

A sauropodomorph dinosaur from the ?Early Jurassic of Lusitu, Zambia

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Dinosaur material has been reported from Zambia but remains undescribed. The first record, from the upper Luangwa Valley, was mistakenly identified and pertains instead to indeterminate dicynodonts. The only other report on Zambian dinosaur material concerns associated partial hind limb and vertebral material collected from an Upper Karoo sandstone in the vicinity of Lusitu. We provide a description of this specimen, the first definitive dinosaur to be reported from Zambia, and identify it as an indeterminate basal sauropodomorph. Unfortunately, the precise age of the specimen remains unknown, although an Early Jurassic age seems likely.

Keywords: Dinosauria, Early Jurassic, Sauropodomorpha, palaeobiogeography, biostratigraphic correlation.

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INTRODUCTION

Triassic/Jurassic Stormberg Group strata are widely distributed in southern and south-central Africa, with prominent outcrops in South Africa, Lesotho, Zimbabwe, Mozambique, Zambia, Malawi, Botswana and Namibia (Catuneanu *et al.* 2005; Olsen & Galton 1984; Raath 1969, 1977; Rubidge 2005). Although these sedimentary rocks (particularly the Elliot and Clarens Formations and their equivalents) preserve a diverse and relatively well-known non-avian dinosaur fauna in South Africa, Lesotho and Zimbabwe, those from adjacent territories have been poorly explored for dinosaur fossils (Catuneanu *et al.* 2005; Olsen & Galton 1984). For example, the Mesozoic Namibian dinosaur record consists of a few small indeterminate fragments described by von Huene (1925), and the Mesozoic dinosaurian record of Mozambique is limited to a diaphyseal fragment possibly from a large theropod (Dixey & Campbell-Smith 1929). A search through compilations of Mesozoic dinosaur distribution data, such as Weishampel *et al.* (2004) and FossilWorks (<http://fossilworks.org>) and The Paleobiology Database (<http://paleobiodb.org>), yielded no known dinosaur collections records from Zambia, Botswana or Swaziland.

There are several Karoo-age rift basins in Zambia (Catuneanu *et al.* 2005; Daly *et al.* 1989), and in particular the Luangwa Basin is known for its abundant tetrapod fossils (Drysdall & Kitching 1962, 1963). These fossils have formed the basis for biostratigraphical correlations between the Luangwa Basin sedimentary sequences and those of Beaufort Group deposits in the main Karoo basin of South Africa, but the Luangwa Basin appears to lack Stormberg Group time-equivalent strata (Catuneanu *et al.* 2005). Nevertheless, rare tetrapod fossils have been reported from hypothesized equivalents of Stormberg

Group rocks in Zambia (Dixey 1937; Drysdall & Kitching 1963). Any dinosaur material from these areas would be of enormous regional significance because it would potentially enable biostratigraphic correlations with the upper portions of neighbouring Karoo-aged basins (Catuneanu *et al.* 2005), allow further determination of the geographic and ecological range of iconic Stormberg dinosaurs, and provide information on faunal composition during this poorly-known interval in this region.

Dixey (1937: 69–70) noted the presence of rolled reptile bones at several sites in the upper Luangwa Valley, Zambia (then Northern Rhodesia), from strata he considered to be lateral equivalents of the Lower Cretaceous ‘Dinosaur Beds’ that he had examined in Nyasaland (now Malawi). Bone fragments from at least one of these localities were sent to W.E. Swinton of the British Museum (Natural History) (now Natural History Museum, London) who identified them as dinosaurian (Dixey 1937). Although the original locality is not mentioned in Dixey’s publication, it is listed in his field notes, which are archived at the British Geological Survey (S. Tolan, pers. comm., January 2015) and the specimens were recently re-located in the collections of the NHMUK by P.M.B., where they are catalogued as NHMUK PV R5904. These specimens bear the field number ‘R.57’ and Dixey’s field notes state that they were obtained from ‘near Katumbi, on Ntawere track, c. 2 m [miles] S of Ntawere’ (S. Tolan, pers. comm., January 2015). NHMUK PV R5904 consists of 12 bone fragments (Dixey originally listed 14 in his field notes: S. Tolan, pers. comm., January 2015) many of which are broken and poorly preserved partial limb bones. None of this material possesses any features consistent with referral to Dinosauria in terms of either autapomorphies or general anatomical resemblance. However, the presence of a large tusk-like tooth suggests that the ‘dinosaur’ specimen

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pertains to a large dicynodont (J.N.C. and P.M.B., pers. obs.) and the limb bone fragments are also consistent with this interpretation (K. Angielczyk, pers. comm., January 2015). Moreover, subsequent work by Drysdall & Kitching (1963) demonstrated that these strata were not lateral equivalents of the Cretaceous-aged Dinosaur Beds of Malawi and instead referred these deposits to the Triassic Ntawere Formation. Although Drysdall & Kitching (1963) reported bones from these deposits, none of their finds could be identified as dinosaurian and the fragments they collected were listed as anomodonts (*ibid.*: 12). Dixey (1937) briefly mentioned other dinosaur material from his Zambian 'Dinosaur Beds' (= Ntawere Formation) with the field numbers R.56–R.63: the relevant localities and specimens are also listed in his field notes (S. Tolan, pers. comm., January 2015). All of the tetrapod material collected by Dixey during his Zambian surveys (R.1–R.66, but minus R.57) was sent to L.D. Boonstra at the South African Museum (now the Iziko South African Museum) in Cape Town for identification. Boonstra (1938) reported that the majority of the collection was not identifiable and made no mention of dinosaur material: this circumstantial evidence suggests that Boonstra rejected Dixey's field identifications of R.56 and R.58–R.63 as dinosaurian. Subsequent biostratigraphic work (Catuneanu *et al.* 2005; Peacock *et al.* 2013; Rubidge 2005; Wopfner 2002) strongly suggests that the Upper Ntawere is time-equivalent with the Middle Triassic *Cynognathus* subzone C (Hancox *et al.* 1995) of South Africa and the Manda Beds of Tanzania, further increasing the likelihood that this material is not dinosaurian.

Here we provide the first description of the only other previously reported dinosaur specimen from Zambia (see Drysdall & Kitching 1963), which now represents the first definitive dinosaur specimen to have been collected from this country.

MATERIAL

All of the material is catalogued under the accession number BP/I/4559. It was donated to the Bernard Price Institute (BPI) by Dr. A.M.J. de Swardt, Director of the Geological Survey, Northern Rhodesia. The exact date of this donation was not recorded, but likely to be no later than 1963, the last year James Kitching worked in Northern Rhodesia, acting as a guide to the BM(NH) Expedition to the Luangwa Valley. BP/I/4559 was collected along the bank of the Lusitu River, in the vicinity of Lusitu village, Zambia (de Swardt 1962; Fig. 1). This area has numerous exposures of Karoo sediments that were divided by Gair (1959) into two unnamed units: a lower 'Sandstone Interbedded Mudstone' and upper 'Red Sandstone'. As these horizons are conformable and lack a clear boundary, Gair's (1959) map of the area does not distinguish between them (Fig. 1B, C). Both units were correlated with the upper part of the Karoo succession in Zimbabwe (Forest Sandstone and Nyamandhlovu formations: Gair 1959). BP/I/4559 was collected from a formation that was described as an 'Upper Karoo sandstone' that might have been an equivalent of the 'Molteno fauna or a higher horizon' (Drysdall & Kitching 1963: 39), but it was not

stated whether this unit was the 'Sandstone Interbedded Mudstone' or the 'Red Sandstone'. A note from J.W. Kitching appended to the ESI collections catalogue noted the horizon as an 'equivalent of the Forest Sandstone'. Brown (1967) noted later that the dinosaur remains had been recovered from the 'Red Sandstone' and this interpretation is followed herein. This bed is usually correlated with the Forest Sandstone and Clarens Sandstone Formations of Zimbabwe and South Africa (Brown, 1967; Drysdall and Kitching, 1963; Gair, 1959); consequently, it is considered to be of Early Jurassic age, although its exact age remains unknown.

BP/I/4559 was initially identified as an indeterminate dinosaur (Drysdall & Kitching 1963: 39), but the collections catalogue of the ESI contains an entry by A. Yates from 2007 identifying it as an indeterminate sauropodomorph. It consists of a partial, poorly preserved right hind limb and associated vertebral material (Figs 2–5). Included within this material are: a complete right femur, complete right tibia, four vertebral centra of unknown position and preserved in unpreparable small blocks, two complete caudal vertebrae (one middle, one distal), a chevron, three non-ungual pedal phalanges, parts of the metatarsus preserved in several additional unpreparable blocks, and numerous broken fragments.

The right femur and tibia are preserved in direct articulation, with the femur folded over the tibia, and the chevron and one of the pedal phalanges are preserved in close association with the distal end of the tibia.

Lithology

BP/I/4559 is preserved in well-indurated, fine-grained, pink sandstone without obvious bedding, and with a siliceous cement. Most of the bones are grey to white in colour, but several poorly preserved vertebrae are a deep blue (Fig. 3B). It is unknown whether this blue color is of diagenetic origin or whether it represents a byproduct of the initial preparation and consolidation of the specimen. All bone surfaces are extensively cracked and were weathered before burial and fossilization. In localized areas, a fine purple iron mineral precipitate layer approximately 1 mm thick adheres to the fossilized bone. The unprepared matrix contains a number of resistant sub-cylindrical features (Fig. 4D), which are likely to represent small invertebrate burrow infills. These extend throughout the matrix surrounding the bones.

Preparation

The specimen was collected from the field using unknown methods and was partially prepared prior to our recent investigations. Our re-preparation of the material was performed as follows: rock matrix was removed from the specimen in the laboratory primarily via the use of hand-held pneumatic airscribes. Fossilized bone was consolidated using an approximately 10% solution of Paraloid B-72 solid grade thermoplastic acrylic resin in 100% acetone solvent. Individual pieces of bone were glued together using a highly concentrated (~30%) solution of Paraloid B-72 in 100% acetone solvent.

The remainder of the specimen is fragmentary and the

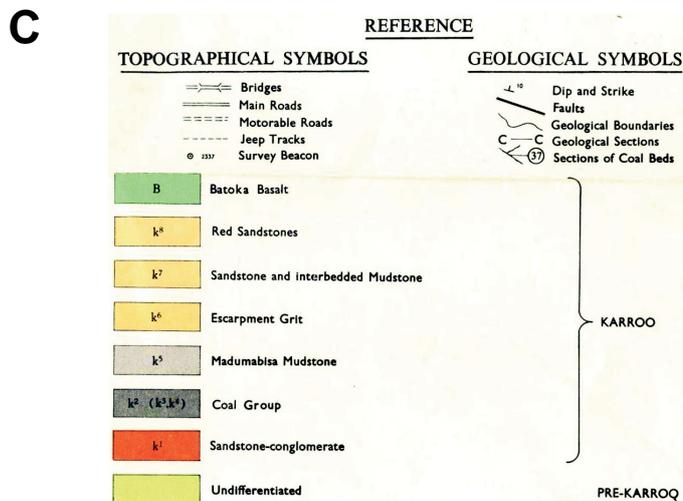
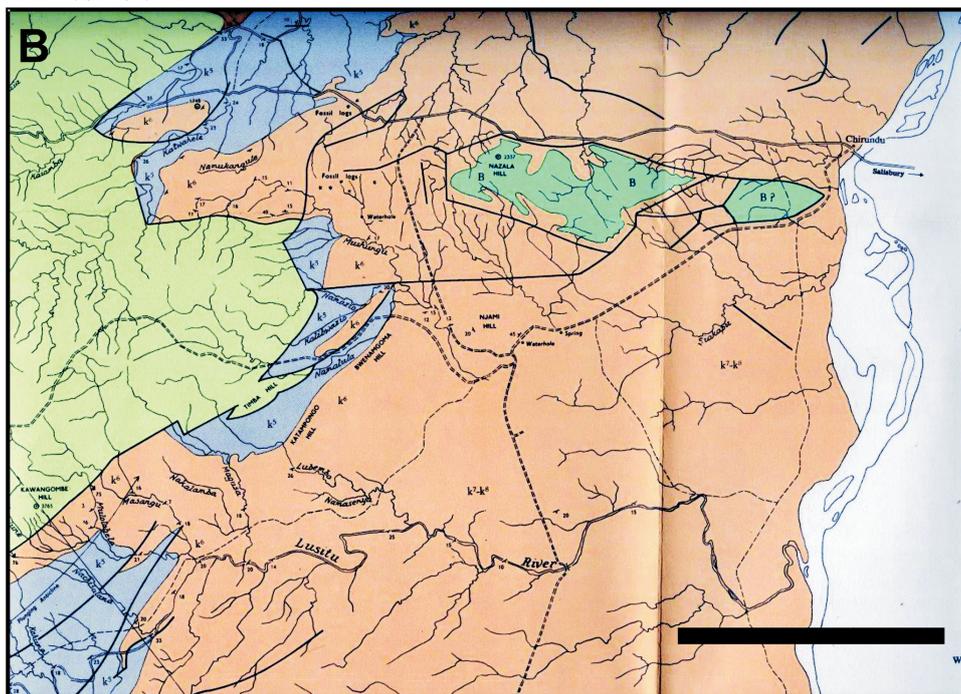
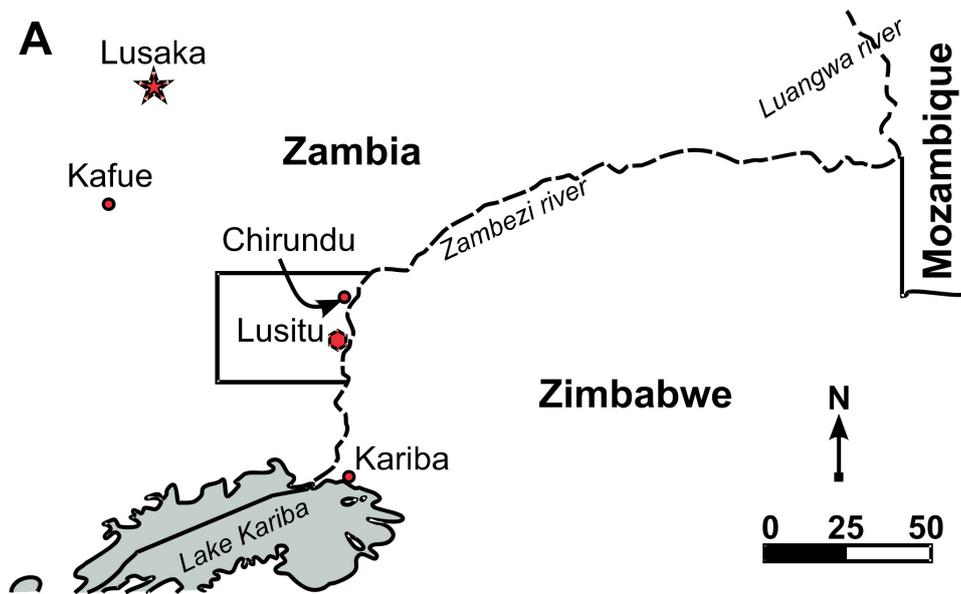


Fig. 1. Maps showing approximate collection locality of BP/1/4559. A, schematic map showing political boundaries and major waterways; B, map detail from Gair, 1959, showing rock units near Lusitu; C, legend for B. Green-shaded area in A shows approximate extent of B. Thick dashed line in B shows likely area where BP/1/4559 was collected from. Thin dashed lines, international boundaries formed by rivers; solid lines, international boundaries. Scale units in A are in km; scale bar in B is approximately 10 km.

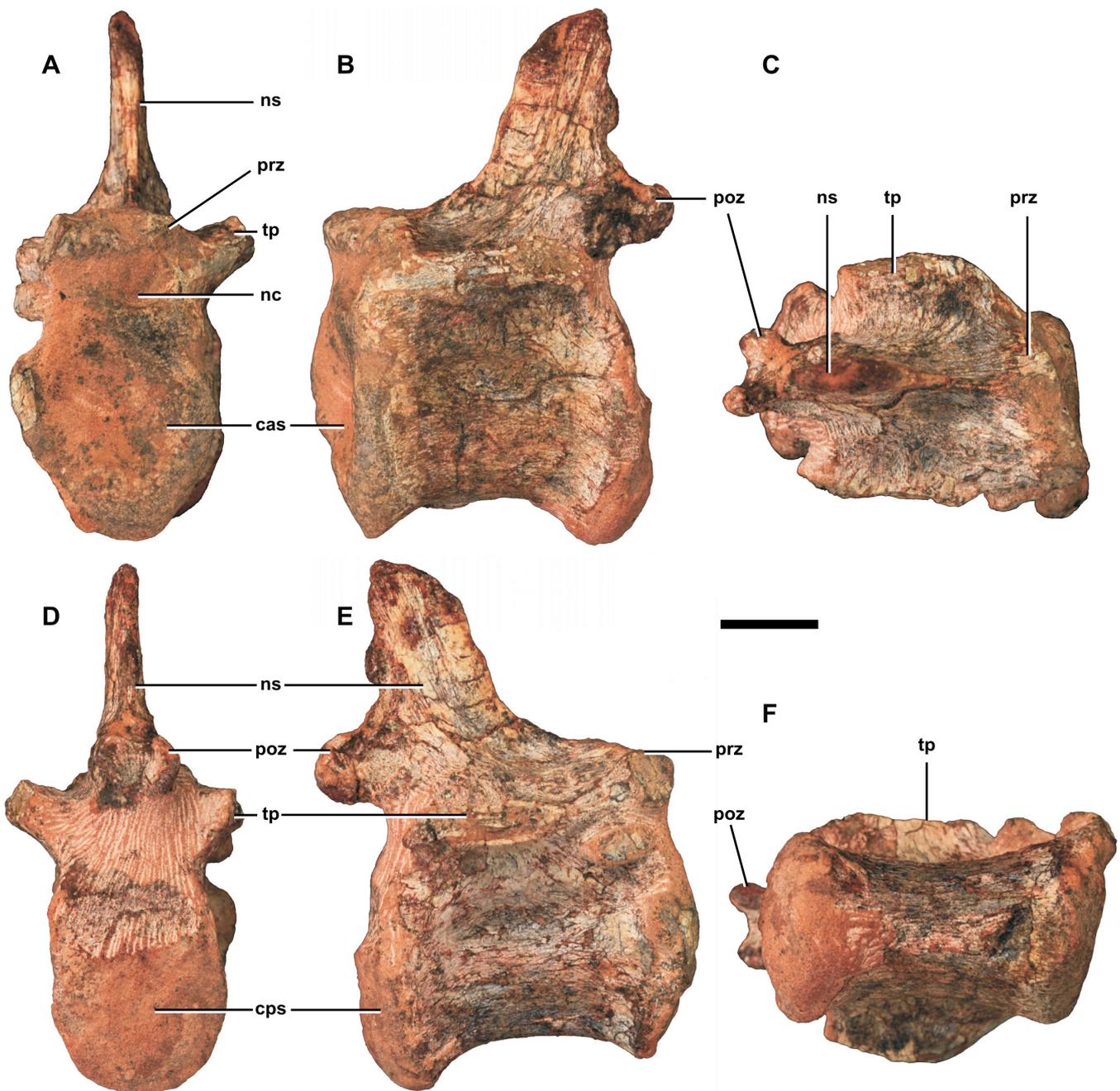


Fig. 2. Middle caudal vertebra of BP/1/4559. A, anterior; B, left lateral; C, dorsal; D, posterior; E, right lateral; and F, ventral views. Scale bar equals 1 cm.

exposed bone is poorly preserved. Due to the discrepancy between the hardness of the sandstone and the softness of the bone, further preparation is not desirable.

SYSTEMATIC PALAEOLOGY

Dinosauria Owen, 1842

Saurischia Seeley, 1887

Sauropodomorpha von Huene, 1932

Sauropodomorpha indet., Figs 2–5

DESCRIPTION

Vertebrae

Two complete caudal vertebrae are preserved with the specimen, one middle caudal (Fig. 2) and one distal caudal (Fig. 3A). Several partial centra are also preserved (Fig. 3B; measurements in Table 1).

Middle caudal vertebra

The middle caudal vertebra has a subelliptical anterior articular surface that is taller dorsoventrally than it is wide mediolaterally. The anterior articular surface is shallowly concave and surrounded by a raised rim of bone laterally and ventrally. A small, undivided chevron facet with a trapezoidal outline is present. The posterior articular surface is more rounded, and shield-shaped in outline. Its ventral margin is abraded and covered with matrix, but slightly bevelled suggesting that it also ended in a small chevron facet. In lateral view, the centrum has straight anterior and posterior margins and a gently concave ventral margin that is accentuated by the ventral projections of the chevron facets. It is slightly longer anteroposteriorly than tall dorsoventrally. The lateral surfaces of the centrum are gently concave anteroposteriorly and convex dorsolaterally to produce a saddle-shaped morphology.

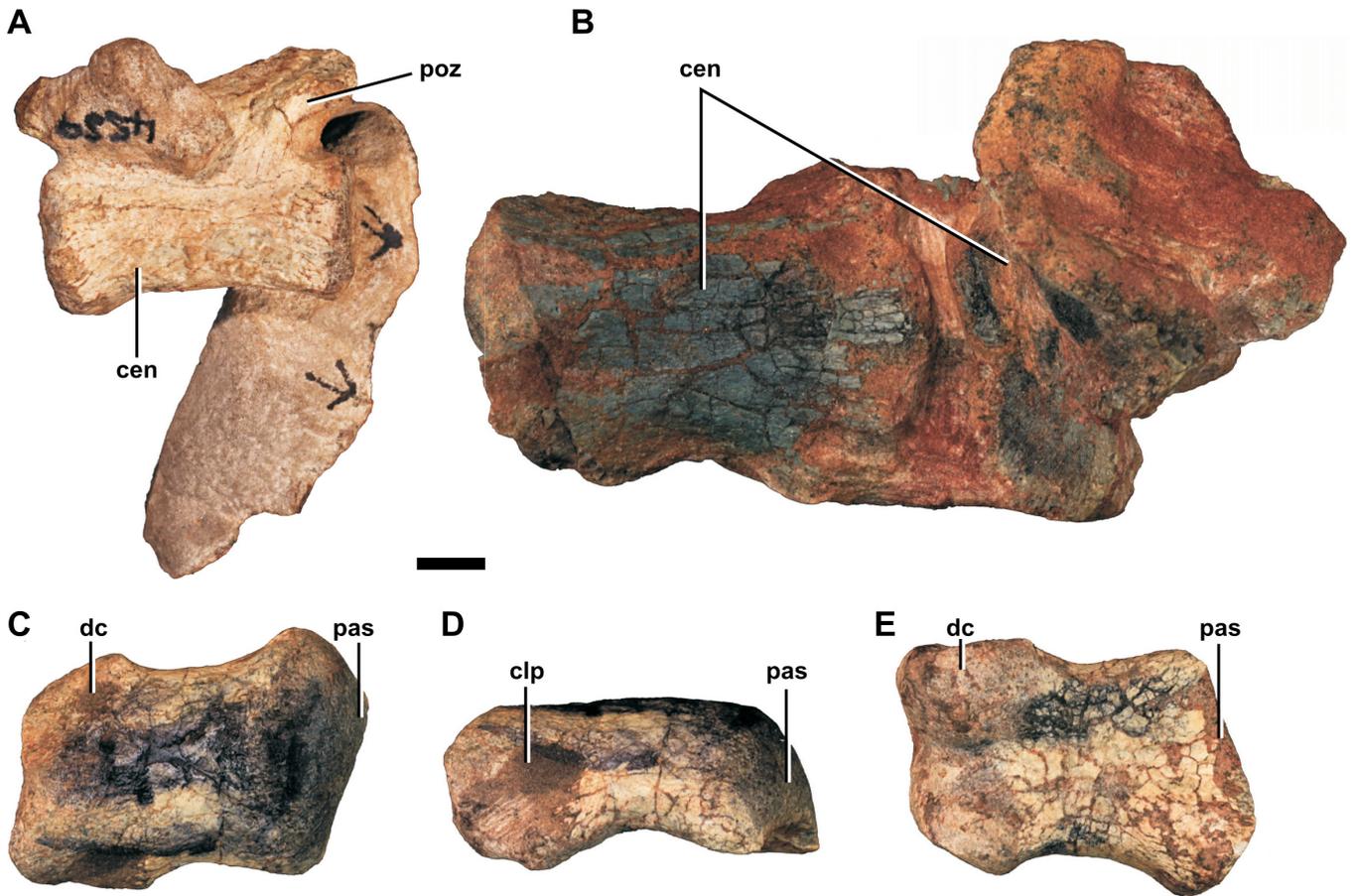


Fig. 3. Vertebral and skeletal elements of BP/1/4559. A, distal caudal vertebra in left lateral view; B, block with partial centra; C–E, pedal phalanx in: C, dorsal, D, lateral, and E, ventral views. Scale bar equals 0.5 cm.

A very shallow, slit-like excavation is present on the lateral surfaces just ventral to the neurocentral suture and extended along the middle part of the centrum. It does not appear to contain any pneumatic openings. The ventral surface of the centrum is slightly offset from the lateral surfaces by rounded breaks in slope, so that it forms a distinct surface. A shallow, but broad and well-defined midline groove is present that extends for almost the full length of the centrum.

A neurocentral suture is still visible on both sides of the posterior part of the vertebra. The anterior opening of the neural canal has a circular outline, but the posterior opening is obscured by matrix. The tips of the prezygapophyses are broken, but their bases show that they had a triangular transverse cross-section and a small matrix-filled space at their confluence might represent a small prespinal fossa. A small bone fragment adhered to the right side of the neural arch might represent the broken tip of this prezygapophysis. A thin web of bone connects the posterior margin of the better-preserved right prezygapophysis with the caudal rib in a position equivalent to a prezygodiapophyseal lamina. Both caudal ribs are broken, but their bases show that in lateral view they extended for most of the length of the centrum, with their anterior margins displaced from the anterior articular surface. They terminated just anterior to the posterior end of the centrum. The bases of the ribs are thin, dorsoventrally compressed plates with shallowly convex dorsal and ventral surfaces, and show that the ribs projected

laterally and slightly dorsally. In dorsal view, the ribs are canted slightly posteriorly. The neural spine is a dorsoventrally tall, anteroposteriorly short transversely compressed plate. It has subparallel anterior and posterior margins that merge via a gently curved dorsal margin. A small projection is present on the posterior margin of the spine at midheight, which might reflect either a tendon attachment site or an adhered bone fragment. The postzygapophyses are small and situated on the posteroventral margin of the neural spine. They extend slightly beyond the posterior margin of the vertebra and diverge at an angle of approximately 30 degrees in dorsal view.

Distal caudal vertebra

The anterior and posterior articular surfaces have ovate outlines that are broadest dorsally, but the anterior surface is flat, whereas the posterior surface is gently concave. Chevron facets are absent both anteriorly and posteriorly. In lateral view, the centrum is elongate, with a length to dorsoventral height ratio of approximately 2.25. The lateral surfaces of the centrum are very shallowly concave anteroposteriorly and flat dorsoventrally and do not bear the slit present in the middle caudal. They are offset from the ventral margin of the centrum, by clear and abrupt breaks in slope that form distinct longitudinal ridges. The ventral margin of the centrum is flat to very gently concave longitudinally and lacks either a groove or keel.

In anterior view, the neural canal has an elliptical outline with its long axis oriented mediolaterally. The bases of the

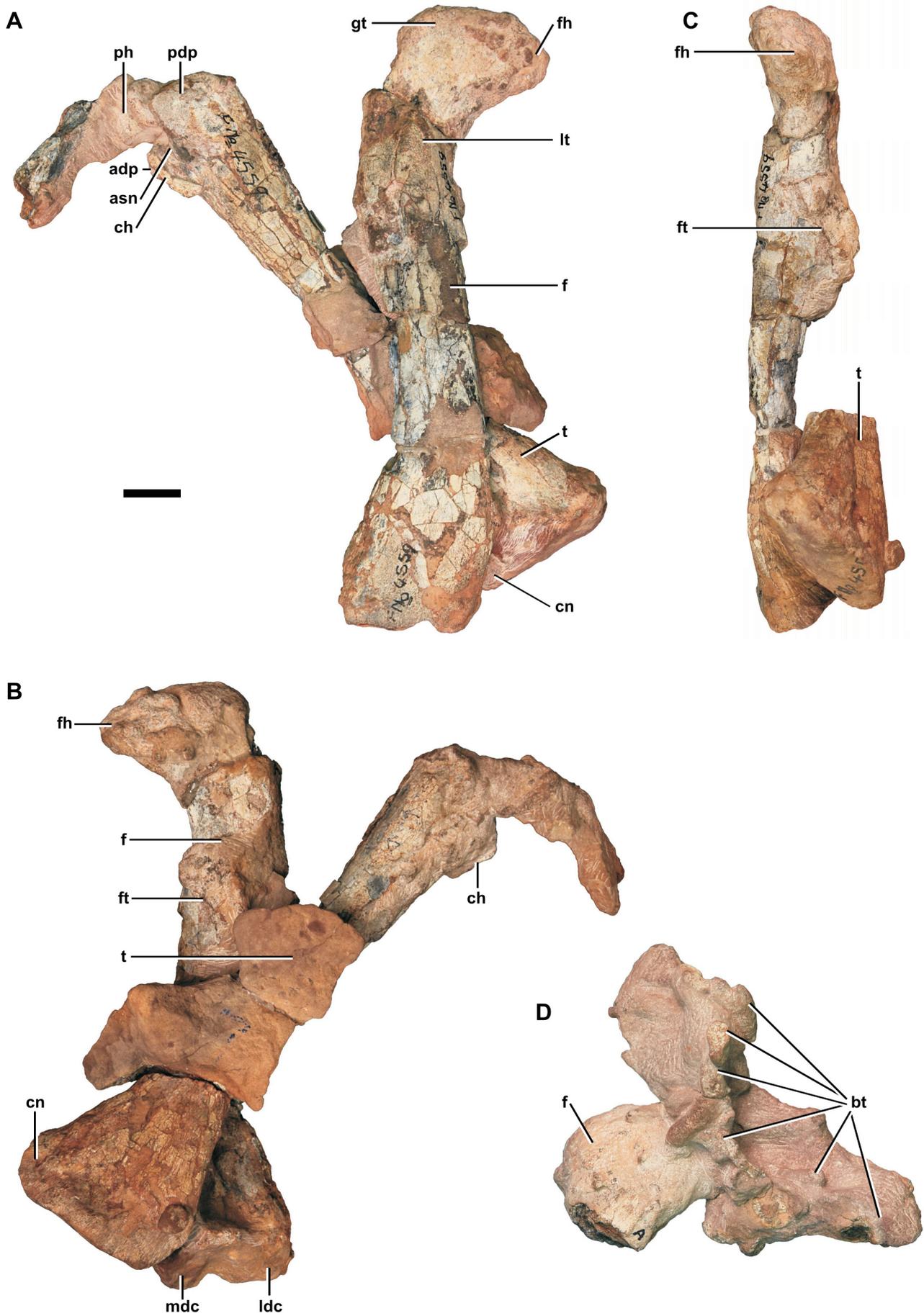


Fig. 4. Femur, tibia, chevron and pedal phalanx of BP/1/4559. A, partially articulated femur and tibia, femur in anterior view, tibia in posterolateral view; B, a partially articulated femur and tibia, femur in posteromedial view, tibia in medial view; C, a femur removed from association with tibia in medial view; D, proximal end of femur before prep showing burrows in matrix. Scale bar equals 2 cm.

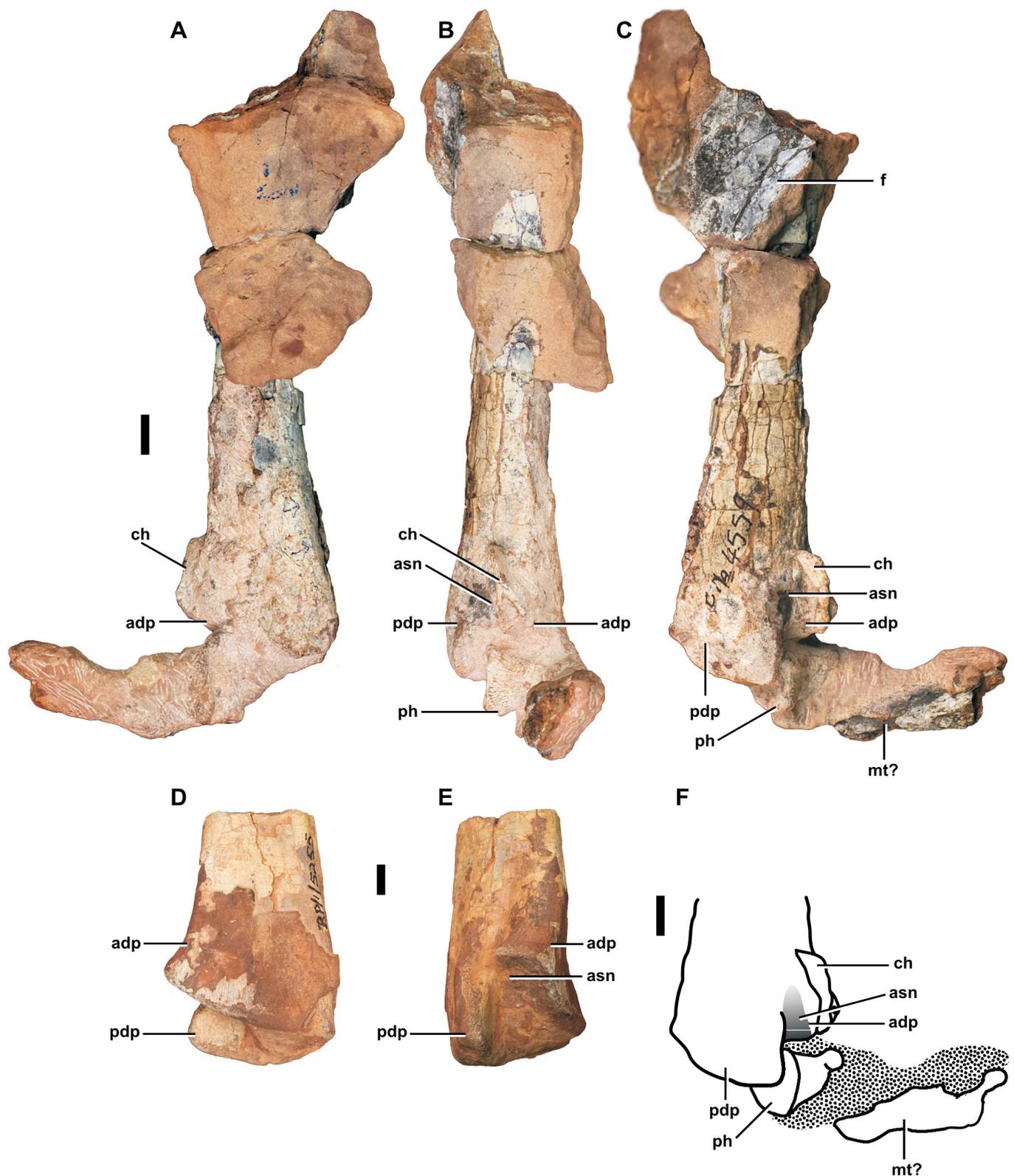


Figure 5. A–C, F: Distal portion of tibia of BP/1/4559 isolated from associated femur; D, E: distal portion of tibia of BP/1/5255, *Massospondylus carinatus*. A, D, anterior; B, E, lateral; C, posterior; F, line drawing of C. Scale bars equal 2 cm.

prezygapophyses are subtriangular in transverse cross-section and in dorsal view they diverged from each other by an angle of approximately 30 degrees. The postzygapophyses have merged into a single midline structure that is elevated on a short stalk that extends posterodorsally from the posterior part of the neural arch. There is no indication that either a neural spine or caudal ribs were present:

these structures were clearly lost by this point in the caudal series.

Other vertebrae

Four additional vertebral centra are present, but all are poorly preserved. Two have been fully prepared, but are incomplete. The other centra are associated in a block of

Table 1. List of measurements of BP/1/4559

Element	Measurement	Value (mm)	Notes
Mid-caudal vertebra	Anteroposterior length	30	
	Dorsoventral height of anterior surface	24	
	Including chevron facet		
	Mediolateral width of anterior surface	20	
	Dorsoventral height of posterior surface	20	
	Mediolateral width of posterior surface	18	
	Total height of vertebra*	53	From base of centrum to top of neural spine
Distal caudal vertebra	Anteroposterior length of centrum	25	
	Dorsoventral height of anterior articular surface of centrum	12	
	Mediolateral width of anterior articular surface	11	
	Dorsoventral height of posterior articular surface of centrum	11	
	Mediolateral width of posterior articular surface	10	
	Total height of vertebra*	19	From base of centrum to dorsal margin of postzygapophysis
Femur	Total length*	208	
	Mediolateral width of proximal end*	51	
	Minimum midshaft diameter	24	
	Midshaft circumference	71	
	Mediolateral width of distal end	27	
Tibia	Total length	201	
	Anteroposterior length of proximal end	60	
	Minimum midshaft diameter	20	
	Anteroposterior length of distal end	28	
	Mediolateral width of distal end (posterior descending process)	33	
Complete phalanx	Length*	29	
	Maximum width proximal expansion	21	
	Maximum width distal expansion	20	
	Maximum height of proximal expansion	13	
	Maximum height of distal expansion	11	

matrix that is only partially prepared and that exposes only parts of their dorsal and anterior surfaces (Fig. 3). None of the vertebrae are preserved well enough to establish their positions in the vertebral column and they offer no useful anatomical details beyond the observation that they were shallowly amphicoelous.

Chevron

A single chevron is preserved lying adjacent to the astragalar notch on the distal end of the right tibia (Figs 4, 5). The proximal end of the chevron is eroded, but enough is preserved to determine that it bears a single process on each side that would have contacted the caudal vertebral centra. The opening in the chevron is teardrop-shaped and relatively large, extending distally to approximately the midpoint of the bone. At midshaft, the chevron is cylindrical, with a subcircular cross-section, but distal to this point it is flattened mediolaterally and expands slightly in the anteroposterior direction, forming a blade-like morphology common in proximal chevrons of most dinosaurian taxa. The distalmost end of the chevron is broken.

Femur

The right femur is nearly complete, missing only its distal condyles (Figs 4, 5C; measurements in Table 1). In anterior view, and with the distal condyles oriented horizontally, the femur has a sigmoidal profile. Its long axis trends later-

ally in the dorsal half of the element and then swings medially in its ventral portion. The proximal end, comprising the greater trochanter laterally and femoral head medially, has a shallowly convex dorsal margin. The femoral head is medially inturned and projects slightly ventrally with respect to the dorsal margin of the greater trochanter. A trochanteric fossa appears to have been absent. The medial and ventral margins of the femoral head are separated by a smooth and gradual change in slope, but this region is covered by matrix, which may be obscuring aspects of the original morphology. Similarly, the junction between the ventral margin of the head and the medial margin of the femoral shaft is also smoothly concave. The anterior surface of the proximal end is transversely convex and lacks distinct intramuscular lines or muscle scars. A low, elongate and ridge-like anterior trochanter is situated on the anterior surface of the proximal shaft and is shifted towards its medial margin. The dorsal-most margin of the anterior trochanter is positioned approximately 10 mm ventral to the point at which the ventral margin of the head merges with the medial shaft margin and merges into the body of the shaft: it is not separated by a cleft. The femoral shaft narrows mediolaterally ventral to the proximal end and remains parallel-sided until a point just dorsal to the distal margin, where it expands again to form the distal condyles. The anterior surface of the distal end possesses a broad, medially situated ridge-like structure that partially

bounds a depression on the anterior surface immediately dorsal to the ventral margin of the femur: however, both of these features are potentially artifacts that are accentuated by deformation.

In lateral view, the shaft of the femur is bowed gently anteriorly. The lateral surface of the greater trochanter has approximately the same anteroposterior width as the rest of the shaft. The distal end of the shaft expands posteriorly to form the femoral epicondyles, although these are only partially preserved. The shaft has been crushed antero-posteriorly, but it appears to have had a sub-elliptical transverse cross-section at midlength.

The posterior surface of the shaft bears the base of an elongate, straight and vertically oriented fourth trochanter, though this area is broken and obscured by matrix, obscuring its original morphology. Nevertheless, the preserved portion indicates that it was likely pendant. As the base of the trochanter is situated close to the midline of the shaft it is possible that it was not visible in anterior view (though this would depend upon the length of the missing portion and its orientation). The distal end of the femur is missing: however, it is clear that a deep posterior groove was present between the two epicondyles.

Tibia

The right tibia is complete, but the proximal- and distal-most ends of the epiphyses are poorly preserved and the boundary between fossilized bone and matrix is unclear in some areas (Figs 4, 5; measurements in Table 1). The middle portion of the tibial shaft is partially obscured by tightly adhering matrix and a portion of the overlapping femoral shaft. A small, likely posterior chevron, a non-ungual pedal phalanx, and an unidentified long bone shaft are tightly adhered to the lateral surface of the distal end (Figs. 4,5).

The proximal end of the tibia is approximately three times as long anteroposteriorly as it is wide mediolaterally. It bears a prominent cnemial crest that arcs anteriorly and laterally. The proximal surface of this crest is level with the proximal surface of the posterior condylar portion of the proximal tibia. The fibular condyle was clearly present, but it is badly eroded. It extends for approximately half of the anteroposterior length of the proximal end of the tibia and projects strictly laterally as a low swelling. It is poorly differentiated from the medial condyle on the posterolateral margin of the proximal tibia, exhibiting only a shallowly offset notch. The posterior end of the medial condyle is eroded, but it clearly extends posteriorly well beyond the level of the fibular condyle. The medial margin of the proximal end of the tibia is shallowly convex and extends in a smooth arc from the medial side of the medial condyle to the cnemial crest.

The medial surface of the proximal end of the tibia has been crushed, creating an artificial fossa, but in life it is likely that the surface would have been shallowly convex. It tapers in anteroposterior length as it extends distally, grading shallowly into the tibial shaft. The proximoposterior corner forms a subtriangular, tab-like extension in medial view. The lateral surface of the proximal end is mostly obscured by matrix and the adhering femur, but the poste-

rior margin bears a shallow fossa immediately distal to the notch between the fibular and medial condyles.

The tibial shaft is relatively slender, and sub-circular in cross-section. It undergoes only modest expansion as it approaches the distal end. The distal end of the tibia is sub-square in outline in distal view. It bears a prominent posterior descending process and anterior descending process for articulation with the astragalus. The posterior descending process is relatively small and tab-like. Its medial margin and distal margin meet at approximately right angles, and a small indentation on the posterior surface of the tibia immediately proximal to the process gives it a sub-rectangular shape in posterior view. It is clearly visible in anterior view and extends to a level far distal to the distal margin of the anterior descending process and only somewhat lateral to the lateral margin of the anterior descending process. The anterior descending process is partially obscured in anterior view by adhering matrix and an overlapping chevron. It is small, sub-triangular, and extends only a short distance laterally from the lateral margin of the anterior surface of the distal end of the tibia. A deep, 'U'-shaped notch in the lateral side of the distal end of the tibia separates the two processes, and this notch extends for a short distance proximally as a shallow groove on the lateral side of the tibial shaft. The posterior surface of the distal end of the tibia bears a broad, low ridge that extends vertically and grades into the diaphysis.

Metatarsus?

Several fragmentary long bones are present, each of which consists of a broken sub-circular to sub-triangular hollow shaft with diameters of approximately 10–13 mm (not figured). Several of these are preserved in cross-section in a single partially prepared block of matrix, and other fragments are present in a smaller block. None of these can be fitted together confidently. As the rest of the specimen consists largely of hind limb and caudal vertebral material, it seems most likely that these long bone fragments represent part of the right metatarsus, but the hardness of the matrix surrounding them prevents further preparation to confirm this suggestion. These fragments offer no other useful anatomical information.

Phalanges

Three non-ungual ?pedal phalanges are present. One is almost complete, but has suffered some abrasion (Fig. 4C, D, E), another consists of the distal articular region only (not figured), and the third is adhered to the distal tibia and is complete but covered by matrix (Fig. 4A; 5B, C, F). The following description is based only on the abraded phalanx as the others offer no additional information (Figs 4, 5). The phalanx is described as though the foot is held in a plantigrade position.

In dorsal view, the proximal and distal ends of the phalanx are mediolaterally expanded to the same extent relative to the shaft, giving it an hourglass-shaped outline. The dorsal surface is gently convex mediolaterally and grades smoothly into the lateral surfaces. In lateral view, the proximal and distal ends are ventrally expanded rela-

tive to the shaft, so that the ventral margin of the phalanx is upwardly concave, while its dorsal margin is gently convex. The proximal end of the phalanx is slightly more expanded ventrally than the distal end.

In ventral view, a shallow groove divides the distal expansion into distinct medial and lateral ginglymi and this groove continues onto the distal end surface. The dorsolateral corners of the distal expansion bear very shallow, sub-circular collateral ligament pits. The proximal end is broken and abraded so details of the articular facet are unavailable. As preserved, both the proximal and distal expansions have a sub-crescentic outline. The phalanx is slightly longer anteroposteriorly than it is wide medio-laterally.

IDENTIFICATIONS AND COMPARISONS

Several anatomical features allow us to identify this specimen as an indeterminate sauropodomorph dinosaur.

Three features of BP/1/4559 allow it to be referred to the Dinosauria. The fourth trochanter is developed as a sharp, blade-like structure (Nesbitt 2011: char. 316, state 1), the cnemial crest arcs anterolaterally (Nesbitt 2011: char. 328, state 2), and a distinct ridge extends proximodistally across the posterior surface of the distal end of the tibia (Nesbitt 2011: char. 336, state 1).

Other synapomorphies suggest a more specific position within Dinosauria. The posterolateral margin of the distal tibia is shallowly concave, matching the condition in theropods and sauropodomorph dinosaurs such as *Massospondylus* (Nesbitt 2011: char. 335, state 1) and therefore suggesting saurischian affinities. In proximal view, the posterior margin of the proximal end of the fibular condyle of the tibia is located at a level anterior to the posterior end of the proximal tibia (Yates 2007), a synapomorphy of Sauropodomorpha (Apaldetti *et al.* 2011). The anterior and posterior descending processes of the distal tibia are developed to the same level laterally, indicating that the Zambian material is likely from a sauropodomorph basal to Anchisauria (Apaldetti *et al.* 2011; McPhee *et al.* 2014; Wilson & Sereno 1998; Yates 2007). The gross morphology of the tibia is almost identical to those of basal sauropodomorphs such as *Lufengosaurus* (Young, 1941; IVPP V15) *Massospondylus* (BP/1/4998; BP/1/5255) (see Fig. 5E) and *Plateosaurus* (e.g. Huene 1932). For example, in distal end view, the tibiae of many basal sauropodomorphs possess a deep notch that incises its posterolateral margin: this notch is much shallower in basal theropods like *Herrerasaurus* (Novas, 1993). In addition, this notch divides the distal end of the tibia into distinct anterior (cranio-lateral) and posterior (caudolateral) descending processes in basal sauropodomorphs, whereas these 'processes' are low tuberosities in *Herrerasaurus* (Novas 1993; Yates 2004). Finally, in *Herrerasaurus* and basal sauropodomorphs, the anterior and posterior descending processes each extend for sub-equal distances from the shaft in distal end view, whereas in other early theropods and basal sauropods either the posterior descending process (theropods) or anterior descending process (sauropods) is significantly longer than the other distal condyle (Yates 2004) (see

Figs 4, 5). Although the incomplete nature of the specimen prevents the identification of further synapomorphies, these features of the hind limb are consistent with an identification of BP/1/4559 as a small-bodied, basal sauropodomorph dinosaur.

CONCLUSIONS

BP/1/4559 represents the first dinosaurian material described from Zambia. Features of the tibia allow this fossil to be identified as an indeterminate non-sauropodan sauropodomorph. Although the exact provenance of the specimen is unknown, its geographic location near Lusitu strongly suggests that it is from Upper Karoo deposits that are equivalents of the Stormberg Group, from beds that are coeval with the upper Elliot/lower Clarens interval. If so, this would make it the first known member of a dinosaurian fauna that should ultimately prove to be similar to that of South Africa, Lesotho and Zimbabwe.

ABBREVIATIONS

Institutional

BP and ESI	Evolutionary Studies Institute (formerly Bernard Price Institute), University of the Witwatersrand, Johannesburg, South Africa
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China
NHMUK	Natural History Museum, London, UK.

Anatomical

adp	anterior descending process
asn	astragalar notch
bt	bioturbation
cas	centrum anterior surface
cen	centrum
ch	chevron
clp	collateral ligament pit
cn	cnemial crest
cps	centrum posterior surface
dc	distal condyle
f	femur
fh	femoral head
ft	fourth trochanter
gt	greater trochanter
ldc	lateral distal condyle
lt	lesser trochanter
mdc	medial distal condyle
mt	metatarsal
nc	neural canal
ns	neural spine
pas	proximal articular surface
pdp	posterior descending process
ph	phalanx
poz	postzygapophysis
prz	prezygapophysis
t	tibia
tp	transverse process

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REFERENCES

APALDETTI, C., MARTINEZ, R.N., ALCOBER, O.A. & POL, D. 2011. A new basal sauropodomorph (Dinosauria: Saurischia) from Quebrada del Barro Formation (Marayes-El Carrizal Basin), northwestern

- Argentina. *PLOS ONE* **6**(11), e26964. 10.1371/journal.pone.0026964
- BOONSTRA, L.D. 1938. A report on some Karroo reptiles from the Luangwa Valley, Northern Rhodesia. *Quarterly Journal of the Geological Society* **94**(1-4), 371–384.
- BROWN, A.G. 1967. The geology of the Chikankata area: explanation of degree sheet 1628, NW. quarter; pp. 1–42, Report of the Geological Survey, Republic of Zambia, Ministry of Lands and Mines.
- CATUNEANU, O., WOPFNER, H., ERIKSSON, P.G., CAIRCROSS, B., RUBIDGE, B.S., SMITH, R.M.H. & HANCOX, P.J. 2005. The Karoo basins of south-central Africa. *Journal of African Earth Sciences* **43**(1–3), 211–253. <http://dx.doi.org/10.1016/j.jafrearsci.2005.07.007>
- DALY, M.C., CHOROWICZ, J. & FAIRHEAD, J.D. 1989. Rift basin evolution in Africa: the influence of reactivated steep basement shear zones. *Geological Society, London, Special Publications* **44**, 309–344.
- DE SWARDT, A.M.J. 1962. *Northern Rhodesia Geological Survey Department Annual Report 1961*. Lusaka, Government Printing Office, 1–14.
- DIXEY, F. 1937. The geology of part of the Upper Luangwa Valley, North-Eastern Rhodesia. *Quarterly Journal of the Geological Society* **93**, 52–76.
- DIXEY, F. & CAMPBELL-SMITH, W. 1929. The Rocks of the Lupata Gorge and the North Side of the Lower Zambezi. *Geological Magazine* **66**(06), 241–259. doi:10.1017/S0016756800100366
- DRYSDALL, A.R. & KITCHING, J.W. 1962. The Karoo succession of the Upper Luangwa Valley, Northern Rhodesia. *Transactions of the Geological Society of South Africa*.
- DRYSDALL, A.R. & KITCHING, J.W. 1963. A re-examination of the Karoo succession and fossil localities of part of the Upper Luangwa Valley. *Memoir of the Geological Survey of Northern Rhodesia* **1**, 1–62.
- GAIR, H. 1959. The Karoo System and coal resources of the Gwembe district, north-east section. Geological Survey Department Northern Rhodesia (Zambia). *Bulletin*(1).
- HANCOX, P., SHISHKIN, M., RUBIDGE, B. & KITCHING, J. 1995. A threefold subdivision of the Cynognathus Assemblage Zone (Beaufort Group, South-Africa) and its paleogeographic implications. *South African Journal of Science* **91**(3), 143–144.
- HUENE, F.V. 1925. Ausgedehnte Karroo-Komplexe mit Fossilführung im nordöstlichen Südwestafrika [Extensive Karoo complexes with fossil management in northeastern Southwest Africa]. *Centralblatt für Mineralogie, Geologie und Paläontologie, Abteilung B: Geologie und Paläontologie* **5**, 151–156.
- HUENE, F.V. 1932. Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. *Monographien zur Geologie und Paläontologie, series 1*, **4**, 1–361.
- MCPHEE, B.W., YATES, A.M., CHOINIERE, J.N. & ABDALA, F. 2014. The complete anatomy and phylogenetic relationships of *Antetonitrus ingenipes* (Sauropodiformes, Dinosauria): implications for the origins of Sauropoda. *Zoological Journal of the Linnean Society* **171**, 151–205.
- NESBITT, S.J. 2011. The early evolution of archosaurs: relationships and the origin of major clades. *Bulletin of the American Museum of Natural History* **352**, 1–291.
- NOVAS, F.E. 1993. New information on the systematics and postcranial skeleton of *Herrerasaurus ischigualastensis* (Theropoda: Herrerasauridae) from the Ischigualasto Formation (Upper Triassic) of Argentina. *Journal of Vertebrate Paleontology* **13**(4), 400–423.
- OLSEN, P.E. & GALTON, P.M. 1984. A review of the reptile and amphibian assemblages from the Stormberg of southern Africa, with special emphasis on the footprints and the age of the Stormberg. *Palaeontologia africana* **25**, 87–110.
- OWEN, R. 1842. Report on British fossil reptiles, part II. *Reports from the British Association for the Advancement of Sciences* **1841**, 60–204.
- PEECOOK, B.R., SIDOR, C.A., NESBITT, S.J., SMITH, R.M., STEYER, J.S. & ANGIELCZYK, K.D. 2013. A new silesaurid from the upper Ntawere Formation of Zambia (Middle Triassic) demonstrates the rapid diversification of Silesauridae (Avenetatarsalia, Dinosauriformes). *Journal of Vertebrate Paleontology* **33**(5), 1127–1137.
- RAATH, M.A. 1969. A new coelurosaurian dinosaur from the Forest Sandstone of Rhodesia. *Arnoldia (Rhodesia)* **4**(28), 1–25.
- RAATH, M.A. 1977. The anatomy of the Triassic theropod *Syntarsus rhodesiensis* (Saurischia: Podokeosauridae) and a consideration of its biology. Doctor of Philosophy, Rhodes University: Salisbury, Rhodesia.
- RUBIDGE, B.S. 2005. 27th Du Toit Memorial Lecture Re-uniting lost continents—Fossil reptiles from the ancient Karoo and their wanderlust. *South African Journal of Geology* **108**(1), 135–172.
- SEELEY, H.G. 1887. On the classification of animals commonly called Dinosauria. *Proceedings of the Royal Society of London* **43**, 165–171.
- WEISHAMPPEL, D.B., BARRETT, P.M., CORIA, R.A., LOEUFF, J.L., XING, X., XIJIN, Z., SAHNI, A., GOMANI, E.M.P. & NOTO, C.R. 2004. Dinosaur distribution. In: Weishampel, D.B., Dodson, P. & Osmolska H. (eds), *The Dinosauria*, 517–626. University of California Press, Berkeley, Los Angeles, London.
- WILSON, J.A. & SERENO, P.C. 1998. Early evolution and higher level phylogeny of sauropod dinosaurs. *Society of Vertebrate Paleontology Memoir* **5**, 1–68.
- WOPFNER, H. 2002. Tectonic and climatic events controlling deposition in Tanzanian Karoo basins. *Journal of African Earth Sciences* **34**(3–4), 167–177. [http://dx.doi.org/10.1016/S0899-5362\(02\)00016-7](http://dx.doi.org/10.1016/S0899-5362(02)00016-7)
- YATES, A.M. 2004. *Anchisaurus polyzelus* (Hitchcock): the smallest known sauropod dinosaur and the evolution of gigantism amongst sauropodomorph dinosaurs. *Postilla* **230**, 1–58.
- YATES, A.M. 2007. The first complete skull of the Triassic dinosaur *Melanorosaurus* Haughton (Sauropodomorpha: Anchisauria). *Special Papers in Palaeontology* **77**, 9–55.
- YOUNG, C.-C. 1941. A complete osteology of *Lufengosaurus huenei* Yong (gen. et sp. nov.). *Palaeontologica Sinica, Series C* **7**, 1–53.