sufficient diagnosis of *"O. hilsensis"* is not possible, and the taxon has to be regarded a *nomen dubium*. Although there exist a number of skeletal records for moderately to large-sized theropods from various clades in the Lower Cretaceous of Europe (*e.g.* Owen, 1849-1884; Pérez-Moreno *et al.*, 1993; Hutt *et al.*, 2001; Allain, 2005; Brusatte *et al.*, 2008; Ortega *et al.*, 2010), none of them preserve pedal phalanx I-1 for a direct comparison.

However, it can be affirmed that *"O. hilsensis"* definitely lacks pterosaurian synapomorphies (Wellnhofer, 1978), confirming its referral to Theropoda (following Meyer, 1884). The difficulties of identification experienced already by Koken (1883) can be explained by the fact that the morphological peculiarities of phalanx I-1 in non-avian theropods were not well documented at the end of the 19th century, contributing to an ongoing confusion over the specimen in later studies.

The fossil documents the presence of an large-sized theropod in the Valanginian-Hauterivian of northern Germany from a period in which the theropod record is excruciatingly sparse, especially in Europe. The specimen was transported from a terrestrial environment at the shores located closely to the south (Mutterlose, 1984: Fig. 1B). The concentration of aquatic and terrestrial vertebrate remains in a distinct single layer, intercalated to the marine claystone (Koch & Dunker, 1837), suggests that the type horizon may have formed as a storm-generated bonebed.

The specimen also has some historical interest, as it was for the first time mentioned in the same year when *Plateosaurus engelhardti* von Meyer, 1837 was described. Although it became identified correctly only much later, it therefore rivals the latter to be the first dinosaur discovered in Germany.

Conclusions

Based on morphology, the probably lost holotype of *"Ornithocheirus hilsensis"* is unambiguously identified as the distal part of the proximal pedal phalanx from right digit I of a large-sized theropod. The distinctness in the morphology of the distal epiphysis of this element from that present in the manus and in pedal digits II-IV of most theropods may have contributed to the ambiguous interpretation of this specimen in in the course of discussion since the 1880s.

The purported pneumaticity of the bone – a main argument in favour of a pterosaur affiliation – cannot be ascertained without the original specimen. In the light of the morphological congruence to theropod phalanges, alternative taphonomic and diagenetic explanations for the apparently thin substantia compacta and missing substantia spongiosa appear more probable than the presence of true pneumaticity.

Although clearly a *nomen dubium*, *"Ornithocheirus hilsensis"* is a precious record of a large theropod near the Valanginian/Hauterivian boundary of Central Europe. Mentioned for the first time in 1837, it is furthermore of significance as one of the historically earliest documented remains of a dinosaur from Germany.

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