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The 'fabrosaurid' ornithischian dinosaurs of the Upper Elliot Formation (Lower Jurassic) of South Africa and Lesotho

RICHARD J. BUTLER*

Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EQ, UK, and Department of Palaeontology, The Natural History Museum, Cromwell Road, London, SW7 5BD, UK

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The Upper Elliot Formation of South Africa and Lesotho contains the world's most diverse fauna of early Jurassic ornithischian dinosaurs. Nevertheless, despite four decades of work on this fauna there remains significant taxonomic confusion and many important specimens remain undescribed. A review of the non-heterodontosaurid ('fabrosaurid') ornithischians of the Upper Elliot Formation is presented, following re-examination of all known ornithischian material from the Elliot Formation. '*Fabrosaurus australis*' is based upon a single undiagnostic dentary, and is here considered a *nomen dubium*. *Lesothosaurus diagnosticus* is considered to be valid and is rediagnosed based upon a unique combination of plesiomorphic and derived characteristics. ***Stormbergia dangershoeki* gen. et. sp. nov.** is described from three partial skeletons including numerous postcranial material. ***Stormbergia dangershoeki*** is significantly larger than previously described Elliot Formation ornithischians, and can be recognized on the basis of a unique combination of characters, the most important of which is the possession of a distinctive tab-shaped obturator process on the ischium. A preliminary systematic analysis is presented, the results of which differ significantly from other recent ornithischian phylogenies. © 2005 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2005, **145**, 175–218.

ADDITIONAL KEYWORDS: Archosauria – heterodontosaurs – osteology – phylogenetics – systematics.

INTRODUCTION

The ornithischian dinosaurs were among the most important terrestrial herbivores of the Mesozoic Era (Sereno, 1997, 1999). During the Late Triassic–Middle Jurassic interval ornithischians have a poor fossil record and appear to have been a relatively minor component of ecosystems. The earliest reported ornithischians are from Late Triassic rocks of Argentina (Casamiquela, 1967) and the western USA (Chatterjee, 1984; Hunt & Lucas, 1994), although some authors consider *Azendohsaurus laaroussii* Detuit (1972) from the Upper Triassic of Morocco to at least partially comprise ornithischian material (e.g. see: Detuit, 1972; Galton, 1990; Gauffre, 1993). Particularly important discoveries of early Jurassic ornithischian dinosaurs have been made from the Stormberg Group of Southern Africa (Fig. 1A), in particular from the upper portion of the Elliot Formation (see review, below). The Upper Elliot has yielded the most diverse and well-studied fauna of early Jurassic dinosaurs known anywhere in the world, including some exquisitely preserved articulated material (e.g. Santa Luca, 1980), although most material represents disarticulated, partial skeletons and isolated elements (e.g. Thulborn, 1970, 1971a, 1972, 1974). To date, six genera have been named from the Upper Elliot (see below), representing the majority of well-known early Jurassic ornithischian taxa.

Other important early Jurassic ornithischian specimens are known from the USA, China and Europe. The Kayenta Formation (Sinemurian–Pliensbachian) of Arizona has yielded the primitive thyreophoran *Scutellosaurus lawleri* Colbert, 1981, as well as an undescribed heterodontosaurid (MCZ 9092; P. C. Sereno, pers. comm., 2004). Several fragmentary primitive thyreophorans (Simmons, 1965; Dong, 2001) are

*E-mail: rbut02@esc.cam.ac.uk

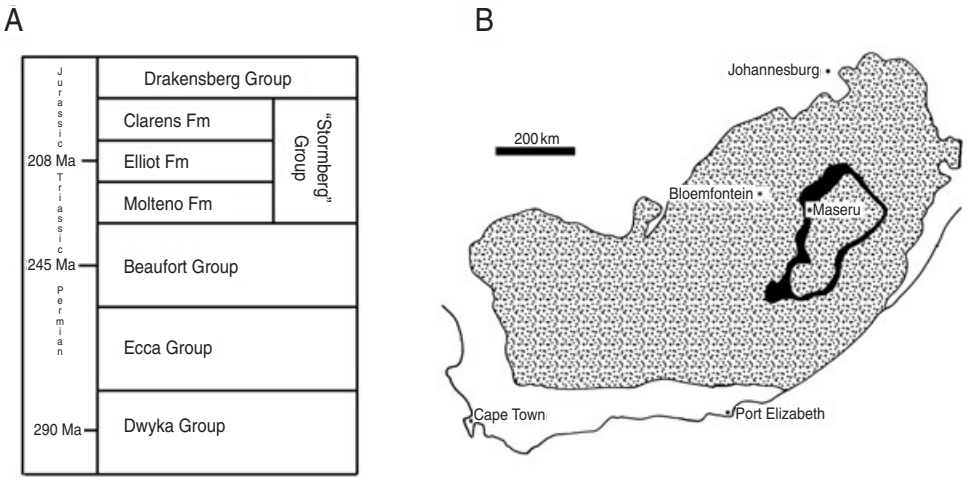

Figure 1. Stratigraphical log showing the subdivisions of the Karoo Supergroup (A), including the Elliot Formation. Map of outcrop of the Elliot Formation in southern Africa (B). Stippled area is the outcrop of the Karoo Supergroup; area shaded black is the outcrop of the Elliot Formation.

known from the Lower Lufeng Formation (Sinemurian) of Yunnan Province, China. The basal thyreophoran dinosaur *Scelidosaurus harrisonii* Owen, 1861a, is well-known from a number of specimens from the Lower Lias (Sinemurian) of Dorset, England, while a single, fragmentary specimen of another thyreophoran, *Emausaurus ernsti* Haubold, 1990, is known from Toarcian deposits of Mecklenburg, Germany.

History of ornithischian discoveries in the Upper Elliot Formation

The first remains of ornithischian dinosaurs found in the Stormberg Group were a partial jaw and fragmentary postcranium from the Clarens Formation (= Cave Sandstone), described as *Geranosaurus atavus* Broom, 1911. This was for some time the earliest known ornithischian. During 1959 the first ornithischian material was collected from the Upper Elliot Formation, at Likhoele, Lesotho, by a French team including F. Ellenberger, J. Fabre and L. Ginsburg. This material is now in the collections of the Museum d'Histoire Naturelle, Paris (Knoll & Battail, 2001; Knoll, 2002a, b).

In the 1960s, South African–British–American expeditions prospected the Upper Elliot Formation of Lesotho and South Africa and recovered substantial ornithischian material, most of which is now held in the collections of the South African Museum (Iziko Museums of Cape Town), and the Natural History Museum, London (Crompton, 1968). These specimens represent the majority of the known ornithischian material from the Upper Elliot, forming the basis for most subsequent studies.

Previous authors noted that the ornithischian dinosaurs of the Upper Elliot formation could be divided into two groups (e.g. Charig & Crompton, 1974: 168): the heterodontosaurids and a group now informally referred to as 'fabrosaurids'. Heterodontosaurids are easily defined by a unique suite of characters, including the wedge-shaped predentary bone, premaxillary and dentary canines and chisel-shaped cheek teeth (e.g. Sereno, 1986; Weishampel & Witmer, 1990b). Crompton & Charig (1962) described *Heterodontosaurus tucki*, and recognized the heterodontosaurid affinities of two previously named taxa, *Geranosaurus atavus* and *Lycorhinus angustidens* Haughton, 1924. Subsequently, two further heterodontosaurid taxa have been named (*Lanasaurus scalpridens* Gow, 1975 and *Abrictosaurus consors* Hopson, 1975); however, most recent authors (e.g. Weishampel & Witmer, 1990b; Norman *et al*., 2004c) recognize only *Lycorhinus, Heterodontosaurus* and *Abrictosaurus* as valid genera. Unfortunately much essential work remains to be carried out on these animals, and several important specimens remain unpublished. A forthcoming description of the skull of *Heterodontosaurus* (D. B. Norman, pers. comm., 2004) and redescription of *Abrictosaurus* (P. M. Barrett, pers. comm., 2004) should help to clarify the anatomy and systematics of the group. A detailed review of heterodontosaurids is beyond the scope of this paper; here I will focus on those Upper Elliot ornithischians that have been referred to as 'fabrosaurids'.

A history of published work on the Elliot Formation 'fabrosaurid' ornithischians is given below, followed by a detailed review and redescription of this material. The 'fabrosaurids' have traditionally been viewed as representative of a primitive ornithischian family, the

Fabrosauridae (Galton, 1978). Consequently, they have played a key role in studies of ornithischian evolution, often being considered as the model for an 'ancestral' ornithischian. Clarification of the anatomy, taxonomy and systematic position of these taxa therefore has wide-ranging implications for future work on the phylogeny and evolutionary history of ornithischian dinosaurs.

Stratigraphy and dating of the Elliot Formation

The Elliot Formation forms part of the Stormberg Group of the Karoo Supergroup (Fig. 1A). The Karoo Supergroup comprises a sequence of terrestrial deposits ranging from the Upper Carboniferous (deposited *c*. 300 Mya) to the Lower Jurassic (deposited *c*. 190 Mya), and is best exposed in the Karoo Basin of South Africa and Lesotho. The sequence is commonly divided into the basal Dwyka Group, the Ecca and Beaufort Groups, and the Stormberg Group, capped by the Drakensberg Group, which marks the onset of volcanism and the end of sedimentation in the Lower Jurassic (Fig. 1A; Smith, Eriksson & Botha, 1993). The Stormberg Group is further subdivided into the Molteno, Elliot (= Red Beds) and Clarens (= Cave Sandstone) formations (Smith *et al*., 1993).

The Elliot Formation (Fig. 1B) is a continental redbed sequence comprising fine- to medium-grained sandstones interbedded with mudstones. The succession appears to represent meandering stream, floodfan and aeolian dune facies deposited under semiarid climatic conditions (Visser & Botha, 1980; Smith *et al*., 1993). The sequence is commonly divided into a two-fold biozonation based on the distribution of basal sauropodomorph dinosaurs: the Lower Elliot ('*Euskelosaurus* range zone'; Kitching & Raath, 1984) and Upper Elliot ('*Massospondylus* range zone'; Kitching & Raath, 1984) assemblages. The Lower Elliot assemblage is not considered in detail here, but has a rich fauna of basal sauropodomorphs (Yates, 2003; Yates & Kitching, 2003), an undescribed ornithischian (SAM-PK-K8025; R. J. Butler & R. M. H. Smith, unpubl. data), rare temnospondyls, a traversodontid cynodont and a possible rauisuchian archosaur (Kitching & Raath, 1984; Galton & Van Heerden, 1998; Lucas & Hancox, 2001). The Upper Elliot assemblage is much more diverse, containing cynodonts, early mammals, amphibians, turtles, sphenosuchian archosaurs, basal sauropodomorphs, a basal theropod and several basal ornithischians (Kitching & Raath, 1984; Lucas & Hancox, 2001); the affinities of some of the latter are discussed in this paper.

The Lower Elliot assemblage has commonly been assigned either a Carnian (e.g. Galton & Van Heerden, 1998; Warren & Damiani, 1999) or Norian (e.g. Lucas & Hancox, 2001; Yates, 2003) age. Lucas & Hancox (2001) reviewed the evidence and cautiously suggested a Norian age based upon the dominance of basal sauropodomorphs, the footprint ichnofauna and the seeming lack of an unconformity between the Lower Elliot assemblage and the apparently Lower Jurassic Upper Elliot assemblage.

The Upper Elliot Formation and overlying Clarens Formation were long considered to be Late Triassic in age, but have been reinterpreted as Lower Jurassic (Olsen & Galton, 1984; Lucas & Hancox, 2001) based upon biostratigraphical correlation with Lower Jurassic deposits elsewhere (e.g. the Glen Canyon Group of the south-western USA and the Lower Lufeng Formation of China). The Upper Elliot is therefore generally referred to the Hettangian–Sinemurian stages, and this interpretation is followed here.

Institutional abbreviations: BMNH, The Natural History Museum, London, UK; BP, Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa; BRSMG, Bristol City Museum and Art Gallery, Bristol, UK; IGCAGS, Institute of Geology, Chinese Academy of Sciences, Beijing, People's Republic of China; IVPP, Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing; MCZ, Museum of Comparative Zoology, Harvard, USA; MNA, Museum of Northern Arizona, Flagstaff, Arizona, USA; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MOR, Museum of the Rockies, Bozeman, Montana, USA; NM, Nasionale Museum, Bloemfontein, South Africa; SAM, South African Museum (Iziko Museums of Cape Town), Cape Town, South Africa; UC, University of Chicago, Chicago, USA; UCMP, University of California Museum of Palaeontology, Berkeley, USA; ZDM, Zigong Dinosaur Museum, Dashanpu, People's Republic of China.

TAXONOMIC REVIEW OF UPPER ELLIOT FORMATION NON-HETERODONTOSAURID ORNITHISCHIANS

Previous work

Ginsburg (1964) described an isolated right dentary (MNHN LES9), collected in 1959 from Likhoele, Lesotho, which he considered to be similar to that of the English Lower Jurassic ornithischian *Scelidosaurus harrisoni*. He named it *Fabrosaurus australis* in honour of the geologist Jean Fabre. In retrospect, it is perhaps unfortunate that such fragmentary material was named, as the ensuing nomenclatural confusion demonstrates (Galton, 1978; Gow, 1981; Sereno, 1991; Thulborn, 1992).

More complete ornithischian material was collected in 1963–64 in Lesotho by an expedition from University College, London, and was referred to *Fabrosaurus*

australis in a series of papers (Thulborn, 1970, 1971a, 1972). The material described includes an assemblage containing the remains of at least two individuals (BMNH RUB17) and a well-preserved skull (BMNH RUB23).

The holotype of *Fabrosaurus australis* was considered a *nomen dubium* by Charig & Crompton (1974), who suggested that its characteristics would prove to be widespread in basal ornithischians. Galton (1978) considered *Fabrosaurus australis* to represent a valid genus, but referred the specimens described by Thulborn (1970, 1971a, 1972) to a new genus and species, *Lesothosaurus diagnosticus*. BMNH RUB17 and RUB23 were therefore made syntypes of *Lesothosaurus diagnosticus*, which was distinguished from *Fabrosaurus australis* on the basis of tooth and dentary morphology. Galton (1978) referred *Fabrosaurus* and *Lesothosaurus* (as well as *Echinodon becklesii* Owen, 1861b and *Nanosaurus agilis* Marsh, 1877) to the family Fabrosauridae.

Further cranial and postcranial ornithischian remains were collected in 1967–68 in Lesotho by a joint expedition from the British Museum (Natural History), Birkbeck College (University of London), Yale University and the South African Museum. Some of the postcranial material from this expedition was described by Santa Luca (1984), while much of the cranial material was described by Sereno (1991). Santa Luca (1984) described the postcranial portions of three 'fabrosaurid' specimens (SAM-PK-K400, K401, K1106). He considered most of the minor differences between this material and the *Lesothosaurus* syntype series (BMNH RUB17, RUB23) to represent intraspecific variation; however, he did consider the sacral rib scars on the ilium to show a significantly different pattern of attachments. This was based upon a comparison with the sacral rib scars of BMNH RUB17 as figured by Thulborn (1972: fig. 8); however, Thulborn's interpretation was in error (see Sereno, 1991: 171, 193) and the material described by Santa Luca has since been referred to *Lesothosaurus diagnosticus* (Sereno, 1991).

Sereno (1991) reviewed and revised the anatomy and systematics of *Fabrosaurus* and *Lesothosaurus*. He redescribed the holotype of *Fabrosaurus australis* and followed Charig & Crompton (1974) in considering it a *nomen dubium*. He listed a partial skull (BMNH R11956) as belonging to the syntype series of *Lesothosaurus diagnosticus*; however, the syntypes erected by Galton (1978) are BMNH RUB17 and BMNH RUB23. BMNH R11956 should therefore be considered as a referred specimen of the species *Lesothosaurus diagnosticus*, not a syntype. Sereno (1991) additionally referred several other specimens, including those described by Santa Luca (1984), to *Lesothosaurus*.

Further material from the Elliot Formation of Lesotho has been described recently (Knoll & Battail, 2001; Knoll, 2002a, b). This material includes two partial skulls (MNHN LES 17, LES 18) and fragmentary postcranial material. All of this material has been referred to as *Lesothosaurus* sp., pending a detailed review of the anatomy of an undescribed new ornithischian from the Elliot Formation (see below).

Reference to an undescribed basal ornithischian from the Elliot Formation, larger than *Lesothosaurus diagnosticus*, is fairly common in the literature, although no detailed diagnosis or description of this taxon has been produced. Crompton & Attridge (1986: 228) refer to: 'at least one undescribed skeleton of what appears to be a fabrosaurid in the South African Museum [which] reaches the dimensions of a medium-sized *Massospondylus*'. Sereno (1986: 247) notes that: 'the obturator process is present in an undescribed, primitive ornithischian from the Stormberg Group of South Africa of possible close affinity to *Lesothosaurus*'. Sereno (1991: 171) records that: 'a larger undescribed basal ornithischian from the same horizon as *Lesothosaurus* also has short forelimbs and a reduced pedal digit I, and these apomorphic characters may eventually emerge as synapomorphies for these taxa'.

Knoll (2002a, b) has recently discussed this basal ornithischian, which he refers to as a 'large fabrosaurid'. He suggests that this animal is a larger species of *Lesothosaurus* from the Upper Elliot Formation and is represented by three specimens held in The Natural History Museum, London, the Museum of Comparative Zoology (MCZ), Harvard (all South African 'fabrosaurid' material held at the MCZ was, until recently, on loan from the South African Museum and has now been returned), and the Nasionale Museum, Bloemfontein. Knoll (2002a, b) only lists a specimen number (NM QR 3076) for one of these specimens, although it is likely that the other specimens referred to are BMNH R11000 and SAM-PK-K1105 (both discussed below). Noting the range of sizes present in Upper Elliot ornithischian material, Knoll (2002a: 601) recognized that ontogenetic variation or sexual dimorphism cannot be ruled out. However, Knoll (2002b: 242) asserted that: 'a fabrosaurid clade of two congeneric species seems to occur in the Upper Elliot Formation of southern Africa, even if it cannot be ruled out that these species are in fact the same'.

The majority of authors agree that (i) *Fabrosaurus* is a *nomen dubium*, (ii) *Lesothosaurus* is valid, and (iii) that there is an undescribed larger ornithischian present in the Upper Elliot Formation, which is possibly phylogenetically close to *Lesothosaurus*. However, not all workers concur with these conclusions (e.g. Thulborn, 1992; Hunt & Lucas, 1994). Clarification of the status of Upper Elliot ornithischians, based upon detailed examination of all-known material, is a necessary precursor to further work on basal ornithischian anatomy, phylogeny and evolution: this work is

Table 1. Specimens discussed in the text, with previous identification and identications proposed herein. A number of extremely fragmentary specimens discussed by Knoll & Battail (2001) are not listed here, but are considered Ornithischia indet

Specimen number	Previous identification	Current Identification
MNHN LES9	*Fabrosaurus australis* (Ginsburg, 1964; Galton, 1978); *'Fabrosaurus australis'* (*nomen dubium*) (Charig & Crompton, 1974; Sereno, 1991)	*'Fabrosaurus australis'* (*nomen dubium*)
BMNH RUB17	*Lesothosaurus diagnosticus* syntype (Galton, 1978; Sereno, 1991)	*Lesothosaurus diagnosticus* syntype
BMNH RUB23	*Lesothosaurus diagnosticus* syntype (Galton, 1978; Sereno, 1991)	*Lesothosaurus diagnosticus* syntype
BMNH R11956	*Lesothosaurus diagnosticus* syntype (Sereno, 1991)	*Lesothosaurus diagnosticus* (referred)
BMNH R11004	*Lesothosaurus diagnosticus* (referred: Sereno, 1991)	*Lesothosaurus diagnosticus* (referred)
BMNH R8501	*Lesothosaurus diagnosticus* (referred: Sereno, 1991)	*Lesothosaurus diagnosticus* (referred)
SAM-PK-K400	Fabrosauridae indet. (Santa Luca, 1984) *Lesothosaurus diagnosticus* (referred: Sereno, 1991)	*Lesothosaurus diagnosticus* (referred)
SAM-PK-K401	Fabrosauridae indet. (Santa Luca, 1984) *Lesothosaurus diagnosticus* (referred: Sereno, 1991)	*Lesothosaurus diagnosticus* (referred)
SAM-PK-1106	Fabrosauridae indet. (Santa Luca, 1984) *Lesothosaurus diagnosticus* (referred: Sereno, 1991)	*Lesothosaurus diagnosticus* (referred)
SAM-PK-K1105	'Large fabrosaurid' (Knoll, 2002a, b)	***Stormbergia dangershoeki*** holotype
BMNH R11000	'Large fabrosaurid' (Knoll, 2002a, b)	***Stormbergia dangershoeki*** paratype
BP/1/4885	*Lesothosaurus* (Knoll, 2002a, b)	***Stormbergia dangershoeki*** referred
SAM-PK-K1107	No previous identification	cf. ***Stormbergia dangershoeki***
NM QR 3076	'Large fabrosaurid' (Knoll, 2002a, b)	cf. ***Stormbergia*** & *Lesothosaurus*
MNHN LES 17	*Lesothosaurus* sp. (Knoll, 2002b)	cf. ***Stormbergia*** & *Lesothosaurus*
MNHN LES 18	*Lesothosaurus* sp. (Knoll, 2002a)	cf. ***Stormbergia*** & *Lesothosaurus*
BMNH R11002	*Lesothosaurus diagnosticus* (Sereno, 1991)	cf. ***Stormbergia*** & *Lesothosaurus*
BMNH R11003	*Lesothosaurus diagnosticus* (Sereno, 1991)	cf. Heterodontosauridae

presented here. Table 1 provides a summary of specimens discussed in the text, with previous identifications and identifications suggested herein.

DINOSAURIA OWEN, 1842
ORNITHISCHIA SEELEY, 1887
FABROSAURUS AUSTRALIS GINSBURG, 1964

Diagnosis: Fabrosaurus australis is not diagnosable on the basis of unique characters, or on the basis of a unique combination of characters, and is here regarded as a *nomen dubium*; the holotype is considered Ornithischia indet.

Holotype: MNHN LES9, partial dentary with three teeth (Ginsburg, 1964; Galton, 1978: fig. 6; Sereno, 1991: fig. 1; Thulborn, 1992: fig. 1).

Horizon: Upper Elliot Formation (Hettangian–Sinemurian), Likhoele, Lesotho.

Discussion: There has been substantial debate regarding whether the holotype of *Fabrosaurus* (MNHN LES9) possesses any unique characters that would support the validity of the genus. Charig & Crompton (1974: 167–168) argued that the teeth of *Fabrosaurus* were symplesiomorphic for Ornithischia, and therefore undiagnostic; they considered it a *nomen dubium*. Galton (1978) considered *Fabrosaurus* as valid, but removed the specimens referred to *Fabrosaurus* by Thulborn (1970, 1971a, 1972) into a new genus, *Lesothosaurus diagnosticus*. He suggested that *Fabrosaurus* was distinct on the basis of its broader dentary, possession of 'special foramina', and minor differences in tooth height/width ratios. Gow (1981) showed that all of these features were undiagnostic, and could be the result of ontogenetic or individual variation. Sereno (1991) redescribed the holotype of *Fabrosaurus* (Sereno, 1991: fig. 1); he concluded that the holotype lacked autapomorphies and could not be distinguished from other basal ornithischians.

Thulborn (1992: 286) and Hunt & Lucas (1994: 238) have argued that no other ornithischian taxon shares the same tooth morphology as *Fabrosaurus* and that, although autapomorphic characters are clearly absent, the holotype dentary can be diagnosed by a unique combination of primitive characters [i.e. a metataxon (*sensu* Gauthier, 1986)]. Knoll (2002b: 238)

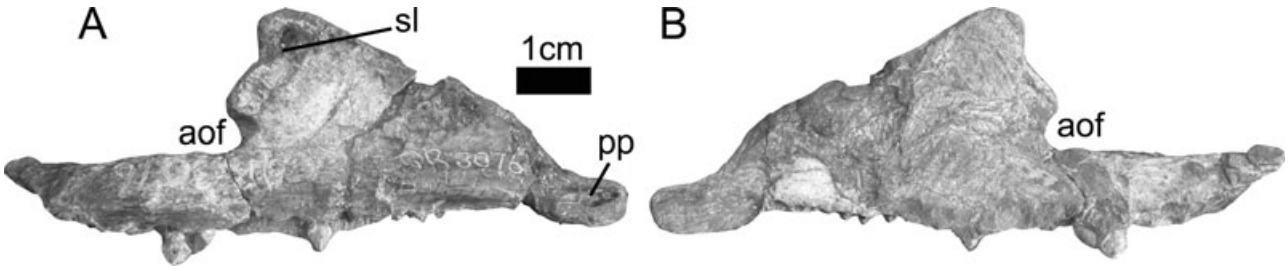

Figure 2. Ornithischia *incertae sedis*. NM QR 3076, left maxilla, medial view (A) and lateral (B) views. Abbreviations: aof, antorbital fossa; pp, premaxillary process; sl, slot in the dorsal process of the maxilla, apparently to receive the lacrimal.

noted that the same tooth morphology is present in an undescribed basal ornithischian from the Upper Elliot Formation; this demonstrates that the tooth morphology of *Fabrosaurus* is shared by more than one taxon, with the consequence that *Fabrosaurus* should be considered a *nomen dubium*. The taxonomic affinities of the specimen (NM QR 3076) used by Knoll to support this supposition are here considered uncertain (see below). However, the same tooth morphology is also recognized in an undescribed new taxon from the Lower Elliot Formation (SAM-PK-K8025) and is very similar to that of other basal ornithischians such as *Scutellosaurus lawleri* (see Colbert, 1981: figs 9, 10; Sereno, 1991: 173–174). This tooth morphology is therefore widespread in basal ornithischians, as first suggested by Charig & Crompton (1974: 167–168). Here I follow most recent authors (Weishampel & Witmer, 1990a; Sereno, 1991; Knoll, 2002a, b; Norman, Witmer & Weishampel, 2004a) in considering *Fabrosaurus australis* to be a *nomen dubium*. *Lesothosaurus diagnosticus* is accepted as the valid binomial for the specimens referred to '*Fabrosaurus*' by Thulborn (1970, 1971a, 1972). Although the holotype of '*Fabrosaurus*' (MNHN LES9) is clearly ornithischian, its phylogenetic position within the clade cannot be determined owing to the fragmentary nature of the specimen and its lack of phylogenetically informative character states; for this reason it should be considered as Ornithischia indet. (Sereno, 1991).

LESOTHOSAURUS DIAGNOSTICUS GALTON, 1978 (FIGS 3A–B, E–F, 4, 24B)

Diagnosis: Lesothosaurus diagnosticus cannot be diagnosed on the basis of autapomorphic features. However, it is distinguishable from all other ornithischians on the basis of a unique combination of primitive and derived character states and should be considered a metataxon (*sensu* Gauthier, 1986), pending further discoveries. This unique character combination comprises: anterior premaxillary foramen present; slot in maxilla for lacrimal present; six premaxillary teeth present; absence of diastema between the premaxillary and maxillary teeth; maxillary teeth lack apicobasally extending ridges on their lingual and labial faces; manual phalanges lacking prominent intercondylar processes; ilium with well-developed supraacetabular flange and ventromedially angling brevis shelf visible in lateral view; dorsal groove on the ischial shaft present; shaft of ischium twists through 90° along its length, forms an elongate symphysis with the opposing ischial blade, and lacks a tab-shaped obturator process; prepubic process short and mediolaterally flattened rather than rodlike and does not extend beyond the end of the preacetabular process of the ilium; postcranial osteoderms absent.

Syntypes: BMNH RUB17, mostly disarticulated remains of at least two individuals, one larger than the other, including most of one articulated skull (Figs 3A–B, 4, 24B; Thulborn, 1970: figs 2–7; Thulborn, 1971a: figs 1–4, 8; Thulborn, 1972: figs 2–12; Galton, 1978: fig. 2; Sereno, 1991: figs 6, 7, 8B–F, 9A–B, E–F); BMNH RUB 23, partial skull (Thulborn, 1970: fig. 1; Thulborn, 1971a: fig. 7).

Referred material: BMNH R11956, partial skull; BMNH R8501, nearly complete, disarticulated skull (Sereno, 1991: fig. 2); BMNH R11004, partially articulated posterior skull and anterior neck, including the braincase, parietals, right squamosal, right quadrate, right posterior lower jaw, axis and third cervical (Sereno, 1991: fig. 8A; SAM-PK-K400, partial postcranium (Santa Luca, 1984: figs 10, 11); SAM-PK-K401, partial postcranium, including proximal ischia (Fig. 3E–F; Santa Luca, 1984: figs 12, 13, 18, 20, 24, 25, 27–32); SAM-PK-K1106, partial postcranium, including proximal ischia (Santa Luca, 1984: figs 1–9, 19, 21–23, 26).

Horizon: All known specimens of *Lesothosaurus* are derived from the Upper Elliot Formation (Lower Jurassic: Hettangian-Sinemurian) of South Africa and Lesotho. Locality details can be found in Thulborn (1970, 1972) and Santa Luca (1984).

Discussion: Sereno (1991: 172) revised the diagnosis of *Lesothosaurus* and suggested six characters as

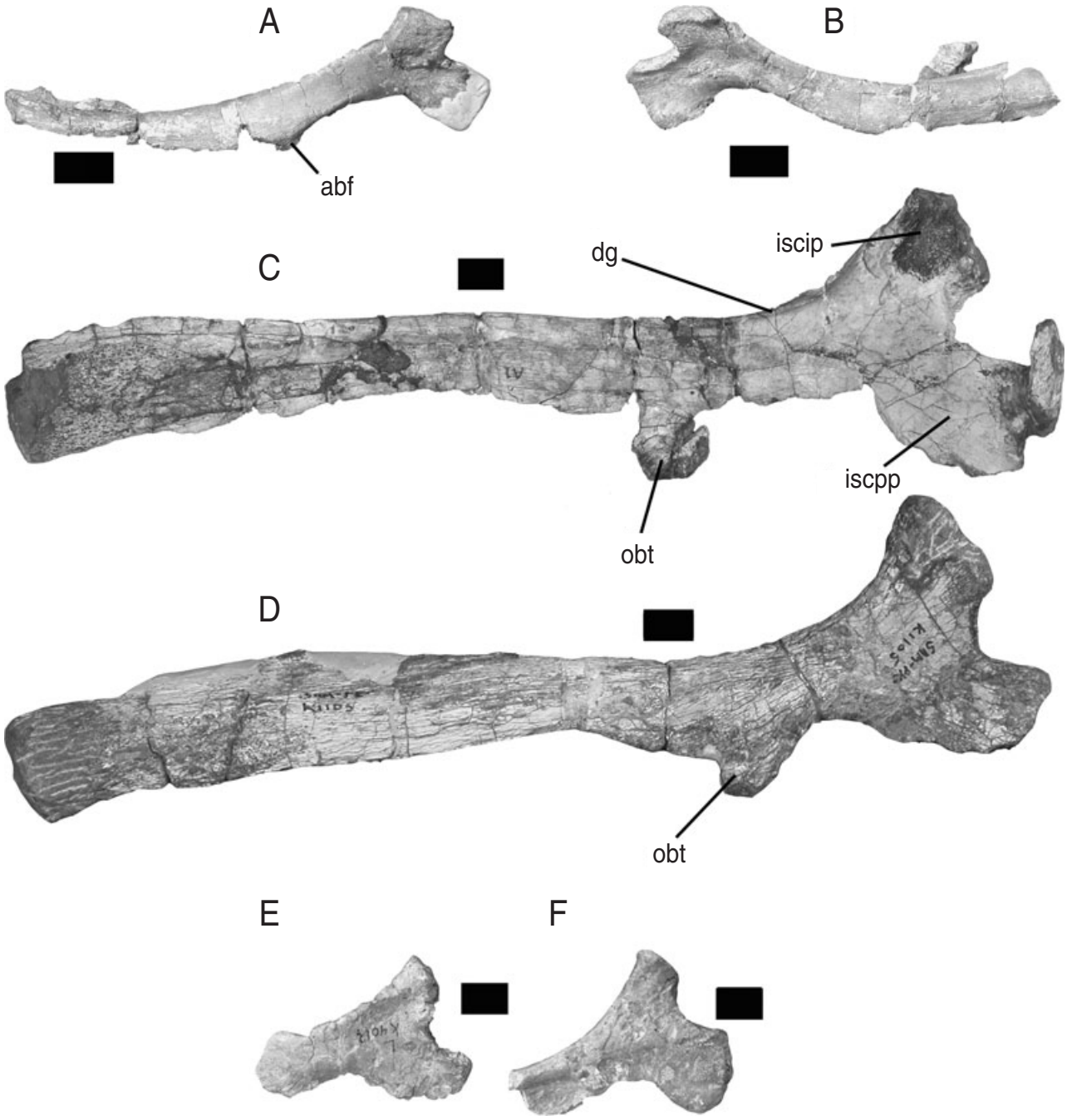

Figure 3. Ischia of Elliot Formation ornithischians. A, B. *Lesothosaurus diagnosticus*, BMNH RUB17 (syntype); left (A) and right (B) ischia in medial views. A tab-shaped obturator process is absent in both specimens. Bone fragments erroneously glued to the ventral margin of the left ischium (abf) create the false impression that an obturator process is present in this specimen. C. ***Stormbergia dangershoeki* gen. et sp. nov.** BMNH R11000 (paratype), right ischium, lateral view. D. SAM-PK-K1105 (holotype), left ischium, medial view. Note the tab-shaped obturator process present in both BMNH R11000 and SAM-PK-K1105. E, F. *Lesothosaurus diagnosticus*, SAM-PK-K401; left (E) and right (F) proximal ischia in medial (E) and lateral (F) views. SAM-PK-K401 was depicted by Santa Luca (1984) and some authors have suggested that it demonstrates an obturator process in *Lesothosaurus*. Note, however, that both ischia are too incomplete to support or deny the presence of an obturator process. All scale bars equal 1 cm. Abbreviations: abf, attached bone fragment; dg, dorsal groove on shaft of ischium; iscip, iliac process; obt, tab-shaped obturator process; iscpp, pubic process.

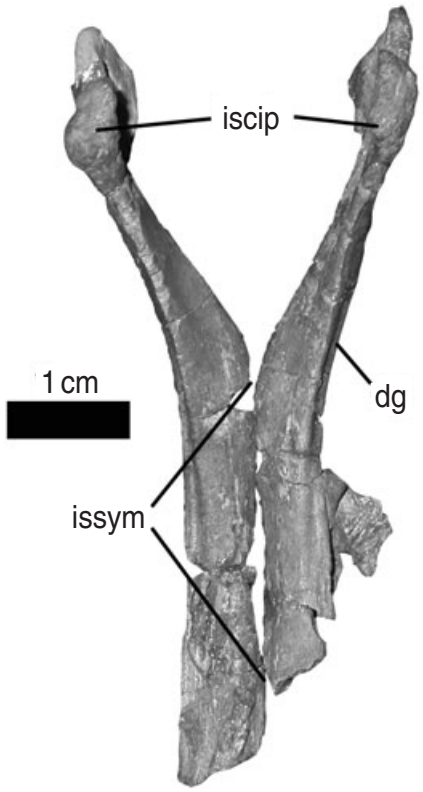

Figure 4. Ischia of *Lesothosaurus diagnosticus* (BMNH RUB17, syntype) in presumed articulation (posterodorsal view). Note the elongate ischial symphysis (issym), the strong torsion of the shaft and the dorsal groove (dg). Abbreviation: iscip, iliac process.

potential autapomorphies, but noted that: 'they may also characterize an undescribed larger ornithischian from the same formation'. Subsequent work and description of new taxa has shown that most of these characters have a more widespread distribution than realized previously (Peng, 1992, 1997; Xu, Wang & You, 2000), and most of them appear to be present in the larger basal ornithischian (described below as *Stormbergia dangershoeki* gen. et sp. nov.) from the same formation. The distribution of the six diagnostic features of *Lesothosaurus* proposed by Sereno (1991) is discussed below:

1. 'Slot in maxilla for lacrimal'. Peng (1997) reported the presence of this feature in *Agilisaurus louderbacki* Peng, 1990; a basal ornithischian from the Middle Jurassic of Sichuan, China. It has also been reported for *Jeholosaurus shangyuanensis* Xu *et al.*, 2000, from the Early Cretaceous of Liaoning (Xu *et al*., 2000: 320). However, the holotype skulls of both *Agilisaurus* (ZDM T6011), and *Jeholosaurus* (IVPP V12529), are preserved in articulation and the nature of the maxilla-lacrimal contact cannot be confirmed (pers. observ.). Knoll (2002a, b) reports the presence of this feature in NM QR 3076, a specimen which he considers to represent a 'large fabrosaurid'. Although the feature does indeed appear to be present (Fig. 2: sl), NM QR 3076 is here considered to be of uncertain affinities (see below). The distribution of this character must thus be considered uncertain at present, and so cannot be confirmed as autapomorphic for *Lesothosaurus*.
2. 'Anterior premaxillary foramen'. Most ornithischians have a premaxillary foramen positioned at the anteroventral corner of the external naris. In *Lesothosaurus* (BMNH RUB17, R8501) a groove passes anteroventrally from the premaxillary foramen to a second foramen which Sereno (1991) termed the anterior premaxillary foramen. This foramen opens into a canal that appears to open onto the premaxillary palate just anterior to the first premaxillary tooth (Sereno, 1991). Knoll (2002a, 2002b) notes that the feature is present in NM QR 3076, but this specimen is here considered to be of uncertain affinities (see below). An anterior premaxillary foramen in an equivalent position is present on the lateral margin of the premaxilla of *Hypsilophodon foxii*, Huxley, 1869 (BMNH R2477) and is connected to the premaxillary foramen by a shallow incised groove. The presence of this foramen was noted by Sereno (1991) who claimed that it opened into an internal cavity of the premaxilla rather than onto the premaxillary palate. However, the anteriormost portion of the premaxilla of BMNH R2477 is damaged and it is not possible to ascertain the position of the canal opening. It seems possible that the anterior premaxillary foramen of *Hypsilophodon* is homologous with that of *Lesothosaurus*. The premaxillae of many basal ornithischians are unknown (e.g. Bonaparte, 1976), or poorly preserved anteriorly (e.g. Colbert, 1981; Haubold, 1991), so this character may have had a wider distribution than previously realized. Although this feature may turn out to be an autapomorphy of *Lesothosaurus*, this cannot be confirmed at present.
3. 'Short forelimb'. The forelimb is highly reduced in *Agilisaurus* (ZDM T6011; Peng, 1992, 1997), *Stormbergia* (SAM-PK-K1105; Table 2) and in an undescribed basal ornithischian from the Upper Triassic Lower Elliot Formation of South Africa (SAM-PK-K8025). This character cannot be considered autapomorphic for *Lesothosaurus*.
4. 'Lateral exposure of brevis surface on the postacetabular process [of the ilium]'. As noted by Sereno (1991: 172) this feature is present in *Scelidosaurus* (BMNH R1111, R6704, see Fig. 24B). It is also seen in *Agilisaurus* (Peng, 1992: fig. 5; Peng, 1997; ZDM

Table 2. Measurements of principal specimens discussed in the text. For SAM-PK-K1105 measurements of left (L), and right (R), elements are provided where present. BMNH RUB17 is an assemblage containing a larger (LI) and a smaller (SI) individual (Thulborn, 1972); measurements are included for both where possible

	SAM-PK-K1105 (***Stormbergia*** holotype)	BMNH R11000 (***Stormbergia*** paratype)	BP/1/4885 (***Stormbergia*** referred)	SAM-PK-1107 (cf. ***Stormbergia***)	BMNH RUB17 (*Lesothosaurus* syntype)
Scapula					
Length		173		+143	73 (LI); 66 (SI)
Max. proximal expansion		73		61	
Max. distal expansion		64			+23 (LI)
Min. shaft width		20		18.5	9.5 (LI)
Coracoid					
Max. length	41 (L); 40 (R)	53		45.5	
Max. height	+45 (L); +43 (R)	73		65	
Humerus					
Length				98	66 (LI); 58 (SI)
Max. proximal expansion				41	19 (LI)
Max. distal expansion				20	15 (LI)
Radius					
Length	65				37 (SI)
Ulna					
Length	69				40 (SI)
Ilium					
Length		198	114		+78.8 (SI)
Preacetabular process, length		76			31.2 (SI)
Postacetabular process, length		62			+18 (SI)
Ischium					
Length	199	217			+78.1 (SI)
Distance to end of base of obturator process	70	74			–
Pubis					
Length	232				+111.8 (SI)
Femur					
Length	202		147	193	103 (SI)
Distance to end of fourth trochanter	92			83.5	45 (SI)
Tibia					
Length	238 (L); 236 (R)				129 (SI)
Max. proximal expansion	68 (L); 64.5 (R)		38		29.5 (SI)
Max. distal expansion	65 (L); 61 (R)	64			23.5 (SI)
Metatarsals					
MT1, length	56 (R)				30 (SI)
MT2, length	92.5 (L); 97 (R)				58 (SI)
MT3, length	111 (L); 114 (R)				67 (SI)
MT4, length	97 (L)				56 (SI)

T6011), *Stormbergia* (BMNH R11000, see Fig. 13) and in the undescribed Lower Elliot Formation taxon (SAM-PK-K8025). Indeed, this feature appears to be plesiomorphic for Ornithischia as a whole (Knoll, 2002a, b).

5. 'Dorsal groove on the ischial shaft'. This feature is present in *Agilisaurus* (Peng, 1997; ZDM T6011), in the undescribed Lower Elliot Formation taxon (SAM-PK-K8025), and weakly present in some individuals of *Stormbergia* (BMNH R11000, Fig. 3C; Knoll 2002a, b), although apparently not in others (SAM-PK-K1105, Fig. 3D). Therefore, this feature cannot be considered autapomorphic for *Lesothosaurus diagnosticus*.

6. 'Pedal digit 1 reduced'. The reduction of pedal digit 1 occurs widely in basal ornithischians including *Agilisaurus* (Peng, 1992: fig. 6C; ZDM T6011), *Othnielia rex* Galton, 1977 (Galton & Jensen, 1973: fig. 6D, *'Yandusaurus' multidens* (He & Cai, 1984: fig. 20C; ZDM T6001) and *Jeholosaurus* (Xu *et al*., 2000; IVPP V12529) and also occurs in *Stormbergia* (SAM-PK-K1105, see Fig. 17B). This feature cannot be considered autapomorphic for *Lesothosaurus diagnosticus*.

In addition, Norman *et al*. (2004a) suggest that *Lesothosaurus* is characterized by: a prominent crested obturator process on the ischium, and metatarsal V was either absent or 'strongly reduced'. However, as argued below, a true tab-shaped obturator process is absent in *Lesothosaurus* (BMNH RUB17, Figs 3A–B, 4). The distinct ventral corner that occurs in a similar position on the ischium is not unique to *Lesothosaurus*, but is present in the undescribed Lower Elliot Formation ornithischian (SAM-PK-K8025) and may be present in the basal thyreophoran *Scutellosaurus lawleri* (UCMP 130580: Rosenbaum & Padian, 2000: figs 2, 4) and the basal genasaurian *Agilisaurus* (ZDM T6011; pers. observ.). The apparent complete loss of metatarsal V is also seen in *Stormbergia* (SAM-PK-K1105, see Fig. 17B). In many other basal ornithischians such as *Agilisaurus* (Peng, 1992: fig. 6) and *Othnielia* (Galton & Jensen, 1973: fig. 6A) metatarsal V is extremely reduced.

Consequently, *Lesothosaurus diagnosticus* is difficult to diagnose on the basis of autapomorphies. However, the syntype specimens BMNH RUB17 and BMNH RUB23 can be differentiated from all other known basal ornithischians; including: *Pisanosaurus mertii* Casamiquela, 1967 from the Late Triassic of Argentina (Bonaparte, 1976; Sereno, 1991); an undescribed basal ornithischian from the Late Triassic of South Africa (SAM-PK-K8025); *Stormbergia dangerhoeki* gen. et sp. nov. and the heterodontosaurids *Heterodontosaurus tucki* (Santa Luca, 1980) and *Abrictosaurus consors* (Thulborn, 1974), all of which are from the Lower Jurassic of South Africa; the basal thyreophoran *Scutellosaurus lawleri* from the Lower Jurassic of Arizona (Colbert, 1981; Rosenbaum & Padian, 2000); and *Agilisaurus louderbacki* and *'Yandusaurus' multidens*, both from the Middle Jurassic of China (He & Cai, 1984; Peng, 1992, 1997).

Pisanosaurus mertii is known from a single fragmentary skeleton, collected from the Ischigualasto Formation (Carnian) of Argentina, and has been considered the basalmost known ornithischian (Sereno, 1991). There is some doubt as to whether the elements which comprise the partial skeleton belong together, or whether the taxon is a composite (Sereno, 1991). Nearly all elements show substantial differences from *Lesothosaurus*. The preserved cranial elements demonstrate features apparently derived with respect to *Lesothosaurus*, in particular the presence of well-developed wear facets on the teeth. Postcranially, however, *Pisanosaurus* appears very primitive, possibly lacking a prepubic process, and with a poorly developed lateral expansion of the distal tibia (Bonaparte, 1976; Sereno, 1991).

A single ornithischian specimen (SAM-PK-K8025) known from the Late Triassic Lower Elliot Formation of South Africa appears to represent a new taxon of basal ornithischian (R. J. Butler & R. M. H. Smith, unpubl. data) and can be distinguished from *Lesothosaurus* by several features, including the retention of a relatively large manus, the phalanges of which have prominent proximal intercondylar processes and distinct dorsal pits on their distal ends. These features are absent in *Lesothosaurus* (BMNH RUB17; Sereno, 1991, fig. 8B).

The anatomical features which distinguish *Lesothosaurus* from *Stormbergia dangerhoeki* gen. et sp. nov. are discussed below.

Heterodontosaurus tucki, *Abrictosaurus consors*, *Echinodon becklesii* (Norman & Barrett, 2002) and undescribed taxa from the Lower Jurassic Kayenta Formation of Arizona (P. C. Sereno, pers. comm., 2004) and the Upper Jurassic Morrison Formation of Colorado (P. M. Galton, pers. comm., 2004), apparently form a clade of heterodontosaurids (Weishampel & Witmer, 1990b; R. J. Butler, unpubl. data), which can be distinguished from *Lesothosaurus* by a large number of derived features. These include: premaxillary tooth count reduced to three or less, arched diastema present between premaxilla and maxilla, wedge-shaped predentary present, supraacetabular flange of the ilium absent, brevis shelf reduced and horizontal.

Scutellosaurus lawleri, a primitive thyreophoran known from numerous partial skeletons (Colbert, 1981; Rosenbaum & Padian, 2000; MCZ unpubl. material) from the Kayenta Formation of Arizona, is plesiomorphic in most of its features, and no autapomorphies appear to be present (although it can be diagnosed using a combination of primitive and derived characters). Its anatomy is therefore very similar to that of *Lesothosaurus*, but it can clearly be distinguished from the latter by the presence of postcranial osteoderms. As yet, no ornithischian osteoderms have been found in the Elliot Formation.

Agilisaurus louderbacki is known from an articulated and nearly complete skeleton (ZDM T6011) from the Lower Shaximiao Formation (Middle Jurassic) of Dashanpu, Sichuan Province, China. Although *Agilisaurus* has been considered by some authors as a basal ornithopod (Sues & Norman, 1990; Weishampel & Heinrich, 1992; Weishampel *et al*., 2003), it is apparently a more basal ornithischian

(Barrett, Butler & Knoll, in press) with numerous similarities (e.g. the presence of a groove on the ischium, shortened forelimb and reduced pedal digit one) to *Lesothosaurus* (Peng, 1997). However, these similarities are probably plesiomorphic as *Agilisaurus* has a large number of derived features absent in *Lesothosaurus*. These include: premaxillary tooth count reduced to five, prepubic process elongated, reaching almost to the end of the preacetabular process of the ilium (ZDM T6011; Peng, 1997), and a tab-shaped obturator process on the ischium (Peng, 1992, 1997). *Agilisaurus* additionally has a number of unusual, autapomorphic, features which are absent in *Lesothosaurus* (pers. observ. of ZDM T6011; Barrett *et al.*, in press), including the presence of a strongly heterodont dentary dentition and a palpebral bone which traverses the entire width of the orbit.

The alpha-level taxonomy of the genus *Yandusaurus* is currently unstable. Barrett *et al*. (in press) consider the species '*Yandusaurus' multidens* to be generically distinct from the genus *Yandusaurus* and the genus *Agilisaurus*. This conclusion is followed herein, with '*Yandusaurus' multidens* being represented by the holotype (ZDM T6001) and paratype (ZDM T6002) specimens, which are both from the same locality as the holotype of *Agilisaurus louderbacki* (see above). '*Y' multidens* retains numerous ornithischian plesiomorphies (ZDM T6001; He & Cai, 1984) but has a large number of derived features which clearly distinguish it from *Lesothosaurus*, including the presence of some apico-basally extending ridges on the maxillary crowns (ZDM T6001), the absence of a supraacetabular flange on the ilium, a horizontal, rather than ventromedially angling, brevis shelf (ZDM T6001, pers. observ.), and a prepubic process which is elongate and rod-shaped, and extends beyond the anterior end of the preacetabular process (He & Cai, 1984: fig. 17A).

STORMBERGIA DANGERSHOEKI GEN. ET SP. NOV.
(FIGS 3C–D, 5, 7–19)

Etymology: Genus name refers to the Stormberg Group of South Africa and Lesotho, the rock sequence that has provided so much information on early dinosaurs. Species epithet refers to the locality from which the holotype (SAM-PK-K1105) was collected.

Diagnosis: A relatively large (around 2 m length) basal ornithischian, lacking unambiguous autapomorphies but distinguished by a unique combination of character states, not seen in other basal ornithischians, including: ilium with a robust, elongate, pubic peduncle, well-developed supra-acetabular flange and ventromedially angling brevis shelf; acetabulum partially closed medially by a ventral flange of the ilium; ischial symphysis present distally only; ischium with an essentially untwisted shaft and a well-developed, proximal tab-shaped obturator process; prepubic process short and mediolaterally flattened.

Holotype: SAM-PK-K1105 (Figs 3D, 7, 8C–G, 9C–D, 11, 12, 14–17, 19), a partial postcranial skeleton, including the axial neural arch, cervical neural arches and centra, dorsal neural arches and centra, two sacral neural arches and sacral ribs, caudal vertebrae, coracoids, fragmentary humeri, left radius and ulna, left ischium, proximal right ischium, pubes, femora, tibiae, tarsals and metatarsals, numerous disarticulated phalangeal elements. Collected from Dangershoek Farm, Herschel District, eastern Cape Province, Republic of South Africa by C. E. Gow. This specimen was previously on loan to the Museum of Comparative Zoology, Harvard, and has been referred to by Knoll (2002a: 601; 2002b: 242).

Paratype: BMNH R11000 (Figs 3C, 8A–B, 9A–B, 10, 13, 18), partial postcranial skeleton, including a dorsal neural arch, complete proximal caudal vertebra, right scapulocoracoid, left ilium, right ischium, proximal left femur, distal left tibia and partial right fibula. This specimen was collected from Pokane, Lesotho by a 1966–67 British Museum/University of London expedition team, and has been referred to by Knoll (2002a: 601; 2002b: 242).

Referred specimen: BP/1/4885 (Fig. 5), in part, collected from Mequatling, Clocolon District, Free State Province by L. Huma in 1980. This specimen number includes portions of several different taxa (including the synapsid *Tritylodon*), but an articulated portion is here considered to represent a juvenile individual of *Stormbergia* and was referred to by Knoll (2002a: 601; 2002b: 242) as an individual of *Lesothosaurus diagnosticus*.

Horizon: All known specimens are from the 'Red Beds' of the Upper Elliot Formation (Lower Jurassic: Hettangian–Sinemurian).

Discussion: As noted by Knoll (2002a: 601), the specimens here referred to *Stormbergia* are very similar in morphology to the syntype (BMNH RUB17) and referred material of *Lesothosaurus diagnosticus*. Indeed, Knoll (2002a) has speculated that *Stormbergia* may represent adults of *Lesothosaurus diagnosticus*, implying that the *Lesothosaurus* syntypes and referred material represent juveniles. The subadult status of the *Lesothosaurus* material may be supported by the lack of neurocentral fusion in the vertebral column and lack of sacral fusion (however, fusion is also absent in the individuals referred here to *Stormbergia* and may be a persistent feature of basal ornithischians).

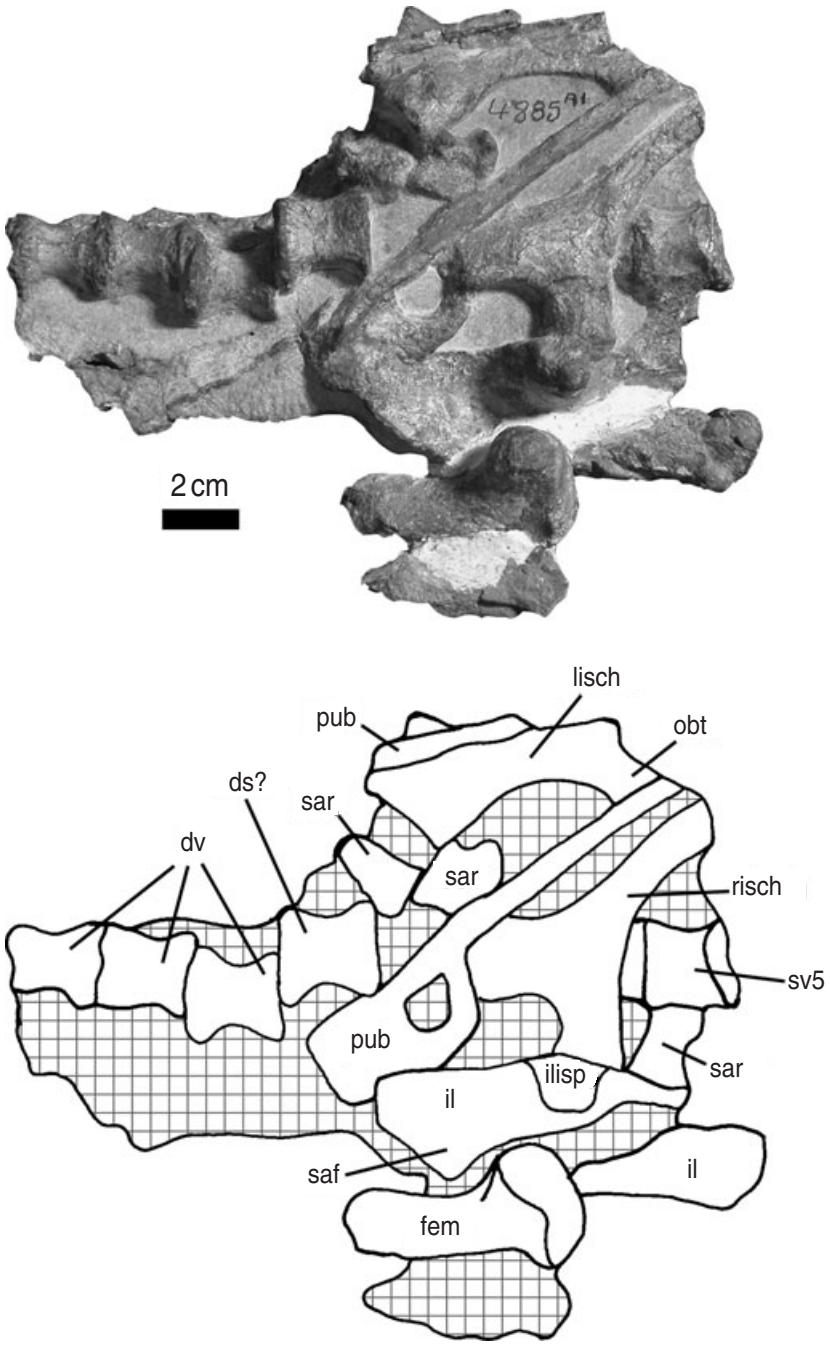

Figure 5. ***Stormbergia dangershoeki*** **gen. et sp. nov.** BP/1/4885 (referred specimen), sacral block in ventral view. Note the presence of a tab-shaped obturator process, as in SAM-PK-K1105 and BMNH R11000. Abbreviations: ds, dorsosacral vertebra; dv, dorsal vertebra; il, ilium; ilisp, ischiadic peduncle of the ilium; fem, femur; lisch, left ischium; obt, tab-shaped obturator process; pub, pubis; risch, right ischium; saf, supraacetabular flange; sar, sacral rib; sv5, posteriormost sacral vertebrae.

The form of the ischium clearly distinguishes *Stormbergia* from *Lesothosaurus* (Figs 3–5). The ischium of *Stormbergia* has a very well-defined, tab-shaped obturator process (BMNH R11000, Fig. 3C; SAM-PK-K1105, Fig. 3D; BP/1/4885, Fig. 5), similar to that seen in more derived ornithischians traditionally referred to Ornithopoda (e.g. Galton, 1974a). The presence or absence of an obturator process in *Lesothosaurus* has been much debated (Sereno, 1986, 1991; Thulborn, 1992; Knoll, 2002a, b). In an undescribed

new ornithischian from the Lower Elliot Formation (SAM-PK-K8025) the well-preserved proximal ischia show that a tab-shaped obturator process was definitely absent. Rather, the shaft is strongly twisted such that the medial surface turns to face dorsally, and its ventral or anterior surface (which actually is directed medially due to the torsion of the shaft) curves to form a distinct corner. The ischia of *Lesothosaurus* (BMNH RUB17, Figs 3A–B, 4) are very similar, also showing this strong torsion, the distinct corner ('prominent angle' of Sereno, 1991) and lacking development of a tab-shaped obturator process (Sereno, 1991; pers. observ.). The suggestion that an obturator process was present in *Lesothosaurus* (Thulborn, 1972) is based upon the left ischium of BMNH RUB17 (Figs 3A, 4), which is damaged along its ventral surface. As noted by Sereno (1991), two fragments glued to this damaged ventral margin have been misidentified as the obturator process (see: Fig. 3A). The more complete right ischium clearly lacks this 'process' (Fig. 3B; Sereno, 1991).

The strong torsion of the ischial shaft and the development of a distinct anteroventral corner to the shaft appear to be linked to the presence of an elongate ischial symphysis in *Lesothosaurus* (Fig. 4). The anteroventral corner marks the most proximal extension of this symphysis, which would have extended for at least 50% of the length of the ischium (Fig. 4). Sereno (1986) suggested that an ischial symphysis restricted to the distal end of the ischia was a synapomorphy of ornithischians; however, an elongate ischial symphysis appears to be retained in a number of basal ornithischians, including *Lesothosaurus*, an undescribed basal ornithischian from the Lower Elliot Formation (SAM-PK-K8025), *Agilisaurus louderbacki* (ZDM T6011; pers. observ.) and possibly *Scutellosaurus lawleri* (UCMP 130580: Rosenbaum & Padian, 2000: figs 2, 4). By contrast, the ischial symphysis of *Stormbergia* (SAM-PK-K1105, BMNH R11000) was present distally only, and the ischial shaft undergoes little torsion along its length. The loss of an elongate ischial symphysis is a derived state shared with most other ornithischians.

None of the specimens (SAM-PK-K401, Fig. 3E–F; SAM-PK-K1106) described by Santa Luca (1984: figs 18, 19) have the distal portions of their ischia preserved or exposed, and so do not demonstrate a tab-shaped obturator process, but appear instead to be very similar in morphology to the ischia of BMNH RUB17 (*contra* Norman *et al*., 2004a: 331).

Knoll (2002b) has suggested that 'the specimen BPI 4885 [sic] pleads for the presence of an obturator process in *Lesothosaurus diagnosticus*'. This specimen number (correctly BP/1/4885) includes a large amount of material, much unprepared, which includes some definite ornithischian material, plentiful material of the synapsid *Tritylodon* and possible saurischian dinosaurs. The clearly associated, articulated ornithischian material includes a series of posterior dorsals, sacrals and anterior caudals, pelves and partial hindlimbs (Fig. 5). The length of the ilia and femora indicate that, although this is a relatively small individual, this material is of a slightly larger animal than the syntypes of *Lesothosaurus* (BMNH RUB17, RUB23). A number of features of this material suggest immaturity: although usually closely articulated the neurocentral sutures are not fused, the sacral and caudal ribs are separate and the sacral vertebrae are not fused (but as noted above, lack of vertebral fusion may be a persistent feature of basal ornithischians).

The ischium of BP/1/4885 clearly has a well-defined, tab-like obturator process (Fig. 5), which is comparable to that of SAM-PK-K1105 and BMNH R11000; this process is not seen in *Lesothosaurus* (Figs 3A–B, 4; see above). Although Knoll (2002a, b) considered BP/1/4885 to be an individual of *Lesothosaurus*, no characters (other than perhaps the relatively small size) support this referral. With the exception of the obturator process, the rest of the preserved material is morphologically indistinguishable from both *Lesothosaurus* and *Stormbergia*. Thus, BP/1/4885 cannot be used to infer the presence of an obturator process in *Lesothosaurus diagnosticus*; the only specimen that can legitimately be used for that purpose is the syntype BMNH RUB17, and this specimen (as noted above) demonstrates that an ornithopod-like obturator process is clearly absent. The ornithischian material in BP/1/4885 is here considered to represent a juvenile individual of *Stormbergia* based upon the presence of the tab-shaped obturator process.

BP/1/4885 further supports the hypothesis that the *Lesothosaurus diagnosticus* syntypes (BMNH RUB17, RUB23) are not juveniles of *Stormbergia*: a well-formed obturator process is seen in an individual that is only 20% larger than BMNH RUB17. Evidence from a growth series of *Hypsilophodon* (BMNH R195, R193, R5830) suggests that the obturator is fully formed in relatively young individuals and does not change significantly during ontogeny.

The features that distinguish *Stormbergia* from *Lesothosaurus* are not autapomorphies. A tab-shaped obturator process is seen in some basal ornithischians (e.g. *Agilisaurus,* Peng, 1997; '*Y.*' *multidens,* He & Cai, 1984) and ornithopods (e.g. *Hypsilophodon*, Galton, 1974a), while the loss of an elongate ischial symphysis characterizes nearly all ornithischians. However, a combination of plesiomorphic and derived features allow *Stormbergia* to be distinguished from all other basal ornithischians, as in *Lesothosaurus*.

Several derived postcranial features are present which distinguish *Stormbergia* from *Pisanosaurus*. These include the presence of an opisthopubic pubis,

development of a prepubic process, and the well-developed lateral flange of the distal tibia, all of which are absent in *Pisanosaurus* (Sereno, 1991). The presence of an untwisted ischial shaft, with a well-developed, tab-shaped obturator process, distinguishes *Stormbergia* from an undescribed basal ornithischian from the Late Triassic Lower Elliot Formation of South Africa (SAM-PK-K8025). Although cranial material of *Stormbergia* is unknown, postcranial anatomy distinguishes *Stormbergia* from the heterodontosaurs *Heterodontosaurus* and *Abrictosaurus*. Both these taxa have the derived conditions of a horizontal (and greatly reduced) brevis shelf, a fully open acetabulum and the absence of a supraacetabular flange. Additionally, a tab-shaped obturator process is absent from the ischium of *Heterodontosaurus*. Finally, *Stormbergia* can be distinguished from *Agilisaurus* and '*Y.*' *multidens* by the retention of an elongate pubic peduncle of the ilium and a short prepubic process of the pubis, and additionally from '*Y.*' *multidens* by the retention of a supraacetabular flange and ventromedially angling brevis shelf on the ilium.

CF. *STORMBERGIA*

SAM-PK-K1107

A partial postcranial skeleton of a basal ornithischian, SAM-PK-K1107 (Figs 20–23), was collected from the same site as the holotype of *Stormbergia* (SAM-PK-K1105) by AW Crompton. It appears to represent an individual of roughly the same size as SAM-PK-K1105, based on the length of the femur (Table 2). The large size of this specimen, and the presence of features (particularly of the humerus) that clearly distinguish it from *Lesothosaurus* (see below), suggest that SAM-PK-K1107 may be referable to *Stormbergia*. However, referral of SAM-PK-K1107 is complicated by the lack of overlap of diagnostic elements between it and the holotype (SAM-PK-K1105) and paratype (BMNH R11000) specimens of *Stormbergia*. For example, an ischium is unknown in SAM-PK-K1107. The humerus of SAM-PK-K1107 is distinctive (Fig. 23), yet is poorly known in SAM-PK-K1105 and BMNH R11000.

For these reasons, I do not herein refer SAM-PK-K1107 to *Stormbergia*, although further discoveries of Upper Elliot Formation ornithischians may allow that referral. The anatomy of SAM-PK-K1107 is described separately below.

CF. *STORMBERGIA* & *LESOTHOSAURUS*

NM QR 3076

NM QR 3076 (Figs 2, 6) was collected at Spitskop Farm, Jamestown, Eastern Cape by J. Welman in 1989 and referred to by Knoll (2002a: 601; 2002b: 242) as a 'large fabrosaurid'. This specimen is mostly preserved semiarticulated on a bedding plane and includes a partial, disarticulated skull and postcranial material, some of which is articulated (Fig. 6). A small amount of isolated material is also catalogued under this specimen number, but some of this clearly represents a basal sauropodomorph, and at least some of the remainder pertains to a second ornithischian individual. This isolated material includes a maxilla (Fig. 2) mentioned by Knoll (2002a: 601; 2002b: 242).

The specimen is much larger than any known specimens of *Lesothosaurus*, and it was probably this large size that led Knoll (2002a: 601; 2002b: 242) to consider NM QR 3076 to be at least specifically distinct. Body size is an insufficient criterion for taxonomic distinction however, and so referral of this material to either *Stormbergia* or *Lesothosaurus* must be based upon anatomical comparison.

An isolated partial ischium is preserved in NM QR 3076, but it is unclear whether this ischium is associated with the semiarticulated ornithischian specimen preserved on the bedding plane. The ischium is poorly preserved and not fully prepared. Its ventral margin is damaged and it is unclear whether or not a tab-shaped obturator process was present. The torsion of the shaft is relatively minor, which is similar to the situation in *Stormbergia*. The rest of the preserved postcranial material shows equal similarity to material of both *Stormbergia* and *Lesothosaurus*.

The partial skull of NM QR 3076 is crushed, but includes a premaxilla, quadrate, prefrontal, palpebral and partial mandible. As noted by Knoll (2002a: 601; 2002b: 242) the premaxilla appears to have an anterior premaxillary foramen (suggested by Sereno (1991: 172) to be an autapomorphy of *Lesothosaurus*). However, the skull of *Stormbergia* is unknown, and, as noted above, the distribution of this feature may be wider than previously realized. Knoll (2002a: 601; 2002b: 242) also noted that an isolated maxilla in NM QR 3076 apparently has a notch for the lacrimal (Fig. 2: sl), a feature also suggested to be an autapomorphy of *Lesothosaurus* (Sereno, 1991: 172). The association of the isolated maxilla with the partially articulated skeleton of NM QR 3076 is uncertain, and a notch for the lacrimal may be present in a variety of basal ornithischians (see above).

Referral of NM QR 3076 to either *Stormbergia* or *Lesothosaurus* cannot be justified, and the specimen is best considered as Ornithischia *incertae sedis*, pending further preparation and study.

Other specimens

Several specimens previously referred to *Lesothosaurus diagnosticus* cannot be assigned to either *Lesothosaurus* or *Stormbergia* with certainty. Knoll (2002a,

Figure 6. Ornithischia *incertae sedis.* NM QR 3076, semiarticulated specimen, as preserved on bedding plane. Abbreviations: ast, astragalus; ax, axis; calc, calcaneum; cv, cervical vertebra; dcav, distal caudal vertebrae; dv, dorsal vertebrae; fem, femur; il, ilium; md, posterior portion of mandible; mts, metatarsals; pal, palpebral; pcav, proximal caudal vertebra; ph, phalanges; pm, premaxilla; pub, pubis; qd, quadrate; ra, radius; scap, scapula; tib, tibia; ul, ulna.

2002b) described two ornithischian skulls (MNHN LES 17, LES 18) from the Elliot Formation as *Lesothosaurus* sp. He listed minor differences between these skulls and described *Lesothosaurus* material (BMNH RUB 17, RUB 23, R11956, R8501) and noted the larger size of MNHN LES17 and LES18. However, until cranial material of *Stormbergia* is identified, the taxonomic position of these skulls is uncertain, especially as *Lesothosaurus diagnosticus* lacks cranial autapomorphies. The same conclusion applies to the

fragmentary postcranial material (MNHN IG 21–30) described by Knoll & Battail (2001).

Sereno (1991) referred BMNH R11002 (a right ilium) and BMNH R11003 (a left ilium) to *Lesothosaurus diagnosticus*, but such fragmentary material cannot be referred to either *Lesothosaurus* or *Stormbergia*. In fact, BMNH R11003 may represent a heterodontosaur ilium, as it lacks a well-developed acetabular flange and has a narrow and horizontal brevis shelf, retains an elongate pubic peduncle and has a sinuous dorsal margin. This combination of features is shared with the ilia of *Heterodontosaurus tucki* (SAM-PK-K1332) and *Abrictosaurus consors* (BMNH RUB 54), both from the Upper Elliot Formation. Knoll & Battail (2001: 418) list several 'fabrosaurid' specimens that have not been discussed here; most of these specimens are extremely fragmentary and possess no character states that would permit their referral to *Lesothosaurus*, *Stormbergia* or any other established taxon.

ANATOMICAL DESCRIPTION OF *STORMBERGIA DANGERSHOEKI* GEN. ET SP. NOV.

AXIAL SKELETON

The axial skeleton (Figs 7–9) is poorly represented in specimens of *Stormbergia*, and only a brief description can be provided. The dorsal and sacral regions are well preserved in SAM-PK-K1107, which may be referable to *Stormbergia*, and this specimen is described in detail below.

The axis of SAM-PK-K1105 (Fig. 7A) is represented by the neural arch only, which has a similar morphology to that of *Lesothosaurus* (BMNH R11004; Sereno 1991: fig. 8), with a deep neural canal. The neural spine is mediolaterally compressed except at its posterior margin where it flares laterally. The prezygapophyses are not preserved, while the poorly preserved postzygapophyses face ventrolaterally.

In SAM-PK-K1105 four fragmentary neural arches and two centra pertain to the anterior of the cervical region. Two of the neural arches are very fragmentary (lacking the pre- and postzygapophyses and neural spine) and will not be described further. The remaining neural arches (Fig. 7B–C) show that the neural canal is deep. Prezygapophyses are elongate and face dorsomedially at about 30° to the horizontal; postzygapophyses are longer and face ventrolaterally at a similar angle. The diapophysis, although well-defined as a lateral process, remains short and relatively low on the neural arch. The neural spine is not preserved.

The cervical centra have an asymmetrical shape, with the articular faces of the centra offset with respect to each other, strongly pinched flanks and a ventral keel. The parapophysis is situated on the anterior margin of the centrum. Two other isolated centra are probably situated close to the cervical–dorsal transition; although much more spool-like, they retain a moderate ventral keel and a slight asymmetry. As a consequence of erosion, the position of the parapophysis cannot be confirmed and thus these isolated centra may represent either anterior dorsals or posterior cervicals.

A single dorsal neural arch is preserved in BMNH R11000 (Fig. 8A–B). SAM-PK-K1105 preserves four dorsal neural arches (Fig. 8C) and nine centra (Fig. 8D–E), but the preservation of the arches is invariably poor. BP/1/4885 preserves the posterior three dorsals (Fig. 5), but they are poorly exposed. The dorsal neural arch of BMNH R11000 (Fig. 8A–B) bears short, stout, slightly dorsally inclined transverse processes. The parapophyses are situated at the anterior base of the processes, while the diapophyses are located at the tips of the processes. The neural spine is low and posteriorly inclined. Zygapophyses are inclined at a low angle (about 20 °) to the horizon-

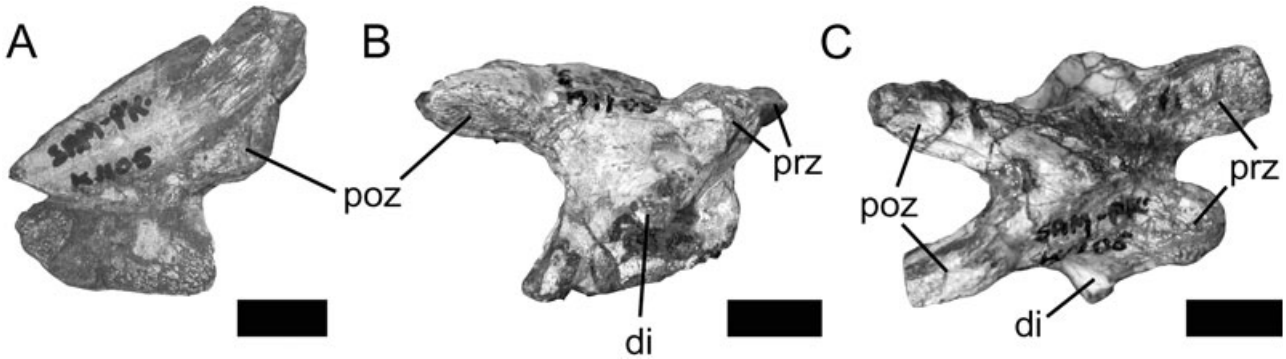

Figure 7. *Stormbergia dangershoeki* gen. et sp. nov. SAM-PK-K1105 (holotype): axial neural arch, left lateral view (A); anterior cervical neural arch in right lateral (B) and dorsal (C) views. All scale bars equal 1 cm. Abbreviations: di, diapophysis; poz, postzygapophyses; prz, prezygapophyes.

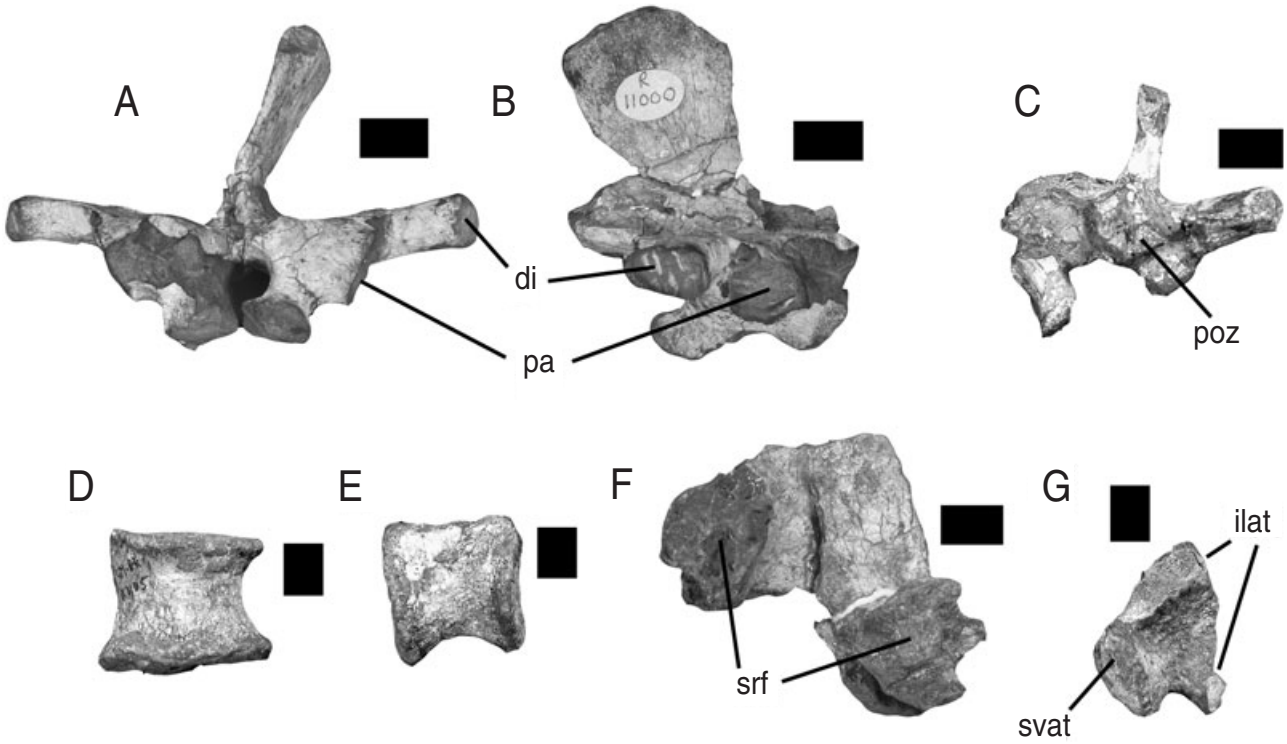

Figure 8. ***Stormbergia dangershoeki*** **gen. et sp. nov.** BMNH R11000 (paratype), mid-dorsal neural arch in anterior (A) and right lateral (B) views. SAM-PK-K1105 (holotype): mid-dorsal neural arch, posterior view (C); dorsal centrum in ventral (D) and lateral (E) views; sacral neural arches in lateral view (F); unidentified sacral rib, from right side of sacrum, in?anterior view (G). Abbreviations: di, diapophysis; ilat, articulation surface for the ilium; pa, parapophysis; poz, postzygapophyses; srf, facet for sacral rib; svat, articulation surface for sacral vertebra.

tal. Little can be noted about the dorsal centra (Fig. 8D–E): they are typically spool-like with flat to slightly concave articular faces.

SAM-PK-K1105 preserves only two sacral neural arches (Fig. 8F) and four isolated sacral ribs (Fig. 8G). The sacral neural arches have large and spacious neural canals, anteroposteriorly expanded neural spines and abbreviated transverse processes, which end in large, ventrolaterally facing facets for the sacral ribs. BP/1/4885 (Fig. 5) preserves the sacral region, but the vertebrae are unfused to each other, and to their neural arches and sacral ribs. At least four, and possibly five, sacrals are present, but they are poorly exposed and yield little information. The first sacral rib attached to the base of the preacetabualar process of the ilium, the second attached to the ilium medial to the pubic peduncle, while the third and fourth sacral ribs attached to the medial surface of the brevis shelf. This corresponds with the pattern of sacral rib scars on the ilium of *Lesothosaurus* (Sereno, 1991: fig. 9C; BMNH RUB17) as well as with the sacrum of SAM-PK-K1107 (see Fig. 22).

Two of the isolated sacral ribs of SAM-PK-K1105 (Fig. 8F) are mirror images of one another and thus form the ribs for a single sacral vertebra (probably the third or fourth). Three of the ribs have flanges of bone developed either posteriorly or anteriorly – these would probably have attached to adjacent sacral ribs. The single sacral rib that lacks such a flange probably belonged to the posteriormost sacral (by comparison with the sacrum of SAM-PK-K1107: see below).

BMNH R11000 preserves a single proximal caudal (Fig. 9A–B). BP/1/4885 preserves caudals 1–3, and several damaged caudals are known for SAM-PK-K1105 (Fig. 9C–D). The anterior caudals of *Stormbergia* are typical of basal ornithischians (Fig. 9A–B; cf. Galton, 1974a: fig. 28A). They have elongate, horizontally orientated, slender caudal ribs, the length of which is approximately equal to the height of the neural spine. Anterior and posterior facets chevron facets first appear on caudal 3 (BP/1/4885) and the first chevron would have articulated between caudals 3 and 4. The posterior chevron facet is inclined much more steeply ventrally than the anterior. Proximal caudal centra are anteroposteriorly short with extensively excavated sides and a ventral keel. Their near-circular faces are slightly concave. Zygapophyses are inclined at a high angle to the horizontal. The tall neural spine

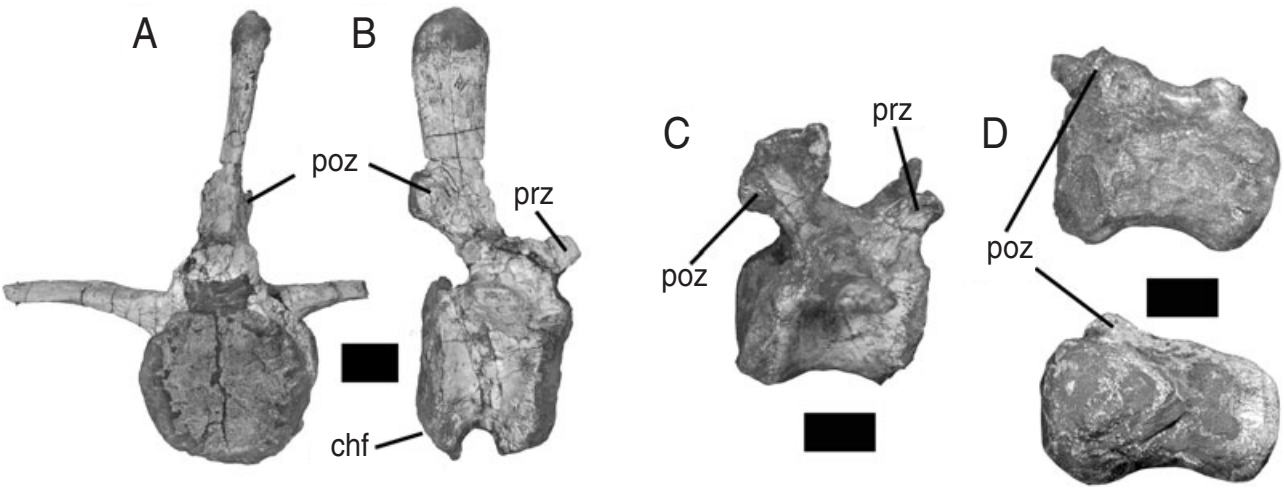

Figure 9. ***Stormbergia dangershoeki*** **gen. et sp. nov.** BMNH R11000 (paratype), anterior caudal in right lateral (A) and anterior (B) views. SAM-PK-K1105 (holotype): mid-caudal in right lateral view (C); posterior caudals in right lateral view (D). All scale bars equal 1 cm. Abbreviations: chf, chrevron facet; poz, postzygapophysis; prz, prezygapophysis.

is near vertical and is slightly expanded mediolaterally and anteroposteriorly at its tip.

The poorly preserved mid-posterior caudals of SAM-PK-K1105 (Fig. 9C–D) are the only vertebrae of the specimen in which the neural arches, centra and ribs are fused. Fusion of the caudals, but not the dorsals, is seen in BMNH R11000 (Figs 8A–B, 9A–B). Vertebral fusion may thus have begun in the caudal region. The neural spines and caudal ribs of the mid-posterior caudals are either reduced or lost (Fig. 9C–D); distally the centra become more elongate, with strongly concave articular faces.

Ossified tendons were present in at least the sacral region of *Stormbergia* (BP/1/4885), but preservation is poor, and the distribution of tendons along the vertebral column remains unknown.

Appendicular skeleton

The scapula and coracoid are fused in BMNH R11000 (Fig. 10) but separate in SAM-PK-K1105 (which only preserves the isolated coracoids, Fig. 11). The general form of the scapula (Fig. 10) is very similar to that of *Lesothosaurus* (BMNH RUB17, Thulborn, 1972: fig. 6) and is fairly typical of basal ornithischians in general (cf. He & Cai, 1984: fig. 15A–B). It is elongate and blade-like. The proximal end is strongly expanded with a large, anterodorsally projecting, acromion process (Fig. 10A–B), which creates a large surface for articulation with the coracoid. A laterally prominent ridge runs along the posterodorsal margin of the acromion, with the result that the acromion faces anterolaterally rather than laterally. The lateral face of the proximal end is shallowly concave. The glenoid cavity opens ventrolaterally and is composed mainly by the scapula. The dorsal blade margin is relatively straight, whereas the ventral margin is somewhat convex, curving ventrally to accommodate the asymmetrical distal expansion of the blade. The distal blade has a thickened, porous irregular texture and probably bore a cartilaginous suprascapula in life. In dorsal view the blade is strongly curved to follow the ribcage (Fig. 10C).

The coracoid (Figs 10A–C, 11) is relatively short with its dorsoventral height being greater than its anteroposterior length. The lateral surface is slightly convex, whereas the medial surface is depressed and concave. There is a short anteroventrally developed 'hook', separated from the glenoid cavity by a ventral embayment. The coracoid makes only a small contribution to the glenoid cavity. The coracoid foramen (which transmitted the scapulocoracoid nerve) is located well within the lateral face, as in most basal ornithischians, and passes posteromedially through the bone. Medially it exits along the coracoid-scapula suture, adjacent to a corresponding groove on the medial surface of the scapula.

SAM-PK-K1105 preserves short portions of the shafts of both humeri, but no useful anatomical information can be obtained. The left radius and ulna are present in SAM-PK-K1105 (Fig. 12). As preserved, the two bones cross along their length: the ulna is set slightly posterior to the radius at their proximal end and the ulna is set slightly anteriorly at the distal end. The proximal end of the ulna is triangular with the apex pointing somewhat medially. There is a well-developed olecranon process. The shaft is somewhat sigmoidal, but this may be a result of postmortem damage. The distal articular surface of the ulna is anteroposteriorly flattened. The radius is moderately

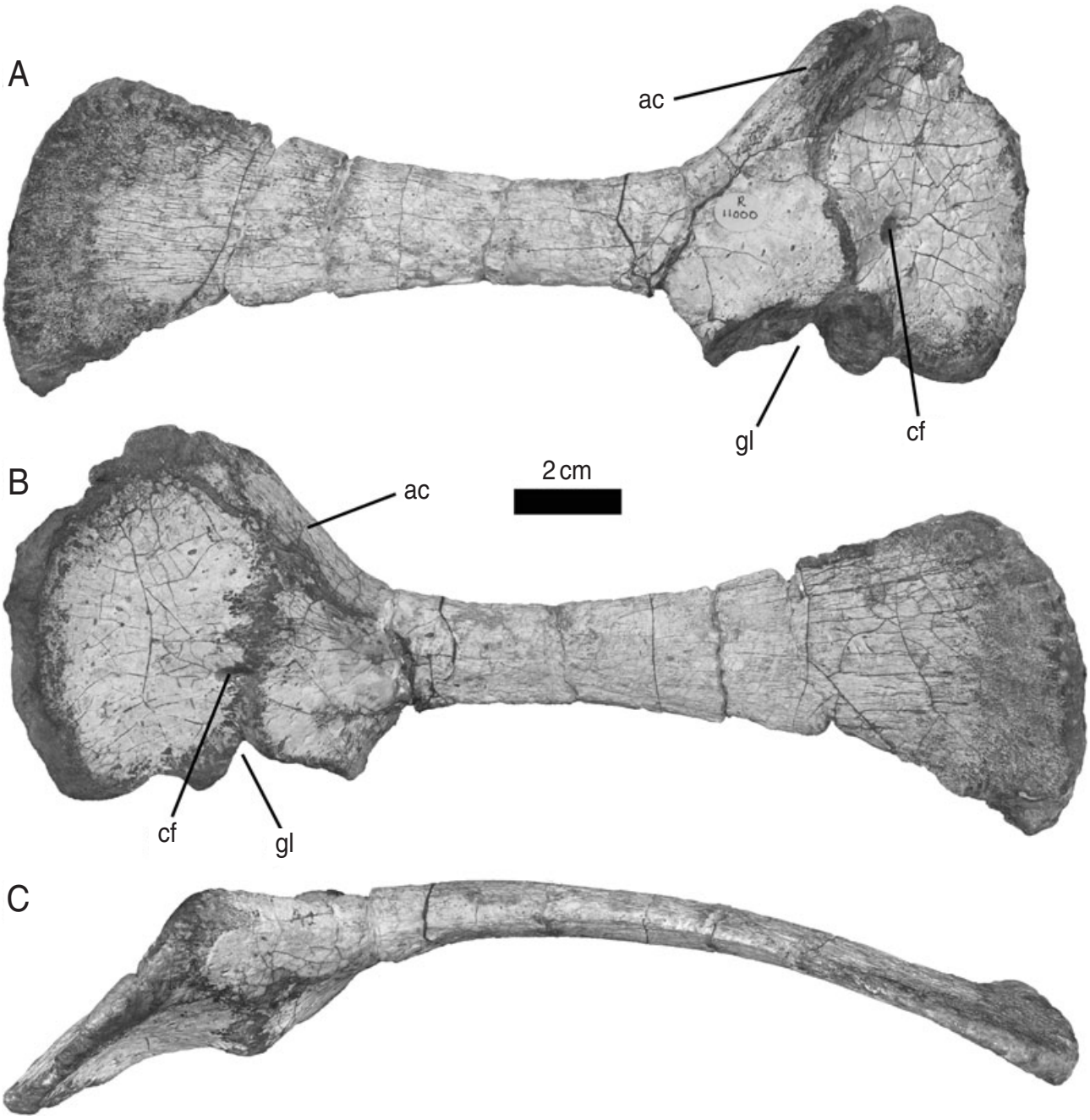

Figure 10. ***Stormbergia dangershoeki*** **gen. et sp. nov.** BMNH R11000 (paratype), scapulocoracoid in lateral (A), medial (B) and dorsal (C) views. Abbreviations: ac, acromion process; cf, coracoid foramen; gl, glenoid.

shorter than the ulna. Its proximal surface is mediolaterally compressed and flattened laterally where it is appressed against the ulna. Distally the radius has a subcircular cross section.

The ilia are well-preserved in BMNH R11000 (Fig. 13A–C) and BP/1/4885 (Fig. 5), but are unknown in SAM-PK-K1105. The ilium is blade-like with long preacetabular and postacetabular processes (Fig. 13A–C). The preacetabular process curves gently ventrally and moderately laterally, as in *Lesothosaurus* (BMNH RUB17, R11002, Fig. 24B). There is a slight shelf-like medial expansion to the ventral surface of the process. Striations representing sites of muscular origin and attachment are common on the lateral surface of the ilium and the dorsal margin is slightly thickened.

A strong lateral expansion (the supraacetabular flange) of the dorsal acetabular margin is seen

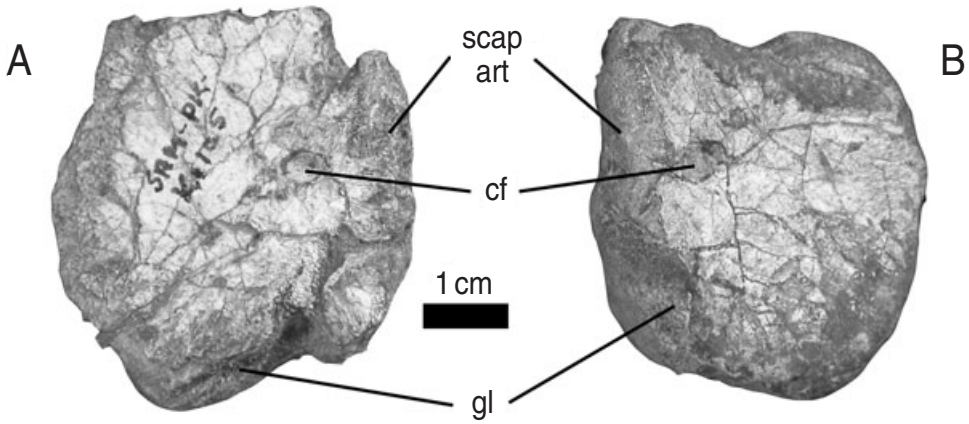

Figure 11. ***Stormbergia dangershoeki*** **gen. et sp. nov.** SAM-PK-K1105 (holotype), left (A) and right (B) coracoids in lateral view. Abbreviations: cf, coracoid foramen; gl, glenoid; scap art, articular suface for the scapula.

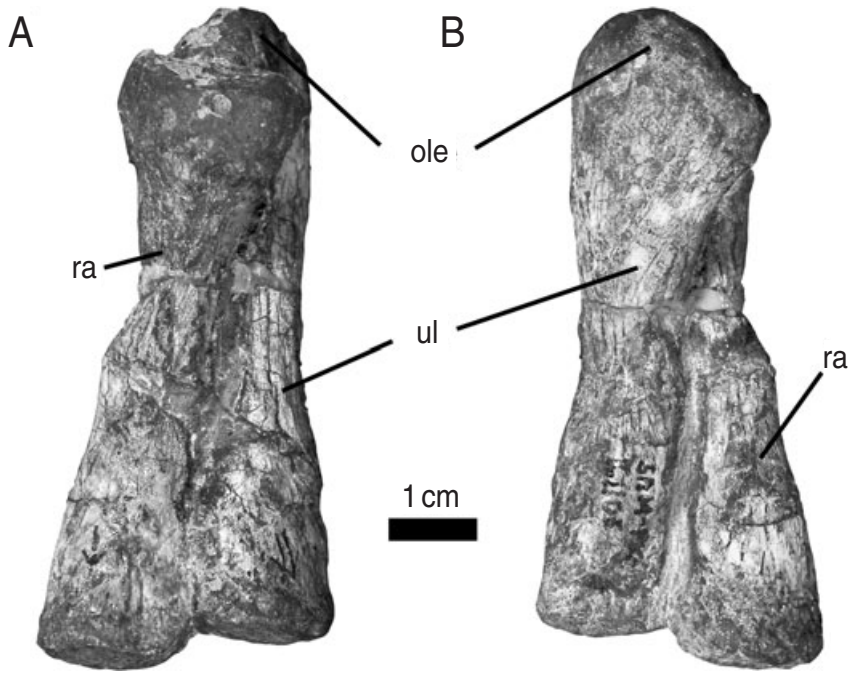

Figure 12. ***Stormbergia dangershoeki*** **gen. et sp. nov.** SAM-PK-K1105 (holotype), ulna and radius in anterior (A) and posterior (B) views. Abbreviations: ole, olecranon process; ra, radius; ul, ulna.

(Fig. 13A–C), forming a deep acetabulum. This lateral expansion is greatest at the anterodorsal corner of the acetabulum and decreases in width posteriorly, disappearing at the posterodorsal corner of the acetabulum. A strong medial expansion of the dorsal acetabular margin is also seen, angling somewhat ventrally to form a medioventral wall to the acetabulum (Fig. 13A), so that the acetabulum is not fully perforate. A similar, but less pronounced, ventral flange is seen in *Lesothosaurus* (BMNH RUB17, R11002, Fig. 24B). The medial expansion is greatest at the anterodorsal margin of the acetabulum, where it is subequal to the lateral expansion, and decreases slightly in width posteriorly to the ischiadic peduncle.

The stout ischiadic peduncle projects ventrally and has a roughly triangular cross-section. There is a triangular raised area of finely porous texture situated adjacent to the peduncle's articular surface, recognized in *Lesothosaurus* as the ischial contribution to the primitive dinosaurian antitrochanter (Sereno, 1991).

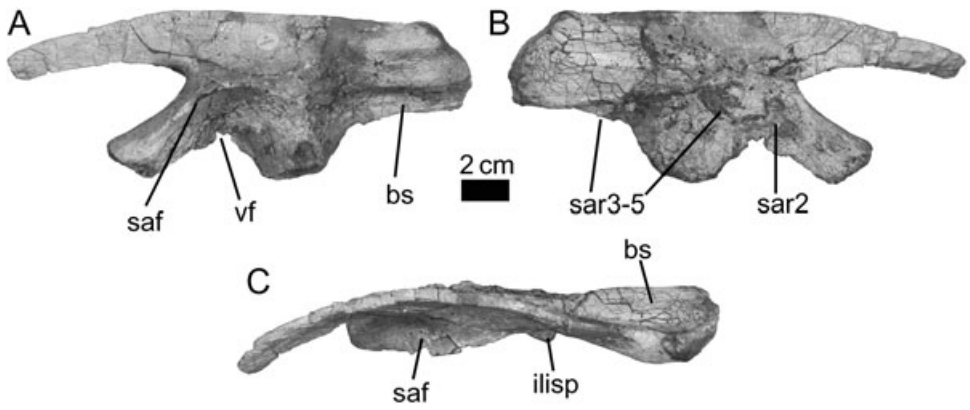

Figure 13. ***Stormbergia dangershoeki*** **gen. et sp. nov.** BMNH R11000 (paratype), left ilium in lateral (A), medial (B) and dorsal (C) views. Abbreviations: bs, brevis shelf; ilisp, ischiadic peduncle; saf, supraacetabular flange; sar2, scar for sacral rib 2; sar3–5, scars for sacral ribs 3–5; vf, ventral flange partially backing the acetabulum.

The postacetabular process is laterally convex and robust. It is relatively wider than the slender process of *Lesothosaurus*. Its dorsal-most part is dorsolaterally facing and has a fibrous bone texture, indicating muscle attachment. Ventrally the process is expanded into a ventromedially directed brevis shelf (Figs 13A, C), which is visible in lateral view, as in *Lesothosaurus* (Sereno, 1991) and other basal ornithischians (e.g. *Agilisaurus*, ZDM T6011; see above). Medially, the pattern of sacral attachment scars is identical to that of *Lesothosaurus* (BMNH R11002; Sereno, 1991: fig. 9). A broad area of scarring medial and posterior to the pubic peduncle and ventral to the brevis shelf is associated with the posterior three sacral ribs, which were probably conjoined. The rib of sacral 2 attaches to the base of the pubic peduncle via a prominent scar. A depression at the base of the preacetabular process of the left ilium may represent the scar for the first sacral rib (Sereno, 1991).

The ischium is well-preserved in BMNH R11000 (Fig. 3C) and SAM-PK-K1105 (Fig. 3D). BP/1/4885 (Fig. 5) preserves the proximal portion of the left ischium. The ischium is blade like and posteroventrally directed (Fig. 3C–D). The proximal end is developed into the iliac and pubic processes. Both processes are laterally convex and medially concave. The pubic process has a triangular cross-section that thickens dorsally towards the acetabular margin. The articular surface for the pubis is flat. The shaft is straight and mediolaterally flattened. Its dorsal margin is rounded and rather broad, the ventral margin is narrow and sharp. The shaft is twisted so that the medial surface faces somewhat dorsally and the obturator process is ventromedially directed, but this is not comparable to *Lesothosaurus* (Figs 3A–B, 4; BMNH RUB17) where the shaft twists through nearly 90° so that the medial surface would have turned to face almost entirely dorsally. Proximally the shaft is mediolaterally compressed, with a rounded posterior margin and a sharp anterior margin; distally the shaft is expanded so that it is bar-like. The ischial symphysis was restricted to the distalmost portion of the blade, and is marked by an area roughened bone texture.

There is a shallow dorsal groove on the proximal shaft on the ischium of BMNH R11000 (Fig. 3C); this is not present in SAM-PK-K1105 (Fig. 3D). Proximally this groove is present in lateral view but it moves medially, distally. In BMNH R11000, SAM-PK-K1105 and BP/1/4885 there is a well-defined tab-like obturator process on the proximal shaft (Figs 3C–D, 5). The presence of this feature clearly distinguishes *Stormbergia* from *Lesothosaurus (*see above).

The pubes are well-preserved in SAM-PK-K1105 (Fig. 14) and BP/1/4885 (Fig. 5). The pubis has a rod-like, posteroventrally directed shaft and a moderately developed prepubic process. There is a very high angle of approximately 170 degrees between the prepubis and the postpubis. The prepubis is mediolaterally flattened and similar to that of *Lesothosaurus* (BMNH RUB17; Thulborn, 1972: fig. 9D–E). There is an obturator notch in SAM-PK-K1105 (Fig. 14) that would have been closed by the pubic peduncle of the ischium, although an obturator foramen is present in BP/1/4885 (Fig. 5). However, the presence of an obturator notch or foramen appears to be subject to intraspecific variation: in *Hypsilophodon* (Galton, 1974a) an obturator notch is present in some individuals (BMNH R195, R5829), while a foramen is present in others (BMNH R193, R196).

The femur is best represented in SAM-PK-K1105 (Fig. 15) and BP/1/4885. A crushed proximal left femur is present in BMNH R11000. The femur (Fig. 15) is straight in anterior or posterior view, but is bowed strongly anteriorly in lateral view. The head is

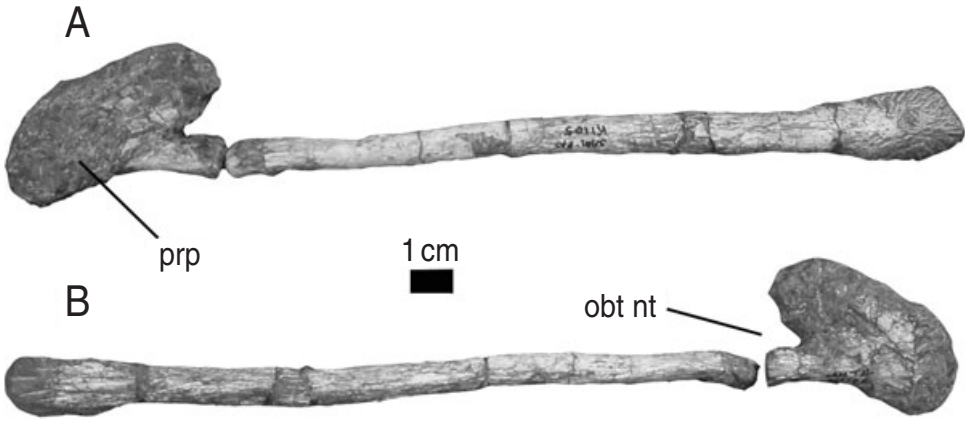

Figure 14. ***Stormbergia dangershoeki*** **gen. et sp. nov.** SAM-PK-K1105 (holotype), right pubis, medial (A) and lateral (B) views. Abbreviations: obt nt, obturator notch; prp, prepubic process.

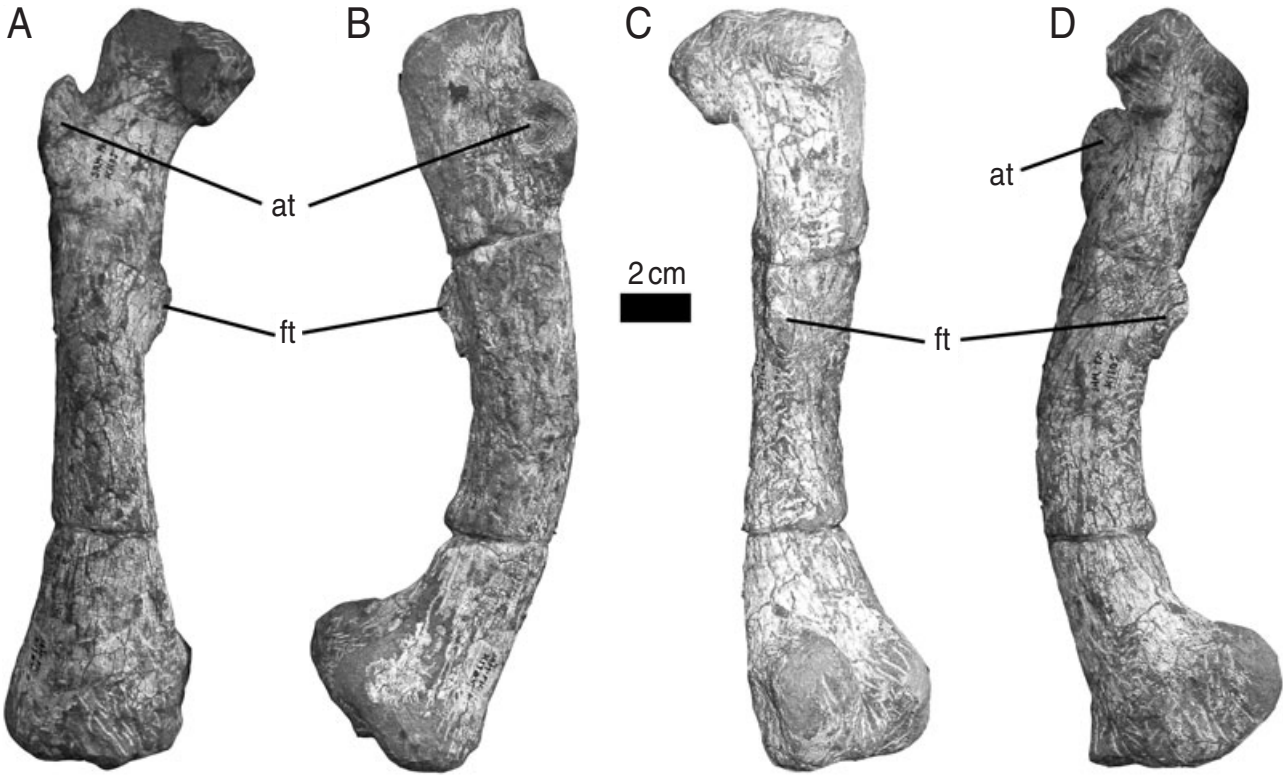

Figure 15. ***Stormbergia dangershoeki*** **gen. et sp. nov.** SAM-PK-K1105 (holotype), right femur in anterior (A), lateral (B), posterior (C) and medial (D) views. Abbreviations: at, anterior trochanter; ft, fourth trochanter.

directed ventromedially and is not differentiated from the greater trochanter by a groove or depression. As in *Lesothosaurus* (BMNH RUB17), the head angles somewhat anteromedially in proximal view relative to the distal condyles. The anterior proximal surface is convex and the posterior surface is relatively flat. The blade-like anterior trochanter is separated from the greater trochanter by a prominent cleft, is set medial to the greater trochanter, and is much lower than the level of the head. The fourth trochanter is incompletely preserved in SAM-PK-K1105 (Fig. 15), so it cannot be determined for certain whether it was pendent or not. It is located proximally, with its distal attachment point lying at approximately 45% of the distance from the proximal end of the femur. Distally, the medial condyle is somewhat enlarged relative to

the lateral, which is moderately inset from the lateral margin. There is a deep posterior intercondylar groove, but no anterior groove is present. Overall the femur is very similar to that of *Lesothosaurus* (BMNH RUB17; Sereno, 1991: fig. 8C–D) and other basal ornithischians such as *Scutellosaurus* (Colbert, 1981), *Scelidosaurus* (BMNH R1111), *Agilisaurus* (Peng, 1992) and '*Yandusaurus' multidens* (He & Cai, 1984).

The tibiae are very well-preserved in SAM-PK-K1105. BMNH R11000 preserves only the distal portion of the left tibia. The tibiae of SAM-PK-K1105 (Figs 16, 17A) are longer (118%) than the femur, as in most basal ornithischians (e.g. Thulborn, 1972; He & Cai, 1984; Peng, 1992). The left tibia is preserved in isolation (Fig. 16), although it articulates tightly with the left astragalus, and calcaneum. The right tibia is present, but is broken into two pieces. The proximal portion is obscured laterally by sediment and has a portion of the shaft of the right fibula attached to it. Distally the astragalus remains attached (but not fused) in its original articulation (Fig. 17A).

The proximal end of the tibia is expanded anteroposteriorly (Fig. 16), and the distal end is expanded mediolaterally at approximately 90° to it. This means there is substantial torsion along the length of the shaft. At the proximal end there is a well-developed cnemial crest that extends down the anteromedial side and is still discernable until 40–45% of tibial length. This cnemial crest is better developed than in *Lesothosaurus* (BMNH RUB17; Thulborn, 1972: fig. 11A–B). A well-developed fibular condyle is present on the lateral margin and continues down the shaft, eventually forming the sharp lateral edge of the tibial shaft. A short accessory condyle is developed anteriorly to this, as in *Lesothosaurus* (BMNH RUB17; Thulborn, 1972). The well-developed inner or posterior condyle is separated from the fibular condyle by a deep sulcus. It can be traced down the posterior margin of the tibia as a distinct ridge.

The shaft is somewhat sinuous in anterior or posterior view. At midlength the shaft is triangular in cross-section, with the anterior surface being rather flat and the posterior margin convex. Distally, the lateral malleolus extends further than the medial one. The anterior surface of the distal end is rather flat, but the medial condyle is somewhat swollen above the astragular articular surface. The distal end is triangular in distal view, with the apex on the posterior side and offset medially, such that the medial side is generally much wider than the lateral side. Facets are developed for articulation with the calcaneum and astragalus.

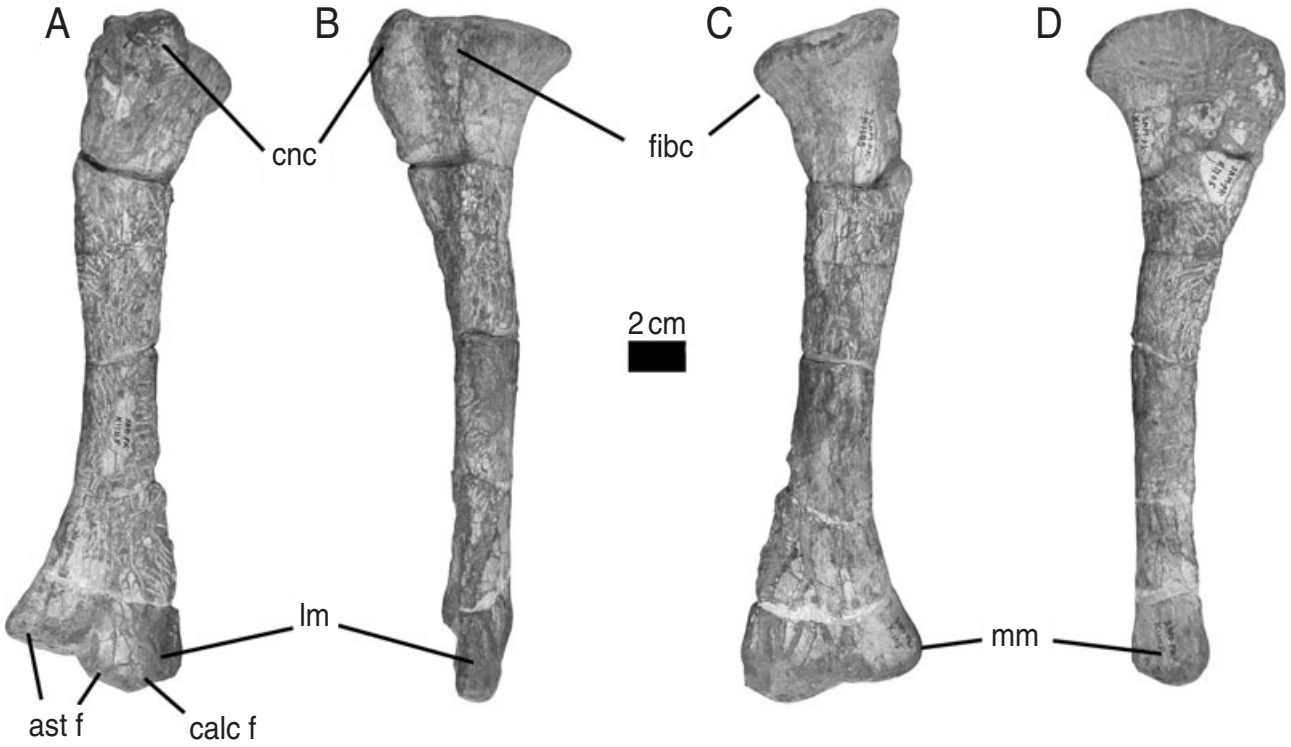

Figure 16. ***Stormbergia dangershoeki*** **gen. et sp. nov.** SAM-PK-K1105 (holotype), left tibia in anterior (A), lateral (B), posterior (C) and medial (D) views. Abbreviations: ast f, astragular facet; calc f, calcaneum facet; cnc, cnemial crest; fibc, fibular condyle; lm, lateral malleolus; mm, medial malleolus.

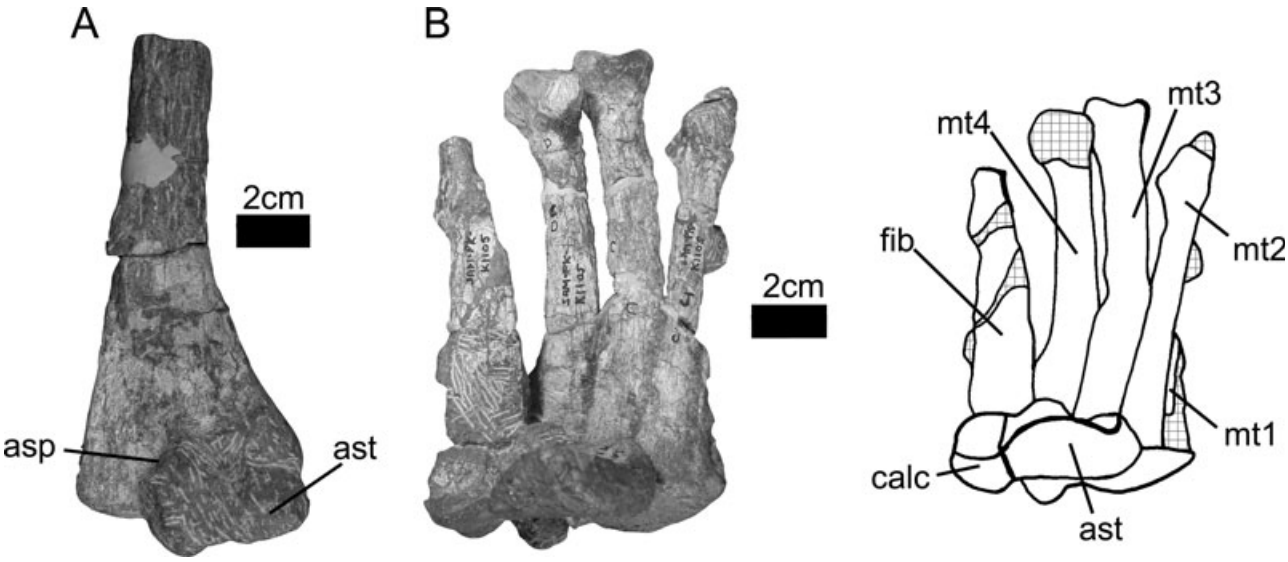

Figure 17. ***Stormbergia dangershoeki*** **gen. et sp. nov.** SAM-PK-K1105 (holotype): right tibia and astragalus in anterior view (A); left distal fibula, astragalus, calcaneum and metatarsus (B). Fibula, astragalus and calcaneum are in posterior view, metatarsals in anterior view. Abbreviations: asp, ascending process of astragalus; ast, astragalus; calc, calcaneum; fib, fibula; mt1, mt2, mt3, mt4, metatarsals.

Overall, the tibia of *Stormbergia* is slightly shorter relative to the femur (118%) than in *Lesothosaurus (*124%, BMNH RUB17), and has a moderately better developed cnemial crest and fibula condyle.

The right fibula is well-preserved in BMNH R11000 (Fig. 18); portions of the left and right fibulae are present in SAM-PK-K1105 (Fig. 17B). The fibula of BMNH R11000 is nearly complete, although it has lost its distalmost portion. It is expanded both proximally and distally and is twisted along its length with the distal end at an angle of about 70° to the proximal end. The proximal end is flat medially and concave laterally.

Astragali are preserved in SAM-PK-K1105 (Fig. 17A–B). The astragalus is widest and deepest anteriorly and tapers posteriorly in both mediolateral width and dorsoventral height. There is a high, well-developed ascending process that is set laterally (as in other basal ornithischians). Two facets are developed on the lateral margin: one for articulation with the calcaneum and an anteroproximal one for articulation with the medial edge of the distal fibula. The astragalus wraps around the distal end of the medial tibia and has a low posterior process. The internal surface of the astragalus is divided into two surfaces. The medial one is higher and articulates with the medial malleolus of the tibia, whereas the lower ventral surface slopes ventrolaterally and receives the medial and ventral surfaces of the tibia's lateral malleolus.

The calcanea are well-preserved in articulation with the astragali in SAM-PK-K1105 (Fig. 17B). The calca-

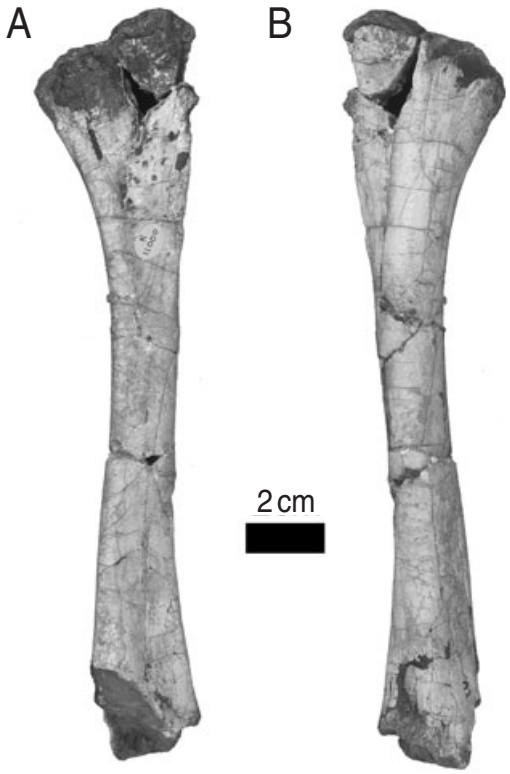

Figure 18. ***Stormbergia dangershoeki*** **gen. et sp. nov.** BMNH R11000 (paratype), right fibula in lateral (A) and medial (B) view.

neum is mediolaterally narrow relative to the astragalus. It has an anterior surface that articulates with the fibula, and a posterior cupped surface for the lateral condyle of the tibia.

The metatarsus is preserved only in SAM-PK-K1105 (Fig. 17B). Metatarsal 1 is reduced and splint-like as in *Lesothosaurus* (Thulborn, 1972; Sereno, 1991). Its proximal end is very slender and articulates with the dorsomedial surface of metatarsal 2. It is orientated such that the first digit angles somewhat posteroventrally relative to the axis of the other three metatarsals. Metatarsal 2 is mediolaterally compressed and dorsoventrally expanded proximally. Although closely appressed to metatarsal 3 along most of its length, distally it curves somewhat medially. Its distal articular surface is not well preserved. Metatarsal 3 is the longest in the pes. Proximally it is mediolaterally compressed while distally it is mediolaterally expanded into a robust articular surface. It has a rather sigmoidal shaft. Metatarsal 4 is shorter and is only appressed to metatarsal 3 proximally; more distally it curves laterally. Proximally it is mediolaterally expanded. It also has a somewhat sigmoidal shape. There is no trace of metatarsal 5.

Although 19 phalanges, including six unguals, are known for SAM-PK-K1105 (Fig. 19), virtually all are disarticulated and so little information on the pedal formula is available, although digit 2 appears to have had three phalanges (Fig. 19B) as in other ornithischians. Phalanges (Fig. 19) are identical in morphology to those seen in other basal ornithischians (e.g. *Lesothosaurus*: Thulborn, 1972; *Agilisaurus*: Peng, 1992) and the unguals (Fig. 19E) are narrow and claw-like.

ANATOMICAL DESCRIPTION OF SAM-PK-K1107

The anatomy of SAM-PK-K1107 is essentially indistinguishable from that of *Stormbergia*. However, because SAM-PK-K1107 does not preserve an ischium the specimen is not herein referred to the genus *Stormbergia*, although it may be referable in the future (see above). In the following description of SAM-PK-K1107 I concentrate on elements that are not represented in specimens of *Stormbergia*.

The atlas is present, but is only represented by the odontoid process and the intercentrum. The odontoid is fused to the axis (Fig. 20A). The intercentrum is kidney-shaped in dorsal view (Fig. 20B), and crescentic in anterior view. The dorsal surface is mediolaterally concave. Anteriorly this concave surface would have received the occipital condyle. Posteriorly a prominent, crescentic groove is present that received the convex ventral surface of the odontoid process. The neural arches would have articulated with the dorsolateral margins of the intercentrum; ventrally there are prominent facets for the atlantal ribs.

The dorsal margin of the odontoid is concave adjacent to the axial neural canal, but becomes flat anteriorly. The ventral margin is transversely convex and is developed into a low lip anteriorly at its articulation

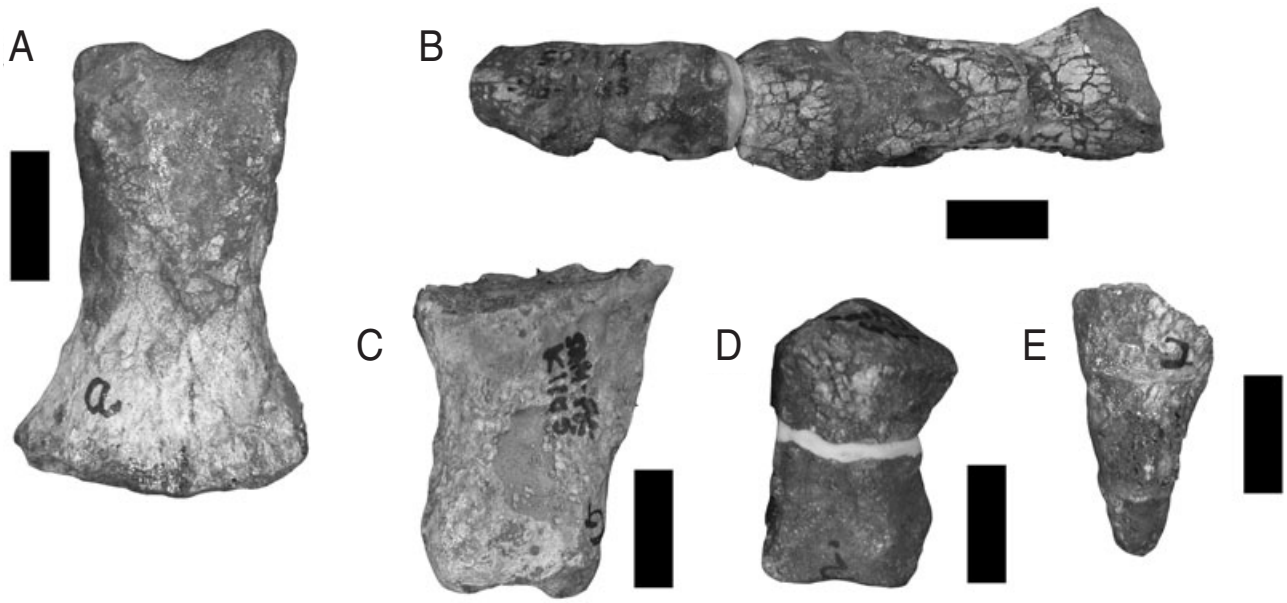

Figure 19. ***Stormbergia dangershoeki*** **gen. et sp. nov.** SAM-PK-K1105 (holotype): phalanx 1, digit 3, dorsal view (A); digit 2, right pes, phalanges 1–3 in dorsal view (B); unidentified phalanges (C, D) in dorsal view; unidentified ungual (E) in dorsal view. All scale-bars equal 1 cm.

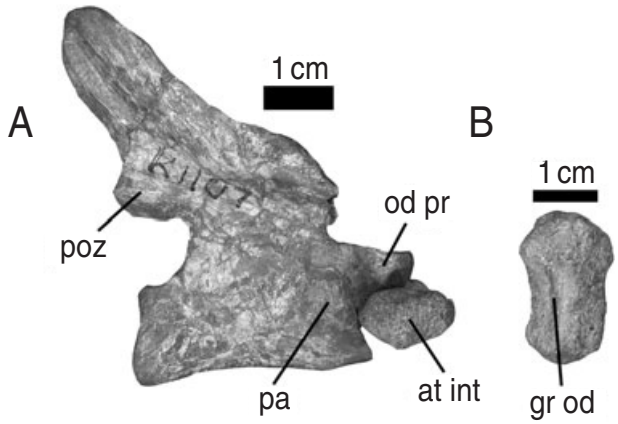

Figure 20. cf. ***Stormbergia*.** SAM-PK-K1107: axis and atlas, right lateral view (A); atlantal intercentrum, dorsal view (B). Abbreviations: at int, atlantal intercentrum; gr od, groove, for odontoid process, on dorsal surface of atlantal intercentrum; od pr, odontoid process; pa, parapophysis; poz, postzygapophysis.

with the atlantal intercentrum. The anterior surface is reniform and flat.

The centrum of the well-preserved axis (Fig. 20A) is relatively long and low, with moderately constricted lateral walls and concave articular faces. A swelling of the anterior rim of the centrum, just posteroventral to the odontoid, represents the parapophysis. There is no obvious diapophysis: the rib was presumably single-headed. A ventral keel is absent. The neural arch is tall, roofing a large neural canal. A strong neural spine projects posterodorsally at about 50° to the long axis of the centrum. The neural spine is lateromedially compressed except at its posterior margin where it flares outwards to form two lateral flanges, which extend ventrally and anteriorly from the distal tip of the spine to the postzygapophyses. The postzygapophyses are well-preserved and face ventrolaterally at about 20° to the horizontal. The prezygapophyses are not preserved in any specimen.

The dorsal region is well-preserved (Figs 21, 23), with 14 dorsals represented. Although the complete

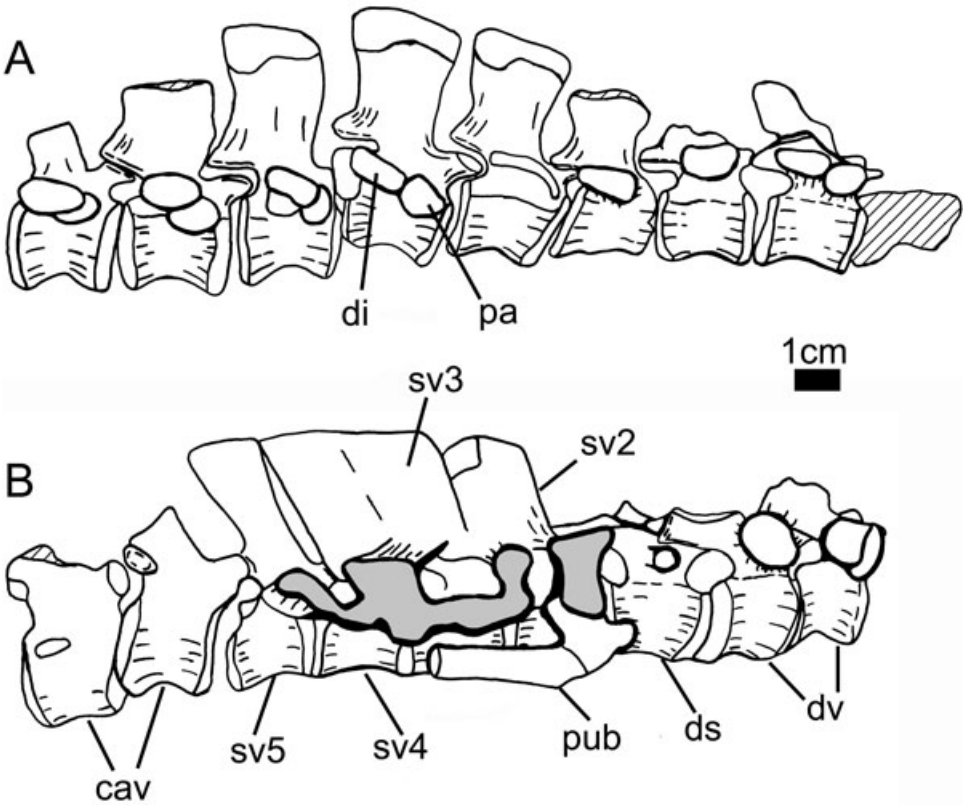

Figure 21. cf. ***Stormbergia*.** SAM-PK-K1107, anterior-mid dorsal series in right lateral view (A). These vertebrae have been articulated together as labelled by the preparator, and appear to fit reasonably well, but the original association is not known. SAM-PK-K1107, posterior dorsals, sacrum and anterior caudals in right lateral view (B). Abbreviations: cav, caudal vertebrae; di, diapophysis; ds, dorsosacral; pa, parapophysis; dv, posterior dorsals; pub, fragment of pubic shaft; sv2, sv3, sv4, sv5, 'true' sacral vertebrae, i.e. those vertebrae which have ribs which articulate with the ilium.

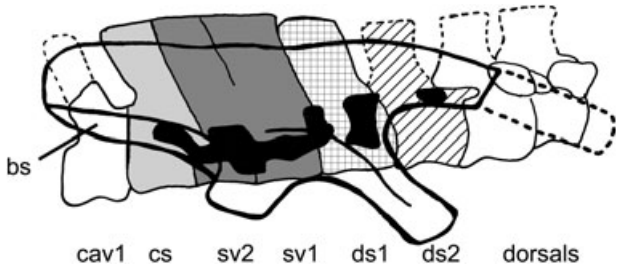

Figure 22. cf. ***Stormbergia*.** SAM-PK-K1107, reconstruction of posterior dorsals, sacrum and anterior caudals in articulation with the right ilium, to show positions of sacral rib attachment and probable incorporation of vertebrae into sacrum. The ancestral two sacrals are shown in dark grey, the caudosacral (sacral 5) is shown in light grey, the first dorsosacral (sacral 2) is cross-hatched and the second dorsosacral is shown with a fill of parallel, diagonally orientated lines. Matt black areas represent the attachment of the sacral ribs to the medial surface of the ilium. Labels refer to the vertebrae directly above them. Abbreviations: bs, brevis shelf; cav1, caudal 1; cs, caudosacral; ds1, ds2, dorsacrals 1 and 2; sv1, sv2, ancestral sacrals 1 and 2.

dorsal count is unknown, it is likely that there were 15 vertebrae, as in other basal ornithischians (e.g. '*Yandusaurus' multidens*, ZDM T6001). Dorsal centra are generally spool-like (Fig. 21). Anteriorly, the centra are rather narrow compared to their lengths and have a small ventral keel, a trace of which is preserved until the 9th dorsal. Posteriorly, the centra maintain a fairly constant length, but become noticeably wider and somewhat higher. Anteriorly, the central faces have approximately equal widths and heights; posteriorly, the faces become somewhat wider relative to height. All central faces are flat to very slightly concave. In lateral view, the planes formed by the anterior and posterior surfaces converge somewhat ventrally, which would have caused an arching of the dorsal series as a whole.

The neural arch becomes somewhat lower posteriorly and the circular neural canal widens moderately. Transverse processes project upwards at about 30° to the horizontal in the anterior dorsals; this decreases posteriorly and the processes are near horizontal by the presumed 13th dorsal. In the anterior dorsals the parapophysis is positioned on the neural arch, just anterior to the base of the transverse process, and has the form of a crater-like facet for the rib capitulum. Posteriorly, the parapophysis migrates dorsally and laterally towards the diapophysis. The diapophysis is positioned at the end of an elongate transverse process in anterior dorsals; transverse processes decrease in length posteriorly causing the diapophysis to converge with the parapophysis. In the presumed 13th dorsal the parapophysis and diapophysis are very close; in the presumed 14th dorsal they are almost continuous; and in the last true dorsal they fuse to form a single surface. Pre- and postzygapophyses extend from the neural arch at around 20° throughout the dorsal series. Prezygapophyses are supported on long arched processes and are widely divergent; postzygapophyses are anchored to the base of the neural spine and lie closer to the midline.

The sacrum of SAM-PK-K1107 (Fig. 21B) contains five fused vertebrae, but the second has been sheared through, so that the first sacral (and some of the second) is preserved with the posterior dorsals, whereas most of the poorly preserved second sacral is attached to the other three sacrals. Only the four posterior sacrals bear stout, dorsoventrally deep sacral ribs that articulated with the medial surface of the ilium (i.e. are 'true' sacrals). The anteriormost fused vertebra lacks such ribs; it has rather weak transverse processes that are incomplete distally. These would have born a single-headed rib that may have contacted the preacetabular process of the ilium, though this cannot be confirmed. Owing to this uncertainty, this vertebra will be referred to as a dorsosacral. The four true sacrals posterior to it will be referred to as sacrals 2–5 in the following description.

The sacral centra are wide and low, with a somewhat flattened appearance. The sides are gently excavated and a weak ventral keel is discernable (further distinguishing the dorsosacral from preceding dorsals). The posterior surface of the last sacral is exposed, and appears somewhat concave, although it may be distorted. Most of the pre- and postzygapophyses are fused with each other and cannot be distinguished; exceptions are the postzygapophyses of sacral 5, which articulate with the preserved first caudal. These are situated fairly close together and are inclined at a high angle as in the caudal series (see below). The sacral neural spines are tall and posteriorly inclined. The spines of sacrals 3–4 are fused. The dorsoventrally broad sacral ribs of sacrals 2–5 are fused to the horizontal transverse processes and it is not possible to identify sutures. The base of the neural spine and the transverse process are anteriorly positioned in sacrals 2–5. This means that the anterior edge of each rib is partially borne by the centrum of the preceding vertebra, as in *Hypsilophodon* (Galton, 1974a). The ribs of sacrals 3–5 are fused to each other ventrally, but the rib of sacral 2 is separate.

The lateral ends of the exposed sacral ribs correspond to scars on the medial side of the right ilium (Fig. 22). A broad area of scarring medial and posterior to the pubic peduncle and ventral to the brevis shelf is associated with the conjoined sacral ribs (3–5). These sacral ribs therefore attach posterior to the partially closed acetabulum. The rib of sacral 2 attaches to the base of the pubic peduncle via a prominent scar. The rib of the dorsosacral may have articulated with

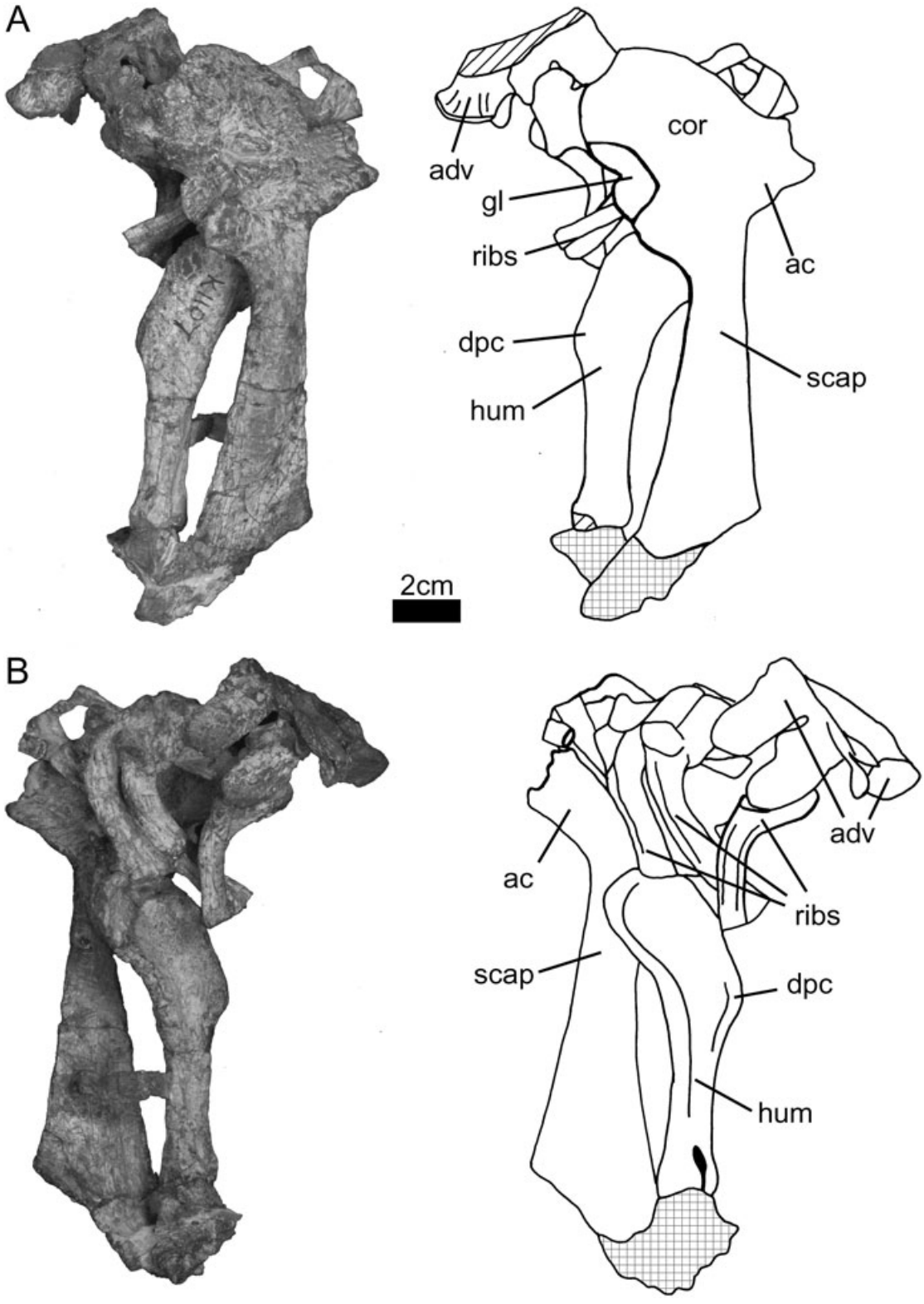

Figure 23. cf. ***Stormbergia.*** SAM-PK-K1107, photos of block of articulated material including portions of two anterior dorsals, rib fragments, left scapulocoracoid and left humerus. Humerus is exposed in anterolateral (A) and posteromedial (B) views. Abbreviations: ac, acromion process; adv, anterior dorsal; cor, coracoid; dpc, deltopectoral crest of the humerus; gl, glenoid; hum, humerus; scap, scapula.

the preacetabular process as suggested for *Lesothosaurus* (Sereno, 1991) – a bone fragment on the preacetabular process of the right ilium of SAM-PK-K1107 may represent part of this rib. Additionally a depression at the base of the preacetabular process of the left ilium may represent the scar for the first sacral rib.

Sacral 2 lies medial to the pubic peduncle (Fig. 22). According to Novas (1996), this vertebra would therefore represent a dorsosacral that has become incorporated into the sacrum in addition to the two sacrals that are primitive for Ornithodira. Sacral 3 also has a robust sacral rib, which attaches to the ilium medial to the posterior acetabulum and the ischiadic peduncle. This is in an equivalent position to the first sacral of *Marasuchus* and *Herrerasaurus* (Novas, 1996) and thus represents the first of the two ancestral sacrals. Sacral 4 must therefore represent the second of the ancestral sacrals; this is supported by its robust sacral rib and its attachment to the brevis shelf posterior to the ischiadic peduncle. Finally, sacral 5 represents an incorporated caudosacral; its sacral rib is not as robust as those of sacrals 2–4. It is dorsoventrally narrow and attaches to the neurocentral boundary, somewhat lower than in the preceding sacrals, but in a similar position to the attachment points of the caudal ribs. Fusion of the caudo-sacral with the sacrum is not as complete as for sacrals 2–4; the neural spine of the former is somewhat separated, a clear suture is visible between its centrum and the preceding one (sutures are obliterated between centra 2–4), and the contact of its prezygapophyses with the postzygapophyses of sacral 4 can be discerned.

Novas (1996) considered the addition of a dorsosacral to the ancestral two sacrals to be a synapomorphy of Dinosauria; this was challenged by Galton (1999a) who suggested that the plesiomorphic dinosaurian condition was the presence of two ancestral sacrals, to which different clades independently added dorsosacrals or caudosacrals. Based upon the development of the sacral ribs, the order of incorporation of vertebrae into the sacrum in SAM-PK-K1107 can be tentatively reconstructed (Fig. 22). Sacral 2, a dorsosacral, was probably incorporated first, followed by sacral 5, a caudosacral. Sacral 1, an additional dorsosacral, is in the process of being incorporated into the sacrum. This interpretation supports that of Novas (1996).

The fused left scapulocoracoid (Fig. 23) is very similar to that of *Stormbergia* (see above) and other basal ornithischians; measurements are provided in Table 2. The left humerus (Fig. 23) is well-preserved and has a straight, stout and broad shaft. The proximal expansion is significantly larger than the distal expansion. The head is obscured but appears to have been situated in the centre of the posterior proximal surface, as in other basal ornithischians (e.g. Thulborn, 1972). Medial to it is a well-developed depression or tubercle, which is similar to that seen in *Heterodontosaurus* (Santa Luca, 1980: fig. 11), but that is absent in *Lesothosaurus* (BMNH RUB17). The well-developed deltopectoral crest projects strongly anteriorly and extends for 45% of humeral length. This is similar to the value for *Lesothosaurus* (BMNH RUB17) and slightly greater than that for *Heterodontosaurus* (42%; Santa Luca, 1980). There is a deep posterior intercondylar groove between the slightly expanded distal condyles. The medial (ulnar) condyle extends slightly further distally than the lateral (radial) condyle. The former is broad and rounded anteriorly but narrow and sharp posteriorly, giving it a rather triangular outline. The lateral radial condyle is narrow anteriorly and becomes somewhat broader posteriorly. There is no evidence of an entepicondyle, which is present in *Heterodontosaurus* (SAM-PK-K1332; Santa Luca, 1980).

The preserved length of the scapula (Table 2) in SAM-PK-K1107 is at least 124% the length of the humerus. However, the distal end of the scapula is broken, and its actual length must have been even greater. In *Lesothosaurus* (Table 2) the scapula is only 110% the size of humeral length. Scapula: humerus ratios in other basal ornithischians are: *Heterodontosaurus*, 105% (Santa Luca, 1980); *Hypsilophodon*, 100–102% (Galton, 1974a); '*Yandusaurus' multidens*, 78–87% (He & Cai, 1984); *Agilisaurus*, 84% (Peng, 1992).

The humerus is also short relative to the femur, at 51% of femoral length. In *Lesothosaurus* the humerus is 55% of femoral length (Table 2). Humerus: femur ratios in other basal ornithischians are: '*Yandusaurus' multidens*, 65% (He & Cai, 1984); *Heterodontosaurus*, 73% (Santa Luca, 1980); *Scutellosaurus*, 73% (Colbert, 1981). While Peng (1992) does not provide measurements for the humerus of *Agilisaurus*, he noted that the humerus is about half the length of the femur.

The left ilium and femur are preserved, but are identical to those already described for *Stormbergia*. Measurements are provided in Table 2.

SAM-PK-K1107 differs from *Lesothosaurus*. The humerus (Fig. 23) has a well-developed tubercle medial to the head, and is notably short relative to the femur and scapula. If, as noted above, SAM-PK-K1107 eventually proves to be referable to *Stormbergia*, these features will further distinguish *Stormbergia* from *Lesothosaurus*.

PHYLOGENETIC RELATIONSHIPS OF UPPER ELLIOT ORNITHISCHIANS

PREVIOUS WORK

The phylogeny of basal Ornithischia has been little-studied, especially when compared to recent advances

in basal saurischian phylogeny (e.g. Rauhut, 2003; references therein). A succession of papers discussing ornithischian phylogeny within a cladistic framework appeared in the early 1980s (Maryańska & Osmólska, 1984, 1985; Norman, 1984; Sereno, 1984; Cooper, 1985; Sereno, 1986) with that of Sereno (1986) proving the most influential. Most subsequent authors have limited their analyses to more derived clades within Ornithischia.

Sereno (1984, 1986) proposed that *Lesothosaurus* was the sister-group to Genasauria, a group comprising all other ornithischians ('*Ankylosaurus, Triceratops*, their most recent common ancestor and all descendents'; Sereno, 1998), a view approximately equivalent to the precladistic analyses of Galton (1972), and this interpretation has been followed by later authors (e.g. Weishampel & Witmer, 1990a). This contrasts with previous views of ornithischian phylogeny (Thulborn, 1971b; Norman, 1984; Cooper, 1985; Maryańska & Osmólska, 1985), which usually considered *Lesothosaurus* to have affinities with Ornithopoda, and sometimes a larger group that additionally included the pachycephalosaurs and ceratopsians (Norman, 1984). Sereno (1991, 1997, 1999) slightly modified his earlier hypothesis by considering *Pisanosaurus mertii*, from the Upper Triassic of Argentina, as the most basal ornithischian, with *Lesothosaurus* still positioned as the sister-group of Genasauria. This interpretation of the position of *Lesothosaurus* is based upon a number of putative synapomorphies supposedly shared by Genasauria, and absent in *Lesothosaurus*. The distribution of these putative synapomorphies is discussed below:

- Maxillary dentition offset medially (Sereno, 1984, 1986, 1999). Sereno (1991: 178) noted that there is a weak linear prominence present on the lateral maxilla, above the row of external maxillary foramina, and that the surface of the maxilla is everted near the maxilla-jugal suture. However, Sereno (1991) claimed that this was not homologous with the more marked medial offset of the entire maxillary tooth row seen in other ornithischians. The maxillary tooth row is slightly inset along its length in *Lesothosaurus (*e.g. Sereno, 1991; fig. 5; BMNH R8501), in an identical position to other ornithischians. The condition in *Lesothosaurus* is herein viewed as homologous with the emargination in other ornithischians, *contra* Sereno (1991). A comparably weak emargination is seen in the genasaurians *Scutellosaurus* (Colbert, 1981), *Echinodon* (Norman & Barrett, 2002) and *Abrictosaurus* (BMNH RUB54).
- Spout-shaped mandibular symphysis (Sereno, 1984, 1986). Shown to be present in *Lesothosaurus* by Sereno (1991).
- Coronoid process, depth more than 50% of the depth of the dentary (Sereno, 1986, 1999). The coronoid eminence is weak in *Lesothosaurus*, but is no better developed in basal thyreophorans (*Scutellosaurus*, Colbert, 1981; *Emausaurus*, Haubold, 1990; fig. 2).
- Edentulous anterior portion of the premaxilla present (Sereno, 1986). Sereno (1991) has since reported a short edentulous anterior portion of the premaxilla in *Lesothosaurus*. An edentulous portion is absent in the genasaurian *Bugenasaura* (Galton, 1999b; SDSM 7210). Although this feature has been reported as absent in *Agilisaurus* (Peng, 1992), a short edentulous portion, similar to that developed in *Lesothosaurus*, is in fact present (ZDM T6011). The premaxilla of the holotype specimen of *Jeholosaurus* (IVPP V12529) is damaged, and so the presence or absence of an edentulous portion in this taxon cannot be determined (*contra* Xu *et al*., 2000).
- Entire margin of the antorbital fossa sharply defined (Sereno, 1986). This is a difficult character to define in practice as the degree to which the margin of the antorbital fossa is sharply defined is extremely variable in basal ornithischian taxa. The genasaurians *Emausaurus* (Haubold, 1990: fig. 2) and *Lycorhinus* (Gow, 1975) have an identical state to that seen in *Lesothosaurus*. The primitive thyreophoran, *Scelidosaurus*, has an antorbital fossa that is weakly defined along its entire margin (BMNH R1111).
- External mandibular fenestra relatively smaller (Sereno, 1986). The mandibular fenestra of *Lesothosaurus* is not significantly larger than that seen in heterodontosaurids (*Heterodontosaurus,* SAM K1332; *Abrictosaurus*, BMNH RUB54) or basal thyreophorans (*Emausaurus*, Haubold, 1990; fig. 2).
- Pubic peduncle of ilium relatively less robust than ischial peduncle (Sereno, 1986, 1999). *Scelidosaurus*, the only basal thyreophoran for which the ilium is adequately known, has a very similar pubic peduncle (Fig. 24B; BMNH R1111, R6704) to that of *Lesothosaurus* (Fig. 24A). The pubic peduncle is also robust in *Heterodontosaurus* (SAM-PK-K1332) and *Abrictosaurus* (BMNH RUB54). The pubic peduncle is reduced in many derived taxa, such as *Hypsilophodon* (Fig. 24C).

Thus, none of the putative synapomorphies apparently defining a monophyletic Genasauria to the exclusion of *Lesothosaurus* actually appear to unambiguously support this hypothesis. Other hypotheses regarding the phylogenetic position of *Lesothosaurus* have been generated. Galton (1972, 1978) considered *Lesothosaurus* to belong to the family Fabrosauridae, envisioned as the basal group of ornithischians, which also included *Nanosaurus* and *Echinodon*. Sereno (1991) demonstrated the polyphyletic

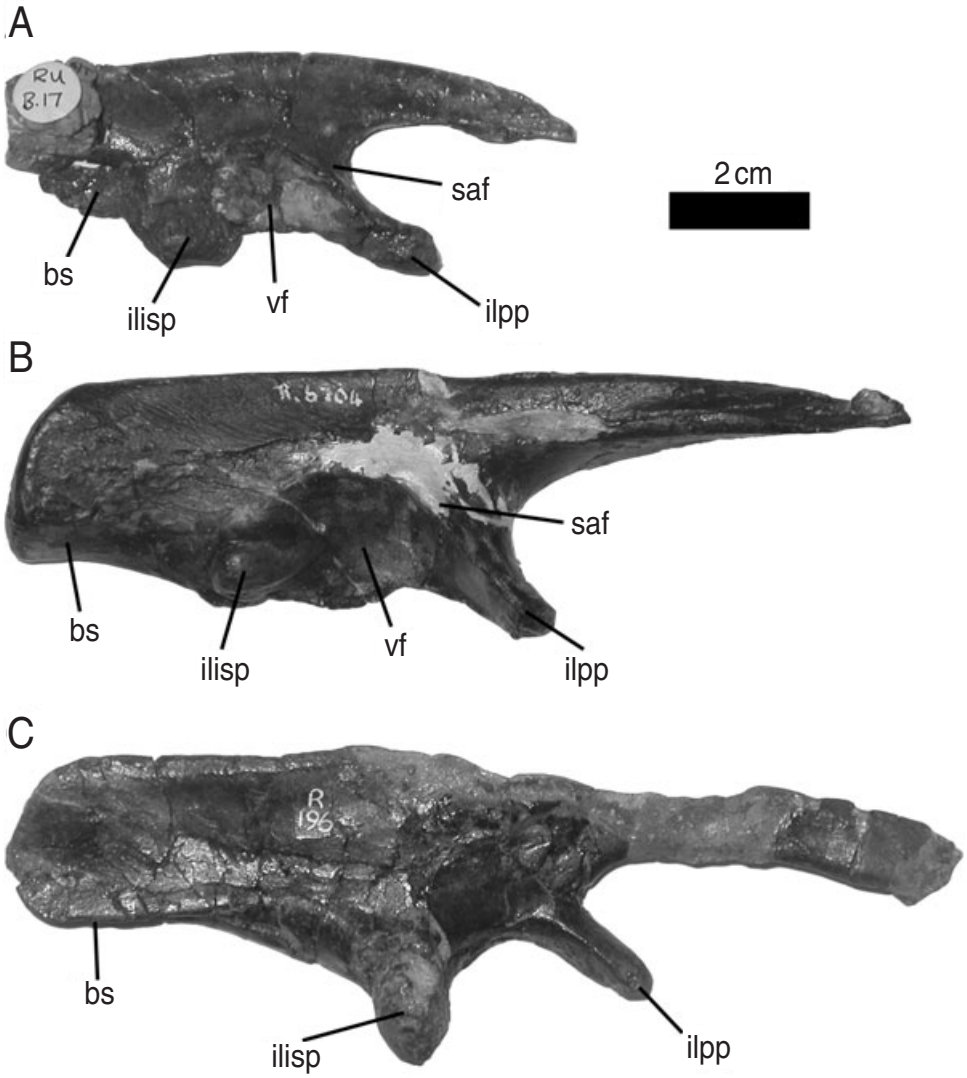

Figure 24. Right ilia of *Lesothosaurus diagnosticus* (A: BMNH RUB17), *Scelidosaurus harrisoni* (B: BMNH R6704) and *Hypsilophodon foxii* (C: BMNH R196). Note the plesiomorphic retention of a supraacetabular flange and a ventral flange backing the acetabulum in *Lesothosaurus* and *Scelidosaurus*; both these features are lost in *Hypsilophodon*. The pubic peduncle is elongate, and larger than the ischiadic peduncle, in both *Lesothosaurus* and *Scelidosaurus*. The brevis shelf angles ventromedially in *Lesothosaurus* and *Scelidosaurus* and is visible in lateral view, creating a deep postacetabular portion of the ilium. The brevis shelf of *Hypsilophodon* is horizontal. Abbreviations: bs, brevis shelf; ilpp, peduncle; ilisp, ischiadic peduncle; saf, supraacetabular flange; vf, ventral flange partially backing the acetabulum.

nature of this family, which had been used as a taxonomic 'waste basket' for all small primitive ornithischians. Peng (1997) revived the family and included within it *Lesothosaurus* and three Chinese taxa *Agilisaurus*, *'Yandusaurus' multidens* and *Gongbusaurus*. The latter taxa have been considered to be hypsilophodontids by other authors (Sues & Norman, 1990; Weishampel & Heinrich, 1992), but the monophyly of Hypsilophodontidae is poorly supported (Weishampel *et al*., 2003). Peng (1997) suggested a number of characters to diagnose Fabrosauridae, most of which were suggested by Sereno (1991) as autapomorphic for *Lesothosaurus*. The distribution of these characters has been discussed in the previous section on *Lesothosaurus* taxonomy.

Finally, although the phylogenetic position of *Stormbergia* has never been formally analysed, Knoll (2002a, b) considered *Stormbergia* (referred to as 'the large fabrosaurid') to form an Upper Elliot Formation 'fabrosaurid clade' with *Lesothosaurus*.

PHYLOGENETIC ANALYSIS

In order to assess the affinities of *Stormbergia*, and to test the hypothesis that *Lesothosaurus* represents the

sister-group of almost all other ornithischians (Sereno, 1986, 1999), a preliminary phylogenetic analysis was carried out. A more detailed review of ornithischian phylogeny is currently in preparation by the author. The analysis included a variety of important basal ornithischians, with data collected from first-hand examination and the literature (Table 3); more derived ornithischian groups that are widely considered to be monophyletic (Ceratopsia, Pachycephalosauria, Stegosauria, Ankylosauria) were coded as composite taxa. The interrelationships of the basal Thyreophora were not considered in detail, as they are not of primary concern here, but will be considered elsewhere. Iguanodontia (*sensu* Weishampel *et al*., 2003) was coded as a composite taxon comprising *Tenontosaurus* and more derived ornithopods. The monophyly of this group has withstood widespread scrutiny (e.g. Sereno, 1986; Weishampel & Heinrich, 1992; Coria & Salgado, 1996; Winkler, Murry & Jacobs, 1997; Weishampel *et al*., 2003).

A number of important potentially basal taxa (e.g. *Bugenasaura, Othnielia, Orodromeus*) were not included here, either because of their fragmentary nature or because they have not, as yet, been examined at first hand by the author. These taxa will be included in the more comprehensive analysis mentioned above.

The analysis assumed a topology in which Dinosauria is a monophyletic taxon divided into the clades Ornithischia and Saurischia. *Marasuchus*, *Lagerpeton*, Pterosauria and *Euparkeria* form successively more distant outgroups to Dinosauria. Two taxa were here coded to polarize character state transformations. Saurischia is coded based upon the literature and personal observations of basal theropods and sauropodomorphs (Table 3), while *Marasuchus* is coded from the literature (Table 3).

The analysis included 23 terminal taxa, and a matrix of 73 characters (Appendices 1–2). Characters were culled from the literature and personal observations. Analyses of the data matrix (Appendix 1) were carried out using PAUP* v.4.0b10 (Swofford, 1998). Characters 39 and 67 were ordered as they were deemed to form part of transformation series; all other characters were considered unordered. A branch-and-bound search was carried out which generated 48 most parsimonious trees (MPTs) with a length of 157 steps (CI = 0.776). Strict (Fig. 25), 50% majority rule (Fig. 26) and Adams consensus trees were generated. Character states were optimized onto the strict consensus tree; synapomorphies supporting each node are given in Appendix 3.

A bootstrap analysis of the data was carried out with 1000 replicates. Very few ornithischian clades were well-supported by the analysis (Fig. 25). Decay analysis was also carried out. Most clades have a decay index of one: that is they are not recovered in the strict consensus of all trees one step longer than the most parsimonious trees. A few clades (e.g. Neornithischia, Heterodontosauridae, Marginocephalia, Eurypoda) have decay indices higher than one (Fig. 25), which are generally those clades with high bootstrap values.

RESULTS

The resulting phylogeny (Figs 25, 26) differs significantly from the analyses of Sereno (1986, 1999). *Lesothosaurus* does not appear as the sister-group of Genasauria (Fig. 25: B); rather the basal split within Ornithischia is between Thyreophora (including *Scutellosaurus, Emausaurus, Scelidosaurus*, ankylosaurs and stegosaurs) and a branch (Fig. 25: C) consisting of all other ornithischians (except *Pisanosaurus*), which should be termed Neornithischia according to previous phylogenetic definitions ('All genasaurs closer to *Triceratops* than to *Ankylosaurus*'; Sereno, 1998). However, the monophyly of Neornithischia is weakly supported by this analysis and the clade does not appear in the 50% majority rule bootstrap tree.

The position of *Lesothosaurus* within Neornithischia is supported by three unequivocal characters: reduction of the forelimb to less than 40% of the hindlimb length (47), presence of a dorsal groove on the ischium (57) and a strongly reduced, splint-like metatarsal one (69). *Lesothosaurus* and the undescribed Lower Elliot Formation ornithischian (SAM-PK-K8025) form an unresolved polytomy with more derived taxa at the base of Neornithischia. *Stormbergia* appears to be more derived within Neornithischia than *Lesothosaurus*; this is supported by one unequivocal character (55: presence of a tab-shaped obturator process) and three equivocal character under accelerated transformation (ACCTRAN). Only one of these (56: loss of an elongate ischial symphysis) is herein viewed as significant; the other two (37, 39) refer to cranial states that are unknown in *Stormbergia*. There is no evidence for a clade containing *Stormbergia* and *Lesothosaurus* to the exclusion of other ornithischians.

Two Chinese taxa (*Agilisaurus, 'Yandusaurus' multidens*) are positioned outside of Ornithopoda as basal neornithischians (Figs 25, 26). This conflicts with previous interpretations (Sues & Norman, 1990; Weishampel & Heinrich, 1992; Weishampel *et al*., 2003; Norman *et al*., 2004c) of *Agilisaurus* and *'Y.' multidens* as basal ornithopods, but is closer to the work of Peng (1992, 1997) who identified *Agilisaurus* as a basal ornithischian. *'Y.' multidens* and *Agilisaurus* form serially more distant outgroups to a clade consisting of Heterodontosauridae, Marginocephalia and

Table 3. Operational taxonomic units (OTU) used in the phylogenetic analysis, and the sources from which anatomical information was obtained

OTU	Specimens examined	References used
Marasuchus lilloensis		Sereno & Arcucci (1994)
Saurischia	SAM-PK-1314, BP/1/4376, 4693, 5241 (all *Massospondylus*); MCZ 7063, 7064 (*Herrerasaurus*); MCZ 9331, UC, casts of *Eoraptor*	Cooper (1981); Welles (1984); Colbert (1989); Novas (1993); Sereno (1993); Sereno & Novas (1993); Langer (2004); Galton & Upchurch (2004a)
Pisanosaurus merti		Casamiquela (1967); Bonaparte (1976); Sereno (1991)
Lesothosaurus diagnosticus	BMNH RUB17 (syntype), RUB23 (syntype), R11965, R11004, R8501; SAM-PK-400, 401, 1106	Thulborn (1970), (1972); Santa Luca (1984); Sereno (1991)
Lower Elliot Formation taxon	SAM-PK-K8025	
Stormbergia dangershoeki	SAM-PK-K1105 (holotype); BMNH R11000 (paratype); BP/1/4885	
Heterodontosaurus tucki	SAM-PK-K337 (holotype), K1332	Weishampel & Witmer (1990b); Norman *et al*. (2004c)
Abrictosaurus consors	BMNH RUB54 (holotype)	Thulborn (1974)
Agilisaurus louderbacki	ZDM T6011 (holotype)	Peng (1992), (1997)
Jeholosaurus shangyuanensis	IVPP V12529 (holotype), V12530	Xu *et al*. (2000)
'Yandusaurus' multidens	ZDM T6001 (holotype)	He & Cai (1984)
Hypsilophodon foxii	BMNH R196, R197 (holotype), R2477	Galton (1974a)
Gasparinisaura cincosaltensis		Coria & Salgado (1996); Salgado, Coria & Heredia (1997)
Thescelosaurus neglectus		Gilmore (1915); Sternberg (1940); Galton (1974b), (1997)
Parksosaurus warreni		Parks (1926); Galton (1973)
Iguanodontia	BMNH numerous bones (*Zalmoxes robustus*); MCZ 4205, MOR 682 (both *Tenontosaurus*)	Norman (1980); Galton (1981); (1983); Forster (1990); Weishampel *et al*. (2003); Norman (2004)
Scelidosaurus harrisonii	BMNH R1111 (holotype), R6704; BRSMG Ce12785	Barrett (2001); Norman, Witmer & Weishampel (2004b)
Scutellosaurus lawleri	MNA P1.175 (holotype), P1. 1752 (paratype); MCZ numerous fragmentary specimens	Colbert (1981); Rosenbaum & Padian (2000)
Emausaurus ernsti		Haubold (1990)
Stegosauria	IVPP V6728 (holotype of *Huayangosaurus*); ZDM 7001(*Huayangosaurus*) BMNH 46013 (holotype of *Dacentrurus*), R1989 (holotype of *Lexovisaurus*)	Sereno & Dong (1992); Galton & Upchurch (2004b)
Ankylosauria	IVPP V12560 (holotype of *Liaoningosaurus*) (2004)	Vickaryous, Maryańska & Weishampel
Pachycephalosauria	IVPP V4447 (holotype of *Wannanosaurus*); BMNH R10055 (cast of *Stegoceras*)	Maryańska & Osmólska (1974); Maryańska, Chapman & Weishampel (2004)
Ceratopsia	IGCAGS V371 (holotype of *Chaoyangsaurus*); IVPP V12704 (holotype of *Hongshanosaurus*), V12738 (holotype of *Liaoceratops*), V11114, V11115 (holotype and paratype of *Archaeoceratops*)	Sereno (1987); You & Dodson (2004)

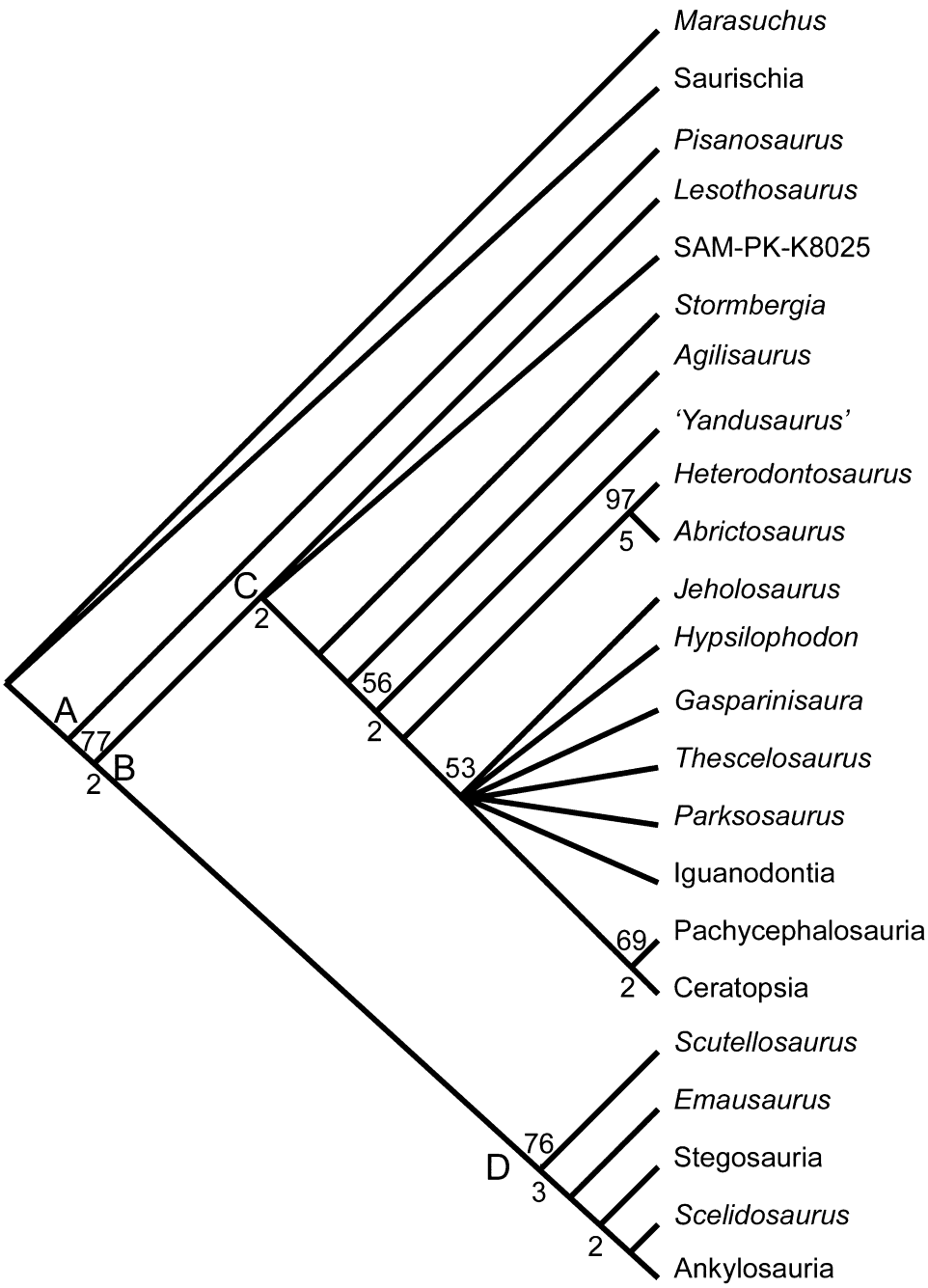

Figure 25. Strict consensus of 48 most parsimonious trees. Letters correspond to names of clades: A, Ornithischia; B, Genasauria; C, Neornithischia; D, Thyreophora. The numbers above nodes represent bootstrap values. Unnumbered nodes have a bootstrap value of less than 50%. Numbers beneath nodes are the decay indices for those nodes. Unnumbered nodes have a decay index of 1.

Ornithopoda. There is no evidence for a 'fabrosaurid' clade consisting of *Lesothosaurus*, *Agilisaurus* and '*Yandusaurus' multidens*, as suggested by Peng (1997).

Heterodontosauridae is positioned as the sister-group to a clade consisting of Ornithopoda and Marginocephalia. This is in contrast with analyses that suggest a robust link for Heterodontosauridae with Hypsilophodontidae and Iguanodontia (Sereno, 1986, 1999) or with Marginocephalia (Maryańska & Osmólska, 1984; Cooper, 1985; You, Xu & Wang, 2003), but equivalent to the position proposed by Maryańska & Osmólska (1985). Heterodontosaurs are phylogenetically problematic for several reasons. The skull of *Heterodontosaurus* has never received a complete

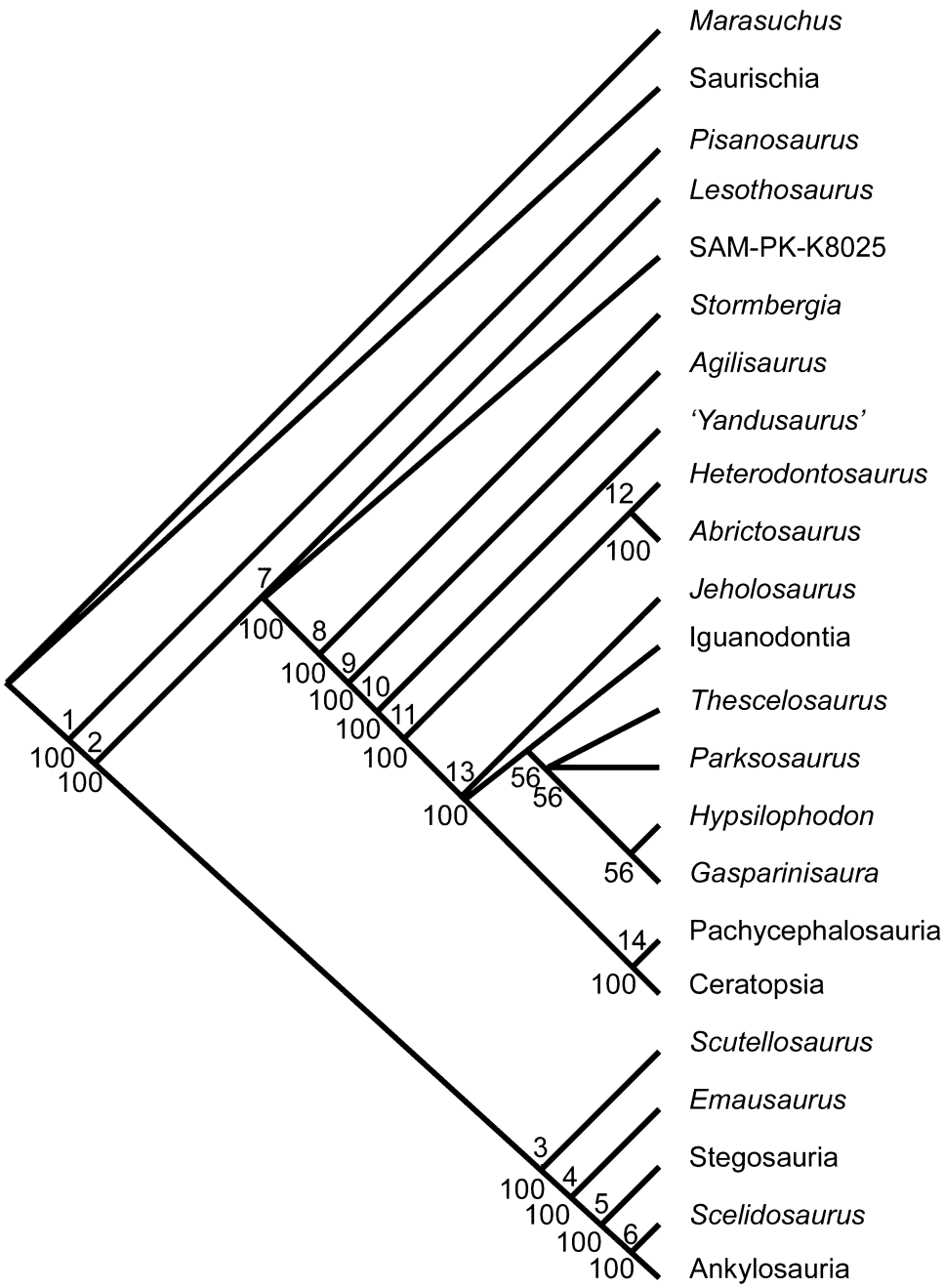

Figure 26. 50% majority-rule consensus of 23 most parsimonious trees (MPTs). Numbers beneath nodes represent the percentage of MPTs in which that clade appears. The numbers above each node refer to the list of character-state transformations provided in Appendix 3.

description, and some details of the description of the skull of *Abrictosaurus* (Thulborn, 1974) are inaccurate. Many workers have compounded this problem by coding only *Heterodontosaurus* (as the most completely known taxon) in phylogenetic analyses. However, *Heterodontosaurus* is apparently derived in many of its features; more basal heterodontosaurs (*Abrictosaurus*, *Echinodon*, undescribed heterodontosaur material from the Kayenta and Morrison Formations) retain many primitive features. Thus characters that have been cited to link *Heterodontosaurus* with marginocephalians or ornithopods are often absent in more primitive heterodontosaurs, suggesting that they were acquired in parallel. A detailed review of the phylogenetic position of heterodontosaurs is in preparation by the author.

The monophyly of Hypsilophodontidae is very weakly supported by this analysis. However, most recent work (e.g. Scheetz, 1999; Weishampel *et al*., 2003; Norman *et al*., 2004c) has considered them a paraphyletic grade of ornithopods. A full discussion of hypsilophodontid monophyly will be provided elsewhere.

SUMMARY AND CONCLUSIONS

The Upper Elliot Formation (Lower Jurassic) of South Africa and Lesotho yields one of the world's most important faunae of basal ornithischian dinosaurs. A review of the anatomy, taxonomy and systematics of the non-heterodontosaurid ornithischians of this fauna has been carried out, based upon the examination of all known Upper Elliot material. '*Fabrosaurus australis*' Ginsburg, 1964 is considered a *nomen dubium*. Two valid non-heterodontosaurid ornithischians are recognized from the Upper Elliot: *Lesothosaurus diagnosticus* Galton (1978) and *Stormbergia dangershoeki* gen. et sp. nov. *Lesothosaurus* is rediagnosed based upon the possession of a unique combination of characters. *Stormbergia dangershoeki* is described and figured based upon three partial skeletons. A fourth partial skeleton (SAM-PK-K1107) may also be referable to *Stormbergia*, but further discoveries are needed to ascertain this. *Stormbergia* is distinguished from other Elliot Formation non-heterodontosaurid ornithischians by its large size, an untwisted ischial shaft with a tab-shaped obturator process, and a short ischial symphysis. It adds to the known diversity of Lower Jurassic ornithischians, and demonstrates an earlier acquisition of moderately large body size in basal ornithischians than previously recognized. The plesiomorphic similarity of known material of *Lesothosaurus* and *Stormbergia* means that it is difficult to refer many specimens to either taxon with certainty, and caution should be exercised.

The palaeoecology of *Lesothosaurus* is reviewed by Norman *et al*. (2004a); their interpretations are relevant to *Stormbergia*, with its closely similar morphology. The forelimb of *Stormbergia* is poorly known, but was clearly strongly reduced relative to the hindlimb. This suggests a predominantly bipedal form, with the forearms free for use in foraging. The tibia and metatarsals are elongate relative to the femur (although not as elongate as in *Lesothosaurus*) and these proportions suggest a relatively agile, active lifestyle. The pes contained only three functional, weight-bearing, digits.

Some puzzling aspects of the Upper Elliot fauna should be mentioned. The first is the abundance of predominantly herbivorous dinosaurs in what has traditionally been considered a semiarid desert environment. To date at least one basal sauropodomorph (*Massospondylus*), three heterodontosaurids (*Heterodontosaurus*, *Abrictosaurus*, *Lycorhinus*) and two basal ornithischians (*Lesothosaurus*, *Stormbergia*) are recognized as valid taxa, and this seems diverse given the seemingly harsh, arid Elliot environment. Weishampel & Witmer (1990b) speculated that at least some of the dinosaur remains may have been transported into the area of deposition by floods, but this remains unsubstantiated by sedimentological evidence. However, Barrett (2000) interprets basal sauropodomorphs, basal ornithischians and heterodontosaurids as facultative omnivores, so the problem may be more apparent than real. There is also an apparent absence of large predators feeding on this diversity of herbivores. Fragmentary remains of a small coelurosaurian dinosaur, referred to *Syntarsus rhodesiensis* (Raath, 1980), represent the only known theropod.

The systematics of basal ornithischians requires extensive future work. Preliminary analyses position *Lesothosaurus* basally within Neornithischia, rather than as the sister-group of Genasauria as proposed in previous analyses (Sereno, 1986, 1999). However, evidence in support of this position is weak. The structure of the ischium indicates that *Stormbergia* is more derived within Ornithischia than *Lesothosaurus*. No evidence is found to support a monophyletic Fabrosauridae; rather, the taxa previously referred to Fabrosauridae by Peng (1997) appear to form a pectinate series of outgroups to more derived neornithischians.

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APPENDIX 1

TAXON CHARACTER-STATE MATRIX

	10	20	30	40
Marasuchus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? 1
Saurischia	1 0 1 0 – 0 0 0 0 0	P 0 0 0 0 0 0 0 0 0	0 0 – – 0 0 0 0 0 0	0 0 – – 0 0 0 0 0 0
Pisanosaurus	? ? ? ? ? ? ? 0 0 0	? ? ? ? ? ? ? 1 ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? 0 1 1 1 ?
Lesothosaurus	0 1 0 0 – 0 0 0 0 1	1 0 0 1 0 0 1 1 0 0	0 1 0 0 0 0 0 0 0 0	? 1 0 0 1 0 0 1 1 0
SAM-PK-K8025	? ? ? ? ? 0 0 0 ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? 1 0 0 1 1 ?
Stormbergia	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? 0
Heterodontosaurus	2 1 1 1 1 1 1 1 1 0	1 1 1 0 0 1 1 0 0 1	0 1 0 0 0 0 0 ? 0 1	0 1 0 1 0 0 1 1 1 0
Abrictosaurus	2 1 1 1 ? 1 1 1 1 0	1 0 1 0 0 0 1 0 0 ?	0 1 0 0 ? ? ? ? ? ?	? 1 1 1 0 0 1 1 1 ?
Agilisaurus	1 1 0 0 – 0 0 0 0 ?	1 0 0 ? 0 1 1 ? 0 0	0 1 0 0 0 ? 1 0 0 1	? 1 0 0 1 0 1 1 2 1
Jeholosaurus	0 1 0 1 0 0 ? 0 ? ?	1 1 0 ? 0 1 1 ? 1 0	0 ? ? ? 1 ? ? ? 0 ?	? 1 1 0 1 0 ? 1 2 ?
Yandsaurus'	? ? ? ? ? 0 0 0 0 ?	1 0 ? ? 0 ? 1 ? 1 0	0 1 0 1 0 0 0 0 0 1	? 1 ? ? 1 0 1 1 ? 1
Hypsilophodon	1 1 0 1 0 0 1 1 0 1	1 0 1 1 0 1 1 0 1 0	0 1 0 1 1 1 0 1 0 1	0 1 1 0 1 0 1 1 2 1
Gasparinisaura	? ? ? ? ? ? 0 ? 1 0 ?	? ? ? ? 1 1 1 0 1 0	0 1 0 0 0 0 0 ? 0 0	? 1 ? ? ? 0 1 1 2 ?
Thescelosaurus	? ? ? ? ? ? 0 1 ? 0 ?	? ? ? ? ? ? ? 1 ? 1 0	0 1 0 1 ? ? 0 1 0 ?	? 1 ? ? 1 0 1 1 2 ?
Parksosaurus	? ? ? ? ? ? 0 ? 0 0 1	1 0 ? ? 1 1 1 0 1 0	0 ? ? ? ? ? ? 0 ? 0 ?	? 1 ? ? ? ? 0 ? ? ? ?
Iguanodontia	2 1 0 1 0 0 1 0 0 1	1 1 1 0 1 1 1 0 P 0	0 1 0 P P 1 0 0 0 P	0 1 1 0 1 0 1 1 2 1
Scelidosaurus	1 ? 0 0 – 0 0 2 0 1	1 0 0 ? 1 0 1 0 0 0	1 1 1 ? 0 1 1 0 0 0	0 1 ? ? 1 1 0 1 2 0
Scutellosaurus	0 ? ? ? ? ? 0 0 ? ? 1	? 0 ? ? ? ? ? 1 ? ? 0	1 ? ? ? ? ? ? 1 1 ? ?	? ? ? ? ? ? 0 0 1 ? ?
Emausaurus	1 ? 0 0 – 0 0 2 0 1	1 0 0 0 0 0 0 1 0 0 0	1 1 0 1 0 1 1 0 0 ?	? 1 0 0 1 1 0 1 1 ?
Stegosauria	0 1 0 0 – 0 0 2 0 1	1 0 0 0 1 1 1 0 0 0	1 1 1 ? 0 1 1 0 0 P	0 1 0 0 1 1 0 1 1 1
Ankylosauria	? 1 0 0 – 0 0 2 0 1	1 ? 0 0 2 – 1 ? ? ?	1 1 1 ? ? ? 1 0 0 0	0 1 0 1 1 1 1 1 2 1
Pachycephalosauria	2 1 0 1 1 0 ? 0 0 1	1 0 P 0 2 – 1 0 1 1	0 1 1 ? 0 1 0 0 1 1	1 1 0 ? 0 0 0 1 2 ?
Ceratopsia	2 1 0 1 0 P 1 1 0 1	1 P 0 0 P 1 1 0 0 1	0 1 0 1 0 1 0 0 1 P	1 1 1 0 1 0 1 1 2 1

	50	60	70	
Marasuchus	1 ? 0 0 ? 0 0 0 0 –	0 0 1 0 0 0 0 0 – –	0 0 0 0 0 0 0 0 0 0	0 0 0
Saurischia	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 P 0 – –	0 0 0 0 0 0 0 0 0 0	0 0 0
Pisanosaurus	? ? ? ? ? ? ? ? ? ?	? 0 ? ? ? 0 ? 0 ? ?	? ? ? ? ? ? 1 ? ? ?	? 0 0
Lesothosaurus	1 ? 1 ? 0 0 1 1 0 0	0 0 0 0 0 0 0 1 1 0 0	0 0 1 0 0 0 2 1 1 0	1 0 0
SAM-PK-K8025	? ? 1 ? 0 0 1 1 0 0	0 0 0 0 0 0 0 1 1 0 0	0 0 1 0 0 0 2 ? ? ?	1 0 0
Stormbergia	1 ? 1 ? 0 0 1 1 0 0	0 0 0 0 1 1 1 1 0 0	0 0 1 0 0 0 2 1 1 0	1 0 0
Heterodontosaurus	1 2 2 0 0 1 0 1 0 1	0 1 1 0 0 1 0 1 0 0	0 0 ? 1 1 0 2 1 1 0	1 0 0
Abrictosaurus	? ? 1 ? 0 ? 0 1 0 1	0 1 1 0 0 ? ? 1 ? ?	? 0 1 0 1 0 2 ? ? ?	? 0 0
Agilisaurus	1 0 1 0 1 0 1 1 1 0	0 0 0 0 1 0 1 1 1 0	0 0 1 0 0 0 2 1 1 0	1 0 0
Jeholosaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? 0 2 0 ? 0 2 1 1 ?	? 0 0
Yandsaurus'	1 0 1 0 1 0 1 1 1 1	0 0 1 0 1 1 1 0 1 1 1	0 0 1 0 0 0 2 1 1 ?	1 0 0
Hypsilophodon	1 0 2 1 0 0 0 1 1 1	2 1 1 1 1 1 1 0 1 1 1	1 0 2 0 1 0 2 1 0 1	1 0 0
Gasparinisaura	1 ? 2 ? ? 0 ? 1 1 1	0 1 1 1 1 1 1 0 1 1 1	1 0 ? 1 1 ? 2 1 ? 1	1 0 0
Thescelosaurus	? 1 1 1 0 0 0 1 1 1	0 1 1 ? 1 1 1 0 1 1 1	1 1 2 0 1 1 2 1 0 1	1 0 0
Parksosaurus	? 1 2 1 0 0 0 1 1 1	0 ? 1 ? 1 1 1 0 1 1 1	1 1 2 1 1 1 0 2 1 0 1	1 0 0
Iguanodontia	1 1 2 0 0 0 0 1 1 1	0 1 1 1 1 1 1 0 1 1 0	1 1 2 0 1 1 2 1 1 P	1 0 0
Scelidosaurus	0 0 1 0 0 0 0 1 0 0	1 0 0 0 0 1 0 1 0 0	0 0 1 0 0 1 2 1 0 0	1 1 1
Scutellosaurus	? 0 1 ? 0 0 0 1 ? ?	0 ? ? 0 0 0 ? 1 ? ?	0 0 1 0 0 0 2 ? ? ?	1 1 0
Emausaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? 1 0
Stegosauria	1 ? 1 0 0 0 0 1 0 ?	1 0 0 0 0 1 0 1 1 0	0 P ? 1 ? 1 2 1 2 0	0 1 0
Ankylosauria	1 ? 1 0 0 0 0 1 ? ?	1 0 ? 0 0 1 0 1 0 ?	0 P ? 1 ? 1 2 1 0 0	1 1 1
Pachycephalosauria	? ? 2 ? 0 1 1 1 1 1	2 1 1 1 0 1 0 1 1 0	1 0 ? 0 1 0 2 ? ? 1	1 0 1
Ceratopsia	1 2 2 0 0 P 0 1 1 1	2 1 1 1 0 1 0 1 P P	1 0 2 0 1 0 2 1 0 0	1 0 0

APPENDIX 2

CHARACTER-STATE LISTING

Characters drawn and rescored from the literature, including: Norman (1984), Sereno (1984, 1986, 1991, 1999), Weishampel & Witmer (1990b), Weishampel & Heinrich (1992), Coria & Salgado (1996), Norman & Barrett (2002) and Weishampel *et al*. (2003).

1. Premaxillary teeth: 6 or more (0); 4–5 (1); 3 or less (2).
2. Premaxilla, edentulous anterior portion: absent (0); first premaxillary tooth inset the width of one or more crowns (1).
3. Premaxillary teeth, crown shape: recurved, transversely flattened, constricted at base (0); straight, subcylindrical, unconstricted (1).
4. Premaxilla-maxilla diastema: absent (0); present (1).
5. Premaxilla-maxilla diastema: absent or flat (0); arched with caniform anterior dentary tooth (1).
6. Denticles restricted to apical third of crown of maxillary/dentary teeth: absent (0); present (1).
7. Enamel on cheek teeth: symmetrical (0); asymmetrical (1).
8. Maxillary teeth, number: 14–18 (0); 12 or less (1); more than 20 (2).
9. Anterior two dentary teeth lack denticles, first tooth strongly reduced: absent (0); present (1).
10. Special foramina medial to dentary and maxillary tooth rows: absent (0); present (1).
11. Premaxillary, posterolateral process: absent (0); present, maxilla excluded from nasal margin (1).
12. Premaxillary, posterolateral process: does not reach lacrimal (0); contacts lacrimal, excludes maxilla – nasal contact (1).
13. Position of the ventral margin of the premaxilla: level with the maxillary tooth row (0) deflected ventral to tooth row (1).
14. Anterior premaxillary foramen: absent (0); present (1).
15. Antorbital fossa, size: large, 15–25% basal skull length (0); reduced (1); absent (2).
16. Antorbital fossa: rounds smoothly onto the maxilla, at least along some part of its margin (0); sharply defined or extended as a secondary lateral wall enclosing the fossa (1).
17. Maxilla, buccal emargination: absent (0); present (1).
18. Notch in maxilla for lacrimal: absent (0); present (1).
19. Exclusion of the jugal from the margin of the antorbital fossa by lacrimal-maxilla contact: absent (0); present (1).
20. Jugal boss or lateral extension: absent (0); present (1).
21. Jugal orbital ramus, depth vs. transverse breadth: deeper (0); broader (1).
22. Accessory ossification (palpebral/supraorbital): absent (0); present (1).
23. Palpebral/supraorbital: free, projects into orbit from contact with lacrimal/prefrontal (0); incorporated into orbital margin (1).
24. Free palpebral, length, relative to anteroposterior width of orbit: long, 70–100% of orbital width (0); reduced (1).
25. Large quadratojugal foramen: absent (0); present (1).
26. Contact between dorsal process of quadratojugal and descending process of the squamosal: present (0); absent (1).
27. Mandibular articulation: condyles subequal (0); medial condyle larger (1).
28. Paired frontals: wider than long (0); longer than wide (1).
29. Parietosquamosal shelf, absent (0); present (1).
30. Paroccipital processes: extend laterally and are slightly expanded distally (0) distal end pendent and ventrally extending (1).
31. Premaxillary border of internal nares: present (0); absent (1).
32. Predentary: absent (0); present (1).
33. Predentary size: less than (0); or equal (1) to the length of the premaxilla.
34. Predentary, ventral process: present (0); very reduced or absent (1).
35. Dentary symphysis: V-shaped (0); spout-shaped (1).
36. Dentary tooth row in lateral view: straight (0); sinuous (1).
37. Coronoid process; absent or weak, posterodorsally oblique (0); well-developed, distinctly elevated (1).
38. Anterior portion of coronoid process formed by posterior process of dentary: absent (0); present (1).
39. External mandibular fenestra, situated on dentary–surangular–angular boundary: large (anteroposterior length more than maximum depth of dentary ramus) (0); reduced (anteroposterior length less than maximum depth of dentary ramus) (1); absent (2) [ORDERED].
40. Epipophyses on anterior cervical 3: present (0); absent (1).
41. Axial epipophyses: at least vestigally present (0); absent (1).
42. Dorsals, number: 15 (0); 16 or more (1); 12–13 (2).
43. Sacrals, number: 2–3 (0); 4–5 (1); 6 or more (2).
44. Ossified sternal ribs: absent (0); present (1).
45. Proportions of humerus and scapula: scapula longer or subequal in length to humerus (0); humerus much longer than scapula (1).

46. Scapula blade: relatively short, length is 5–8 times minimum width (0); elongate and strap-like, length is at least 9 times the minimum width (1).
47. Forelimb, reduced to 40% of hindlimb length: absent (0); present (1).
48. Preacetabular process, shape/length: triangular, distal end is posterior to pubic peduncle (0); strap-like, distal end is anterior to pubic peduncle (1).
49. Pubic peduncle of the ilium: more robust than the ischial peduncle, expands in lateral view (0); reduced, tapers (1).
50. Ilium with vertical brevis shelf: present (0); absent (1).
51. Length of the postacetabular process as a percentage of the ilium length: 30% (0); 20% or less (1); 40% or more (2).
52. Ventral acetabular flange: present (0); absent (1).
53. Supracetabular rim: present (0); absent (1).
54. Lateral swelling of the ischiadic peduncle of the ilium: not broadly swollen (0); broad swelling (1).
55. Tab-shaped obturator process on ischium: absent (0); present (1).
56. Ischial symphysis: along at least 50% of ischial length (0); distally only (1).
57. Dorsal groove on the ischium: absent (0); present (1).
58. Pubis, orientation: anteroventral (0); posteroventrally rotated (1).
59. Prepubic process, length (from obturator notch) as percentage of ilium length: poorly developed, less than 20% (0); elongated into elongate process (1).
60. Prepubic process: laterally flattened (0); rod-like (1); dorsoventrally flattened (2).
61. Femur, saddle-shaped 'trench' between greater trochanter and head: absent, greater trochanter and head continuous (0); present, greater trochanter and head distinct (1).
62. Fourth trochanter, position: proximal half of the femur (0); positioned at midlength or more distal (1).
63. Anterior trochanter: prominent crest (0); wide, similar in width to the greater trochanter, and separated from it by a wide cleft (1); narrow, closely appressed to the expanded greater trochanter (2).
64. Cleft (intertrochantic notch) between anterior and greater trochanters: present (0); absent, trochanters fused (1).
65. Level of anterior trochanter relative to femoral head: at significantly lower level (0); at approximately the same level (1).
66. Femoral length: shorter or equal in length to tibia (0); longer than tibia (1).
67. Tibial posterior flange, lateral extension: does not reach fibula (0); extends posterior to medial margin of fibula (1); extends posterior to entire distal end of fibula and calcaneum (2) [ORDERED].
68. Metatarsal 5 development: 40–50% of metatarsal 3 (0); less than 25% of metatarsal 3 (1).
69. Metatarsal 1: MT1 well-developed (0); MT1 reduced to less than 50% of MT3, proximally splint like, but distally bears digits (1) MT1 absent (2).
70. Ossified hypaxial tendons, present on caudal vertebrae: absent (0); present (1).
71. Epaxial ossified tendons: absent (0); present (1).
72. Postcranial osteoderms: absent (0); present (1).
73. Dermal sculpturing of the skull/mandible: absent (0); present (1).

APPENDIX 3

TREE DESCRIPTION

The 'tree description' option of PAUP and the 'character tracing' option of MacClade were used to interpret character state transformations. Transformation was evaluated under accelerated transformation (ACCTRAN) and delayed transformation (DELTRAN) options: ACCTRAN favours reversals over convergences and assumes character transformation at the lowest possible node; DELTRAN favours convergences over reversals and assumes character transformations at the highest possible node. Node numbers refer to Figure 26. Character state transformations are not provided for clades that do not appear in the majority-rule consensus. For simple 0–1 state changes only the character number is given; for others the type of change is specified in parentheses.

Node 1: Ornithischia
Unambiguous: 17, 38, 39, 67 (0–1).
ACCTRAN: 2, 22, 32, 35, 43, 48, 63, 68, 71

Node 2: Genasauria (Thyreophora + Neornithischia)
Unambiguous: 10, 58, 67 (1–2)
DELTRAN: 2, 22, 32, 35, 43, 48, 63, 68, 71

Node 3. *Scutellosaurus* + (*Emausaurus* + Eurypoda)
Unambiguous: 21, 27, 72
ACCTRAN –8, 24, 26

Node 4. *Emausaurus* + Eurypoda
Unambiguous: 36
ACCTRAN: 51, 56, 64, 66
DELTRAN: 8 (0–2), 26, 36

Node 5. Eurypoda (Ankylosauria + Stegosauria)
Unambiguous: 15, 23
DELTRAN: 51, 56, 66

Node 6. *Scelidosaurus* + other ankylosaurs
Unambiguous: 39 (1–2), 73
ACCTRAN: 34

Node 7. *Lesothosaurus* + SAM-PK-K8025 + more derived neornithischians
Unambiguous: 47, 57, 69

Node 8. *Stormbergia* + more derived neornithischians
Unambiguous: 55
ACCTRAN: 37, 39 (1–2), 56

Node 9. *Agilisaurus* + more derived neornithischians
Unambiguous: 49, 59
ACCTRAN: 45
DELTRAN: 16, 30, 37

Node 10. '*Yandusaurus*' + more derived neornithischians
Unambiguous: 47 (1–0), 50, 53, 57 (0–1)
ACCTRAN: 1 (1–2), 4, 19, 33
DELTRAN: 56

Node 11. Heterodontosauridae + Cerapoda
Unambiguous: 7, 42, 52, 65
ACCTRAN: 43, 45
DELTRAN: 1 (1–2), 4

Node 12. Heterodontosauridae
Unambiguous: 3, 6, 8, 9, 10 (1–0), 13, 34, 35 (1–0), 49 (1–0), 55 (1–0)
ACCTRAN: 5, 19 (1–0), 20, 39 (2–1), 40 (1–0), 46, 59 (1–0)

Node 13. 'Cerapoda' (unresolved node)
Unambiguous: 54, 61, 63 (1–2)
ACCTRAN: 24, 26, 39 (1–2), 43 (1–2), 51, 54, 70

Node 14. Ceratopsia + Pachycephalosauria
Unambiguous: 20, 29, 31, 51, 55
ACCTRAN: 46