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2016-03

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New specimens of the basal ornithischian dinosaur *Lesothosaurus diagnosticus* Galton, 1978 from the Early Jurassic of South Africa

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Received 7 December 2015. Accepted 1 March 2016

We describe new specimens of the basal ornithischian dinosaur *Lesothosaurus diagnosticus* Galton, 1978 collected from a bonebed in the Fouriesburg district of the Free State, South Africa. The material was collected from the upper Elliot Formation (Early Jurassic) and represents the remains of at least three individuals. These individuals are larger in body size than those already known in museum collections and offer additional information on cranial ontogeny in the taxon. Moreover, they are similar in size to the sympatric taxon *Stormbergia dangershoeki*. The discovery of three individuals at this locality might imply group-living behaviour in this early ornithischian.

Keywords: Ornithischia, Free State, upper Elliot Formation, ontogeny, sociality.

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INTRODUCTION

The Early Jurassic upper Elliot Formation of South Africa and Lesotho has yielded abundant material of primitive ornithischian dinosaurs and currently represents the best available window on early ornithischian evolution. The fauna includes four heterodontosaurid taxa (*Abrictosaurus consors*, *Heterodontosaurus tucki*, *Lycorhinus angustidens* and *Pegomastax africanus*: e.g. Porro *et al*. 2011; Sereno 2012) and the basal ornithischians *Lesothosaurus diagnosticus* and *Stormbergia dangershoeki* (e.g. Butler 2005). Several of these taxa are represented by multiple individuals and include excellently preserved skull and postcranial material as in *Heterodontosaurus* (Santa Luca *et al*. 1976; Santa Luca 1980; Butler *et al*. 2008a; Norman *et al*. 2011; Sereno 2012; Galton 2014) and *Lesothosaurus* (Thulborn 1970, 1972; Galton 1978; Santa Luca 1984; Sereno 1991; Knoll 2002a,b; Porro *et al*. 2015). However, although *Lesothosaurus* is known on the basis of three-dimensionally preserved skulls and partial postcranial material, complete skeletons have yet to be recovered. Moreover, numerous features of the skull anatomy (e.g. relatively large orbits, lack of fusion between braincase elements), the small size of the material, and some histological evidence suggests that all of the specimens referred to this taxon thus far are juvenile individuals (e.g. Knoll *et al*. 2010; Porro *et al*. 2015).

The lack of larger subadult or adult material for *Lesothosaurus* poses two problems for our current understanding of early ornithischian diversity and evolution. The first of these is taxonomic: it has been suggested that *Stormbergia* might be an adult morph of *Lesothosaurus* rather than a distinct genus (Knoll *et al*. 2010). *Stormbergia* was distinguished from *Lesothosaurus* on the basis of ischial morphology (Butler 2005), but all of the available specimens of *Stormbergia* represent individuals that are substantially larger than those referred to *Lesothosaurus*. Consequently, it has been suggested that the proposed ischial differences might be of ontogenetic, rather than taxonomic, significance (Knoll *et al*. 2010). Secondly, the lack of adult material may affect the position of *Lesothosaurus* in phylogenetic analyses. *Lesothosaurus* has been recovered in several positions within the ornithischian tree, including as a non-genasaurian ornithischian, a non-cerapodan neornithischian, and a basal thyreophoran (Sereno 1986, 1999; Butler *et al*. 2007, 2008b; Boyd 2015). This instability may be the result of genuine character conflict, lack of key character data, or incomplete lineage sorting close to the base of the ornithischian tree, but it

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might also result from the phenomenon whereby juvenile individuals included in analyses cause taxa to move stem-ward due to the absence of more derived, adult morphologies (e.g. Tsuihiji *et al*. 2011; Campione *et al*. 2013).

Here we describe new material of *Lesothosaurus* representing a minimum of three individuals derived from a single bonebed. Two of these are larger than either of the syntype specimens of *Lesothosaurus* or of any of the referred specimens previously reported in the literature (Thulborn 1970, 1972; Santa Luca 1984; Sereno 1991; Knoll 2002a,b; Butler 2005).

LOCALITY AND HORIZON

In 2007, the Keyser family mentioned the presence of dinosaur bones on their property, known as Aushan Grey, to A.M.Y. Subsequent investigations by A.M.Y. in March 2007 revealed that Aushan Grey (formerly part of the farm Landkloof 73: situated at S 28°35′25.6″ E 28°03′0.56″), in the Fouriesburg district of Free State Province, South Africa, contained exposures of the upper part of the 'Stormberg group' (the upper part of the Karoo Supergroup) and that the dinosaur bones originated from the upper part of the Elliot Formation (dated as either Hettangian–Sinemurian or Pliensbachian: Olsen & Galton 1984; Yates *et al*. 2004). The bulk of the deposit at this site consisted of laminated overbank siltstones and mudstones. The ornithischian specimens described here were found in a layer sitting on a resistant, bench-forming pedogenic nodule bed, or were found *ex situ* immediately below this bench. The ornithischian fossils were distributed over a 6 m stretch of exposure. No other taxa were found at this level although sauropodomorph dinosaurs and a tritylodontid cynodont were found at other stratigraphic levels.

MATERIAL AND IDENTIFICATION

The majority of the ornithischian specimens were found in situ in a small dense accumulation of bones a few tens of centimetres across, but one of the specimens (BP/1/6581) was found ex situ lying immediately below the level of the bench, although it is likely that it was derived from the same accumulation. Two isolated bones, a surangular (BP/1/6580) and a scapula (BP/1/6583) were found in the same horizon a few metres distant from the main accumulation. At least three individuals are represented within the sample on the basis of scapula size, with scapula midshaft diameters of 11, 18 and 27 mm, in BP/1/6581, BP/1/6582 and BP/1/6583, respectively. It is possible that the isolated surangular (BP/1/6580) pertained to one of the larger individuals present (e.g. BP/1/6582), but it might also represent a fourth individual. Charlton Dube (BP), A.M.Y. and Scott Moore-Fay (formerly NHMUK) prepared the fossils mechanically using an airscribe. Breaks were repaired with cyanoacrylate glue. Some fossil bones were consolidated after preparation with an approximately 10% solution of Paraloid B-72 solid grade thermoplastic acrylic resin in 100% acetone solvent.

Although the available material of the individuals present is largely non-overlapping, there are no clear differences in morphology that suggest the presence of more than one ornithischian taxon in the sample. Each element in the assemblage is consistent in anatomy with other specimens referred to *Lesothosaurus diagnosticus* (see Thulborn 1970, 1972; Santa Luca 1984; Sereno 1991; Knoll 2002a,b; Butler 2005; Porro *et al*. 2015). Two cranial features support referral of this material to *Lesothosaurus*: the presence of a shallow groove that extends along the dorsal surface of the surangular, backed by a medial ridge (in BP/1/6580: Fig. 1) and the presence of a tongue-in-groove articulation between the maxilla and lacrimal (in BP/1/6581: Figs 2–3). The combined presence of a dorsal groove and medial ridge on the surangular appears to be unique to *Lesothosaurus* and has been proposed as an autapomorphy of the taxon (Butler 2010). Sereno (1991) proposed that the presence of a tongue-in-groove articulation between the maxilla and lacrimal was autapomor-

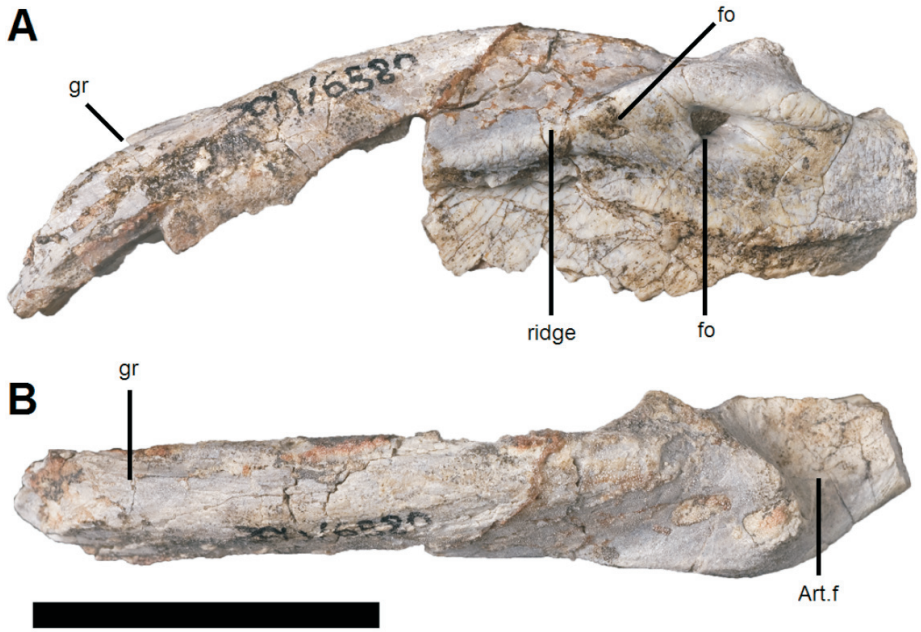

Figure 1. Left surangular (BP/1/6580). **A**, Lateral view; **B**, dorsal view. Scale bar = 20 mm.

phic of *Lesothosaurus*, but this was questioned by Butler (2005) who regarded the distribution of this character as unclear. Nevertheless, no other ornithischians from the Early Jurassic of southern Africa possess this feature (see Sereno 2012) and we regard it as positive evidence for the referral of BP/1/6581 to *Lesothosaurus*. No postcranial autapomorphies currently diagnose *Lesothosaurus* (Butler 2005) and the referral of the two postcranial specimens from this assemblage to this taxon is based on i) their close association with the diagnostic cranial elements and ii) the possibility that the isolated angular might pertain to one of these individuals.

DESCRIPTION

BP/1/6580

This specimen consists of a left surangular that lacks its retroarticular process, rostral-most portion and parts of the ventral margin (Fig. 1). In lateral view, the surangular is shallowly arched and its dorsal margin forms a low coronoid eminence. A strong ridge is present on the caudal part of the lateral surface and extends rostroventrally at approximately 15 degrees to the horizontal, towards the articular surface for the angular (Fig. 1A). The ridge originates at the rostral margin of the articular fossa and extends to a point at least halfway along the length of the coronoid eminence. It delimits the lateral and ventral margins of a dorsally facing concavity that contains a large foramen, which is visible in dorsal view only. Ventral to the ridge, another large foramen is present, which is set within a short, but deep, caudoventrally opening groove. A third smaller foramen lies rostral to the latter, just below the ridge. This lateral ridge is thick and overhangs the anterior part of the articular facet for the angular. This articular facet is striated and depressed relative to the rest of the surangular's lateral surface. The posterior part of the angular articular facet is delimited dorsally by a thin, sharp, horizontally oriented ridge.

In dorsal view, the dorsal surface of the surangular is inflected laterally to form a shallow groove that extends along the element rostrocaudally (Fig. 1B). The medial margin of the groove is formed by a distinct ridge, while the lateral margin is defined by a change in slope. This combination of features is considered to be autapomorphic for *Lesothosaurus* (Butler 2010). Rostrally, the dorsal surface of the surangular is bevelled to form a contact for the coronoid process of the dentary. Immediately caudal to the coronoid eminence, a saddle-shaped sulcus for the reception of the articular is present. This sulcus is delimited rostrally by a prominent transverse ridge, caudally by a low, but distinct, transverse ridge and medially by a low lip of bone, but there is no distinct border laterally. The broken base of retroarticular process has a teardrop-shaped transverse cross-section.

In medial view, the dorsal margin of the surangular overhangs the internal mandibular fossa. This area increases in depth rostrally and its ventral surface is deeply invaginated by the dorsal-most part of the internal mandibular fossa. The area ventral to the articular fossa is shallowly concave for the reception of the prearticular: this region is separated from the internal mandibular fenestra by a low rostroventrally extending ridge that originates from the rostroventral corner of the articular fossa.

BP/1/6581

General comments

This specimen consists of the rostral part of a crushed skull with associated postcranial material (Figs 2–3). The left-hand side of the skull is the most informative, as the right-hand side has been sheared ventrally with respect to the left, has suffered more crushing and disruption, and is obscured by postcranial elements. The left-hand side of the skull includes an incomplete premaxilla, maxilla, lacrimal, parts of the nasal, prefrontal, jugal and palpebral, as well as a partial dentary and splenial (Figs 2A, 3A). Several partial elements from the right-hand side of the skull are preserved, including the premaxilla, maxilla, lacrimal, prefrontal, jugal, ?frontal, palpebral and dentary. Postcranial elements visible on the right-hand side comprise a vertebra, humerus, ?ulna, scapula and ?rib fragments (Figs 2B, 3B). Due to breakage and the close apposition of many elements, only partial descriptions can be provided. Measurements are provided in Table 1.

Table 1. List of measurements BP/1/6581. All measurements in mm. A '*' indicates measurement of an incomplete element, measured as preserved.

Maximum length of maxilla	51*
Maximum length of dentary	55*
Height of dentary immediately anterior to coronoid eminence	17.5
Length of humerus	72
Distal width of humerus	18
Length of scapula	75*
Scapula midshaft height	11

Premaxilla

The premaxillae are poorly preserved and offer few useful details (Figs 2–3). Parts of both elements are present, with the left slightly better represented, but both are extensively cracked and broken. The premaxillae are in articulation, but sheared off rostrally, to reveal the narial cavity in anterior view. The left premaxilla has an elongate, tapering caudolateral process, which is heavily cracked (Figs 2A, 3A). It articulates with the rostrodorsal margin of the maxilla, but breakage obscures the morphology of any premaxillary/nasal/lacrimal contacts. A small sub-triangular flange of bone ventral to the preserved part of the left premaxilla and the rostral border of the left maxilla may represent a strongly deformed caudoventral process. As preserved, the surface of this flange is concave and bounded by a longitudinal ridge along its dorsal margin.

A possible premaxillary tooth is preserved ventral to the right premaxillary fragment. Both the crown and the root are exposed: the root is approximately twice the length of the crown and has a subcircular cross-section, but tapers basally. The root is constricted both labiolingually and mesiodistally immediately basal to the crown. Above this constriction, the crown expands in both directions, but especially mesiodistally. The apicobasal height of the



Figure 2. Stereophotographs of partial skull and articulated postcranial elements of BP/1/6581. **A**, Left lateral view; B, right lateral view. Scale bar = 50 mm.

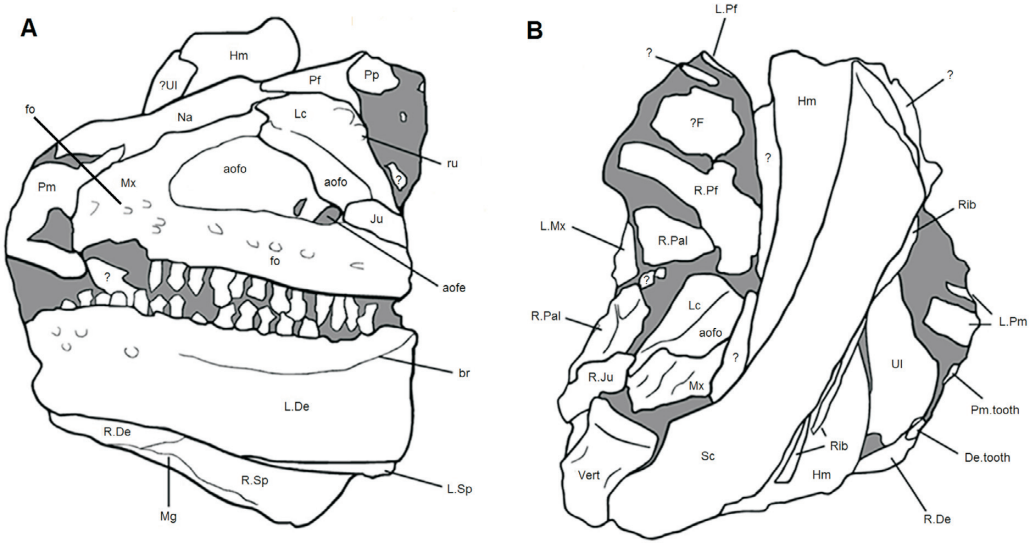

Figure 3. Interpretative line drawings of partial skull and articulated postcranial elements of BP/1/6581. **A**, Left lateral view; **B**, right lateral view.

crown exceeds its mesiodistal width and the crown apex is slightly recurved and lacks denticles.

Maxilla

The left maxilla is missing its rostroventral and caudalmost parts, and the preserved portion has a triangular outline in lateral view (Figs 2A, 3A). The maxilla contacts the premaxilla rostrally, the nasal rostrodorsally, the lacrimal caudodorsally and its tooth-bearing ramus is overlapped by the jugal caudodorsally. Its lateral surface is embayed by a large subtriangular antorbital fossa, which is defined rostrally and ventrally by prominent ridges (the latter corresponding to the 'lateral lamina'). The internal surface of the antorbital fossa is shallowly convex and is depressed in its rostroventral corner and at the point adjacent to its contact with the lacrimal. The maxilla forms an extensive sheet-like medial lamina that closes the fossa medially and which is pierced by a small, elliptical and caudally situated antorbital fenestra. A second smaller elliptical foramen pieces the medial lamina rostral to the antorbital fenestra (Figs 2A, 3A).

In lateral view, the ascending process tapers in rostrocaudal width as it extends dorsally. The apex of the ascending process extends lateral to the rostral part of the lacrimal to form a tongue-in-groove joint with the latter (Figs 2A, 3A). The maxillary toothrow is not inset medially with respect to the rest of the maxillary surface and there is no distinct buccal emargination, although this may have been affected by crushing. There are 13 preserved tooth positions, 12 of which contain teeth. Based on the length of the preserved portion, and comparisons with the proportions of other more complete specimens (e.g. NHMUK PV R8501, NHMUK RU B23), approximately 18 tooth positions would have been present if the maxilla was complete. The tooth-bearing ramus tapers slightly caudally and the dorsal surface of its caudal part is grooved for the reception of the jugal.

Numerous foramina pierce the lateral surface of the maxilla: four of these lie in a distinct cluster rostroventral to the antorbital fossa in the region between the fossa and the premaxillary articulation. These foramina open rostrally and a prominent groove extends rostrally from the dorsal-most foramen to the premaxillary/maxillary articulation. In addition, a line of at least three (possibly four) subcircular nutrient foramina extends parallel to the tooth row (Figs 2A, 3A).

Dental morphology is consistent along the tooth row, although the tooth crowns vary in size. The ninth preserved tooth (counting from the rostral end of the tooth row) is the largest and positioned in the caudal-most third of the tooth row (Figs 2A, 3A). In the rostral half of the preserved tooth row, adjacent tooth crowns do not overlap, although slight imbrication is present between the caudal-most teeth. Tooth crowns are low and triangular in labial view, with apicobasal heights that are subequal to their mesiodistal lengths. The tooth crowns are expanded both labiolingually and especially mesiodistally with respect to the root. The root is slightly constricted in both directions beneath the crown creating a distinct 'neck' and 'cingulum'. The mesial margin of the crown is slightly longer than the distal margin, so that crown apex is slightly offset distally, but there is no recurvature. Coarse denticles are present on both the mesial and distal crown margins. There are 8–10 denticles along each crown margin, though the number is variable between teeth. No primary or secondary ridges are present on any of the tooth crowns, a distinct central eminence is absent, and the mesial- and distal-most denticles are not supported by strong ridges basally. No other crown ornament is present and there is no evidence for tooth wear. In mesial view, the labiolingual expansion of the tooth crowns is asymmetrical, with the greatest expansion on the labial side. Part of the right maxilla is exposed on the reverse of the skull block, in articulation with the jugal, but it offers no useful details.

Lacrimal

Both lacrimals are present, but the following description is based on the more complete left lacrimal (Figs 2A, 3A). The lacrimal has a quadrangular outline in lateral view and forms the caudal margin of the antorbital fossa, the caudodorsal margin of the antorbital fenestra and the rostral border of the orbit. The rostroventral portion of the lateral surface is deeply embayed to form the rostrodorsal section of the antorbital fossa. This embayment is framed by a sharp ridge, which partially overhangs the fossa and extends rostrodorsally from the jugal contact. Ventrally, the lacrimal is overlapped laterally by the jugal, while rostrally its tip bears a 'U'-shaped sulcus that articulates with the ascending process of the maxilla in a tongue-in-groove arrangement, which we consider to be distinctive for *Lesothosaurus* (see above: Sereno 1991). Dorsally, the lacrimal contacts the nasal rostrodorsally and the prefrontal caudodorsally. Ventral to the contact with the prefrontal and adjacent to the palpebral, the lateral surface of the lacrimal is roughened and bears two prominent rugosities or nodes close to the orbital margin.

Jugal

A small subrectangular bone fragment lying dorsal to the caudal part of the left maxilla, and overlapping the ventral part of the lacrimal, probably represents the rostral-most part of the left jugal (Figs 2A, 3A). It forms a small contribution to the caudoventral margin of the antorbital fossa and has a dorsoventrally convex lateral surface. The rostral-most part of the right jugal is also present (Figs 2B, 3B): it is broken into two pieces, with the rostral part preserved in articulation with the right lacrimal and maxilla. The rostral end of the right jugal is slightly embayed by the antorbital fossa.

Nasal

Parts of the left and right nasal are present, positioned between the lacrimal and the caudolateral process of the premaxilla (Figs 2–3). The contact between the nasal and the maxilla is generally a linear butt-joint, although a small, rounded dorsal deviation in the suture appears to be present at the level of the rostrocaudal midpoint of the antorbital fossa. The posterolateral corner of the nasal tapers to a narrow process that extends ventral to the

rostral end of the prefrontal, separating the latter from the lacrimal (Figs 2A, 3A). The lateral surface of this process is faintly rugose. The dorsal surface of the nasal is smooth and bears no foramina or other distinguishing features.

?Frontal

A small, flat quadrangular plate of bone situated between the prefrontals may represent a fragment of one of the frontals, but this identification is based solely on positional evidence (Figs 2B, 3B). It offers no useful anatomical details.

Prefrontal

A triangular plate of bone in contact with the left nasal and lacrimal represents the rostral process of the left prefrontal, but its caudal process is missing and its shape has been affected by crushing and breakage (Figs 2A, 3A). The right prefrontal is also present and incomplete caudally (Figs 2B, 3B). As preserved, the rostral process is broadest caudally and tapers rostrally. Its dorsal surface is shallowly concave rostrally, but planar posteriorly and the whole element is shallowly arched rostrocaudally. The rostral margin of the process extends to a point level with the rostral margin of the lacrimal. Its medial margin, which would have contacted the frontal, forms a straight articular surface. Caudoventrally, the prefrontal is thickened to form the articular region for the palpebral.

Palatine

The right palatine is preserved in dorsal view and lies medial to the right jugal (Figs 2B, 3B). The lateral margin of the element is thickened, forming a distinct ridge. A second subsidiary ridge arises from the lateral margin and divides the dorsal surface into rostral and caudal depressions. The caudal depression is longer and more strongly concave than the rostral depression.

Palpebral

Fragments of both palpebrals are preserved, but include the articular region only (Figs 2–3). The articular region is stout and broad based, with a subpyramidal cross-section.

Dentary

The right dentary is almost completely obscured (Figs 2B, 3B) and the left dentary lacks its rostral and caudal extremities. In lateral view, the dorsal and ventral margins diverge from each other caudally, so that the dentary increases in depth (Figs 2A, 3A). The dorsal expansion of the broken caudal margin indicates that a coronoid eminence would have been present. The rostral-most part of the dentary is slightly downturned and, as a result, the remainder of the ventral margin is sigmoidal, but this may be due to deformation. Rostrally, the tooth row is not inset and the first five teeth are marginally positioned. Caudally, a well-developed buccal emargination is present, which is bounded ventrally by a distinct break in slope. Two large nutrient foramina are positioned ventral to the tooth row, with a third smaller foramen positioned ventral to them: the rostral-most foramen opens into a short canal that extends rostrodorsally at the rostral end of the dentary. A fourth foramen is situated ventral to the fifth dentary tooth, on the margin of the buccal emargination, while a final slit-like foramen is placed approximately halfway along the tooth row beneath the ninth and tenth teeth on the buccal ridge.

Thirteen teeth and one empty alveolus are visible in the left dentary. Teeth at the caudal end of the tooth row are obscured by the maxillary teeth and is it possible that at least one, and maybe more, rostrally positioned teeth are missing. Although the exact number of dentary teeth cannot be determined, comparisons with other more complete specimens (e.g. NHMUK PV R8501) suggest that a total tooth count of 18–20 teeth seems likely. The morphology of the dentary teeth is identical to that of maxillary teeth (see above). The largest exposed teeth are in the posterior part of the tooth row, in alveoli 10–12. None of the dentary teeth are worn and there is no overlap between adjacent dentary teeth.

Splenial

Both the left and right splenial are visible in left lateral view, and they are preserved in articulation with their respective dentaries (Figs 2A, 3A). Only a small part of the left splenial is exposed, but most of the medial surface of the right splenial is visible. The right splenial extends for much of the length of the preserved right dentary. It tapers rostrally to a narrow point at the level of the fifth preserved dentary tooth. The medial surface of its ventral margin is faintly rugose.

Vertebra

A small centrum is preserved adjacent to the right jugal (Figs 2B, 3B). One end of the centrum is eroded but the preserved articular surface is concave, with a roughened rugose margin, and the surface is transversely wider than tall (although it cannot be determined if the dorsal margin is the true dorsal margin or broken/obscured). In ventral view, the centrum is hourglass-shaped, has a rounded ventral surface and bears a low midline keel. A small nutrient foramen enters one of the lateral surfaces.

?Dorsal ribs

Several cylindrical bone fragments are present, lying beneath the scapula (Figs 2B, 3B). These are interpreted as the dorsal rib shafts, but offer no useful information.

Scapula

A left scapula is preserved, but can only be observed in medial view (Figs 2B, 3B). The proximal plate is expanded dorsoventrally and has a shallowly concave surface, but most of this area, including the glenoid, is obscured by the presence of a centrum (see above). The acromial region is missing. The dorsal margin of the scapula blade is straight, while the ventral margin is concave, leading to asymmetrical dorsoventral distal expansion of the scapula blade. The medial surface of the blade is strongly convex dorsoventrally. In dorsal view, the scapula blade is almost straight, rather than bowed, but this may be due to crushing.

Humerus

A left humerus lies beneath the scapula and is partially exposed in posterior view (Figs 2B, 3B). Its proximal and distal ends are transversely expanded: the proximal expansion is wider than the distal expansion. Distally, the humerus is divided into medial and lateral condyles that are separated posteriorly by a shallow furrow. The medial condyle extends further distally than the lateral one. In distal view, the medial condyle is longer anteroposteriorly than the lateral condyle.

?Ulna

Adjacent to the humerus another limb element is present that may represent an ulna, as the ?proximal end is transversely expanded in a manner suggestive of an olecranon process. More distally, the shaft tapers ventrally and is subcylindrical in cross-section (Figs 2B, 3B).

BP/1/6582

General comments

This specimen consists solely of postcranial material and incorporates five dorsal and two sacral vertebrae, a ?dorsal neural spine, two partial dorsal ribs, a left coracoid, both scapulae, a right humerus and ulna, a partial left ilium, the proximal end of a right ischium and a left femur (Figs 4–8). Measurements are provided in Tables 2–3.

Dorsal vertebrae

Three of the dorsal vertebrae are preserved in articulation and are held together with matrix, which partially obscures some details of their anatomy (Fig. 4A; Table 2). Each vertebra consists of a complete centrum and partial neural arch. The centra are amphiplatyan to mildly amphicoelous and are longer than they are high. The anterior articular surfaces are approximately equal in dorsoventral height and mediolateral width. In ventral view, the centra are hourglass-shaped. The first vertebra in the series has a moderately developed ventral keel; the second has a more rounded surface; and the third bears a shallow midline groove. In lateral view, the sides of the centra are lightly excavated and are concave anteroposteriorly and mildly convex dorsoventrally. Several small nutrient foramina are present on each side of the centrum at approximately midlength and midheight. The lateral surfaces immediately adjacent to the articular surfaces are strongly sculpted with short longitudinally extending striations. Neurocentral sutures are filled with a thin line of matrix and are clearly visible.

The neural canal has a circular outline in both anterior and posterior views. Small, subcircular parapophyses are present on the anteroventral corners of the neural arch. The prezygapophyses are angled at approximately 40 degrees to the horizontal in lateral view and probably terminated slightly anterior to the articular surface of the centrum. In anterior view, the articular facets of the prezygapophyses are oriented dorsomedially at an angle of approximately 45 degrees to the horizontal. The prezygapophyses are supported ventrally by stout pedicles that merge with the rest of the neural arch ventrally. A small foramen pierces the base of the left prezygapophysis on the first vertebra, but this foramen cannot be identified on any of the other vertebrae.

The right transverse process is preserved in the second vertebra of the series and is horizontally oriented. The underside of the process bears a swelling along its anterior

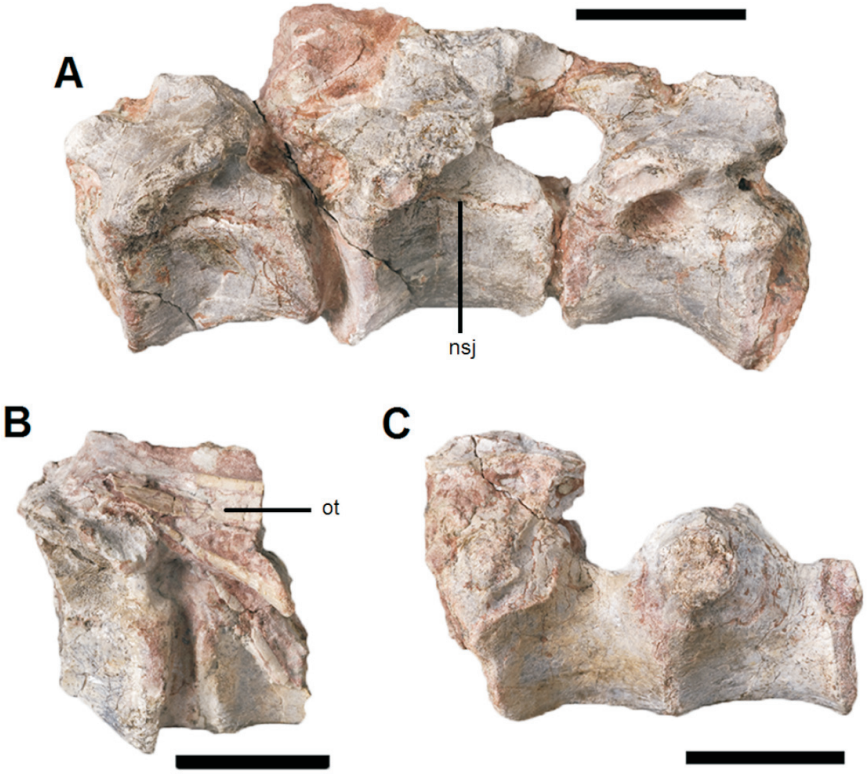

Figure 4. Dorsal and sacral vertebrae of BP/1/6582. **A**, Three articulated dorsal vertebrae in left lateral view; **B**, two partial articulated dorsal vertebrae in left lateral view; **C**, two partial articulated sacral vertebrae in left lateral view. Scale bars = 20 mm.

margin that merges with the base of the arch, in a position equivalent to that of the anterior centrodiapophyseal lamina. A shallow concavity is present at the posteroventral corner of the neural arch, which is bounded anteriorly by a stout buttress that is confluent with the posterior margin of the transverse process and dorsally by the base of the postzygapophysis. This buttress is in a position equivalent to that of the posterior centrodiapophyseal lamina. However, none of the vertebrae show any other evidence of complex neural arch lamination.

Most of the postzygapophyses are broken or obscured by matrix, but those of the second vertebra in the series show that their articular surfaces face ventrolaterally, they extend beyond the posterior articular surface, and they are situated dorsal to the base of the prezygapophysis. There is no evidence for the presence of hyposphenes or hypantra. Small fragments of ossified tendon lie adjacent to the neural arches of the second and third vertebrae. An isolated neural arch is present that cannot be articulated with any of the preserved vertebrae. It is a transversely flattened, subquadrate plate and its posterodorsal corner slightly overhangs its posterior margin in lateral view.

Two additional articulated dorsal vertebrae are included in BP/1/6582, but are poorly preserved. They appear to be identical to the aforementioned vertebrae and are associated with fragments of subcylindrical, rod-like ossified tendons (Fig. 4B). These vertebrae are slightly larger than the other dorsals and the sacral vertebrae, suggesting that they might pertain to the third larger individual in the assemblage that is represented by BP/1/6583, though this cannot be confirmed.

Dorsal ribs

Two dorsal rib heads are preserved. They probably pertain to the anterior part of the vertebral column as the tuberculum and capitulum are widely separated. The base of each rib head is broken just ventral to the area in which the two processes merge and this basal region has a subelliptical transverse cross-section. The tuberculum is broken or obscured in each rib head, although its base can be seen. The capitulum is elongate with a cylindrical cross-section. A partial neural arch is present in the same block of matrix as the rib heads, but offers little information.

Sacral vertebrae

A partial sacrum is preserved consisting of two articulated centra, each of which bears the broken bases of their associated sacral ribs (Fig. 4C; Table 2). The anterior-most centrum bears a partial but very damaged neural arch and the anterior articular surface is damaged and partially obscured by matrix. It is not possible to determine the positions of these vertebrae within the sacrum. The centra are not fully coossified and remain partially separated by a thin line of matrix. The neurocentral sutures and sacral rib articulations of both vertebrae are also unfused.

The anterior articular surface of the anterior sacral is as wide as high with a subcircular outline, whereas its posterior articular surface is wider than high. The lateral surface of the centrum is strongly concave anteroposteriorly and weakly convex dorsoventrally and there is a low, longitudinal break-in-slope that extends along the surface of the centrum approximately one-third of the way up from its ventral margin. Immediately ventral to this break-in-slope, at a point approximately halfway along the centrum, a small elliptical nutrient foramen is present. In ventral view, the centrum is hourglass-shaped and the articular surfaces are subequal in transverse width. The lateral surfaces of the centrum converge ventrally to form a sharp keel that extends along the entire length of the centrum. On the dorsal surface, the neural canal excavates the body of the centrum. Close to the neurocentral suture, at a point immediately posterior to the sacral rib facet, a small depression is present. The sacral ribs are large with a sub-elliptical base but they are broken and no other details can be determined. Although present, the neural arch is too badly preserved to yield any useful information and all of its major processes are missing.

The posterior centrum differs from the preceding one in several respects: its anterior articular surface is wider in ventral view than the posterior articular surface; it lacks a prominent keel (although a slight raised midline eminence is present); it lacks the break-in-slope on the lateral surface and the depression on the neurocentral boundary; and the nutrient foramen is positioned slightly more dorsally on its lateral surface. Both articular surfaces are wider than high and the posterior articular surface has a subelliptical outline. The preserved sacral rib bases are large and cover the anterior two-thirds of the lateral surface of the centrum, and slightly overlap the preceding centrum. Although broken close to their base it can be determined that they tapered distally to some extent. A

Table 2. List of measurements for selected vertebrae in BP/1/6582. All measurements in mm.

Articulated dorsal series: dorsal 1	
Centrum length	23
Centrum anterior height	19
Centrum anterior width	20
Centrum posterior width	22
Centrum posterior height	20
Articulated dorsal series: dorsal 2	
Centrum length	23
Centrum anterior height	20
Centrum anterior width	22
Centrum posterior width	26
Centrum posterior height	17
Articulated dorsal series: dorsal 3	
Centrum length	26
Centrum anterior height	18
Centrum anterior width	24
Centrum posterior width	19
Centrum posterior height	20
Sacral 1	
Centrum length	23
Centrum anterior width (excluding rib)	23.5
Centrum posterior width	25
Centrum posterior height	19
Sacral 2	
Centrum length	23
Centrum anterior height	19
Centrum anterior width (excluding rib)	25
Centrum posterior width	23
Centrum posterior height	17

small fragment of the succeeding vertebra's left sacral rib adheres to the posterior border of the centrum; an obliquely inclined sub-ovate facet is present along the dorsolateral margin of the posterior articular surface (on the right side) which represents an articular surface for the right sacral rib of the next vertebra.

Coracoid

The left coracoid is preserved in articulation with the scapula (Fig. 5). Its dorsal and anterior margins are broken, but it appears to have been subquadrangular in outline. Most of its lateral surface is shallowly concave (Fig. 5A). A large foramen is positioned in the ventral half of the coracoid, just dorsal to the glenoid fossa and slightly anterior to the articulation with the scapula. A low, horizontally oriented and ventrally positioned ridge divides the lateral surface into a small ventrolaterally facing portion and a much larger laterally facing dorsal portion. The coracoid contribution to the glenoid fossa forms the posterior part of the ventral surface and faces posteroventrolaterally. The coracoid contributes approximately one-third of the total length of the glenoid fossa. It has a shallowly concave surface and is separated from the ventrolaterally facing portion of the lateral surface by a distinct rounded ridge. Anterior to this, a shallowly concave, ventrally facing surface makes up the remainder of the coracoid ventral surface, which is downturned to form a distinct (though broken) anteroventral (sternal) process.

Most of the medial surface is convex (both dorsoventrally and anteroposteriorly) although small concavities are present adjacent to the anterodorsal and anteroventral corners of the element (Fig. 5B). A low rounded eminence is present adjacent to the scapula articulation at approximately mid-height, which merges with the rest of the medial surface anteriorly. The coracoid is mediolaterally thickest in the region of the glenoid and the area immediately dorsal to it, and it thins slightly anteriorly and markedly dorsally.

Scapula

Both scapulae are preserved and largely complete, with each missing only small sections of the distal blade (Fig. 5; Table 3). The left scapula is preserved in articulation with the coracoid, but they are unfused and separated by a clear line of matrix. The scapula consists of a proximal plate that supports an elongate, posteriorly extending blade. The proximal plate has a sub-trapezoidal outline in lateral view and much of its lateral surface is covered by a shallow concavity that fades out at the point where the proximal plate meets the blade (Fig. 5A). The proximal plate is strongly expanded dorsoventrally and its dorsal margin is expanded into an anteroposteriorly narrow, but elongate, sub-triangular acromial ridge (Fig. 5A). The anterior margin of the proximal plate is slightly concave. A large oval facet on the anteroventral border of the proximal plate forms the scapula contribution to the glenoid fossa and accounts for approximately two-thirds of the fossa's



Figure 5. Articulated left scapula and coracoid of BP/1/6582. **A**, Lateral view; **B**, medial view. Scale bar = 20 mm.

Table 3. List of measurements for postcranial elements in BP/1/6582. All measurements in mm. '*' indicates measurement of an incomplete element, measured as preserved.

Left scapula	
Length	132
Maximum height of proximal end	43
Minimum width of blade	18
Right scapula	
Length	127
Maximum height of proximal end	53
Minimum width of blade	19
Expansion of the distal blade	61*
Left coracoid	
Maximum length	41*
Maximum height	48*
Right humerus	
Length	112
Width of proximal expansion	43
Width of distal expansion	29.5
Width of shaft at midlength	15
Distance from head to ventral margin of deltopectoral crest	49
Right ulna	
Length	72.5*
Left femur	
Length	189*
Mediolateral wid	
Anteroposterior width of proximal end	39
Distance to base of fourth trochanter from proximal end	80

total length. This facet is oriented ventrolaterally and is concave both anteroposteriorly and mediolaterally. Medially, the surface of the proximal plate is shallowly convex dorsoventrally and mildly concave anteroposteriorly (Fig. 5B). A short, shallow groove lies close to the ventral border of the coracoid articulation, which likely communicates with the coracoid foramen (Fig. 5B). In anterior view, the dorsolateral portion of the coracoid articulation is concave, while the ventromedial portion is convex.

In lateral view, the anterior part of the elongate scapula blade is dorsoventrally narrow and parallel-sided (Fig. 5A). It expands dorsoventrally in its posterior portion to form a fan-like distal end that is greater in height than the proximal plate. This posterior expansion is asymmetrical as it is caused by divergence of the ventral margin so that most of the expansion lies ventral to the scapula long axis. The ventral tip of the distal expansion is somewhat rugose and the posterior margin of the expansion is slightly thickened relative to the rest of the distal blade. The lateral surface of the scapula blade is strongly convex dorsoventrally in its anterior part, but becomes weakly convex to planar in its distal portions. Medially, the proximal part of the blade is dorsoventrally convex and a distinct break in slope creates a shallow excavation along its ventral border that extends for a short distance posteriorly (Fig. 5B). More distally, the medial surface of the blade becomes flat to very shallowly concave dorsoventrally.

In cross-section, the scapula blade is mediolaterally compressed with respect to the proximal plate. Immediately posterior to the proximal plate it has a sub-elliptical cross-section, which becomes subcrescentic more distally. In dorsal view, the entire scapula is moderately bowed laterally.

Humerus

The right humerus is well preserved and almost complete (Fig. 6A–C; Table 3). It consists of a narrow shaft that links the mediolaterally expanded proximal and distal ends. The proximal expansion is medially inclined in anterior view and is asymmetrical, so that most of the expansion lies medial to the humeral long axis (Fig. 6A). The proximal expansion is also twisted at an angle of approximately 30 degrees relative to the transverse axis of the distal expansion. The humeral head is positioned slightly medial to the humeral long axis, at the centre of the proximal expansion and forms the dorsal-most point of the humerus. Medial to the head, the dorsal margin of the humerus forms a straight, ventromedially extending slope that terminates in a prominent medial tubercle, which has a quadrate outline. Lateral to the head, the dorsal margin of the humerus is smoothly convex and confluent with the deltopectoral crest ventrally. The deltopectoral crest has a thickened lateral margin, which extends anteriorly and very slightly medially towards its apex (Fig. 6A, 6C), forming an angle of approximately 90 degrees with the anterior proximal surface. The deltopectoral crest is confined to the proximal half of the bone and forms a narrow, smoothly convex flange in anterior view. The anterior surface of the proximal expansion medial to the deltopectoral crest is gently concave mediolaterally (Fig. 6A).

In proximal view, the humerus has a shallow, 'C'-shaped outline. The humeral head is an indistinct structure that is only slightly thicker than the medial tubercle and it lacks a distinct articular surface. In posterior view, the proximal expansion is transversely convex and the humeral head is supported by a low, indistinct intermuscular line that merges into the proximal end surface at a point level with the dorsal part of the shaft (Fig. 6B). The dorsal part of this surface is striated for muscle attachment areas.

The humeral shaft is slightly crushed, but appears to have had a subelliptical transverse cross-section originally. In anterior or posterior views, the distal expansion is narrower than the proximal expansion and divided into two articular condyles (Fig. 6A–B). Expansion of the distal end is effectively symmetrical around the humeral long axis so that the two condyles are approximately equal in size in anterior and posterior views. The medial condyle is anteroposteriorly expanded relative to the lateral condyle in distal end view and extends slightly further ventrally than the lateral condyle in anterior view. Shallow concavities situated between the condyles on both the anterior and posterior surfaces of the distal expansion expand proximally, although the anterior concavity is the more prominent.

Ulna

The right ulna is present but damaged at its proximal and distal ends and has been slightly crushed. It consists of a narrow, elongate shaft linking proximal and distal ends that are expanded both anteroposteriorly and

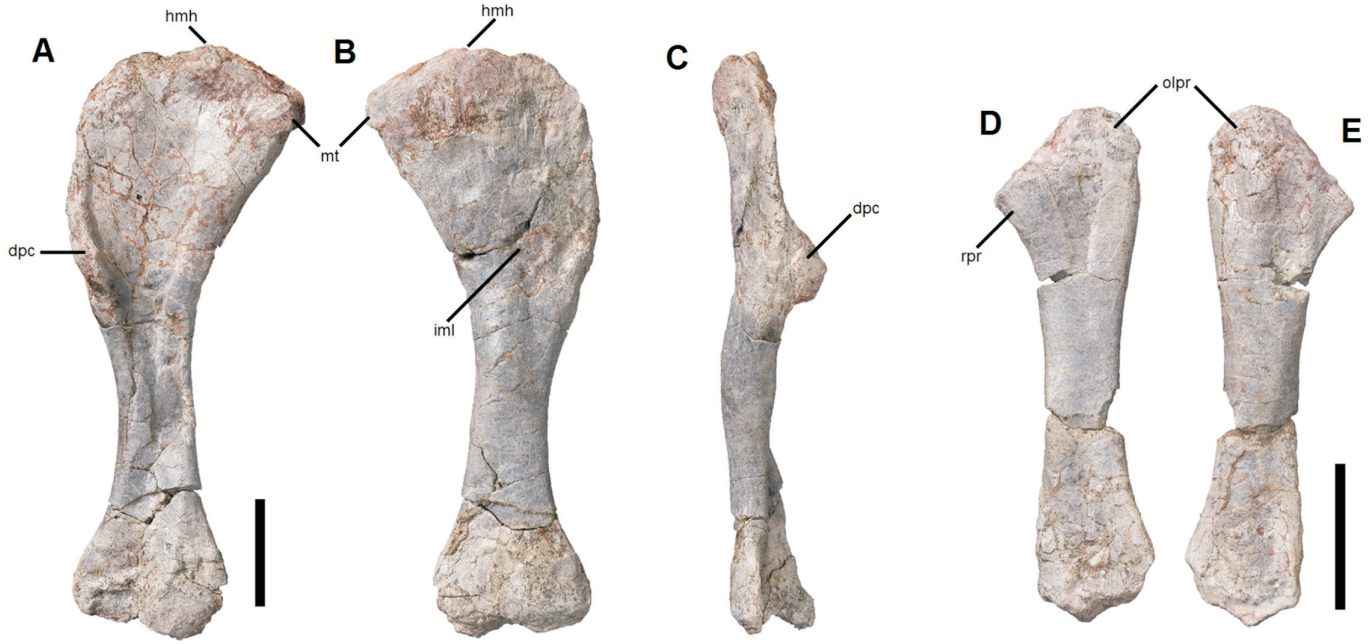

Figure 6. Right forelimb elements of BP/1/6582. **A–C**, Humerus in anterior (**A**), posterior (**B**) and lateral (**C**) views; **D–E**, ulna in medial (**D**) and lateral (**E**) views. Scale bars = 20 mm.

mediolaterally (Fig. 6D–E; Table 3). The proximal end of the bone is expanded to a greater extent than the distal end in both directions. In lateral view, the ulna terminates proximally in a broad, rounded olecranon process that merges anteriorly with a more ventrally situated, triangular radial process, which projects anteriorly. The humeral glenoid is poorly preserved and the articular surface is damaged. The lateral surface of the proximal end is strongly convex anteroposteriorly. In medial view, the proximal end of the shaft is slightly concave, although this has been accentuated by crushing. The ulnar shaft has a semicircular cross-section close to the dorsal expansion with an almost planar medial surface. This cross-section becomes elliptical more distally as the shaft merges into the distal expansion. The distal end is poorly preserved: the articular region is broken ventrally and offers no useful information.

Ilium

A partial left ilium is present that lacks the preacetabular process, the dorsal margin of the main body, most of the postacetabular process and the pubic peduncle (Fig. 7A–B). The main body is expanded laterally dorsal to the acetabulum to form a well-developed supraacetabular flange: this flange is mediolaterally broadest at the base of the pubic peduncle and narrows posteriorly, grading into the lateral surface of the ilium at a point immediately dorsal to the ischiadic peduncle (Fig. 7A). Most of the acetabulum is backed by a complete, ventromedially extending sheet of bone (Fig. 7A). As a consequence, the acetabulum is only partially open: the fenestra would have been small and confined to the ventral part of the hip socket. The acetabular surface is strongly concave both anteroposteriorly and dorsoventrally. Dorsal to the supraacetabular flange, the lateral surface of the ilium is strongly concave dorsoventrally. The ischial peduncle projects ventrally and slightly posteriorly. The lateral surface of the peduncle is slightly raised relative to the rest of the acetabular surface and probably represents part of the antitrochanter. In ventral view, the peduncle has an ovate outline, tapering anteriorly, with its long axis extending anteroposteriorly. Its ventral surface is concave, for articulation with the ischium. This concavity is surrounded by a raised lip of bone.

In medial view, the anterior-most part of the brevis shelf is preserved, but its posterior portion is missing and the form of the brevis fossa cannot be determined (Fig. 7B). This shelf extends anteriorly to form the dorsal border of the sacral rib facets. Three separate sacral rib facets are identifiable: the facet for sacral rib two is incompletely preserved and is positioned close to the base of the preacetabular process/pubic peduncle (Fig. 7B). This is separated from the facet for sacral rib three by a low ridge. The latter facet is positioned on the medial surface of the acetabular wall. Posterior to this a larger incomplete facet represents the attachment for sacral ribs four and five, which extends over the medial surface of the ischiadic peduncle and brevis shelf. Another small concavity is positioned dorsal to the scar for sacral rib two, but might represent damage.

Ischium

The proximal end of the right ischium is preserved. It consists of a proximal plate, which is divided into iliac and pubic processes, and a short section of the shaft (Fig. 7C–E). In lateral view, the pubic and iliac processes are separated from each other by an angle of approximately 80 degrees. The pubic process is anteroposteriorly longer than the iliac process is tall dorsoventrally, has a subquadrate outline and extends anteriorly (Fig. 7C). Its lateral surface is shallowly concave anteroposteriorly, whereas the corresponding medial surface is convex. Its anterior margin is transversely compressed, so that it forms a narrow plate in anterior view. The iliac process

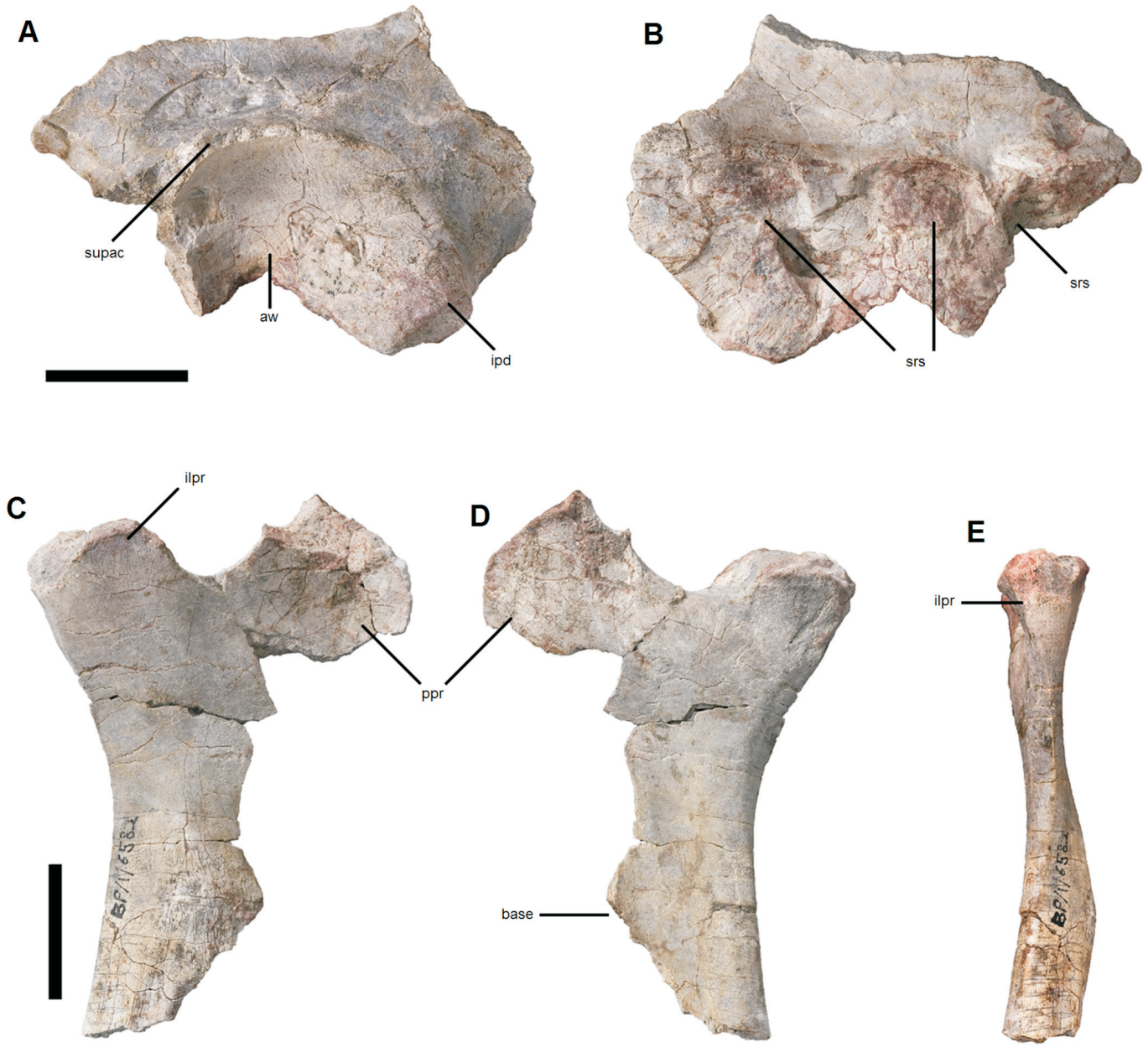

Figure 7. Pelvic girdle elements of BP/1/6582. **A–B**, Left ilium in lateral (**A**) and medial (**B**) views; **C–E**, right ischium in lateral (**C**), medial (**D**) and posterior (**E**) views. Scale bars = 20 mm.

extends dorsally and has a subtriangular cross-section, being broadest anteriorly and tapering posteriorly. Its lateral surface is shallowly convex both dorsoventrally and anteroposteriorly; the corresponding medial surface is slightly concave. The dorsal margin for articulation with the ilium is convex in lateral view. The iliac process exceeds the pubic process in transverse width. The acetabular margin is formed by the dorsal margin of the pubic process and the anterior margin of the iliac process and describes a smooth curve in lateral view. In dorsal view, the acetabular margin is a mediolaterally-expanded shelf, which has a smoothly concave surface.

Posterior to the proximal plate, the ischium narrows dorsoventrally to form the shaft. In lateral view, the proximal-most part of the shaft is dorsoventrally narrow, but the shaft expands ventrally a short distance from the proximal plate, forming a distinctive anteroventral 'shoulder' (Fig. 7C–E). The ventral margin of the shaft is damaged posterior to this point, so the morphology of this region is somewhat equivocal and it is not possible to determine if a tab-like obturator process was present or absent. The lateral surface of the shaft is strongly convex dorsoventrally. A shallow groove extends along the dorsolateral surface of the shaft, originating at a point level with the anteroventral 'shoulder'.

In medial view, the dorsal margin of the shaft is thickened and the surface ventral to this is strongly convex (Fig. 7D). As a result, the shaft cross-section has an inverted comma-like shape in distal view. In dorsal view, the shaft extends slightly medially with respect to the anteroposteriorly extending proximal plate.

Femur

The left femur is nearly complete, but has been strongly compressed transversely (Fig. 8; Table 3). It is strongly bowed anteriorly in lateral view, but is straight in anterior

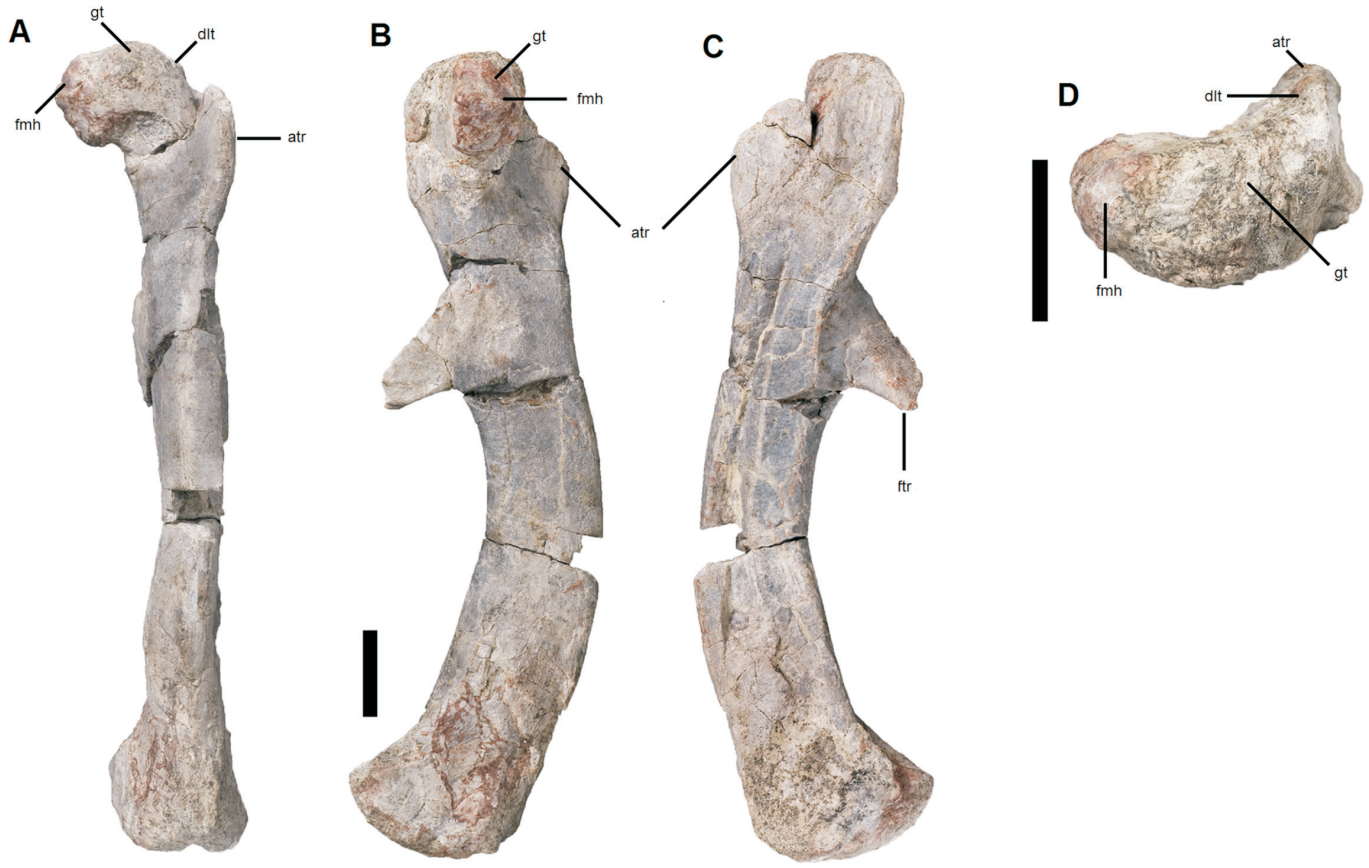

Figure 8. Left femur of BP/1/6582. **A**, Anterior; **B**, medial; **C**, lateral; and **D**, proximal views. Scale bars = 20 mm.

view. In anterior view, the femoral head is in-turned and projects strictly medially. Its dorsal margin is continuous with that of the greater trochanter and their combined dorsal margin is very shallowly convex in anterior view (Fig. 8A). The articular surface of the femoral head is convex: its medial margin is angular in anterior view, with a dorsomedially facing proximal half and a ventromedially facing distal half, although this feature may result from poor preservation. The head is set on a stout neck that is continuous with the greater trochanter. In proximal view, the femur has a slightly convex anterior margin and concave posterior margin (Fig. 8D). A weakly developed groove, the fossa trochantericus, extends across the proximal surface, from the anteromedial corner of the proximal end to the posterolateral corner, dividing the surfaces of the femoral head and greater trochanter. The groove is continuous with a depressed area on the posterolateral corner of the proximal end, the articularis antitrochantericus. There is no development of a medial tuber on the posterior surface. The posterolateral corner of the greater trochanter is thickened and forms a prominent ridge, though this feature may have been accentuated by crushing. Laterally, the greater trochanter is flattened and develops into a small anteriorly extending flange – the dorsolateral trochanter. The dorsal termination of the dorsolateral trochanter lies ventral to the proximal surface of the greater trochanter. In turn, the anterior trochanter is situated anteroventral to the dorsolateral trochanter and is separated from the latter by a deep cleft, which is clearly visible in lateral view (Fig. 8B). The latter two trochanters have subequal anteroposterior widths in lateral view. The anterior trochanter has a mediolaterally flattened, plate-like cross-section that is slightly wider anteriorly than posteriorly. There is a small foramen on the medial surface of the anterior trochanter, positioned ventral to the notch between the anterior trochanter and the dorsolateral trochanter. The lateral surface of the dorsolateral trochanter is concave anteroposteriorly.

The anterior surface of the anterior trochanter continues distally onto the femoral shaft as an anteriorly convex, mediolaterally robust ridge of bone. This ridge gradually tapers into the femoral shaft, and becomes indistinguishable at its midpoint. A small foramen is present on the medial surface of this ridge at a point level with the dorsal margin of the fourth trochanter. The fourth trochanter is located proximally and is pendant with a triangular outline in lateral view. It arises from the posteromedial margin of the shaft and curves laterally along its length. Its medial surface is scarred for muscle attachment as is the posterior part of its lateral surface, including its dorsal margin and apex. These scars represent the insertions for the Mm. caudofemoralis longus (medially) and brevis (laterally) (see Maidment & Barrett 2011). A small foramen is positioned in the base of the fourth trochanter laterally. Due to crushing it is not possible to determine the original cross-section of the shaft. The distal end is divided into lateral and medial condyles, each bearing a posteriorly extending epicondyle. Posteriorly, the condyles are separated by a shallow intercondylar groove, but there is no evidence for a groove or fossa on the anterior surface of

the distal end. Due to damage it is not possible to determine the morphology of the distal end surface.

BP/1/6583

This specimen is a partial left scapula, which is lacking its proximal plate and most of the distal expansion. What remains of the scapula blade is identical in morphology to the scapulae included within BP/1/6581 and BP/1/6582. However, it pertains to much larger individual than either of the latter specimens, with a midshaft depth of 27 mm (compare with measurements in Tables 1 & 3) and so provides evidence for the presence of a third individual in the assemblage.

DISCUSSION

Cranial ontogeny

The partial skull preserved in BP/1/6581 is approximately 55 mm in anteroposterior length, but is missing the temporal region and the snout. Comparisons with other specimens (NHMUK RU B17, NHMUK RU B23, NHMUK PV R8501, NHMUK PV R11956, and those described in Knoll [2002a,b]) suggest a total skull length of approximately 100 mm, which is larger than any of the other skulls available for this taxon. As none of the available skulls of *Lesothosaurus* are complete it is not possible to provide proportional comparisons between them (e.g. relative orbit size, snout length), but maxillary length illustrates the range of sizes available. In the majority of specimens, maxillary length is estimated to range between 28 and 35 mm (NHMUK RU B17, NHMUK RU B23, NHMUK PV R8501, NHMUK PV R11956: though it should be noted that many of the maxillae are missing small portions anteriorly or posteriorly), whereas in BP/1/6581 is it a minimum of 52 mm.

Two features of BP/1/6581 may represent ontogenetic variations based on the larger size of this individual and its presumed greater age. Firstly, a series of small rugosities is present on the lateral surface of the lacrimal in BP/1/6581, close to the orbital margin. No other *Lesothosaurus* specimen preserves this feature (NHMUK RU B17, NHMUK RU B23, NHMUK PV R8501, NHMUK PV R11956; Sereno 1991; Knoll 2002a,b; Porro *et al*. 2015). Similar ontogenetic increases in cranial rugosity are known in other small ornithischian taxa, such as the ornithopod *Jeholosaurus* (Barrett & Han 2009). Secondly, although the maxillary tooth row is incomplete in BP/1/6581, the length of the preserved maxilla (with 13 preserved tooth positions), the extent of the missing posterior process and consideration of tooth size suggests that a minimum of 18 maxillary teeth were present. By contrast, other specimens possess up to 15 maxillary teeth (e.g. NHMUK PV R8501) and might have had a maximum maxillary tooth count of 16–17 when breakage is taken into account. Ontogenetic increases in tooth count are relatively common in dinosaurs and are known in a variety of ornithischian taxa (e.g. Varricchio 1997).

Ontogenetic variation in postcranial characters will be discussed in a separate article providing full redescriptions of the syntype postcrania (NHMUK RU B17; M.G.B. & P.M.B., unpubl. data).

Taxonomic implications

If the Aushan Grey postcranial material is referable to *Lesothosaurus* (see above) it would indicate that larger-bodied individuals of this taxon overlapped in body size with individuals referred to the sympatric taxon *Stormbergia dangershoeki*. Femoral lengths of *Stormbergia* specimens range from 147–202 mm and its minimum scapula shaft widths vary from 18.5–20 mm (Butler 2005), whereas the femoral length of BP/1/6582 is 189 mm and the minimum scapula shaft widths of BP/1/6582 and BP/1/6583 are 18 mm and 27 mm, respectively. However, although this previously undocumented overlap in body size could prove useful in testing the proposed synonymy of these taxa (Knoll *et al*. 2010), as it would remove ontogenetic considerations from the argument, the only preserved ischial fragment in the new assemblage, which is part of BP/1/6582, is incomplete. As a result, it is not possible to determine either the presence/absence of a tab-like obturator process or the relative length of the ischial symphysis, which are the two critical features used to distinguish *Stormbergia* from *Lesothosaurus* (Butler 2005). Nevertheless, at the very least, the new, diagnosable skull specimens described herein offer the possibility of finding other, more completely preserved and large-sized *Lesothosaurus* individuals that might help to resolve this controversy.

Behaviour

The discovery of several *Lesothosaurus* individuals in one locality is potentially significant as it may indicate that these animals formed part of a small social group that perished during the same event. Examples of monotypic ornithischian bonebeds are rare prior to the Cretaceous (Weishampel *et al*. 2004), but a similar discovery of multiple individuals of the Early Jurassic taxon *Laquintasaura* suggests that group-living might have appeared much earlier in ornithischian evolutionary history than usually thought (Barrett *et al*. 2014). Nevertheless, detailed taphonomic information is not currently available for the Aushan Grey locality and it is not clear if the dinosaur assemblage was preserved in a single event, which might support the group-living hypothesis, or whether the remains accumulated over a more protracted period, with different carcasses joining the assemblage at different times. Further sedimentological work is required at the site to distinguish between these possibilities.

CONCLUSIONS

This new material shows that some individuals of *Lesothosaurus diagnosticus* reached similar body sizes to those reported for the sympatric taxon *Stormbergia dangershoeki* and demonstrates the potential for finding other larger individuals that might help resolve the controversial status of the latter taxon. Moreover, these larger specimens document some ontogenetic differences in cranial anatomy, with larger (= older) specimens possessing cranial rugosities that are absent from smaller individuals, as well as higher tooth counts. The discovery of three associated individuals hints at the possibility that *Lesothosaurus* might have lived in small groups, providing

additional circumstantial evidence for the early evolution of sociality in ornithischian dinosaurs.

ABBREVIATIONS

Institutional

BP	ESI Evolutionary Studies Institute (formerly Bernard Price Institute), University of the Witwatersrand, Johannesburg, South Africa.
NHMUK	Natural History Museum, London, U.K.

Anatomical

aofe	antorbital fenestra
aofo	antorbital fossa
Art.f	articular fossa
atr	anterior trochanter
aw	acetabular wall
base	broken base of ischial shaft
br	buccal ridge
Co	coracoid
cofo	coracoid foramen
De	dentary
dlt	dorsolateral trochanter
dpc	deltopectoral crest
F	frontal
fmh	femoral head
fo	foramen
ftr	fourth trochanter
gl	glenoid
gr	groove
gt	greater trochanter
Hm	humerus
hmh	humeral head
ilpr	iliac process
iml	intermuscular line
ipd	ischial peduncle
Ju	jugal
L	left
Lc	lacrimal
Mg	Meckelian groove
mt	medial tubercle
Mx	maxilla
Na	nasal
olpr	olecranon process
ot	ossified tendon
Pal	palatine
Pf	prefrontal
Pm	premaxilla
Pp	palpebral
ppr	pubic process
R	right
rpr	radial process
ru	rugosities
Sc	scapula
Sp	splenial
srs	sacral rib scar
supac	supraacetabular crest
Ul	ulna
Vert	vertebra

A.M.Y. offers his sincere thanks to the Keyser family for permission to collect this material from their property. Funding for P.M.B. and M.G.B. to visit the ESI was provided by grants from The Royal Society, The Natural History Museum, London and NERC (NE/L501578/1'). Funding for J.N.C. was provided by the Friedel Sellschop Award through the University of the Witwatersrand, the DST-NRF Centre of Excellence for Palaeosciences, and by the Palaeontological Trust and its Scatterlings of Africa Programmes. Photographs of the specimens were taken by P. Hurst (NHM Image Resources). P.M.B. and M.G.B. thank A.M.Y. and J.N.C. for their help and hospitality while in Johannesburg and Bernhard Zipfel and Sifelani Jirah for help in accessing collections. We offer our sincere thanks to Clint Boyd, Peter Galton and Laura Porro for their helpful reviews of an earlier version of this article.

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