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Citation for published version:
Ezcurra, MD, Marke, D, Walsh, S & Brusatte, S 2023, 'A revision of the ‘coelophysoid-grade’ theropod specimen from the Lower Jurassic of the Isle of Skye (Scotland)', *Scottish Journal of Geology*, vol. 59. https://doi.org/10.1144/sjg2023-012

Digital Object Identifier (DOI):
10.1144/sjg2023-012

Link:
Link to publication record in Edinburgh Research Explorer

Document Version:
Peer reviewed version

Published In:
Scottish Journal of Geology

A revision of the ‘coelophysoid-grade’ theropod specimen from the Lower Jurassic of the Isle of Skye (Scotland)

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Abbreviated title: Jurassic theropod from the Isle of Skye

Abstract. The broadest diversification of early predatory dinosaurs is represented by the 'coelophysoid-grade' neotheropods, but their Hettangian–Sinemurian (ca. 191–201 Ma) record is scarce worldwide. More information is needed to shed light on the evolution of this dinosaur group after the Triassic-Jurassic mass extinction (ca. 201 Ma). Here we revisit the anatomy and phylogeny of one of these earliest Jurassic neotheropod specimens, an isolated partial tibia from the lower Sinemurian of the Isle of Skye (Scotland) that was previously identified as probably closely related to *Liliensternus liliensterni* and coelophysids. However, we found that the Skye specimen is positioned in the branch leading to Averostra (Ceratosauria + Tetanurae), in a polytomy with *Sarcosaurus woodi* from the late Hettangian–lower Sinemurian of central England and a clade composed of *Tachiraptor admirabilis* and Averostra. The morphology of the Skye specimen is congruent with that of referred specimens of *Sarcosaurus woodi*, but because it probably represents a skeletally immature specimen, we assign it to cf. *Sarcosaurus woodi*. The Skye specimen increases the number of averostran-line neotheropod specimens recorded in the Lower Jurassic of Europe and current evidence indicates that these forms, and not coelophysoids, were relatively common in this part of the world at that time.

Keywords. Dinosauria, Neotheropoda, Sinemurian, United Kingdom, phylogeny.

The end-Triassic mass extinction event (ca. 201 Ma) is one of the five major biotic crises that life faced on Earth (Raup and Sepkoski, 1982). This mass extinction was an inflexion point for the continental tetrapod assemblages because several common Triassic groups went extinct (e.g., aetosaurs, phytosaurs, 'rauisuchians', dicynodonts). Although dinosaurs had already undergone at least 30 million years of evolution when this biotic crisis occurred and some latest Triassic assemblages were already numerically dominated by them (e.g., upper levels of the Los Colorados Formation, Trossingen Formation and Kettgau Formation; Bonaparte, 1972; Sander, 1992), dinosaurs established a clear ecological dominance among medium to large-sized forms after the mass extinction (see reviews by Brusatte et al., 2010; Langer et al., 2010). Also, some dinosaur groups that were extremely rare—or perhaps had not yet appeared—during the Triassic became abundant in the Early Jurassic, such as ornithischians (Irmis et al., 2007; Agnolin and Rozadilla, 2018; Baron, 2019; Desojo et al., 2020). Sauropodomorph dinosaurs—seemingly the most common dinosaurs of the Triassic outside of North America—seem to have not been substantially affected by the end-Triassic mass extinction, in which variations after the biotic crisis were more related to changes of pre-existing lineages rather than the emergence of distinct clades or body plans (Apaldetti et al., 2021). These macroevolutionary patterns are less clear in the case of other Late Triassic–Early Jurassic dinosaurs, particularly theropods.

Theropods—the group of mostly carnivorous dinosaurs that later gave rise to taxa such as *Tyrannosaurus rex*, *Velociraptor mongoliensis*, and birds—originated in the Triassic as generalized species with the size of modern dogs and horses. The more derived neotheropods first proliferated in the Late Triassic and endured the end-Triassic mass extinction. Coelophysoids represent the bulk of neotheropod diversity during the Late Triassic, with at least six nominal species and some other still unnamed forms (Spiekman et al., 2021). Several species that were previously classified within Coelophysoidea are now recovered as successive sister taxa to Averostra (i.e., Certatosauria + Tentanurae) in phylogenetic analyses (e.g., *Dilophosaurus wetherilli*, *Cryolophosaurus ellioti*, *Gojirasaurus quayi*) (e.g., Yates, 2005; Nesbitt et al., 2009; Ezcurra, 2017; Marsh and Rowe, 2020; Spiekman et al., 2021). Coelophysoids and these averostran-line species are informally included among the 'coelophysoid-grade' theropods. The number of recognized averostran-line species has increased in recent years and at least some early-diverging members of this branch are present in the Late Triassic (*Zupaysaurus rougieri*, *Gojirasaurus quayi*, *Notatesseraeraptor frickensis*) (Yates, 2005; Ezcurra, 2017; Zahner and Brinkman, 2019; Marsh and Rowe, 2020; Ezcurra et al., 2021). Thus, a reassessment of the anatomy and phylogeny of Late Triassic and Early Jurassic neotheropod specimens is needed to shed light on the early evolution of the clade.

One of these neotheropod specimens that requires a revision is an isolated partial tibia originally described by Benton et al. (1995), which was the first Early Jurassic dinosaur reported from Scotland. Furthermore, jointly with a Middle Jurassic sauropod limb bone described by Clark et al. (1995) in the same journal issue, this tibia was one of the first two dinosaur bones ever reported from Scotland. The tibia (NMS G.1994.10.1; Figs. 1, 2) was collected from the lower Sinemurian levels of the upper Broadford Beds Formation of the Isle of Skye, Scotland [see Benton et al. (1995) for more details about the geological setting of the specimen]. Benton et al. (1995) identified NMS G.1994.10.1 as a right tibia lacking its distal end and interpreted it as a ceratosaurian theropod, a group which at that time included 'coelophysoid-grade' species and ceratosaurian averostrans (Rowe, 1989; Rowe and Gauthier, 1990). This specimen was sporadically mentioned in the literature in subsequent years. Carrano and Sampson (2004) briefly reassessed NMS G.1994.10.1 and concluded that the specimen is a left tibia originally interpreted upside down. For example, the structure originally interpreted as the cnemial crest is the facet for reception of the ascending process of the astragalus. Carrano and Sampson (2004) did not provide a redescription and noted similarities with *Coelophysis*, ‘*Syntarsus*’, and *Liliensternus*, identifying it as an indeterminate member of Coelophysoidea (a group that at that time included several averostran-line neotheropods, e.g., *Dilophosaurus wetherilli*, *Sarcosaurus woodi*).

As a result of the uncertainty around the phylogenetic relationships of the neotheropod tibia from the Lower Jurassic of the Isle of Skye, here we revisit its anatomy and affinities in the light of the new information published in the last 20 years. This revision is part of a broader study of the Jurassic dinosaurs of Scotland by our research group. The overwhelming majority of these fossils are Middle Jurassic in age and found on the Isle of Skye (see review in Clark, 2018), and include sauropod bones and teeth (Clark et al., 1995; Liston, 2004; Barrett, 2006; Clark and Gavin, 2016), theropod bones and teeth (Brusatte and Clark, 2015; Wills et al., 2014; Young et al., 2019), and probable thyreophoran limb material (Clark, 2001). Far more abundant, however, are trackways, including several newly discovered sites that yield handprints and footprints of sauropods, theropods, stegosaurs, and ornithopods (Brusatte et al., 2016; dePolo et al., 2018, 2020). The neotheropod tibia remains the sole Early Jurassic dinosaur bone definitively known and described from Scotland, making its identification and interpretation all the more important.

Institutional abbreviations

AMNH, American Museum of Natural History, New York, USA; IVIC, Colección Paleontológica del Centro de Ecología, Instituto Venezolano de Investigaciones Científicas, Caracas, Venezuela; LPRP/USP, Laboratório de Paleontologia de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto, Brazil; MACN-Pv, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’, Paleovertebrados, Buenos Aires, Argentina; HMN, Museum für Naturkunde der Humboldt Universität, Berlin, Germany; MNA, Museum of

Northern Arizona, Flagstaff, USA; MPEF, Museo Paleontológico Egidio Feruglio, Trelew, Argentina; NHMB, Natural History Museum of Zimbabwe, Bulawayo, Zimbabwe; NHMUK PV, The Natural History Museum, Palaeontology Vertebrates, London, UK; NMS, National Museums Scotland, Edinburgh, UK; PULR-V, Paleontología, Universidad Nacional de La Rioja, Vertebrados, La Rioja, Argentina; PVL, Paleontología de Vertebrados, Instituto 'Miguel Lillo', San Miguel de Tucumán, Argentina; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; UCM, University of Colorado Museum, Boulder, USA; UCMP, University of California Museum of Paleontology, Berkeley, USA; USNM, National Museum of Natural History (formerly United States National Museum), Smithsonian Institution, Washington D.C., USA; WARMS, Warwickshire Museum, Warwick, UK.

MATERIAL AND METHODS

Phylogenetic analysis

The phylogenetic relationships of the neotheropod tibia from the Lower Jurassic of the Isle of Skye were tested using the phylogenetic dataset of early theropods and close relatives originally published by Nesbitt *et al.* (2009) and iteratively modified by several authors (e.g., Ezcurra and Brusatte, 2011; You et al., 2014; Nesbitt and Ezcurra, 2015; Martill et al., 2016; Ezcurra, 2017; Martínez and Apaldetti, 2017; Marsh et al., 2019; Marsh and Rowe, 2020; Ezcurra et al., 2021; Novas et al., 2021; Spiekman et al., 2021; Kirmse et al., 2023). Here we added NMS G.1994.10.1 and a new character to the most recent iteration of the dataset (Spiekman et al., 2021) (Supplementary Information). The resulting matrix consists of 387 active characters [characters 252 and 352 were deactivated following Novas et al. (2021)] and 59 active terminals. The outgroup choice follows Nesbitt *et al.* (2009) and the following multistate characters were ordered: 9, 18, 30, 67, 128, 129, 174, 184, 197, 207, 213, 219, 231, 236, 248, 253, 254, 273, 329, 343, 345, 347, 349, 354, 366, 371, 374, 377–379, 383 and 384. The data matrix was analysed under equally weighted parsimony using TNT 1.6 (Goloboff and Morales, 2023). A heuristic search of 1,000 replications of Wagner trees (with random addition sequence) followed by TBR branch swapping (holding 10 trees per replicate) was performed. Branches with a maximum possible length of zero among any of the recovered most parsimonious trees (MPTs) were collapsed (rule 3 of Swofford and Begle, 1993; Coddington and Scharff, 1994). As measures of branch support, decay indices (= Bremer support) (Bremer, 1988, 1994) and bootstrap resampling frequencies (Felsenstein, 1985) were calculated, performing 10,000 pseudoreplications in the latter analysis. Both absolute and GC (i.e., difference between the frequency whereby the original group and the most frequent contradictory group are recovered in the pseudoreplications; Goloboff et al., 2003) bootstrap frequencies are reported. Finally, analyses forcing topological constraints were conducted to find the minimum number of steps necessary to force alternative suboptimal positions for NMS G.1994.10.1.

3D model of the specimen

A 3D model of NMS G.1994.10.1 was created using photogrammetry. A tripod mounted Nikon D5100 digital SLR camera with a Nikon 18-55mm VR lens was used to photograph the specimen under artificial lighting against a uniformly coloured and contrasting background. Sixty-four and 31 photographs were taken in a circular path around the specimen for two different orientations, respectively. The software Agisoft PhotoScan Professional edition version 1.0.3 was used to mask the backgrounds of the photographs and create 3D meshes using automated point picking and triangulation of point clouds. Five markers had to be used to generate the full 3D model because of problems during the mesh generation due to the dark surface of the specimen. Two markers were used to scale the specimen (error<0.001 mm). The final surface was textured in PhotoScan and exported as a .ply file. This file is available in the Supplementary Online Information.

SYSTEMATIC PALAEONTOLOGY

Archosauria Cope, 1869–1870 sensu Gauthier and Padian (1985)

Dinosauria Owen, 1842 sensu Padian and May (1993)

Theropoda Marsh, 1881 sensu Gauthier (1986)

Neotheropoda Bakker, 1986 sensu Sereno (1998)

cf. *Sarcosaurus woodi* Andrews, 1921

Material. NMS G.1994.10.1, isolated left tibia lacking its proximal region (Figs. 1, 2).

Ontogenetic stage. The only possible distinct indicator of skeletal maturity preserved in NMS G.1994.10.1 is the absence of co-ossification between tibia and astragalus. The co-ossification between these two bones occurs in specimens of Coelophysoidea (e.g., *Camposaurus arizonensis*, *Coelophysis bauri*, *Megapnosaurus rhodesiensis*, '*Syntarsus*' *kayentakatae*: Raath, 1977; Rowe, 1989; Ezcurra and Brusatte, 2011; Griffin, 2018) and Ceratosauria (e.g., *Ceratosaurus nasicornis*: USNM 4735; *Eoabelisaurus mefi*: MPEF-PV 3990; *Masiakasaurus knopfleri*: Carrano et al., 2002) with a considerable degree of skeletal maturity. Thus, its absence indicates that specimens of these clades were not fully skeletally mature (Tykoski, 2005; Griffin and Nesbitt, 2016; Griffin et al., 2021). However, under current phylogenetic schemes (e.g., Marsh et al., 2020; Novas et al., 2021; Spiekman et al., 2021), it is equally parsimonious to interpret the presence of such co-ossification as an apomorphy of Neotheropoda subsequently lost in Tetanurae or as independently acquired in Coelophysoidea and Ceratosauria. In this latter scenario, the presence of the tibia-astragalus co-ossification is optimized ambiguously in all non-coelophysoid, non-averostran species, even if a putative adult specimen of *Dilophosaurus wetherilli* (UCMP 77270) is interpreted as lacking such condition (see Tykoski, 2005). Indeed, our phylogenetic analysis recovers NMS G.1994.10.1 as a non-coelophysoid, non-averostran neotheropod (see below). In the scenario of two independent acquisitions of co-ossification between tibia and astragalus in early neotheropods, the absence of such condition in NMS G.1994.10.1 would not be an informative feature to assess its skeletal maturity. Therefore, the ontogenetic stage of this specimen should be considered unknown, although its size indicates that it probably was not, at least, an early juvenile (see Discussion).

Type locality and horizon. Heaste, Southern Strath, Isle of Skye, Highland, Scotland, UK. Upper levels of the Broadford Beds Formation, Lias Group, Early Jurassic (early Sinemurian) (Benton et al., 1995).

RESULTS

Description

We agree with Carrano and Sampson (2004) in the reinterpretation of NMS G.1994.10.1 as a left tibia lacking its proximal region (contra Benton et al., 1995). Thus, the cnemial crest, posterior hemicondyles of the proximal end, and the fibular crest are not preserved. However, we have located a photograph of the specimen as it was found in the field and it was originally more complete, preserving both ends, but more than half of the exposed surface of the bone had already eroded away, exposing the thin bony walls (Fig. 1). The bone was exposed mainly in posterior view and the currently missing end is distinctly more expanded than the preserved one, supporting the interpretation that the missing region was the proximal one. Moreover, the proximal end is asymmetric in posterior view, with a posteromedial hemicondyle more proximally developed than the posterolateral one, as occurs in other early neotheropods. The currently preserved total length of NMS G.1994.10.1 is 126.9 mm and its distal end has a transverse width of 21.0 mm and an anteroposterior depth of 14.7 mm. The photograph shows that approximately half of the bone is currently missing and originally should have had a complete length of 23–24 cm, being slightly shorter than the tibiae of the smallest referred specimen of *Sarcosaurus woodi* (29.6–29.7 cm: WARMS G667–690; Ezcurra et al., 2021).

The bone surface is generally well-preserved, but the posterior surface around mid-shaft and the posteromedial corner of the distal end are missing. The currently preserved portion of the tibia is distinctly medially bowed in anterior or posterior view, whereas it is straight in lateral or medial view and only its proximalmost region possesses an incipient anterior bowing. However, the degree of anterior curvature of the bone is probably underestimated because of the current absence of the proximal region of the bone. Distinctly anteriorly bowed tibial shafts are common among early neotheropods (e.g., *Liliensternus liliensterni*: HMN MB.R. 2175; *Megapnosaurus rhodesiensis*: cast of NHMB QG 1). The shaft of the tibia of NMS G.1994.10.1 has a subtriangular cross-section, with anteromedially, anterolaterally, and posteriorly facing, moderately rounded apices. The anterior surface of the shaft is gently transversely convex, whereas the posterior surface is distinctly more convex.

The distal end of the bone is transversely and very gently posteriorly expanded with respect to the shaft. The posterior expansion is a result of the presence of a thick, longitudinal posteromedial ridge (Fig. 2: pmr), a plesiomorphic condition among neotheropods (Nesbitt, 2011). The posteromedial ridge separates a transversely convex posteromedial surface from a flat to incipiently concave posterolateral surface. This ridge is well separated from the medialmost edge of the distal end, being positioned approximately midway between this edge and the tip of the posterolateral process (Fig. 3j: pmr), resembling the condition of coelophysids (e.g., *Coelophysis bauri*: AMNH unnumbered; *Megapnosaurus rhodesiensis*: Raath, 1977), *Liliensternus liliensterni* (HMN MB.R. 2175), *Gojirasaurus quayi* (HMN MB.R. 4232.1, cast of UCM 47221), *Zupaysaurus rougieri* (Ezcurra and Novas, 2007), *Dilophosaurus wetherilli* (Marsh and Rowe, 2020), and *Sarcosaurus woodi* (Ezcurra et al., 2021) (Fig. 3d–i). By contrast, this ridge is positioned distinctly closer to the medial edge of the distal end than to the distal tip of the posterolateral process in *Tachiraptor admirabilis* (LPRP/USP 0747, cast of IVIC-P-2867) and averostrans (e.g., *Ceratosaurus nasicornis*: USNM 4735; *Eoabelisaurus mefi*: MPEF-PV 3990; *Piatnitzkysaurus floresi*: MACN-Pv CH 895; *Allosaurus fragilis*: Madsen, 1976) (Fig. 3k, l). The posterolateral surface possesses a series of mainly longitudinally oriented, thin striations. The presence of the medial diagonal tuberosity (sensu Ezcurra and Brusatte, 2011) that is present in several coelophysoids (e.g., *Camposaurus arizonensis*, *Powellvenator podocitus*, *Megapnosaurus rhodesiensis*; Ezcurra and Brusatte, 2011; Ezcurra, 2017) cannot be determined in NMS G.1994.10.1 because the medial surface of the distal end of the tibia is damaged.

The anterior surface of the distal end of tibia possesses a facet for reception of the ascending process of the astragalus that is proximolaterally to mediodistally oriented at an angle of 27° with respect to the horizontal plane (Figs. 2, 3b: fap), resembling the condition in *Sarcosaurus woodi* (Ezcurra et al., 2021: 25°; Fig. 3c; this angle is ca. 38° in another referred specimen but such high angle could be the result of taphonomic distortion), *Cryolophosaurus ellioti* (Smith et al., 2007: fig. 19b: 24º), *Dilophosaurus wetherilli* (UCMP 77270: 23º), *Tachiraptor admirabilis* (LPRP/USP 0747, cast of IVIC-P-2867: 23º) and *Eoabelisaurus mefi* (MPEF-PV 3990: 24°). By contrast, this angle is lower in *Zupaysaurus rougieri* (PULR-V 076: 19º; Fig. 3A), *Liliensternus liliensterni* (HMN MB.R. 2175: ca. 17º), *Powellvenator podocitus* (PVL 4414-1: 18º), *Procompsognathus triassicus* (SMNS 12591: 17º), and coelophysines (e.g., *Camposaurus arizonensis*: UCMP 34498, 10º; *Coelophysis bauri*: AMNH unnumbered, 18º; *Megapnosaurus rhodesiensis*: cast of NHMB QG 1, 17º). The facet for reception of the ascending process of the astragalus of NMS G.1994.10.1 is similarly proximodistally developed and anteroposteriorly deep to those of *Sarcosaurus* *woodi* (Ezcurra et al., 2021; Fig. 3h, i) and *Tachiraptor admirabilis* (LPRP/USP 0747, cast of IVIC-P-2867; Fig. 3k), which indicate a higher and more laminar ascending process of the astragalus than in coelophysids (e.g., *Coelophysis bauri*: AMNH unnumbered; *Megapnosaurus rhodesiensis*: Raath, 1977), *Liliensternus liliesnterni* (HMN MB.R. 2175), *Gojirasaurus quayi* (HMN MB.R. 4232.1, cast of UCM 47221), *Zupaysaurus rougieri* (Ezcurra and Novas, 2007) and *Dilophosaurus wetherilli* (Marsh and Rowe, 2020) (Fig. 3d–g). By contrast, the facet for reception of the ascending process of the astragalus of NMS G.1994.10.1 is anteroposteriorly thicker than in averostran neotheropods (e.g., *Ceratosaurus nasicornis*: USNM 4735; *Berberosaurus liassicus*: Allain et al., 2007; *Piatnitzkysaurus floresi*: MACN-Pv CH 895) (Fig. 3l).

The anterior surface of the tibia immediately proximal to the facet for reception of the astragalar ascending process lacks the thick anterior diagonal tuberosity present in several coelophysoids (*Procompsognathus triassicus*, *Camposaurus arizonensis*, *Megapnosaurus rhodesiensis*, *Coelophysis bauri*; Ezcurra and Brusatte, 2011; Ezcurra 2017), *Lepidus praecisio* (Nesbitt and Ezcurra, 2015), and one referred specimen of *Sarcosaurus woodi* (Ezcurra et al., 2021). A longitudinal ridge extends along the lateral surface of the distal third of the tibia, resembling the condition of *Camposaurus arizonensis* (Ezcurra and Brusatte, 2011). The posterolateral process of the distal end is directly laterally oriented and it has a lobular profile in anterior or posterior view (Figs. 2, 3b: plp), as in *Sarcosaurus woodi* (Ezcurra et al., 2021), *Tachiraptor admirabilis* (Langer et al., 2014), *Gojirasaurus quayi* (HMN MB.R. 4232.1, cast of UCM 47221), *Powellvenator podocitus* (Ezcurra, 2017), *Megapnosaurus rhodesiensis* (Raath, 1977), *Dilophosaurus wetherilli* (Marsh and Rowe, 2020), and '*Syntarsus*' *kayentakatae* (MNA V2623). By contrast, some other early neotheropods have a posterolateral process with a tabular profile (e.g., *Coelophysis bauri*: Ezcurra and Brusatte, 2011; *Liliensternus liliensterni*: HMN MB.R. 2175; *Zupaysaurus* *rougieri*: Ezcurra and Novas, 2007; Fig. 3a). There is an inflexion that separates the more distally extended posterolateral process from the medial portion of the bone, as occurs in other early neotheropods (Nesbitt and Ezcurra, 2015; Ezcurra, 2017). The medial portion of the distal end has a poorly developed, sub-circular medial expansion (Figs. 2: mex, 3b) that resembles the condition in *Tachiraptor admirabilis* (LPRP/USP 0747, cast of IVIC-P-2867). This expansion is considerably less developed than that in averostrans (e.g., *Ceratosaurus nasicornis*: USNM 4735; *Eoabelisaurus mefi*: MPEF-PV 3990; *Piatnitzkysaurus floresi*: MACN-Pv CH 895).

The distal surface of the tibia possesses a subtriangular outline in distal view (Fig. 2g, h) that closely resembles that present in non-averostran neotheropods (e.g., *Zupaysaurus rougieri*: PULR-V 076; *Liliensternus liliensterni*: HMN MB.R. 2175; *Dilophosaurus wetherilli*: UCMP 77270; *Coelophysis bauri*: AMNH unnumbered; Fig. 3d−g) and, in particular, that of *Sarcosaurus woodi* (Ezcurra et al., 2021; Fig. 3h, i). We cannot determine the ratio between the anteroposterior depth versus transverse width of the distal end of the bone because the medial edge is missing NMS G.1994.10.1. However, the preserved portion indicates that it should have been similar to that of *Sarcosaurus woodi* or the slightly transversely wider end of *Tachiraptor admirabilis* (Fig. 3h−k). Beyond that, it is clear that the distal end of the tibia of NMS G.1994.10.1 was not as transversely broad as that of averostrans (Fig. 3l). The distal surface of the bone seems to lack the posteromedial notch located distal to the posteromedial ridge in other early neotheropods. However, this notch could have been located in the missing posteromedial corner of the distal end of the bone.

Phylogenetic analysis

The analysis of the data matrix found six most parsimonious trees (MPTs) of 1,365 steps with a consistency index (CI) of 0.34579 and a retention index (RI) of 0.67527 (best score hit 907 times of the 1,000 replicates). The overall topology of these MPTs is mostly congruent with those recovered in the analyses of the most recent iterations of this matrix (Novas et al., 2021; Spiekman et al., 2021; Fig. 4). Resembling previous analyses, we found a major dichotomy at the base of Neotheropoda between Coelophysoidea and the averostran-line theropods (i.e., the lineage leading to Averostra). The tibia from the Lower Jurassic of Skye is recovered as an averostran-line neotheropod, in a polytomy also composed of *Sarcosaurus woodi* from the Hettangian–Sinemurian of central England and a clade formed by *Tachiraptor admirabilis* from the Hettangian of Venezuela and Averostra. The clade that includes this trichotomy is supported by the presence of an astragalus with a plate-like ascending process (character 274: 0→1). Among the MPTs, NMS G.1994.10.1 is alternatively found as the sister taxon to *Sarcosaurus woodi*, the sister taxon to *Sarcosaurus woodi* + (*Tachiraptor admirabilis* + Averostra), and the sister taxon to *Tachiraptor admirabilis* + Averostra. However, none of these three alternative positions are supported by synapomorphies. The exclusion of NMS G.1994.10.1 from the clade composed of *Tachiraptor admirabilis* + Averostra is because of the absence of a tibia with a posteromedial ridge distinctly closer to the medial edge of the distal end than to the distal tip of the posterolateral process (character 389: 0→1). The branch supports are relatively low around the position of NMS G.1994.10.1 and only the clade composed of *Tachiraptor admirabilis* + Averostra, Averostra, and Tetanurae have bootstrap frequencies higher than 50%. Under constrained topologies, only one additional step is necessary to force the position of NMS G.1994.10.1 as the sister taxon to Averostra and two additional steps to find this specimen as a non-coelophysine coelophysoid or within Averostra.

DISCUSSION

The morphology of NMS G.1994.10.1 closely resembles that of *Sarcosaurus woodi* from the upper Hettangian–lower Sinemurian of central England and differs from that of other early neotheropods. In addition, the scorings of NMS G.1994.10.1 and *Sarcosaurus woodi* are completely consistent between each other in the phylogenetic data matrix. The position of NMS G.1994.10.1 as the sister taxon to *Sarcosaurus woodi* in some most parsimonious trees and its morphology congruent with the diagnosis of *Sarcosaurus woodi* (sensu Ezcurra et al., 2021) could favour the interpretation that the neotheropod tibia from the Isle of Skye is referrable to the latter species. NMS G.1994.10.1 is smaller than the two referred specimens of *Sarcosaurus woodi* (the holotype does not preserve the tibia), being ca. 50% of the length of the tibia of NHMUK PV R3542 and 80% of the tibiae of WARMS G667–690. Thus, it is possible that NMS G.1994.10.1 could be a juvenile-subadult specimen of this species (see ‘Ontogenetic stage’ in the Systematic Palaeontology section). Early neotheropods show a high degree of intraspecific variability during their ontogeny (Griffin and Nesbitt, 2016; Griffin, 2018) and, thus, it is possible that character states that may differentiate NMS G.1994.10.1 from *Sarcosaurus woodi* had not been expressed yet when the individual died (e.g., development of muscle scars). As a result, we prefer to assign NMS G.1994.10.1 to cf. *Sarcosaurus woodi*.

Our reassessment of the neotheropod tibia from the Isle of Skye constrains its phylogenetic position as one of the closest successive sister taxa to Averostra. This result contrasts with some previous findings that NMS G.1994.10.1 was more similar to *Coelophysis bauri*, ‘*Syntarsus*’ and *Liliensternus liliensterni* among ‘coelophysoid-grade’ neotheropods (Benton et al., 1995; Carrano and Sampson, 2004) and allows us to discuss the European Early Jurassic neotheropod record within an updated phylogenetic context. NMS G.1994.10.1 closely resembles or could be even conspecific with *Sarcosaurus woodi* (see above), which is an approximately contemporary and geographically close species (i.e., late

Hettangian−early Sinemurian of central England; Ezcurra et al., 2021). Another Early Jurassic (Hettangian) neotheropod from Great Britain is *Dracoraptor hanigani* from Wales (Martill et al., 2016). The phylogenetic position of this species is debated, but it is alternatively recovered at the base of Coelophysoidea or at the base of the branch leading to Averostra (Martill et al., 2016; Ezcurra, 2017; Ezcurra, et al., 2021; Spiekman et al., 2021). In any case, *Dracoraptor hanigani* is not closely related to NMS G.1994.10.1, but neither is part of the clade that includes the typical Early Jurassic coelophysoids (e.g., '*Syntarsus*' *kayentakae*, *Megapnosaurus rhodesiensis*, *Panguraptor lufengensis*, *Segisaurus halli*). An isolated fibula from the upper Sinemurian of southwestern England has been identified as belonging to a non-coelophysoid, non-averostran early branching neotheropod (Choiniere et al., 2020). A fragment of tibial shaft from the Hettangian of north-eastern Ireland has been interpreted as an early branching averostran-line taxon or a megalosauroid tetanuran (Simms et al., 2021). Finally, fragmentary specimens from Great Britain and Luxembourg that are represented by isolated teeth or partial hindlimb bones have not been identified beyond Theropoda or Neotheropoda indet. (e.g., Benson and Barrett, 2009; Delsate and Ezcurra, 2014; Norman, 2020) and *Lophostropheus airelensis* from northern France is ambiguously dated as latest Triassic or earliest Jurassic and its phylogenetic relationships need a revision in an updated phylogenetic analysis (Ezcurra and Cuny, 2007).

Thus, the Early Jurassic neotheropod record of Europe is currently composed of at least seven specimens with relatively well constrained phylogenetic positions and none of them seems to be unambiguously a coelophysoid. This contrasts with the presence of coelophysoids in Lower Jurassic rocks of China, the USA, and Zimbabwe (Raath, 1969, 1977; Rowe, 1989; Irmis, 2004; Carrano et al., 2005; You et al., 2014), and in some cases these forms seem to have been, at least regionally, very abundant (e.g., Kayenta Formation, Forest Sandstone Formation; Raath, 1977; Rowe, 1989; Tykoski, 1998). The same or geographically close units that preserve these coelophysoids have also yielded averostran-line neotheropods or even possible early branching averostrans (e.g., *Sinosaurus triassicus* in the Lower Lufeng Formation in China; *Dilophosaurus wetherilli* in the Kayenta Formation in the USA; *Dracovenator regenti* in the upper Elliot Formation in South Africa; Welles, 1954; Yates, 2005; Zhang et al., 2023). As a result, Early Jurassic neotheropods seem to have been phylogenetically diverse in Asia, North America and southern Africa, with the presence of lineages and body plans that extend back from the Late Triassic (coelophysoids) and species more closely related to Averostra, which probably had their origin around the Triassic-Jurassic boundary. By contrast, the current Early Jurassic neotheropod record of Europe is restricted to non-coelophysoid species or at least species that are not deeply nested within Coelophysoidea. This also differs from the Late Triassic European neotheropod record, which includes species deeply nested within Coelophysoidea (e.g., *Pendraig milnerae*; Spiekman et al., 2021) and at the base of Coelophysoidea or close to the base of the branch leading to Averostra (e.g., *Liliensternus liliensterni*, *Notatesseraeraptor frickensis*: Ezcurra, 2017; Zahner and Brinkman, 2019; Spiekman et al., 2021). We need a richer sampling of early neotheropod specimens in the Lower Jurassic rocks of Europe to determine if this is an actual macroevolutionary and biogeographic pattern or is a result of sampling bias. However, beyond that, current evidence indicates that averostran-line neotheropods were relatively common in the Hettangian−Sinemurian dinosaur assemblages of Europe.

ACKNOWLEDGEMENTS

This project began as an undergraduate dissertation at the University of Edinburgh completed by DM, advised by SLB, with the assistance of MDE. The following curators, researchers and collection managers are thanked for providing access to specimens under their care for the purpose of this research: Carl Mehling (AMNH), Max Langer (University of São Paulo), Daniela Schwarz (HMN), Eduardo Ruigomez, José Carballido, and Diego Pol (MPEF), Susannah Maidment, Sandra Chapman and Lorna Steel (NHMUK), Sergio Martin, Emilio Vaccari and Gabriela Cisterna (PULR), Jaime Powell, Pablo Ortíz and Rodrigo Gonzalez (PVL), Rainer Schoch (SMNS), Kevin Padian and Pat Holroyd (UCMP) Michael Brett-Surman and Hans-Dieter Sues (USNM), and Jonathan Radley (WARMS). Access to the free version of TNT 1.6 was possible due to the Willi Henning Society. SLB thanks his many colleagues for collaborative work on Scottish dinosaurs and discussions that informed this manuscript, including Dugald Ross, Tom Challands, Mark Wilkinson, Neil Clark, Nick Fraser, Paige dePolo, and Davide Foffa, and the broader PalAlba Group. We thank Matthias Metz and Ralf Metzdorf for allowing reproducing the photograph of NMS G.1994.10.1 as originally found in the field, and Jeff Liston for information on the local geology on Skye and for help tracking down the discovery site. We thank Christopher Griffin and Adam Marsh for their comments in the peer-review process, which improved the final version of the manuscript. This is PalAlba Publication Number 12.

REFERENCES

Agnolin, F.L. and Rozadilla, S. 2018. Phylogenetic reassessment of *Pisanosaurus mertii* Casamiquela, 1967, a basal dinosauriform from the Late Triassic of Argentina. *Journal of Systematic Palaeontology*, **16**, 853-879.

Allain, R., Tykoski, R., Aquesbi, N., Jalil, N.E., Monbaron, M., Russell, D. and Taquet, P. 2007. An abelisauroid (Dinosauria: Theropoda) from the Early Jurassic of the High Atlas Mountains, Morocco, and the radiation of ceratosaurs. *Journal of Vertebrate Paleontology*, **27**, 610–624.

Andrews, C.W. 1921. On some remains of a theropodous dinosaur from the Lower Lias of Barrow-on-Soar. *Annals and Magazine of Natural History, Series 9*, **8**, 570–576.

Apaldetti, C., Pol, D., Ezcurra, M.D. and Martínez, R.N. 2021. Sauropodomorph evolution across the Triassic–Jurassic boundary: body size, locomotion, and their influence on morphological disparity. *Scientific Reports*, **11**, 22534.

Bakker, R.T. 1986. *The Dinosaur Heresies*. William Morrow, New York.

Baron, M.G. 2019. *Pisanosaurus mertii* and the Triassic ornithischian crisis: could phylogeny offer a solution? *Historical Biology*, **31**, 967–981.

Barrett, P.M. 2006. A sauropod dinosaur tooth from the Middle Jurassic of Skye, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **97**, 25–29.

Benson, R.B.J. and Barrett, P.M. 2009. Dinosaurs of Dorset: Part 1, the carnivorous dinosaurs (Saurischia, Theropoda). *Proceedings of the Dorset Natural History and Archaeological Society*, **130**, 133–147.

Benton, M.J., Martill, D.M. and Taylor, M.A. 1995. The first Lower Jurassic dinosaur from Scotland: limb bone of a ceratosaur theropod from Skye. *Scottish Journal of Geology*, **31**, 177–182.

Bremer, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution*, **42**, 795−803.

Bremer, K. 1994. Branch support and tree stability. *Cladistics*, **10**, 295−304.

Brusatte, S.L. and Clark, N.D.L. 2015. Theropod dinosaurs from the Middle Jurassic (Bajocian–Bathonian) of Skye, Scotland. *Geological Society of London*, **51**, 157–164.

Brusatte, S.L., Nesbitt, S.J., Irmis, R.B., Butler, R.J., Benton, M.J. and Norell, M.A. 2010. The origin and early radiation of dinosaurs. *Earth-Science Reviews*, **101**, 68–100.

Brusatte, S.L., Challands, T.J., Ross, D.A. and Wilkinson, M. 2016. Sauropod dinosaur trackways in a Middle Jurassic lagoon on the Isle of Skye, Scotland. *Scottish Journal of Geology*, **52**, 1–9.

Bonaparte, J.F. 1972. Los tetrápodos del sector superior de la Formación Los Colorados, La Rioja, Argentina. (Triásico Superior) I parte. *Opera Lilloana*, **22**, 1–183.

Carrano, M.T. and Sampson, S.D. 2004. A review of coelophysoids (Dinosauria: Theropoda) from the Early Jurassic of Europe, with comments on the late history of the Coelophysoidea. *Neues Jahrbuch für Geologie und Palaontologie*, **9**, 537−558.

Carrano, M.T., Hutchinson, J.R. and Sampson, S.D. 2005. New information on *Segisaurus halli*, a small theropod dinosaur from the Early Jurassic of Arizona. *Journal of Vertebrate Paleontology,* **25**, 835–849.

Choiniere, J.N., Wills, S., Bennett, S.C. and Barrett, P.M. 2020. A small theropod dinosaur from the Lower Jurassic Lias Group of Charmouth, Dorset. *Proceedings of the Geologists' Association*, **131**, 751–757.

Clark, N.D.L. 2018. Review of the dinosaur remains from the Middle Jurassic of Scotland, UK. *Geosciences*, **8**, 53.

Clark, N.D.L. 2001. A thyreophoran dinosaur from the early Bajocian (Middle Jurassic) of the Isle of Skye, Scotland. *Scottish Journal of Earth Sciences,* **37**, 19–26.

Clark, N.D.L. and Gavin, P. 2016. New Bathonian (Middle Jurassic) sauropod remains from the Valtos Sandstone Formation, Isle of Skye, Scotland. *Scottish Journal of Geology,* **52,** 71–75.

Clark, N.D.L., Boyd, J.D., Dixon, R.J. and Ross, D.A. 1995. The first Middle Jurassic dinosaur from Scotland: a cetiosaurid? (Sauropoda) from the Bathonian of the Isle of Skye. *Scottish Journal of Geology,* **31,** 171–176.

Coddington, J. and Scharff, N. 1994. Problems with zero-length branches. *Cladistics*, **10**, 415−423.

Cope, E.D. 1869–1870. Synopsis of the extinct Batrachia, Reptilia and Aves of North America. *Transactions of the American Philosophical Society*, **14**, 1–252.

Delsate, D. and Ezcurra, M.D. 2014. The first Early Jurassic (late Hettangian) theropod dinosaur remains from the Grand Duchy of Luxembourg. *Geologica Belgica*, **17**, 175–181.

dePolo, P.E., Brusatte, S.L., Challands, T.J., Foffa, D., Ross, D.A., Wilkinson, M. and Yi, H.Y. 2018. A sauropod-dominated tracksite from Rubha nam Brathairean (Brothers' Point), Isle of Skye, Scotland. *Scottish Journal of Geology*, **54**, 1–12.

dePolo, P. E., et al. 2020. Novel track morphotypes from new tracksites indicate increased Middle Jurassic dinosaur diversity on the Isle of Skye, Scotland. *PlosONE*, **15**, e0229640.

Desojo, J.B., et al. 2020. The Late Triassic Ischigualasto Formation at Cerro Las Lajas (La Rioja, Argentina): fossil tetrapods, high-resolution chronostratigraphy, and faunal correlations. *Scientific Reports*, **10**, 1–34.

Ezcurra, M.D. 2017. A new early coelophysoid neotheropod from the Late Triassic of northwestern Argentina. *Ameghiniana*, **54**, 506−539.

Ezcurra, M.D. and Cuny, G. 2007. The coelophysoid *Lophostropheus airelensis* nov. gen.: a review of the systematics of "*Liliensternus*" *airelensis* from the Triassic-Jurassic outcrops of Normandy (France). *Journal of Vertebrate Paleontology,* **27**, 73−86.

Ezcurra, M.D. and Novas, F. E. 2007. Phylogenetic relationships of the Triassic theropod *Zupaysaurus rougieri* from NW Argentina. *Historical Biology*, **19**, 35−72.

Ezcurra, M.D. and Brusatte, S.L. 2011. Taxonomic and phylogenetic reassessment of the early neotheropod dinosaur *Camposaurus arizonensis* from the Late Triassic of North America. *Palaeontology,* **54**, 763−772.

Ezcurra, M.D., Butler, R.J., Maidment, S.C., Sansom, I.J., Meade, L.E. and Radley, J.D. 2021. A revision of the early neotheropod genus *Sarcosaurus* from the Early Jurassic

(Hettangian–Sinemurian) of central England. *Zoological Journal of the Linnean Society*, **191**, 113–149.

Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, **39**, 783–791.

Gauthier, J.A. 1986. Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Science*, **8**, 1−55.

Gauthier, J.A. and Padian, K. 1985. Phylogenetic, functional, and aerodynamic analyses of the origin of birds and their flight. *In*: Hecht, M.K., et al. (eds) *The Beginning of Birds*. Freunde des Jura Museums, 185–197.

Goloboff, P.A. and Morales, M.E. 2023. TNT version 1.6, with a graphical interface for MacOS and Linux, including new routines in parallel. *Cladistics*, **39**, 144–153.

Goloboff, P.A., Farris, J.S., Källersjö, M., Oxelman, B., Ramírez, M. and Szumik, C. 2003. Improvements to resampling measures of group support. *Cladistics*, **19**, 324−332.

Griffin, C.T. 2018. Developmental patterns and variation among early theropods. *Journal of Anatomy*, **232**, 604−640.

Griffin, C.T. and Nesbitt, S.J. 2016. Anomalously high variation in postnatal development is ancestral for dinosaurs but lost in birds. *Proceedings of the National Academy of Sciences*, **113**, 14757−14762.

Griffin, C.T., Stocker, M.R., Colleary, C., Stefanic, C.M., Lessner, E.J., Riegler, M., Formoso, K., Koeller, K. and Nesbitt, S.J. 2021. Assessing ontogenetic maturity in extinct saurian reptiles. *Biological Reviews*, **96**, 470–525.

Irmis, R.B. 2004. First report of *Megapnosaurus* (Theropoda: Coelophysoidea) from China. *PaleoBios*, **24**, 11−18.

Irmis, R.B., Parker, W.G., Nesbitt, S.J. and Liu, J. 2007. Early ornithischian dinosaurs: the Triassic record. *Historical Biology*, **19**, 3–22.

Kirmse, J.P., Benton, M.J., Hildebrandt, C., Langer, M.C. and Marsola, J.C. 2023. A Coelophysoidea (Dinosauria, Therpoda) femur from the Tytherington fissures (Rhaetian, Late Triassic), Bristol, UK. *Proceedings of the Geologists' Association*: 10.1016/j.pgeola.2023.07.005

Langer, M.C., Ezcurra, M.D., Bittencourt, J.S. and Novas, F.E. 2010. The origin and early evolution of dinosaurs. *Biological Reviews*, **85**, 55–110.

Langer, M.C., Rincón, A.D., Ramezani, J., Solórzano, A. and Rauhut, O.W.M. 2014. New dinosaur (Theropoda, stem-Averostra) from the earliest Jurassic of the La Quinta formation, Venezuelan Andes. *Royal Society Open Science*, **1**, 140184.

Liston, J.J. 2004. A re-examination of a Middle Jurassic sauropod limb bone from the Bathonian of the Isle of Skye. *Scottish Journal of Geology*, **40**, 119–122.

Madsen, Jr, J.H. 1976. Allosaurus fragilis: a revised osteology. *Utah Geological and Mining Survey Bulletin*, **109**, 1–163.

Marsh, A.D. Rowe, T.B. 2020. A comprehensive anatomical and phylogenetic evaluation of *Dilophosaurus wetherilli* (Dinosauria, Theropoda) with descriptions of new specimens from the Kayenta Formation of northern Arizona. *Journal of Paleontology*, **94**, 1–103.

Marsh, A.D., Parker, W.G., Langer, M.C. and Nesbitt, S.J. 2019. Redescription of the holotype specimen of *Chindesaurus bryansmalli* Long and Murry, 1995 (Dinosauria, Theropoda), from Petrified Forest National Park, Arizona. *Journal of Vertebrate Paleontology*, **39**, e1645682.

Marsh. O.C. 1881. Principal characters of American Jurassic dinosaurs. *American Journal of Science (3rd series)*, **21**, 417−423.

Martill, D.M., Vidovic, S.U., Howells, C. and Nudds, J.R. 2016. The oldest Jurassic dinosaur: a basal neotheropod from the Hettangian of Great Britain. *PLoS ONE*, **11**, e0145713.

Martínez, R.N. and Apaldetti, C. 2017. A late Norian-Rhaetian coelophysid neotheropod (Dinosauria, Saurischia) from the Quebrada del Barro Formation, northwestern Argentina. *Ameghiniana*, **54**, 488–505.

Nesbitt, S.J. 2011. The early evolution of Archosauria: relationships and the origin of major clades. *Bulletin of the American Museum of Natural History*, **352**, 1−292.

Nesbitt, S.J. and Ezcurra, M.D. 2015. The early fossil record of dinosaurs in North America: A new neotheropod from the base of the Upper Triassic Dockum Group of Texas. *Acta Palaeontologica Polonica*, **60**, 513−526.

Nesbitt, S.J., Smith, N.D., Irmis, R.B., Turner, A.H., Downs, A. and Norell, M.A. 2009. A complete skeleton of a Late Triassic saurischian and the early evolution of dinosaurs. *Science*, 326, 1530−1533.

Norman, D.B. 2020. *Scelidosaurus harrisonii* from the Early Jurassic of Dorset, England: cranial anatomy. *Zoological Journal of the Linnean Society*, **188**, 1–81.

Novas, F.E., Agnolin, F.L., Ezcurra, M.D., Müller, R.T., Martinelli, A.G. and Langer, M.C. 2021. Review of the fossil record of early dinosaurs from South America, and its phylogenetic implications. *Journal of South American Earth Sciences*, **110**, 103341.

Owen, R. 1842. Report on British fossil reptiles. Part 2. *Report of the British Association for the Advancement of Science*, **11**, 60−204.

Padian, K. and May, C.L. 1993. The earliest dinosaurs. The Nonmarine Triassic. *New Mexico Museum of Natural History and Science Bulletin*, **3**, 379−381.

Raath, M.A. 1969. A new coelurosaurian dinosaur from the Forest Sandstone of Rhodesia. *Arnoldia*, **4**, 1−25.

Raath, M.A. 1977. *The anatomy of the Triassic theropods* Syntarsus rhodesiensis *(Saurischia: Podokesauridae) and a consideration of its biology*. PhD thesis, Rhodes University.

Raup, D.M. and Sepkoski Jr, J.J. 1982. Mass extinctions in the marine fossil record. *Science*, **215**, 1501–1503.

Rowe, T. 1989. A new species of the theropod dinosaur *Syntarsus* from the Early Jurassic Kayenta Formation of Arizona. *Journal of Vertebrate Paleontology*, **9**, 125−136.

Rowe, T. and Gauthier, J. 1990. Ceratosauria. *In*: Weishampel, D.B., Dodson, P. and Osmólska, H. (eds.) *The Dinosauria*. University of California Press, 505–518.

Sander, P.M. 1992. The Norian *Plateosaurus* bonebeds of central Europe and their taphonomy. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **93**, 255–299.

Sereno, P.C. 1998. A rationale for phylogenetic definitions, with application to the higher-level taxonomy of Dinosauria. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **210**, 41−83.

Simms, M.J., Smyth, R.S., Martill, D.M., Collins, P.C. and Byrne, R. 2021. First dinosaur remains from Ireland. *Proceedings of the Geologists' Association*, **132**, 771–779.

Smith, N.D., Makovicky, P.J., Hammer, W.R., Currie, P.J. 2007. Osteology of *Cryolophosaurus ellioti* (Dinosauria: Theropoda) from the Early Jurassic of Antarctica and implications for early theropod evolution. *Zoological Journal of the Linnean Society*, **151**, 377−421.

Spiekman, S.N., Ezcurra, M.D., Butler, R.J., Fraser, N.C. and Maidment, S.C. 2021. *Pendraig milnerae*, a new small-sized coelophysoid theropod from the Late Triassic of Wales. *Royal Society Open Science*, **8**, 210915.

Swofford, D.L. and Begle, D.P. 1993. *User's manual for PAUP: phylogenetic analysis using parsimony, Version 3.1*. Smithsonian Institution, Washington D.C., USA.

Tykoski, R.S. 1998. *The osteology of Syntarsus kayentakatae and its implications for ceratosaurid phylogeny*. Master’s thesis, University of Texas.

Welles, S.P. 1954. New Jurassic dinosaur from the Kayenta Formation of Arizona. *Bulletin of the Geological Society of America*, **65**, 591–598.

Wills, S., Barrett, P.M. and Walker, A. 2014. New dinosaur and crocodylomorph material from the Middle Jurassic (Bathonian) Kilmaluag Formation, Skye, Scotland. *Scottish Journal of Geology,* **50**, 183–190.

Yates, A.M. 2005. A new theropod dinosaur from the Early Jurassic of South Africa and its implication for the early evolution of theropods. *Palaeontologia Africana*, **41**, 105−122.

You, H.-L., Azuma, Y., Wang, T., Wang, Y.-M. and Dong, Z.-M. 2014. The first well-preserved coelophysoid theropod dinosaur from Asia. *Zootaxa*, **3873**, 233–249.

Young, C.M.E., Hendrickx , C., Challands, T.J., Foffa, D., Ross, D.A., Butler, I.B. and Brusatte, S.L. 2019. New theropod dinosaur teeth from the Middle Jurassic of the Isle of Skye, Scotland. *Scottish Journal of Geology,* **55**, 7–19.

Zahner, M. and Brinkmann, W. 2019. A Triassic averostran-line theropod from Switzerland and the early evolution of dinosaurs. *Nature Ecology & Evolution*, **3**, 1146–1152.

Zhang, Z.C., Wang, T. and You, H.-L. 2023. A new specimen of *Sinosaurus triassicus* (Dinosauria: Theropoda) from the Early Jurassic of Lufeng, Yunnan, China. *Historical Biology,* 1–15.

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Funding information

MDE research was funded by Agencia Nacional de Promoción Científica y Técnica (PICT 2018–01186) and a Sepkoski Grant 2019 of the Paleontological Society International Research Program. SLB work on the Isle of Skye is funded by the National Geographic Society (GEFNE185-16) and his fossil lab is funded by a Philip Leverhulme Prize.

Data availability statement

All data generated or analysed during this study are included in this published article (and its supplementary information files).

Figure legends

Fig. 1. Isolated left tibia (NMS G.1994.10.1) assigned to cf. *Sarcosaurus woodi* as originally found in the field. The bone is exposed mainly in posterior view. Note that approximately the proximal half of the bone is currently missing (see Fig. 2). Photograph courtesy of Matthias Metz. Scale bar equals 5 cm.

Fig. 2. Isolated left tibia (NMS G.1994.10.1) assigned to cf. *Sarcosaurus woodi* in anterior (a, b), posterior (c), lateral (d, e), medial (f), and distal (g, h) views. (a, c, d, f, g) photographs of the actual specimen and (b, e, h) artificially coloured 3D models. Abbreviations: fap, facet for reception of the ascending process of the astragalus; lg, lateral groove; mex, medial expansion; plp, posterolateral process; pmr, posteromedial ridge. Scale bar equals 2 cm.

Fig. 3. Comparison among Late Triassic−Early Jurassic neotheropod tibiae in anterior (a−c) and distal (d−l) views. (a, f) *Zupaysaurus rougieri* (PULR-V 076), (b, j) cf. *Sarcosaurus woodi* (NMS G.1994.10.1, reversed), (c, h) *Sarcosaurus woodi* (c, WARMS G680; h, composite reconstruction using WARMS G668 and 680), (d) *Coelophysis bauri* (AMNH unnumbered, reversed), (e) *Liliensternus liliensterni* (HMN MB.R. 2175), (g) *Dilophosaurus wetherilli* (UCMP 77270), (i) *Sarcosaurus woodi* (NHMUK PV R3542), (k) *Tachiraptor admirabilis* (LPRP/USP 0747, cast of IVIC-P-2867), and (l) *Piatnitzkysaurus floresi* (MACN-Pv CH 895, reversed). (a, b, d−g, i, k, l) Photographs of actual specimens and (c, h, j) are 3D models. Abbreviations: fap, facet for reception of the ascending process of the astragalus; plp, posterolateral process; pmn, posteromedial notch; pmr, posteromedial ridge. Arrows indicate anterior direction. Specimens not to scale.

Fig. 4. Time-calibrated strict consensus subtree showing the phylogenetic relationships of all neotheropod species sampled in the phylogenetic analysis. Values next to each branch represent Bremer support, absolute bootstrap frequency, and GC bootstrap frequency, respectively. Thick black bars represent the chronostratigraphic uncertainty of taxa.

Supplementary Information

Added character to the data matrix:

389. Tibia, position of the proximodistally oriented posteromedial ridge of the distal end: approximately at mid-width between the medialmost edge of the distal end and the tip of the posterolateral process (0); distinctly closer to the medial edge of the distal end than to the distal tip of the posterolateral (1) (New character).