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## A Coelophysoidea (Dinosauria, Theropoda) femur from the Tytherington fissures (Rhaetian, Late Triassic), Bristol, UK

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### ABSTRACT

Theropods originated in the Late Triassic and their relations and early evolution are still topics of discussion. Within Neotheropoda, coelophysoids represent their earliest worldwide radiation and include most Triassic theropods, but their internal relations remain volatile. In this paper, we discuss the significance of a coelophysoid femur from the Rhaetian Tytherington fissures near Bristol, UK. The specimen belongs to a small-sized individual and is complete, but for the fourth trochanter blade. The most distinctive aspects of the femur are a sharply pointed lateral condyle and the pentagonal distal outline. The features that supposedly correlate with ontogenetic development, in addition to several well-developed scars, indicate it probably pertains to a mature individual. Its inclusion in a taxon-character matrix recovered the specimen within Coelophysoidea, but created a polytomy encompassing all members of the group. A definitive referral of the femur to the previously recorded coelophysoid *Pendraig milnerae* is precluded by the lack of overlap in diagnostic anatomical parts, the paucity of specimens from the Bristol Channel Triassic fissures, and the possible geological age difference between them.

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### 1. Introduction

Theropods are the most diverse group of dinosaurs and the only one that survived the K–Pg extinction event, including the largest land predators of the Mesozoic (Gauthier, 1986; Sereno, 1997; Rauhut, 2003; Holtz and Osmólska, 2004; Hendrickx et al., 2015). Along with other dinosaurs, theropods originated in the Late Triassic, and their early evolution and relations are still subject to discussion, with details, and sometimes general patterns, of their phylogeny, ontogeny, and body size still unclear (Tykoski, 2005; Griffin, 2018, 2019; Zahner and Brinkmann, 2019; Griffin and Nesbitt, 2020; Ezcurra et al., 2021; Griffin et al., 2021; Spiekman et al., 2021).

The inclusiveness of Theropoda is one of those topics open to debate. Several Late Triassic panavians, like herrerasaurs, *Tawa hallae*, *Daemonosaurus chauliodus*, *Eodromaeus murphii*, *Nhandumirim waldsangae*, and *Eoraptor lunensis*, have been found either nested within or outside the lineage (Rauhut, 2003; Sereno et al., 2012; Langer et al., 2017; Marsola et al., 2018; Pacheco et al., 2019; Novas et al., 2021; Nesbitt and Sues, 2021). Within Neotheropoda (the least inclusive

clade that includes *Coelophysis bauri* and Neornithes), the Coelophysoidea lineage was once thought to include forms close to *Dilophosaurus wetherilli* (Gauthier, 1986; Rauhut, 2003), more recently placed along the Averostria branch (Langer et al., 2017; Zahner and Brinkmann, 2019; Marsh and Rowe, 2020; Ezcurra et al., 2021). Indeed, some putative coelophysoids such as *Zupaysaurus rougieri*, *Liliensternus liliensterni*, and *Dracoraptor hanmigani* are also sometimes recovered as early members of the Averostria line (Smith et al., 2007; Martill et al., 2016; Ezcurra, 2017; Langer et al., 2017; Ezcurra et al., 2021; Spiekman et al., 2021). This indicates that the character distribution in early theropod evolution is still unclear, hampering the identification of anchor points and diagnostic characters of the group.

Coelophysoidea represents the most diverse lineage of early theropods. The group minimally includes, along with the name-bearer *Coelophysis bauri* (Colbert, 1989; Griffin, 2018), *Camposaurus arizonensis* (Ezcurra and Brusatte, 2011), *Lucianovenator bonoi* (Martínez and Apaldetti, 2017), *Megapnosaurus rhodesiensis* (Raath, 1969; Griffin, 2018), *Powellvenator podocitus* (Ezcurra, 2017), *Pendraig milnerae* (Spiekman et al., 2021), *Procompsognathus triassicus* (Fraas, 1913; Sereno and Wild, 1992), *Segisaurus halli* (Carrano et al., 2005), and *'Syntarsus' kayentakatae* (Tykoski, 1998). Although aspects of their ecology, ontogeny, and behaviour have recently become much better understood (Tykoski, 2005; Rinehart et al., 2009; Griffin, 2018; Barta et al., 2022), the internal relations of the group are still unclear. For example,

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defined as those taxa more closely related to *Coelophysis bauri* than to *Procompsognathus triassicus*, the composition of Coelophysidae may encompass or not taxa such as '*Syntarsus kayentakatae*, *Megapnosaurus rhodesiensis*, *Segisaurus halli*, and *Camposaurus arizonensis* (Tykoski, 1998, 2005; Carrano et al., 2005; Nesbitt et al., 2009; Nesbitt, 2011; Ezcurra and Brusatte, 2011; Ezcurra, 2017; Nesbitt and Sues, 2021; Spiekman et al., 2021).

Coelophysoids have a worldwide record, with various specimens found in what is now the Northern Hemisphere. From the European Triassic, the first named coelophysoid is the German *Procompsognathus triassicus* (Fraas, 1913). Other records of Triassic age include *Pendraig milnerae* from the Pant-y-Ffynnon fissures in south Wales; first mentioned in 1983, but only named in 2021 (Warrener, 1983; Spiekman et al., 2021), and an isolated right tibia from the Durdham Down fissures in Bristol (Foffa et al., 2014). Here, we describe a coelophysoid femur from the Rhaetian Tytherington fissure locality in Bristol. We aim to provide a complete description for subsequent comparisons with new specimens and to compare with other published theropod specimens of the fissure deposits and the Triassic theropod fauna as a whole, assessing how it fits on the current understanding of theropod ontogeny and the local palaeoecology.

## 2. Methods

BRSUG 28403 consists of an isolated and nearly complete left femur. Despite some weathering on the proximal and distal ends, the bone is well preserved and most relevant features can be discerned. The specimen was collected from the Tytherington fissure 2, which has also yielded sauropodomorph bones and probable theropod teeth, among others (Mussini et al., 2020). It was part of the 1975 find by Mike Curtis and Tom Ralph that was reported to the University of Bristol, and which also includes *Thecodontosaurus antiquus* remains (Ballell et al., 2020) and palynomorph assemblages (Marshall and Whiteside, 1980) and was the basis of the PhD dissertation of Whiteside (1983) and has been continuously studied and prepared through the Bristol Dinosaur Project under the direction of MJB (Benton et al., 2012). It is here compared with several early dinosauriform species, focusing on theropods; the complete list is seen in Supplementary Table 1. In order to better understand how BRSUG 28403 relates to other theropods, it was included in the phylogenetic matrix of Spiekman et al. (2021), originally assembled by Nesbitt et al. (2009), which is the most inclusive and up-to-date dataset focused on the putative position of the new specimen. The selected outgroup was *Erythrosuchus africanus*, with the following characters treated as 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, and 383–384. The matrix was edited in Mesquite and a parsimony analysis was performed in TNT 1.5 (Goloboff and Catalano, 2016) through the Traditional Search algorithm with 10,000 replicates. 1000 bootstrap pseudoreplications and Bremer supports were calculated with the same software.

## 3. Institutional abbreviations

**BRSMG**, Bristol City Museum and Art Gallery, Bristol, UK. **BRSUG**, Earth Science Collections, University of Bristol, Bristol, UK. **AMNH**, American Museum of Natural History, New York, NY, USA. **BP/I**, Bernard Price Institute for Palaeontological Research, University of Witwatersrand, Johannesburg, South Africa. **CAPPA/UFSM**, Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia, Universidade Federal de Santa Maria, São João do Polêsine, RS, Brazil. **FMNH**, Field Museum of Natural History, Chicago, IL, USA. **GR**, Ghost Ranch Ruth Hall Museum of Paleontology, Abiquiu, NM, USA. **HMN**, Museum für Naturkunde Berlin, Germany. **LPRP/USP**, Laboratório de Paleontologia de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto, SP, Brazil. **MCN PV**, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, RS, Brazil. **MCP**, Museu de Ciências e Tecnologia da Pontifícia Universidade

Católica do Rio Grande do Sul, Porto Alegre, RS, Brazil. **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA. **MNA**, Museum of Northern Arizona, Flagstaff, AZ, USA. **NHMUK**, Natural History Museum London, UK. **NMMNHS**, New Mexico Museum of Natural History and Science, Albuquerque, NM, USA. **NMW**, National Museum of Wales, Cardiff, UK. **PVL**, Colección de Paleontología de Vertebrados de la Fundación Instituto Miguel Lillo, San Miguel de Tucumán, TM, Argentina. **PVSJ**, Museo de Ciencias Naturales, Universidade Nacional de San Juan, San Juan, SJ, Argentina. **TMM**, Texas Memorial Museum, Austin, TX, USA. **SMNS**, Staatliches Museum für Naturkunde Stuttgart, BW, Germany. **UCMP**, University of California Museum of Paleontology, Berkeley, CA, USA. **UFRGS PV**, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brazil. **UNLR**, Museo de Ciencias Naturales de la Universidad Nacional de La Rioja, La Rioja, LR, Argentina. **USNM**, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA. **UUVP**, University of Utah Natural History Collections, Salt Lake City, UT, USA. **WARMS**, Warwickshire Museum, UK. **ZPAL**, Instytut Paleobiologii, Polska Akademia Nauk, Warsaw, Mazowieckie, Poland.

## 4. Systematic palaeontology

Dinosauria Owen, 1842

Theropoda Marsh, 1881

Neotheropoda Bakker, 1986, *sensu* Sereno, 1998

Coelophisoidea von Nopcsa, 1928, *sensu* Sereno, 1998

### 4.1. Material

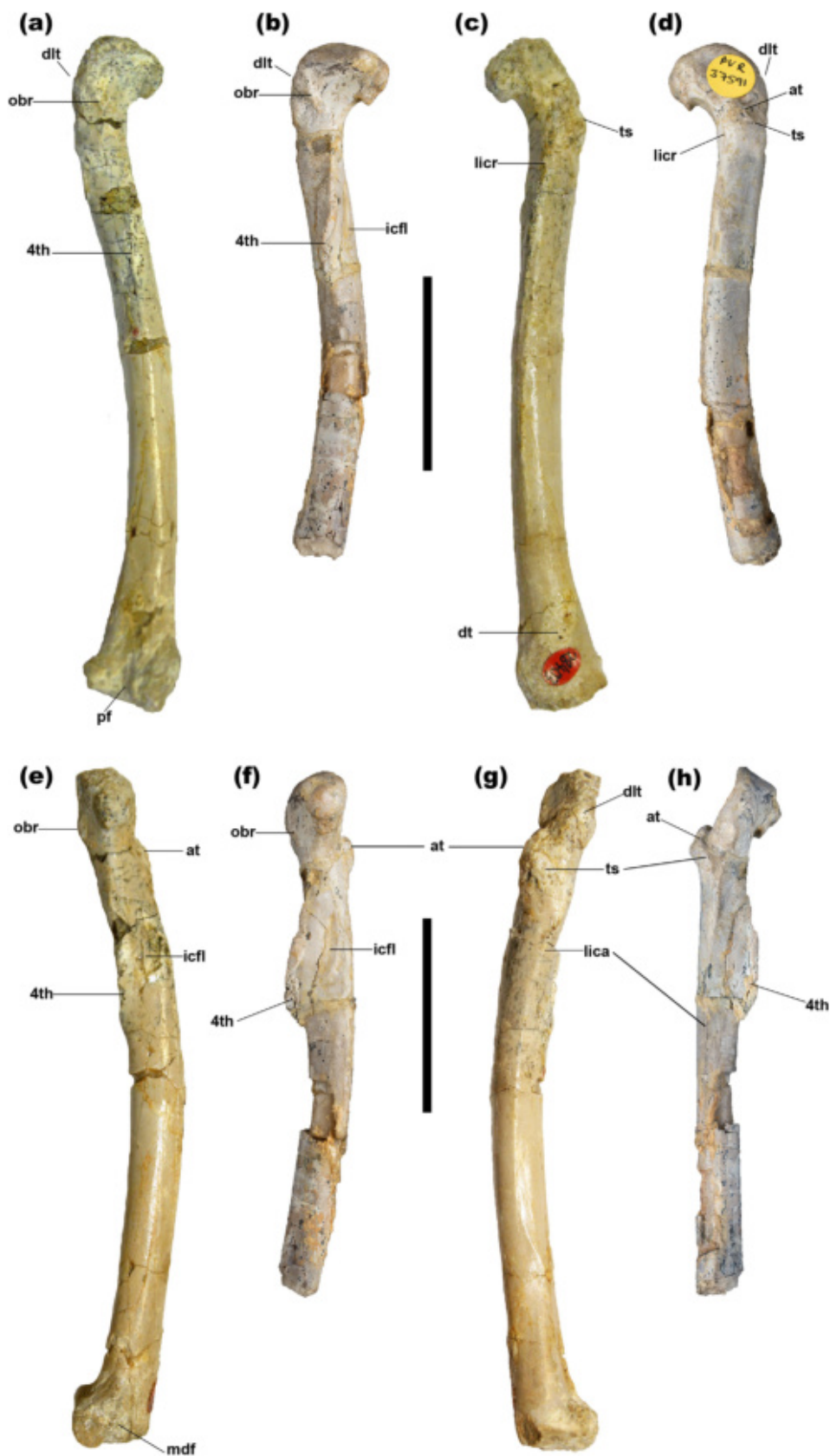
BRSUG 28403, a nearly complete left femur.

### 4.2. Locality and age

The Tytherington fissures, located just under 20 km northeast of Bristol, are part of a wider range of fissures around the Bristol Channel that include, among others, the Durdham Down, Cromhall, and Pant-y-Ffynnon fissures (see Evans and Kermack, 1994, Fraser and Sues, 1994, and Whiteside and Marshall, 2008 for wider overviews). These deposits occur within Carboniferous limestone, filled in a marine/marginal terrestrial landscape, suggesting a palaeoenvironment of small marine islands (Whiteside and Marshall, 2008; Whiteside et al., 2016; Mussini et al., 2020). The fissures, once thought to be Carnian or Norian in age (Fraser and Walkden, 1983; Lucas, 1999), were reanalysed using palynological and faunal biostratigraphy and their age is currently constrained to the Rhaetian (Whiteside and Marshall, 2008). Like the other fissures, those at Tytherington have an extensive fauna, including rhynchocephalians, procolophonids, pterosauroforms, aetosaurs, and drepanosauroforms (Whiteside and Marshall, 2008; Foffa et al., 2014; Mussini et al., 2020). It also includes the sauropodomorph *Thecodontosaurus antiquus*, one of the first named dinosaurs, with remains found at Durdham Down and Tytherington (Riley and Stutchbury, 1836; Whiteside and Marshall, 2008; Mussini et al., 2020; Ballell et al., 2020).

## 5. Comparative description

The femur is thin and subcylindrical, 10.8 cm long proximodistally (Fig. 1; Supplementary Table 2). It is sigmoidal in anterior/posterior views, bowed laterally in its proximal third and medially distal to that, whereas in medial/lateral views it has a more prominent anterior bowing. The femoral head is medially turned, forming an angle of 60° to the anteroposterior axis of the distal end of the bone; as in '*Syntarsus kayentakatae*' (MNA V2623 in Tykoski, 1998, Fig. 2b) and *Pendraig milnerae* (NHMUK PV R 37591 in Spiekman et al., 2021, Fig. 1; exact angle unclear as the distal end is missing), more interned than in most early dinosaurs (e.g., *Thecodontosaurus antiquus* BRSUG 23615, *Saturnalia tupiniquim* MCP 3844-PV, Fig. 2h, *Herrerasaurus*



**Fig. 1.** BRSUG 28403 (a, c, e, g) and Pendraig milnerae NHMUK PV R 37591 (b, d, f, h) in posteromedial (a, b), anterolateral (c, d), anteromedial (e, f), and posterolateral (g, h) views. 4th, fourth trochanter; at, anterior trochanter; dlt, dorsolateral trochanter; dt, distal tuberosity; dlt; icfl, depression associated with the insertion of the *M. caudofemoralis longus*; lica, linea intermuscularis caudalis; licr, linea intermuscularis cranialis; mdf, medial distal fossa; obr, obturator ridge; pf, popliteal fossa; ts, trochanteric shelf. Scale bars are 3 cm.

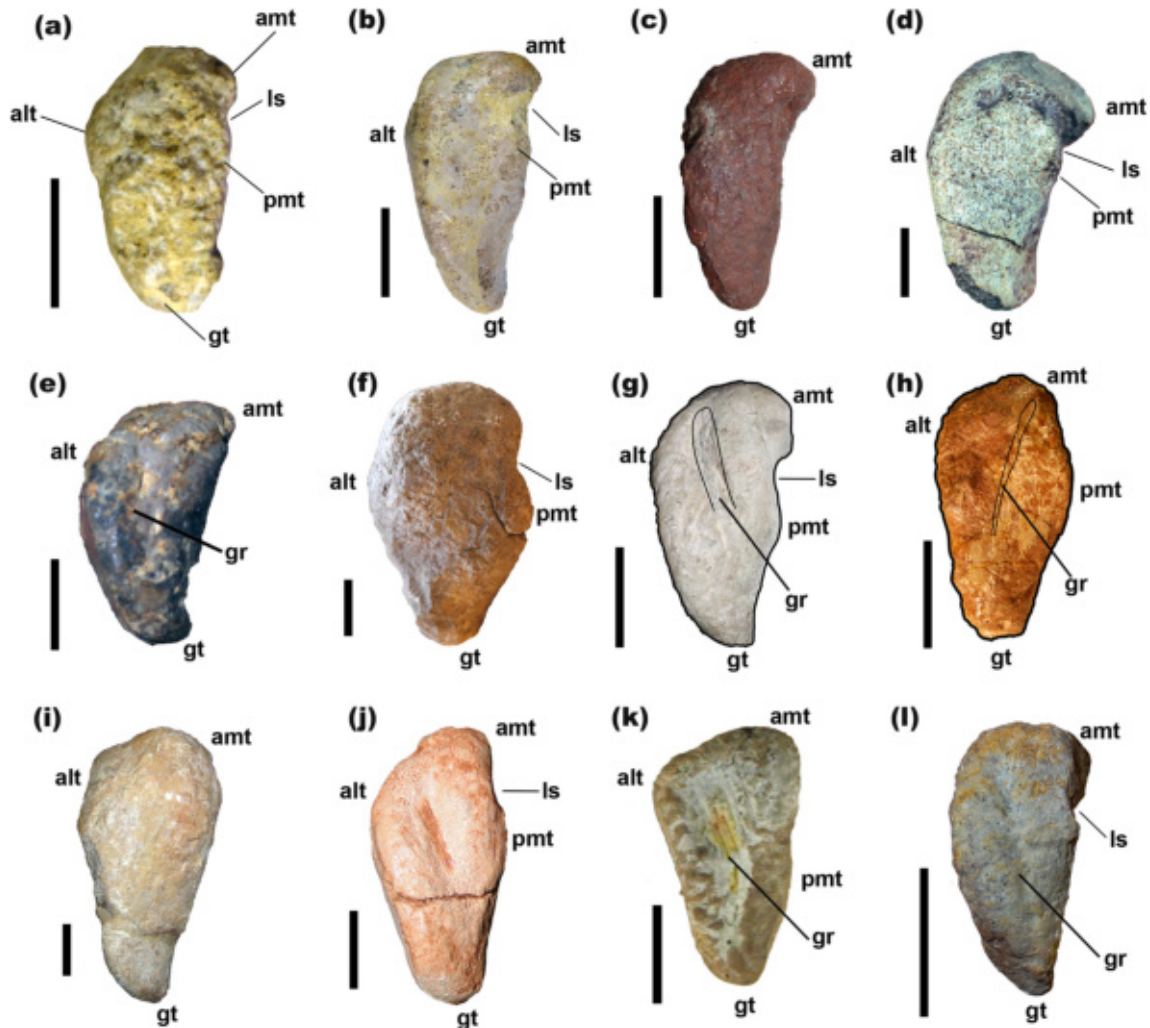


**Fig. 2.** Femora in anterolateral view. (a) BRSUG 28403; (b) *Syntarsus kayentakatae*' MNA V2623; (c) *Dilophosaurus wetherilli* UCMP 37302; (d) *Liliensternus liliensterni* HMN MB.R.2175.7; (e) *Piatnitzkysaurus floresi* PVL 4073; (f) *Tawa hallae* GR 242; (g) *Nhandumirim waldsangae* LPRP/USP 0651; (h) *Saturnalia tupiniquim* MCP 3844 PV. (b, c, d, e, f, h) are mirrored. at, anterior trochanter; dlt, dorsolateral trochanter; dt, distal tuberosity; dlt; licr, linea intermuscularis cranialis; ts, trochanteric shelf. Scale bars are 2 cm in (f); 3 cm in (a, b, g); 5 cm in (d, h); 10 cm in (e).

*ischigualastensis* PVL 2566), but less than in later averostran theropods (e.g., *Cryolophosaurus ellioti* FMNH PR1821 in Smith et al., 2007). The long axis of the femoral head is 14 mm long and anteromedially–posterolaterally extended. The femoral head groove is apparently present, but quite faint (Fig. 3), an uncertainty enhanced by the relatively poor preservation of the head. This condition differs from the clear proximal groove present in *Saturnalia tupiniquim* (MCP 3844-PV), *Thecodontosaurus antiquus* (BRSUG 26655, Fig. 3l), *Staurikosaurus pricei* (MCZ 1669), *Nhandumirim waldsangae* (LPRP/USP 0651, Fig. 3j), *Tawa hallae* (GR 241, Fig. 3e), and *Liliensternus liliensterni* (HMN MB.R.2175.7.1 and .7.2, Fig. 3g). The groove of BRUSG 28403 is similar to the faint ones seen in some *Coelophysis bauri* specimens (NMMNHS 55344), differing from coelophysids that show no proximal groove at all (e.g., *Pendraig milnerae* NHMUK PV R37591 in Spiekman et al., 2021, Fig. 3b, *Coelophysis bauri* AMNH 7224 and MCZ 4331, ‘*Syntarsus kayentakatae*’ MNA V2623 in Tykoski, 2005, Fig. 3d), though this absence might be related to skeletal immaturity (Griffin, 2018).

The anteromedial tuber is distinctive and anteroposteriorly long (Fig. 3a). It is more protuberant than those of *Eoraptor lunensis* (PVSJ 212), *Thecodontosaurus antiquus* (BRSUG 23615, Fig. 3l), and several coelophysids (*Coelophysis bauri* AMNH 2704, 7224 and MCZ 4331, *Megapnosaurus rhodesiensis* BP/1/6612, Fig. 3c, ‘*Syntarsus kayentakatae*

MNA V2623, Fig. 3d), in which the tuber does not project significantly from the main portion of the head, but also distinct from that of *Nhandumirim waldsangae* (LPRP/USP 0651, Fig. 3j), which projects much further anteromedially (Marsola et al., 2018). The projection of the tuber in *Pendraig milnerae* (NHMUK PV R37591, Fig. 3b) is similar to that of BRSUG 28403, but the latter shows a more angled tuber in proximal view. As in *Nhandumirim waldsangae* and coelophysids, the anteromedial tuber of BRSUG 28403 is lateromedially broad, whereas in taxa such as *Dilophosaurus wetherilli* (UCMP 37302, Fig. 3h) and *Liliensternus liliensterni* (HMN MB.R.2174.7.1, Fig. 3g) it is less developed in that axis. In proximal view, the anteriormost margin of the femoral head of BRSUG 28403 is not straight-to-slightly-concave as in most theropods. Instead, it is V-shaped, with a straight margin projecting anterolaterally from the anterior edge of the anteromedial tuber, which abruptly deflects at the lateromedial midpoint of the head to another straight margin that continues posterolaterally up to the anterolateral tuber (Fig. 3a). This tuber is like those of other early theropods (e.g., *Pendraig milnerae* NHMUK PV R 37591, Fig. 3b, *Coelophysis bauri* AMNH 2704, *Dilophosaurus wetherilli* UCMP 37302, Fig. 3h), *Nhandumirim waldsangae* (LPRP/USP 0651, Fig. 3j), and *Eoraptor lunensis* (PVSJ 512), i.e., developed as a swelling in proximal view. As in *Pendraig milnerae* (NHMUK PV R 37591, Fig. 3b), ‘*Syntarsus*



**Fig. 3.** Femoral heads in proximal view. (a) BRSUG 28403; (b) *Pendraig milnerae* NHMUK PV R 37591; (c) *Megapnosaurus rhodesiensis* BP/1/6614; (d) ‘*Syntarsus kayentakatae*’ MNA V2623; (e) *Tawa hallae* GR 242; (f) *Herrerasaurus ischigualastensis* PVL 2566; (g) *Liliensternus liliensterni* HMN MB.R.2175.7; (h) *Dilophosaurus wetherilli* UCMP 37302; (i) *Piatnitzkysaurus floresii* PVL 4073; (j) *Nhandumirim waldsangae* LPRP/USP 0651; (k) *Silesaurus opolenis* ZPAL Ab/III/56317; (l) *Thecodontosaurus antiquus* BRSUG unnumbered. (c, f, i, j) are mirrored. alt, anterolateral trochanter; amt, anteromedial trochanter; gr, proximal groove; gt, greater trochanter; ls, ligament sulcus; pmt, posteromedial trochanter. Scale bars are 5 mm in (b, e, j); 1 cm in (a, c, d, k); 2 cm in (f, g, i, l); 5 cm in (h).

*kayentakatae*' (MNA V2623, Fig. 3d), *Liliensternus liliensterni* (HMN MB.R.2174.7.1, Fig. 3g), and *Nhandumirim waldsangae* (LPRP/USP 0651, Fig. 3j), there is a concave ligament sulcus (Fig. 3a) posterior to the anteromedial tuber in proximal view, in contrast to forms like *Tawa hallae* (GR 242, Fig. 3e) and *Piatnitzkysaurus floresi* (PVL 4073, Fig. 3i), which show no such concavity. BRSUG 28403 shows no large medial expansion in the area of the posteromedial tuber, bearing a virtually straight medial margin posterior to the ligament sulcus (Fig. 3a), as in *Guaibasaurus candelariensis* (MCN PV 2355) and some coelophysoids (e.g., *Pendraig milnerae* NHMUK PV R37591, Fig. 3b), unlike the prominent tuber and sigmoidal medial margin of the femoral head of *Dilophosaurus wetherilli* (UCMP 37302, Fig. 3h), *Liliensternus liliensterni* (HMN MB.R.2175.7.2, Fig. 3g), *Nhandumirim waldsangae* (LPRP/USP 0651, Fig. 3j), and herrerasaurs (*Herrerasaurus ischigualastensis* PVL 2566, Fig. 3f). As in coelophysids (*Coelophysis bauri* AMNH 2704, '*Syntarsus*' *kayentakatae* MNA V2623 in Tykoski, 1998, Fig. 3d), the posterior portion of the head of BRSUG 28403 does not narrow strongly, as its mediolateral breadth is just slightly narrower than that of the anterior part, in contrast with the strongly narrowing seen in *Pendraig milnerae* (NHMUK PV R 37391, Fig. 3b), *Tawa hallae* (GR 242, Fig. 3e), *Nhandumirim waldsangae* (LPRP/USP 0651, Fig. 3j), and early Averostra-line theropods (e.g., *Dilophosaurus wetherilli* UCM 37302, Fig. 3h, *Piatnitzkysaurus floresi* PVL 4073, Fig. 3i).

The femoral head is widest at the anterolateral tuber, with a transverse width of 7 mm, whereas that of the greater trochanter region is 3.5 mm. There is no craniomedial or craniolateral crest on the femoral head, such as those present in *Staurikosaurus pricei* (MCZ 1669) and *Nhandumirim waldsangae* (LPRP/USP 0651). The femoral head of BRSUG 28403 is somewhat curved medially, so that its proximal margin forms an oblique, rather than perpendicular line to the long axis of the bone. Consequently, the medial portion of the head is downturned, and the proximolateral apex of the greater trochanters is inset and proximally expanding, rather than placed near the lateral margin of the bone (Figs. 1, 2, 4). This is different from the condition in *Nhandumirim waldsangae* (LPRP/USP 0651, Fig. 2g), *Dilophosaurus wetherilli* (UCMP

37302, Fig. 2c), and *Pendraig milnerae* (NHMUK PV R37591 in Spiekman et al., 2021, Fig. 1b, d), approaching that of *Tawa hallae* (GR 242, Fig. 2f), '*Syntarsus*' *kayentakatae* (MNA V2623, TMM 43688-1 in Tykoski, 1998, Fig. 2b), *Liliensternus liliensterni* (HMN MB.R.2175.7, Fig. 2d), and *Coelophysis bauri* (AMNH 2704; NMMNH 42351). The dorsolateral trochanter of BRSUG 28403 (Fig. 4a) is not prominent as in '*Syntarsus*' *kayentakatae* (TMM 43688-1 in Tykoski, 1998), *Coelophysis bauri* (AMNH 2074, NMMNH 55344), and *Dilophosaurus wetherilli* (UCMP 37302). It is instead present in the form of a low mound fused to the posterior margin of the greater trochanter and the obturator ridge. This also contrasts with the ridge-like trochanter of *Nhandumirim waldsangae* (LPRP/USP 0651) and *Liliensternus liliensterni* (HMN MB.R.2175.7), and the "transitional" condition seen in *Pendraig milnerae* (NHMUK PV R37591 in Spiekman et al., 2021, Fig. 4b), in which the dorsolateral trochanter is mound-shaped and more closely connected to the shaft, but still prominent in its posterior portion. The shape of the dorsolateral trochanter might be related to ontogeny (Griffin, 2018), with a ridge-like element turning into a mound during development, which is consistent with the mature condition of BRSUG 28403.

The anterior trochanter is a low, lobed expansion that does not reach proximally onto the level of the femoral head (Figs. 1, 4). It is 6 mm in proximodistal length and projects only about 2.5 mm from the femoral shaft. Its shape and connection to the shaft clearly differentiate it from the finger-shaped anterior trochanter of sauropodomorphs (*Saturnalia tupiniquim* MCP 3844-PV, Fig. 2h; *Thecodontosaurus antiquus* BRUSG 23615) and herrerasaurs (*Herrerasaurus ischigualastensis* PVL 2566), which is fully connected to the shaft. It also differs from the wing-shaped trochanters of *Dracoraptor hannigani* (NMW 2015.5G.2a), '*Syntarsus*' *kayentakatae* (MNA V2623 in Tykoski, 1998, Fig. 2b), and averostrans (*Piatnitzkysaurus floresi* PVL 4073, Fig. 2e; *Ceratosaurus* sp. UUV 56 in Madsen and Welles, 2000). The anterior trochanter of *Dilophosaurus wetherilli* (UCMP 37302, Fig. 2c) and *Liliensternus liliensterni* (HMN MB.R.2175.7.1, Fig. 2d), although similarly lobed, are more proximally positioned and slightly separated from the shaft

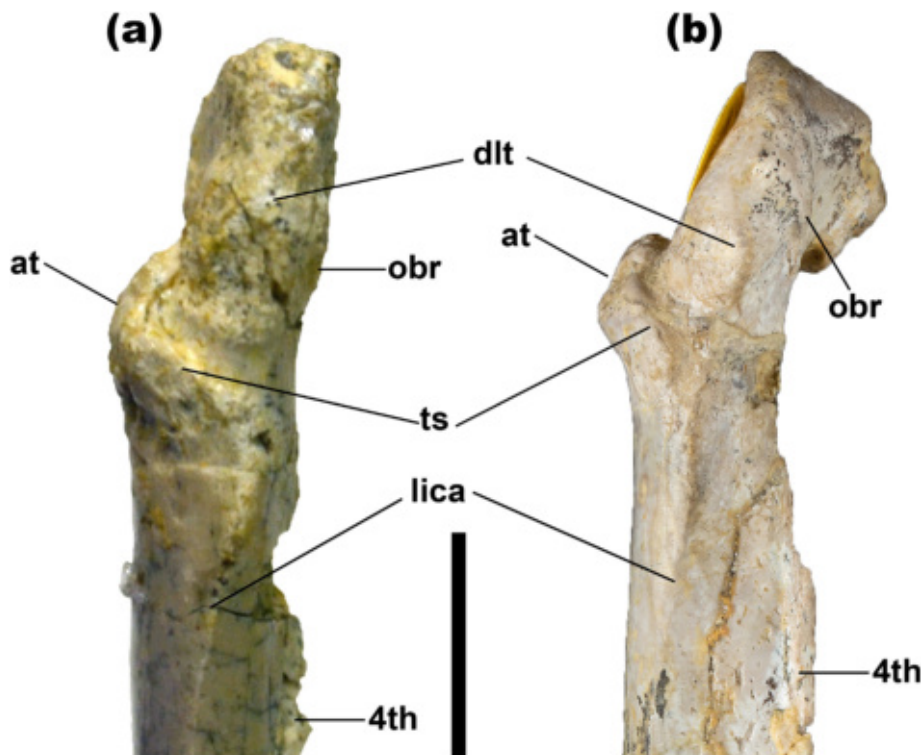


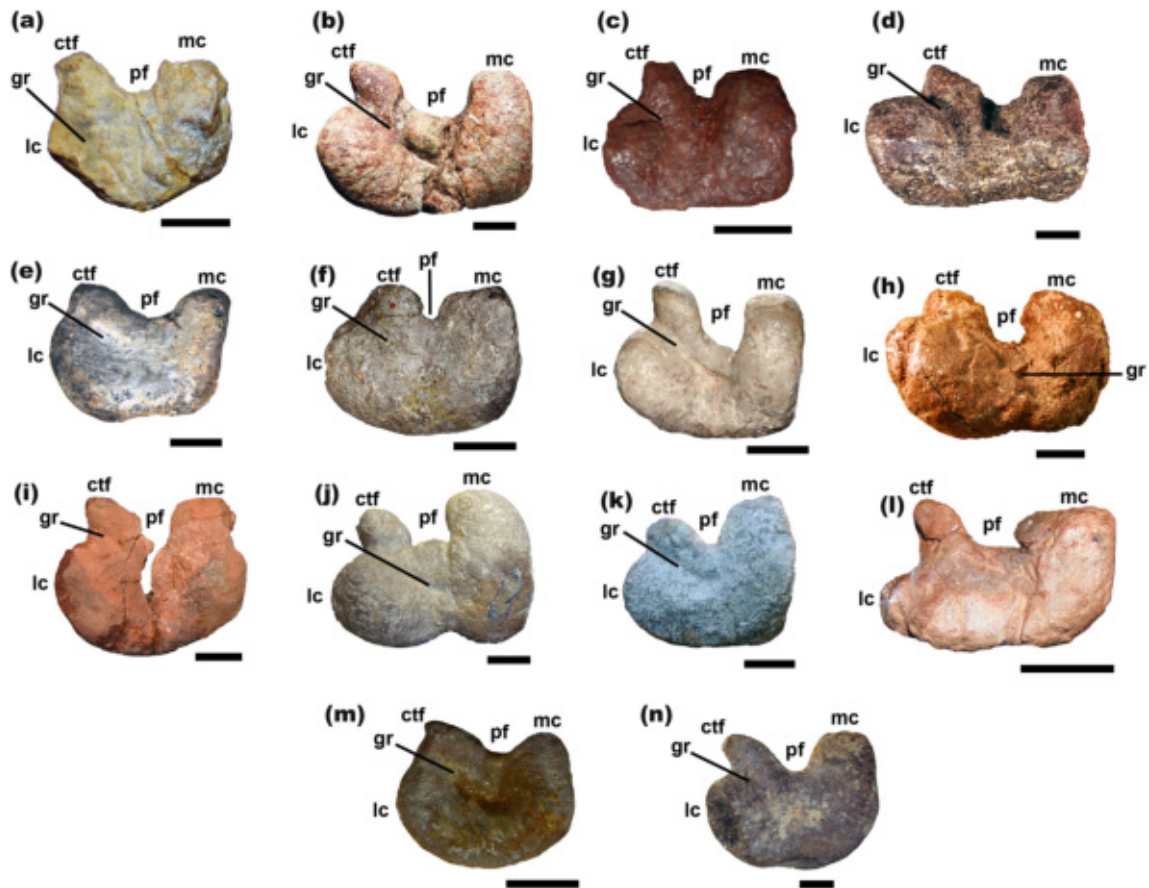
Fig. 4. Proximal portions of the femora of (a) BRSUG 28403 and (b) *Pendraig milnerae* NHMUK PV R 37591 in posterior view. 4th, fourth trochanter; at, anterior trochanter; dlt, dorsolateral trochanter; lica, linea intermuscularis caudalis; obr, obturator ridge; ts, trochanteric shelf. Scale bar is 1 cm.

proximally. The anterior trochanter of BRSUG 28403 is, on the other hand, very similar to those of *Coelophysis bauri* (AMNH 2704, 7224), *Megapnosaurus rhodesiensis* (BP/1/6215), *Tawa hallae* (GR 242, Fig. 2f), and *Pendraig milnerae* (NHMUK PV R37591 in Spiekman et al., 2021, Figs. 1f, h, 4b), the only difference being a slightly more angled profile in the latter two species, as seen in posterior view. Silesaurids also have a similar trochanter, but it is more pronounced in relation to the shaft, as seen in *Silesaurus opolensis* (ZPAL Ab/III/193, 362, 405) and *Sacisaurus agudoensis* (MCN PV 10023, 10024). BRSUG 28403 has a trochanteric shelf (Fig. 4a), resembling *Pendraig milnerae* (NHMUK PV R37591 in Spiekman et al., 2021, Fig. 4b), herrerasaurids (*Herrerasaurus ischigualastensis* PVL 2566), and coelophysids (*Coelophysis bauri* AMNH 2704, 'Syntarsus' *kayentakatae* MNA V2623 in Tykoski, 1998, Fig. 2b), but differing from *Tawa hallae* (GR 242, Fig. 2f), and *Liliensternus liliensterni* (HMN MB.R.2175.7.2, Fig. 2d). As for the orientation of the shelf, BRSUG 28403 most closely resembles the condition in *Pendraig milnerae* and the sauropodomorph *Saturnalia tupiniquim* (MCP 3845 PV, Fig. 2h), as it is horizontally oriented, in contrast with those of herrerasaurs and other coelophysoids, which markedly slope downwards along their length.

In BRSUG 28403, the fourth trochanter extends for about 20 % of the femoral length, and its distal end is located just distal to the proximal third of the bone (Fig. 1e). The proximal position of the trochanter contrasts with that of *Tawa hallae* (GR 242, Fig. 2f), herrerasaurids (*Gnathovorax cabreirai* CAPP/UFMS 0009 in Pacheco et al., 2019), and *Nhandumirim waldsangae* (LPRP/USP 0651), which is much more distally set on the shaft, with the proximal margin distal to the level of the anterior trochanter. Sauropodomorphs (*Bagualosaurus agudoensis*

UFGRS PV1099T, *Thecodontosaurus antiquus* BRSUG 23615), *Dilophosaurus wetherilli* (UCMP 37302), *Liliensternus liliensterni* (HMN MB.R.2175.7.1), *Cryolophosaurus ellioti* (FMNH PR1821 in Smith et al., 2007), and *Pendraig milnerae* (NHMUK PV R37591, Fig. 1f, h) also have a more proximally located fourth trochanter, with a proximal end at the level of the distal end of the anterior trochanter, but that of BRSUG 28403 is even more proximal, as there is an overlap between the fourth and anterior trochanters (Fig. 4a). This condition is also seen in averostrans (*Elaphrosaurus bambergi* HMN MB.R.4960, *Allosaurus* sp. UUVV 6000 in Madsen, 1976) and the coelophysids 'Syntarsus' *kayentakatae* (MNA V2623 in Tykoski, 1998) and *Coelophysis bauri* (AMNH 2704, 7224). The fourth trochanter is not totally preserved, but the low angle formed by its proximal and distal margins to the shaft suggests it was low crest like those of coelophysoids such as *Coelophysis bauri* AMNH 7244 and *Megapnosaurus rhodesiensis* QG 727. Anteromedial to the fourth trochanter, the depression for the insertion of *m. caudofemoralis longus* (Hutchinson, 2001; Carrano and Hutchinson, 2002; Grillo and Azevedo, 2011) is deep and well-defined (Fig. 1e), although its outstanding depth results from a minor collapse of bone in the region. Also of note is that the *linea intermuscularis caudalis* is exceptionally prominent in BRSUG 28403, more than in any other examined taxon, although it is also quite prominent in *Pendraig milnerae* (NHMUK PV R37591) (Fig. 4).

The anterior face of the distal end of the femur does not show an extensor fossa (Figs. 1, 5), which is also lacking in *Dilophosaurus wetherilli* (UCMP 37302, Fig. 5h), *Liliensternus liliensterni* (HMN.MB.R.2175.7.1, Fig. 5g), *Zupaysaurus rougieri* (UNLR 076, Fig. 5i), *Eoraptor lunensis* (PVSJ 559, Fig. 5k), *Guaibasaurus candelariensis* (MCN PV 2355), herrerasaurs



**Fig. 5.** Femora in distal view. (a) BRSUG 28403; (b) *Coelophysis bauri* NMMNH 42351; (c) *Megapnosaurus rhodesiensis* BP/1/6614; (d) 'Syntarsus' *kayentakatae* MNA V2623; (e) *Tawa hallae* GR 242; (f) *Herrerasaurus ischigualastensis* PVSJ 373; (g) *Liliensternus liliensterni* HMN MB.R.2175.7; (h) *Dilophosaurus wetherilli* UCMP 37302; (i) *Zupaysaurus rougieri* UNLR 076; (j) *Piatnitzkysaurus floresi* PVL 4073; (k) *Eoraptor lunensis* PVL 559; (l) *Nhandumirim waldsangae* LPRP/USP 0651; (m) *Silesaurus opolensis* ZPAL Ab/III/405; (n) *Thecodontosaurus antiquus* BRSMG Ca7490. (b, c, d, f, g, j, k, l) are mirrored. ctf, crista tibiofibularis; gr, distal groove; lc, lateral condyle; mc, medial condyle; pf, popliteal fossa. Scale bars are 5 mm in (a), e); 1 cm in (b, c, d, k, l, m, n); 2 cm in (f, g, h, i); 3 cm in (j).

(*Gnathovorax cabreirai* CAPP/UFMS 0009 in Pacheco et al., 2019), and sauropodomorphs (*Saturnalia tupiniquim* MCP 3844 PV; *Thecodontosaurus antiquus* BRSUG 23615, Fig. 5n). This contrasts with averostrans (such as *Piatnitzkysaurus floresi* PVL 4073, Fig. 5j), *Segisaurus halli* (UCMP 32101), *Powellvenator podocitus* (PVL 4414 in Ezcurra, 2017), and most coelophysids, such as *Coelophysis bauri* (USNM 529376) and 'Syntarsus' *kayentakatae* (MNA V2623; Tykoski, 1998), which bear a prominent fossa that extends to the distal portion of the femur and separates the lateral and medial condyles anteriorly in distal view; note that there are specimens of *Coelophysis bauri* with no such fossa (AMNH 2704). BRSUG 28403 does have, however, a diagonal scar for the insertion of *m. femorotibialis externus* (Hutchinson, 2001, Carrano and Hutchinson, 2002 - Fig. 1c), as seen in *Coelophysis bauri* (NMMNHS 55344, USNM 529376), *Dilophosaurus wetherilli* (UCM 37302, Fig. 2c), *Procompsognathus triassicus* (SMNS 12591), and *Sarcosaurus woodi* (WARMS G682). BRSUG 28403 also shows a swelling at the distal tuberosity region, shared in *Zupaysaurus rougieri* (UNLR 076) and *Liliensternus liliensterni* (HMN MB.R.2175.7, Fig. 2d). In addition, there is a fossa on the medial surface of the distal end of the femur (Figs. 1, 2), which is delimited by two ridges, one anterior and another posterior. The latter borders the medial condyle distally, and converges with the anterior ridge proximally, giving the fossa a triangular shape. This differs from the semi lunate medial fossa present in other neotheropods such as *Powellvenator podocitus* (PVL 4414 in Ezcurra, 2017), *Coelophysis bauri* (AMNH 2704), *Megapnosaurus* (NHMUK PV R9585), *Liliensternus liliensterni* (HMN MB.R.2175.7.1 and .7.2), and *Zupaysaurus rougieri* (UNLR 076). Not only is the shape different, but the fossa of BRSUG 28403 is deeper and more rugose than the rest of the element as delimited by the ridges. Moreover, the anterior of these two ridges, possibly the same as the medial distal ridge as described for *Megapnosaurus rhodesiensis* (NHMUK PV R9585), *Powellvenator podocitus* (PVL 4414 in Ezcurra, 2017), *Segisaurus halli* (UCMP 32101 in Ezcurra, 2017), and *Zupaysaurus rougieri* (UNL 076), is less prominent and much less proximally extended in BRSUG 28403 in comparison to these taxa.

The distal end of the femur has a generally pentagonal shape, with no distinct mediolateral or anteroposterior expansion (Fig. 5a). In distal view, the distal tuberosity (=distal rugosity, attachment area for the *M. femorotibialis externus* (Hutchinson, 2001)) is well-marked, the anterior margin of the bone showing a V-shaped profile, with the anteriormost point midway between the medial and lateral condyles. This contrasts with the virtually straight anterior margin of the femur (in distal view) of *Dilophosaurus wetherilli* (UCMP 37302, Fig. 5h) and the sauropodomorph *Thecodontosaurus antiquus* (BRSMG C4530, Fig. 5n), the rounded margin of *Liliensternus liliensterni* (MB.R.2175.7.1, Fig. 5g) and *Zupaysaurus rougieri* (UNLR 076, Fig. 5i), and the excavated one of taxa with prominent extensor fossae such as *Megapnosaurus rhodesiensis* (NHMUK PV R9585), *Segisaurus halli* (UCMP 32101 in Carrano et al., 2005), *Powellvenator podocitus* (PVL 4414 in Ezcurra, 2017), and averostrans (*Piatnitzkysaurus floresi* PVL 4073, Fig. 5j; *Ceratosaurus* sp. UUV 56 in Madsen and Welles, 2000). The medial condyle has a slightly curved medial margin in distal view (Fig. 2), continuous throughout its length, as is the case in most dinosauromorphs, such as *Silesaurus opolensis* (ZPAL Ab/III/405, Fig. 5m), *Eoraptor lunensis* (PVSJ 559, Fig. 5k), *Tawa hallae* (GR 242, Fig. 5e), *Herrerasaurus ischigualastensis* (PVSJ 373, Fig. 5f), 'Syntarsus' *kayentakatae* (MNA V2623, Fig. 5d), *Megapnosaurus rhodesiensis* (NHMUK PV R9585), *Liliensternus liliensterni* (HMN MB.R.2175.7.1), and *Zupaysaurus rougieri* (UNLR 076, Fig. 5i). In contrast, a few early theropods such as *Coelophysis bauri* (NMMNHS 42351, Fig. 5b) and *Piatnitzkysaurus floresi* (PLV 4073, Fig. 5j) have straighter margins. In distal view, the popliteal fossa, and thus the separation between the medial condyle and the crista tibiofibularis, is short and wider than long, representing 26.7% of the mediolateral width and 15.4% of the anteroposterior length of the distal surface of the femur (Fig. 5a). This is similar to the condition in 'Syntarsus' *kayentakatae* (MNA V2623 in Tykoski, 1998, Fig. 5d), *Coelophysis bauri* (AMNH 2704, NMMNHS 42351; USNM 529376, Fig. 5b), *Megapnosaurus rhodesiensis* (NHMUK PV

R9585, BP/1/6215, Fig. 5c), *Powellvenator podocitus* (PVL 4414 in Ezcurra, 2017), *Segisaurus halli* (UCMP 32101 in Carrano et al., 2005), *Nhandumirim waldsangae* (LPRP/USP 0651, Fig. 5l), *Tawa hallae* (GR 241, Fig. 5e), and *Herrerasaurus ischigualastensis* (PVL 2566). In contrast, a distal fossa longer than wide and more deeply excavating the distal end of the femur is seen in *Liliensternus liliensterni* (HMN MB.R.2175.7, Fig. 5g), *Zupaysaurus rougieri* (UNLR 076), *Dilophosaurus wetherilli* (UCMP 37302, Fig. 5h), *Eoraptor lunensis* (PSJ 559), averostrans such as *Piatnitzkysaurus floresi* (PVL 4073, Fig. 5j), and sauropodomorphs such as *Saturnalia tupiniquim* (MCP 3844 PV) and *Thecodontosaurus antiquus* (BRSMG C4530).

The crista tibiofibularis of BRSUG 28403 projects laterally as in most dinosauromorphs (Fig. 5), an exception being *Powellvenator podocitus* (PVL 4414 in Ezcurra, 2017), the crista of which is more posteriorly directed. The notch between the crista and the lateral condyle is short and the lateral condyle projects laterally (Fig. 5a). This condition is seen in *Coelophysis bauri* (AMNH 2704, USNM 259376), *Zupaysaurus rougieri* (UNLR 076, Fig. 5i), *Nhandumirim waldsangae* (LPRP/USP 0651, Fig. 5), *Tawa hallae* (GR 242, Fig. 5e), *Saturnalia tupiniquim* (MCP3844 PV), and *Eoraptor lunensis* (PVSJ 559, Fig. 5k), but not in 'Syntarsus' *kayentakatae* (MNA V2623 in Tykoski, 1998, Fig. 5d), *Megapnosaurus rhodesiensis* (BP/1/6614), *Liliensternus liliensterni* (HMN MB.R.2175.7, Fig. 5g), *Dilophosaurus wetherilli* (UCMP 37302, Fig. 5h), and averostrans (*Piatnitzkysaurus floresi* PVL 4073, Fig. 5j), whose lateral condyle expands laterally and the notch between it and the crista tibiofibularis is more prominent. In BRSUG 28403, the groove that extends from the notch to the anterior margin of the femur (Fig. 5a), on the distal surface of the bone, forms a steeply anteroposteriorly oriented diagonal, as in 'Syntarsus' *kayentakatae* (MNA V2623 in Tykoski, 1998, Fig. 5d), but contrasting with the gentler diagonal groove in all other taxa. The lateral condyle shows a unique expansion (Fig. 2), projecting posterolaterally from the anterior distal tuberosity and anterolaterally from the crista tibiofibularis, the two margins meeting in the anteroposterior midpoint of the distal end. The margins are straight, so that the condyle has an overall sharp triangular aspect in distal view. There are taxa with a similar condition, but the margins and the furthest laterally projected point are rounded, so that the condyle is semi-circular or semioval instead of triangular; this is the case of *Coelophysis bauri* (NMMMS 42351, Fig. 5b), *Liliensternus liliensterni* (HMN BR.R.2175.7, Fig. 5g), *Zupaysaurus rougieri* (UNLR 076, Fig. 5i), *Piatnitzkysaurus floresi* (PVL 4073, Fig. 5j), *Powellvenator podocitus* (PVL 4414 in Ezcurra, 2017), *Saturnalia tupiniquim* (MVP 3844 PV), *Thecodontosaurus antiquus* (BRSMG Ca7490, Fig. 5n), *Eoraptor lunensis* (PVL 559, Fig. 5k), and *Silesaurus opolensis* (ZPAL Ab/III/193, 362, 405, Fig. 5m). On the other hand, *Tawa hallae* (GR 242, Fig. 5e), *Nhandumirim waldsangae* (LPRP/USP 0651, Fig. 5l), and *Dilophosaurus wetherilli* (UCMP 37302, Fig. 5h), although having a rounded margin with a distinct apex, have apices that are either posteriorly or anteriorly deflected, which give them a general aspect that recalls more the rectangular lateral condyles of 'Syntarsus' *kayentakatae* (Tykoski, 1998) and *Megapnosaurus rhodesiensis*. *Herrerasaurus ischigualastensis* (PVL 2566) and some specimens of *Coelophysis bauri* (USNM 529376) have straight lateral condyles that do not project laterally, but this is likely due to taphonomic deformation in the latter case. In fact, it cannot be excluded that the unique sharp aspect of the condyle in BRSUG 28403 was at least partially caused by deformation. However, specimens of related taxa that are taphonomically deformed, such as *Coelophysis bauri* (USNM 529376) and *Powellvenator podocitus* (PVL 4414-8; Ezcurra, 2017) have alterations in the entire distal end of the femur, whereas that would be the case only of the lateral condyle in BRUSG 28403. This suggests that the triangular lateral condyle is autapomorphic for the specimen.

If BRSUG 28403 is scored for the ontogenetic character list of Griffin (2018), it fits the mature condition for all features; note that character 23 on that list was not scored because the fourth trochanter blade is missing. Such features include the absence of a depression on the anterolateral face of the femoral head, a large trochanteric shelf and an obturator ridge. Some of the most prominent differences between BRSUG 28403 and *Pendraig milnerae*, the only named theropod from the UK fissure system,



such as the presence of an anterolateral scar, a scar proximal to the obturator ridge, an insertion scar of the *m. caudofemoralis brevis*, and the more prominent *lineae intermuscularis*, are potentially explained by *Pendraig milnerae* representing an immature individual, whereas BRSUG 28403 is possibly more osteologically mature, following Griffin (2018). On the other hand, the estimated total femoral length of *Pendraig milnerae* is 10.5 cm (Spiekman et al., 2021), which is only marginally shorter than BRUSG 28403, what may jeopardise the inference that they represent ontogenetically disparate individuals.

## 6. Phylogeny and discussion

The inclusion of BRSUG 28403 in the Spiekman et al. (2021) phylogenetic matrix unsurprisingly led to a decrease in resolution of the tree, given the amount of missing data for an OTU composed only by a femur. Fifty-two MPTs were recovered, with 1410 steps. In the strict consensus, all coelophysoids are found in a large polytomy (Fig. 6). The support of the Coelophysoidea clade is low, with a Bremer score of 1 and <50 % Bootstrap support. The majority-rule consensus has

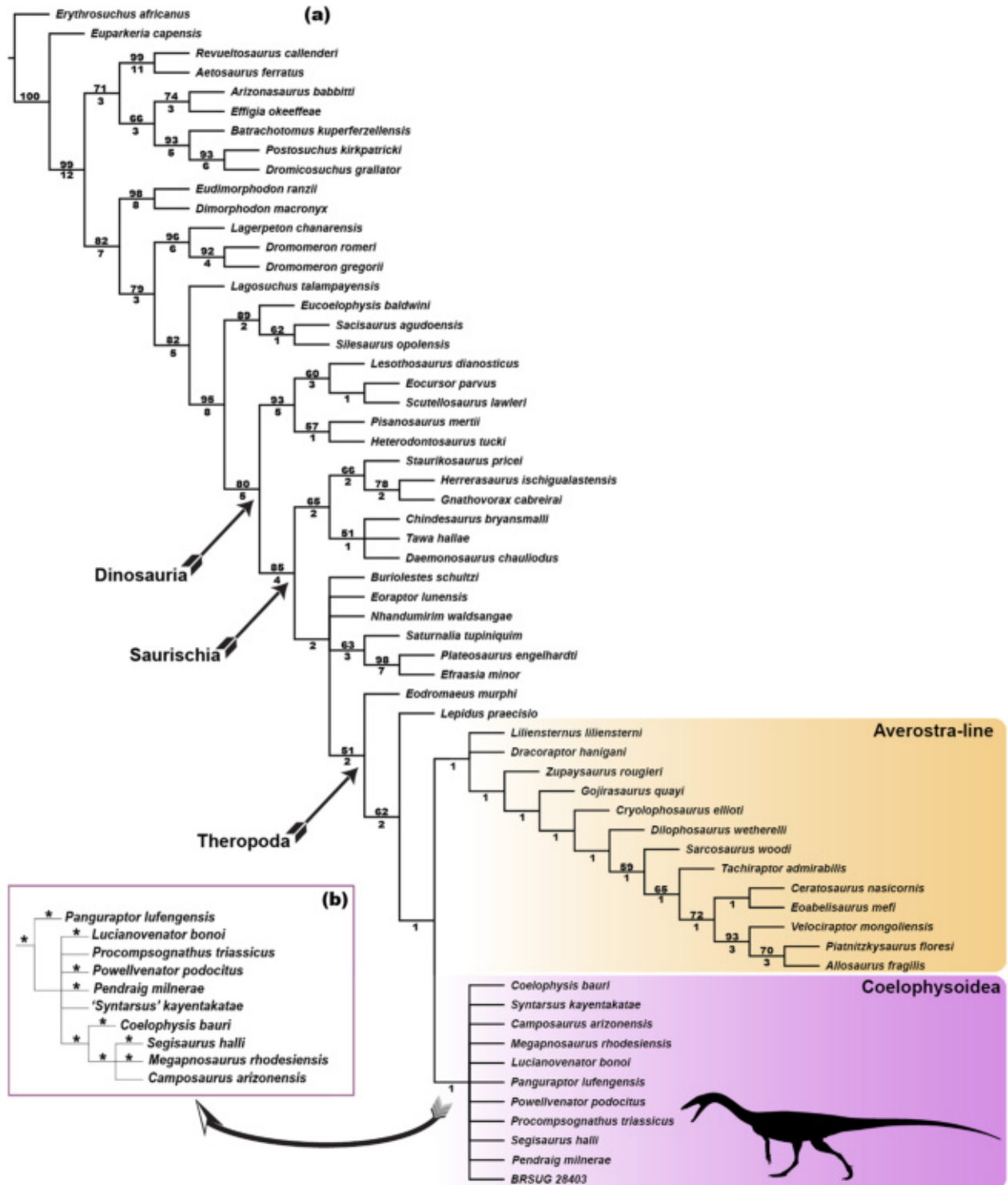


Fig. 6. Strict consensus of 52 MPTs with a score of 1410 (a). Numbers above the lines represent bootstrap support of 1000 pseudoreplications and numbers below are Bremer supports. The inset (b) shows the IterPCR consensus with BRSUG 28403 pruned, and the asterisks mark the different recovered positions of BRSUG 28403 on this scheme.

more resolution (Supplementary Fig. 1), with *Panguraptor lufengensis* as sister to all other coelophysoids and a clade formed by *Coelophysis bauri* and a tritomy of *Segisaurus halli*, *Camposaurus arizonensis*, and *Megapnosaurus rhodesiensis*. On the strict consensus, the position of BRSUG 28403 as a Neotheropod is supported by a medially offset anteromedial tuber (223: 1 → 2) and as a coelophysoid by a rounded dorsolateral trochanter (230: 1 → 2). On the majority consensus, no character scored for BRSUG 28403 is listed as a synapomorphy of the coelophysoid clade that excludes *Panguraptor lufengensis*. In both consensuses, a flat medial articular surface of the femoral head in proximal view (226: 0 → 1) was recovered as a local autapomorphy of BRSUG 28403, as is also the case of an angled anteromedial corner of the distal end (247, 0 → 1) in the majority rule tree.

The iterPCR (Pol and Escapa, 2009 – Details on the Supplementary text) analysis identifies BRUSG 28403 as an unstable taxon and, once it is pruned, the remaining configuration is the same as that of Spiekman et al. (2021), namely a clade of (*C. bauri* (*S. halli*, *M. rhodesiensis*, *C. arizonensis*)) in a polytomy with all other coelophysoids excluding *P. lufengensis*. It is also of note that, when the analysis prunes two taxa, *Powellvenator podocitus* is pruned in addition to BRSUG 28403. In this configuration, *Pendraig milnerae* falls outside the abovementioned polytomy, being instead its sister group.

The putative difference in ontogenetic stages between *Pendraig milnerae* and BRUSG 28403, coupled with the small size difference could have multiple explanations. It might mean that, although immature, the holotype of *Pendraig milnerae* was close to its maximum adult size. Indeed, one of the main observations of Griffin (2018) is the variability in the pattern of ontogenetic changes between *Coelophysis bauri* and *Megapnosaurus rhodesiensis*, and even within the same species. Hence, *Pendraig milnerae* undergoing several changes in skeletal maturation without a significant increase in overall size is a reasonable possibility. As mentioned in Spiekman et al. (2021), the small size of *Pendraig milnerae* could be due to insular dwarfism (MacArthur and Wilson, 1967; Lomolino, 2005), but the immature condition of the holotype and the presence of non-insular small coelophysoids hamper this inference. Indeed, BRSUG 28403 indicates that coelophysoid individuals could reach maturity with an overall small size. Whether the same species or not, this suggests the less mature status of the holotype of *Pendraig milnerae* might not be the only explanation for its small size. Yet, this does not unequivocally suggest insular dwarfism, as the fissure deposit coelophysoids fall within the body size range of other small forms such as *Procompsognathus triassicus*, that were not located on islands (Spiekman et al., 2021).

Conversely, BRSUG 28403 could represent another coelophysoid from the same insular environment, which, given the increase of speciation rates and multiple colonisations that often happen in island chains (MacArthur and Wilson, 1967; Emerson and Kolm, 2005; Whittaker et al., 2007; Losos and Ricklefs, 2009), is also a reasonable possibility. In this case, BRSUG 28403 would represent an overall smaller-sized theropod than *Pendraig milnerae*. Indeed, some differences between the two individuals are not clearly related to ontogeny, such as the flat medial articular surface of the femoral head, the sharper anteromedial condyle, and the relatively wider posterolateral end of the femoral head of BRSUG 28403; and possibly the distally deflected fourth trochanter of *P. milnerae*, which is likely absent in BRSUG 28403 based on what is preserved of its trochanter. Unfortunately, the most distinctive aspect of the BRSUG 28403 femur, the pentagonal-shaped distal end, cannot be compared to *Pendraig milnerae*, which lacks the distal end of the femur. In addition, the height of the fourth trochanter, a distinctive trait of *Pendraig milnerae*, also cannot be observed in BRSUG 28403 either, as the blade of this element is missing. Such lack of overlap of significant features complicates a possible assignment of BRSUG 28403 to *Pendraig milnerae*, and although there are differences that are not clearly ontogenetic, this possibility cannot be dismissed *a priori*. As is often the case, more specimens are needed to define the taxonomic affinities of BRSUG 28403, but it nonetheless adds to the knowledge of the faunal

diversity of the Late Triassic fissure fill deposits of southwestern England and southern Wales.

### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pgeola.2023.07.005>.

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