

A primitive ornithischian dinosaur from the Late Triassic of South Africa, and the early evolution and diversification of Ornithischia

Richard J. Butler^{1,2,*}, Roger M. H. Smith³ and David B. Norman²

¹Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

²Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EQ, UK

³Department of Karoo Palaeontology, Iziko South African Museum, PO Box 61, Cape Town 8000, Republic of South Africa

Although the group played an important role in the evolution of Late Mesozoic terrestrial ecosystems, the early evolutionary history of the ornithischian dinosaurs remains poorly understood. Here, we report on a new primitive ornithischian, *Eocursor parvus* gen. et sp. nov., from the Late Triassic (?Norian) Lower Elliot Formation of South Africa. *Eocursor* is known from a single specimen comprising substantial cranial and postcranial material and represents the most complete Triassic member of Ornithischia, providing the earliest evidence for the acquisition of many key ornithischian postcranial characters, including an opisthopubic pelvis. A new phylogenetic analysis positions this taxon near the base of Ornithischia, as the sister taxon to the important and diverse clade Genasauria. The problematic clade Heterodontosauridae is also positioned basal to Genasauria, suggesting that an enlarged grasping manus may represent a plesiomorphic ornithischian condition. This analysis provides additional phylogenetic support for limited ornithischian diversity during the Late Triassic, and suggests that several major ornithischian clades may have originated later than generally believed. There are few morphological differences between Late Triassic and Early Jurassic ornithischians, supporting previous suggestions that the Early Jurassic ornithischian radiation may simply represent the filling of vacant ecological space following Late Triassic terrestrial extinctions.

Keywords: Ornithischia; Genasauria; Heterodontosauridae; Elliot Formation; Late Triassic

1. INTRODUCTION

Ornithischia was a large and diverse clade of dinosaurs that included well-known forms such as hadrosaurs, ceratopsians, pachycephalosaurs, ankylosaurs and stegosaurs. Ornithischians dominated the herbivorous faunas of many Late Mesozoic terrestrial ecosystems and have provided fertile ground for studies of dinosaur biogeography and palaeobiology; their evolution was characterized by trends including increases in body size, the origin and elaboration of postcranial armour (osteoderms) and the development of sophisticated feeding mechanisms, elaborate cranial ornamentation and complex social behaviours (Sereni 1997; Weishampel *et al.* 2004a). The first ornithischians appeared during the Late Triassic (Bonaparte 1976; Sereni 1997; Báez & Marsicano 2001; Irmis *et al.* 2007); however, ornithischian specimens from this period are exceptionally rare and highly fragmentary, frustrating attempts to study the group's early evolution (Parker *et al.* 2005; Irmis *et al.* 2007). Here we describe a new partial skeleton of a primitive ornithischian from the Late Triassic of South Africa, providing important new information on the early

evolution of the clade. This specimen was previously included as an unnamed taxon in a preliminary phylogenetic analysis of basal ornithischians (Butler 2005a); it possesses several autapomorphies and can furthermore be distinguished from all other early ornithischian taxa by a number of features—as a result, we designate the new specimen as the holotype of a new genus.

2. SYSTEMATIC PALAEONTOLOGY

Dinosauria Owen (1842)

Ornithischia Seeley (1887)

Eocursor parvus gen. et sp. nov.

(a) *Etymology*

From *eos* (Greek, dawn), *cursor* (Latin, runner) and *parvus* (Latin, little), in reference to the early occurrence of this ornithischian, its apparent locomotory abilities and its small size.

(b) *Holotype*

Iziko South African Museum SAM-PK-K8025; disarticulated partial skeleton including parietal, supraoccipital, basisphenoid, parasphenoid, right dentary, surangular and angular, isolated cheek tooth, fragmentary cervical, dorsal, sacral and caudal vertebrae, scapulae, humeri, radius, six manual phalanges, ilia, ischia, pubes, femora, tibiae, fibulae, right metatarsals II and III and three pedal phalanges (figure 2).

* Author and address for correspondence: Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK (r.butler@nhm.ac.uk).

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Figure 1. Skeletal reconstruction of *E. parvus* gen. et sp. nov. based upon SAM-PK-K8025, demonstrating preserved elements and body proportions. Scale bar, 100 mm. Reconstruction by Scott Hartman.

(c) *Locality and horizon*

Damplaats Farm, Ladybrand District, Free State, Republic of South Africa; upper part of the Lower Elliot Formation (Smith *et al.* 1993; Bordy *et al.* 2004), ?Norian stage of the Late Triassic (Lucas & Hancox 2001; see electronic supplementary material for further details).

(d) *Diagnosis*

A basal ornithischian distinguished by the following autapomorphies: accessory fossa present on lateral surface of basisphenoid, posterior to the canal for the internal carotid artery; maximum transverse expansion of the distal end of the humerus is only 50% of maximum transverse expansion of proximal humerus; and pubic obturator foramen subcircular and enlarged (maximum dorsoventral diameter of foramen is twice the maximum diameter of proximal pubic shaft). *Eocursor* can additionally be distinguished from all other basal ornithischian taxa by a unique combination of derived and plesiomorphic features (see electronic supplementary material for details).

(e) *Description*

The holotype skeleton of *Eocursor* comprises a disarticulated but associated partial postcranial skeleton (approx. 25% complete, most large appendicular elements are well preserved) with fragmentary cranial remains (figure 1), representing a single small individual (length approx. 1 m, height at hips approx. 300 mm). Cervical and caudal neurocentral sutures are closed but visible, while dorsal and sacral sutures are unfused, suggesting that this animal represents a subadult (Brochu 1996). The general morphology of *Eocursor* resembles that of Early Jurassic ornithischians including *Lesothosaurus*, *Scelidosaurus*, *Scutellosoaurus* and *Stormbergia* (Colbert 1981; Sereno 1991; Norman *et al.* 2004a,b; Butler 2005), while some elements (notably the manus) show similarities to the basal ornithischian clade, Heterodontosauridae (Santa Luca 1980).

A prominent accessory fossa is present on the lateral surface of the basisphenoid, posterior to the canal for the internal carotid artery (electronic supplementary material, figure S3a). This accessory fossa is unknown in other ornithischians (e.g. Galton 1989; Sereno 1991), and may represent an autapomorphy of *Eocursor*. The lower jaw is elongate with a low coronoid process (figure 2a). The anterior end of the dentary is poorly preserved, so the presence or absence of a predentary cannot be confirmed. As in all ornithischians (Sereno 1999), the anterior margin of the coronoid process is formed by a posterodorsally directed process of the dentary. Anteriorly, the ventral margin of the dentary is weakly inturned to form a

spout-like symphysis. The posterior two-thirds of the tooth row are inset medially, creating a narrow buccal emargination. Posteriorly, the jaw joint is offset a short distance below the dentary tooth row, as occurs in other basal ornithischians (e.g. Sereno 1991; Norman *et al.* 2004a). A short and weakly developed ridge, extending anteroposteriorly, is present on the external surface of the surangular, dorsolateral to the glenoid; a more prominent and elongate surangular ridge is present in a number of other early dinosaurs, including *Herrerasaurus*, *Lesothosaurus* and *Scelidosaurus* (Sereno 1991; Sereno & Novas 1993; Norman *et al.* 2004b). The teeth are low and triangular in labial view, with a weak labiolingual expansion of the crown base (a 'cingulum') and around six enlarged denticles on mesial and distal margins. Tooth-on-tooth wear facets are not present. The morphology of the teeth is suggestive of facultative herbivory in *Eocursor* (Barrett 2000).

The scapula has a well-developed acromion process (figure 2b), but is only weakly expanded at its posterior margin. The humerus (figure 2c) is approximately equal in length to the scapula, and the distal end is notably weakly expanded transversely. The manus (figure 2d; electronic supplementary material, figure S3b,c) of *Eocursor* is incompletely preserved, and positional identifications of manual phalanges are problematic, although a number of unusual features are evident. As in basal saurischians (Sereno 1993) and the Early Jurassic ornithischian *Heterodontosaurus* (Santa Luca 1980), the manus is robust and elongated relative to the humerus when compared with other ornithischians: the longest preserved phalanx is 17% of the length of the humerus, compared with the values of 9–11% in small ornithischians, such as *Lesothosaurus* (Thulborn 1972; Sereno 1991), *Hexinlusaurus* (He & Cai 1984; Barrett *et al.* 2005) and *Hypsilophodon* (Galton 1974), and 19% in *Heterodontosaurus* (Santa Luca 1980). Furthermore, in *Eocursor*, distal manual phalanges exceed proximal manual phalanges in length, and at least some manual phalanges possess tongue-like median dorsal and ventral intercondylar processes proximally and dorsal extensor pits and deep collateral ligament pits distally. These features are also present in heterodontosaurids and some basal saurischians (Santa Luca 1980; Sereno 1993), but absent in other ornithischians (Galton 1974; He & Cai 1984; Sereno 1991).

The pelvis is well preserved (figure 2e–h). The ilium has an elongate strap-like preacetabular process and a quadrangular postacetabular process. As in other early dinosaurs (Novas 1996), the acetabulum was roofed dorsally by a well-developed, laterally projecting supra-acetabular flange. However, unlike the condition in many other early ornithischians (Sereno 1991; Norman *et al.* 2004a,b), the ventromedial flange of the ilium (which partially closed the acetabulum medially) is weakly developed. The brevis shelf is broad and nearly horizontal, unlike the condition in *Agilisaurus* (Peng 1992), *Lesothosaurus* (Sereno 1991) and *Scelidosaurus* (Norman *et al.* 2004b) in which the shelf is steeply inclined and faces ventrolaterally. Scars for sacral ribs indicate that the sacrum was formed by at least four (probably five) sacral vertebrae. The blade of the ischium lacks an obturator process and is twisted through 90° along its length. The ischial shafts meet along an elongate symphysis, as in *Lesothosaurus* and *Scutellosoaurus* (Butler 2005). The pubis

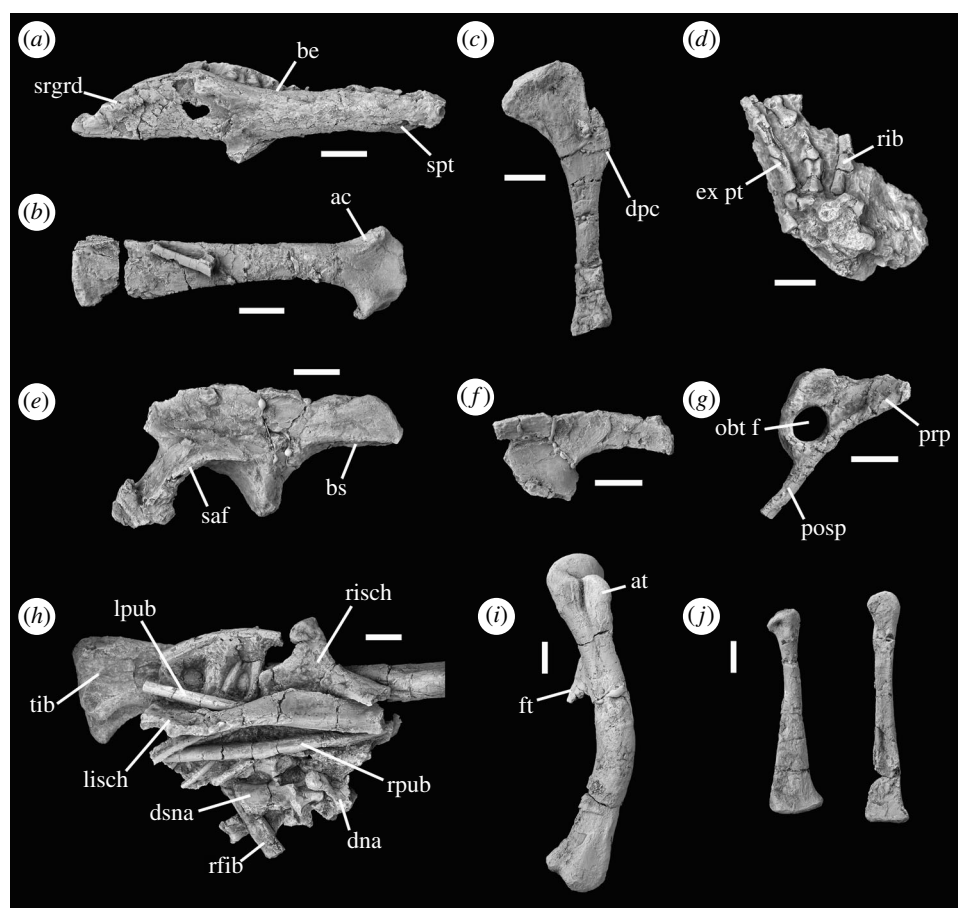


Figure 2. Anatomy of the holotype of *E. parvus* (SAM-PK-K8025). (a) Right mandible in lateral view. (b) Right scapula in lateral view. (c) Right humerus in posterior view. (d) Preserved manual phalanges in dorsal view. (e) Left ilium in lateral view (preacetabular process is missing). (f) Preacetabular process of right ilium in lateral view. (g) Prepubic process of left pubis in medial view. (h) Elements of pelvic region and hindlimb, including dorsal and sacral vertebrae, ischia (right ischium in medial view; left ischium in dorsal view), pubes, right tibia and fibula. (i) Right femur in lateral view. (j) Right metatarsals 2 (left) and 3 (right) in medial view. Scale bars, 10 mm. Abbreviations: ac, acromion process; at, anterior trochanter; be, buccal emargination; bs, brevis shelf; dna, neural arch of dorsal vertebra; dpc, deltopectoral crest; dsna, neural arch of dorsosacral vertebra; ex pt, extensor pit on dorsal surface of distal end of manual phalanx; fib, fibula; ft, fourth trochanter; lisch, left ischium; lpub, left pubis; obt f, obturator foramen; posp, pubic shaft; prp, prepubic process; risch, right ischium; rpub, right pubis; saf, supra-acetabular flange; spt, spout-shaped mandibular symphysis; srgd, weak ridge on lateral surface of surangular; tib, tibia.

is opisthopubic, with a short transversely compressed prepubic process and an elongate rod-like shaft. The portion of the pubis adjacent to the acetabulum is robust with an enlarged subcircular obturator foramen.

The femur (figure 2*i*) is shorter than the tibia, and is bowed gently anteriorly along its length. The turned articular head of the femur is not separated from the proximal trochanters, unlike the condition in many ornithischians (Galton 1974). The blade-like anterior trochanter is positioned medial and distal to the greater trochanter and is separated from it by a deep cleft. The fourth trochanter is pendant, and positioned on the proximal half of the femur. The tibia (figure 2*h*) and preserved elements of the metatarsus (figure 2*j*) and pes resemble those of other early ornithischians (Thulborn 1972; He & Cai 1984; Peng 1992). The tibia and metatarsals are elongated relative to the femur, implying well-developed cursorial abilities (Galton 1971; Thulborn 1972; Carrano 1999).

3. DISCUSSION

The only other relatively well-known Triassic ornithischian is *Pisanosaurus mertii* from the Carnian of Argentina (Bonaparte 1976); however, aspects of the

association and anatomy of the holotype specimen of *Pisanosaurus* are highly controversial (Bonaparte 1976; Sereno 1991; Norman *et al.* 2004a; Irmis *et al.* 2007). Although *Pisanosaurus* clearly demonstrates that some key cranial and dental characters related to herbivory (e.g. well-developed wear facets, inferred presence of cheeks, enlarged dentary) were present in ornithischians by the beginning of the Late Triassic, other ornithischian synapomorphies are either ambiguous (e.g. number of sacral vertebrae, pelvic morphology) or absent (e.g. a distal expansion of the tibia and corresponding features of the tarsus). By contrast, the more complete holotype specimen of *Eocursor* clearly possesses many key ornithischian features, including an increased number of sacral vertebrae, a strap-shaped preacetabular process of the ilium, an opisthopubic pelvis with a well-defined prepubic process, a blade-shaped anterior trochanter, a pendant fourth trochanter and a distally expanded tibia (Sereno 1999). *Eocursor* provides the earliest unambiguous evidence for the evolution of these features.

A phylogenetic analysis (electronic supplementary material) positions *Eocursor* near to the base of Ornithischia as the sister group of Genasauria, but in a

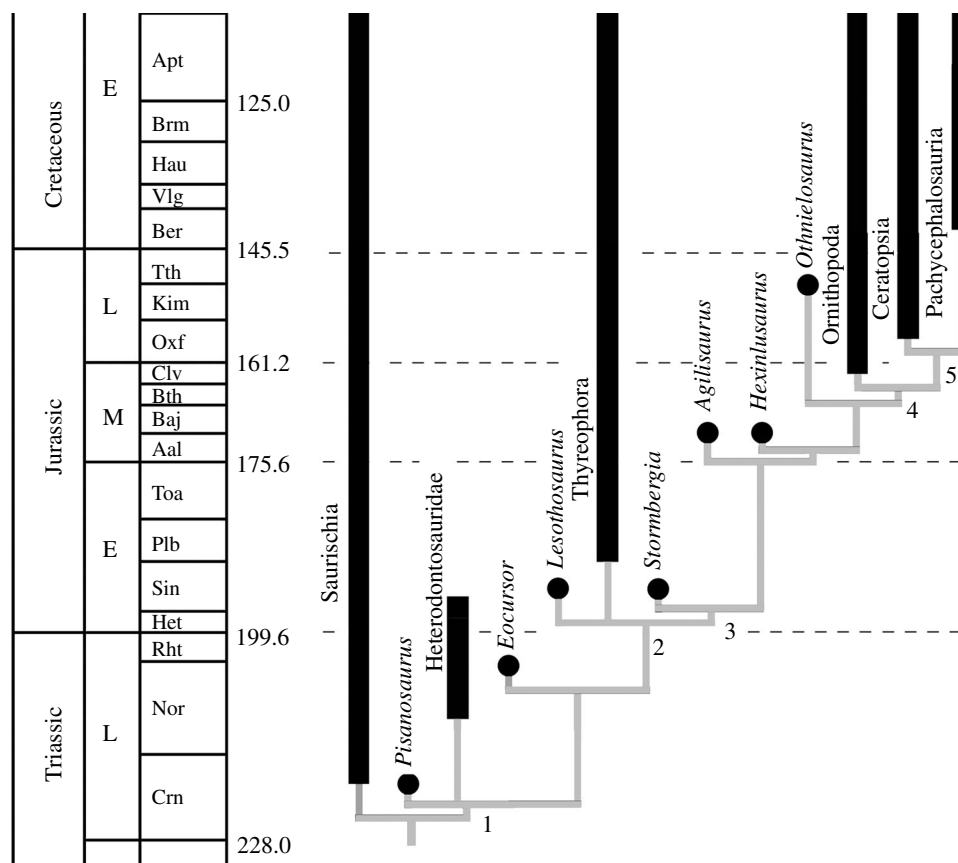


Figure 3. Temporally calibrated phylogeny of early ornithischian dinosaurs. The phylogeny is a simplified version of a cladogram produced by an analysis of 27 taxa and 150 characters (electronic supplementary material). Grey lines indicate ghost lineages. Minimum origination dates for major ornithischian clades include: Carnian (Late Triassic), Ornithischia; Hettangian (Early Jurassic), Genasauria, Thyreophora, Neornithischia; Callovian (Middle Jurassic), Cerapoda, Ornithopoda; Oxfordian (Late Jurassic), Marginocephalia. Numbers indicate clades: 1, Ornithischia; 2, Genasauria; 3, Neornithischia; 4, Cerapoda; 5, Marginocephalia.

more derived position than the enigmatic clade Heterodontosauridae (figure 3; electronic supplementary material, figure S2). Although previous analyses have interpreted the presence of an enlarged grasping manus (with elongated distal manual phalanges, prominent dorsal extensor pits and proximal intercondylar processes) as a feature unique to heterodontosaurids among ornithischians (Sereni 1986), this work suggests that this feature may represent a plesiomorphic dinosaurian condition, present in basal members of the ornithischian outgroup Saurischia (e.g. *Herrerasaurus*), the primitive and stratigraphically early ornithischian clade Heterodontosauridae and *Eocursor*.

Although some previous work has implied a Triassic origin for Genasauria and a significant pre-Jurassic ornithischian radiation (Báez & Marsicano 2001; Irmis *et al.* 2007), this analysis does not support that scenario. All known Triassic ornithischian taxa (*Eocursor*, *Pisanosaurus* (Bonaparte 1976) and Heterodontosauridae (Báez & Marsicano 2001)) are positioned basal to Genasauria in this analysis. It is therefore possible that neornithischian and thyreophoran ornithischians may not have arisen until the earliest Jurassic, while ornithopods and marginocephalians may not have appeared prior to the Middle Jurassic.

An alternative phylogenetic hypothesis for basal ornithischians was recently proposed by Xu *et al.* (2006). They described a new basal ceratopsian, *Yinlong downsi*, and provided character evidence and a

phylogenetic analysis to support a sister group relationship between heterodontosaurids and marginocephalians (this clade was named Heterodontosauriformes). This alternative topology would imply Triassic origins for Ornithopoda, Heterodontosauriformes and Thyreophora, based upon the Triassic occurrence of Heterodontosauridae (Báez & Marsicano 2001). *Yinlong* was included as a terminal taxon in the phylogenetic analysis carried out here, but a sister group relationship between Heterodontosauridae and Marginocephalia was not recovered. Future work on ornithischian phylogeny should concentrate on establishing the position of heterodontosaurids.

Recent work has demonstrated that previous reports of Triassic ornithischians from North America, Europe, North Africa and India are erroneous or at best questionable (Parker *et al.* 2005; Butler *et al.* 2006; Irmis *et al.* 2007). Verifiable ornithischian specimens are extremely scarce in Upper Triassic sediments, and are limited to Gondwana (Argentina and South Africa: Bonaparte 1976; Báez & Marsicano 2001; this paper). In contrast, by the Sinemurian stage of the Early Jurassic, ornithischians had achieved a global distribution and were, at least locally in North America and Africa, comparatively abundant and diverse (Norman *et al.* 2004a,b; Weishampel *et al.* 2004b; Butler 2005a), although they still formed a relatively minor component of global dinosaurian faunas. The fossil record suggests that ornithischians underwent a radiation in taxonomic

diversity, abundance and geographical range across the Triassic–Jurassic boundary (Sereno 1997), although the exact timing and rate of this diversification remains poorly understood.

The general morphology of *Eocursor* is most closely reminiscent of Early Jurassic ornithischians such as *Lesothosaurus* (Thulborn 1972; Sereno 1991) and *Scutelosaurus* (Colbert 1981). Similarly, a jaw fragment described from the Late Triassic of Argentina (Báez & Marsicano 2001) closely resembles *Heterodontosaurus*, otherwise only known from the Early Jurassic of South Africa (Santa Luca 1980). Few significant size-related or morphological differences are present between Norian (Late Triassic) and Sinemurian (Early Jurassic) ornithischians; this suggests that the Triassic–Jurassic ornithischian radiation cannot be linked to the acquisition of ‘key’ characters such as those relating to locomotion or dietary preferences. Instead, as proposed by previous authors (e.g. Sereno 1997), it seems probable that ornithischians radiated to fill ecological space left vacant by the Late Triassic extinctions of several clades of herbivorous synapsids and archosauromorphs (Olsen & Sues 1986).

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