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ABSTRACT

The mid-Cretaceous terrestrial deposits of southeastern Australia have yielded an unusual wealth of small-bodied ornithopod remains. Despite their numerical abundance, particularly from the Barremian–Cenomanian of New South Wales and Victoria, articulated remains are extremely rare. Here, we describe the first articulated remains of a small-bodied ornithopod, consisting of a partial hindlimb, from the Cenomanian Griman Creek Formation, which crops out in central-northern New South Wales. The hindlimb includes a number of unusual features not found in other small ornithopods, including a sharp supracondylar crest on the medial surface of the femur and a notched proximal margin of the ascending process of the astragalus. Although this combination of features appears to be unique, most known Australian taxa, including those from the Griman Creek Formation, are known only from isolated craniodental remains, making comparisons impossible. A phylogenetic analysis recovers the new specimen as an elasmarian with possible close affinities to the South American species *Isasicursor santacrucensis*. As the most complete small-bodied ornithopod yet recovered from the Griman Creek Formation, the new specimen reinforces the elasmarian affinities of at least some Australian ornithopods but also highlights the ongoing difficulties in attempting to resolve their diversity and relationships based on a highly incomplete fossil record.

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SMALL-BODIED, BIPEDAL ornithopods ('basal ornithopods') are typically rare in Cretaceous assemblages worldwide. The mid-Cretaceous exposures of southeastern Australia are a well-known exception to this rule, where small ornithopods are found in abundance in the Albian part of the Eumeralla Formation (Otway Basin) and the upper Barremian–lower Aptian Wonthaggi Formation (upper Strzelecki Group, Gippsland Basin) in Victoria (Rich & Vickers-Rich 1989, 1999, Herne *et al.* 2018, 2019, Poropat *et al.* 2018, Duncan *et al.* 2021) and the Cenomanian Griman Creek Formation (Surat Basin) in New South Wales (Molnar 1980, Molnar & Galton, 1986, Bell *et al.* 2018). Five locally endemic species have been described from the Eumeralla Formation and its lateral (but not entirely coeval) equivalent, the Wonthaggi

Formation (*Atlascopcosaurus loadsi* Rich & Vickers-Rich, 1989, *Diluvicursor pickeringi* Herne, Tait, Weisbecker, Hall, Nair, Cleeland & Salisbury, 2018, *Galleonosaurus dorisae* Herne, Nair, Evans & Tair, 2019, *Leaellynasaura amicagraphica* Rich & Vickers-Rich, 1989, *Qantassaurus intrepidus* Rich & Vickers-Rich, 1999) although there is disagreement as to the validity of some of these taxa, in part owing to the absence of overlapping material (Herne & Salisbury 2009, Agnolin *et al.* 2010, Rich *et al.* 2010, Poropat *et al.* 2018, Duncan *et al.* 2021). Part of this disagreement arises from the fact that most taxa were erected based on isolated craniodental remains, and the assignment of postcranial remains to the type series of *L. amicagraphica* has been viewed as contentious by some (Herne & Salisbury 2009; Herne *et al.* 2016). To complicate matters further, *D. pickeringi* is known only from a partial postcranial skeleton, although it represents one of the most complete skeletons of any Australian ornithopod (Herne *et al.* 2018).

In the Griman Creek Formation (GCF), which crops out near the town of Lightning Ridge in central-northern New South Wales, at least two

(possibly three) small-bodied ornithopods and a larger-bodied forms are known from cranial and post-cranial remains (Molnar & Galton 1986, Molnar 1996, Bell *et al.* 2018, 2019a). The first taxon to be formally described from the GCF was based on an isolated distal femur (NHMUK PV R3719, holotype of *Fulgurotherium australe* von Huene, 1932). The absence of autapomorphies in NHMUK PV R3719 led Agnolin *et al.* (2010) to consider the taxon a *nomen dubium* and all materials assigned to *F. australe*, including those from the Wonthaggi and Eumeralla formations of Victoria (Rich & Vickers-Rich 1989, 1999), are now considered indeterminate non-iguanodontian ornithopods (Agnolin *et al.* 2010). More recently, *Weewarrasaurus pobeni* Bell, Herne, Brougham & Smith, 2018 was named on the basis of a partial dentary from the GCF (Bell *et al.* 2018), and the associated remains of at least four individuals from a monodominant assemblage have been assigned to a second taxon, *Fostoria dhimbangunmal* Bell, Brougham, Herne, Frauenfelder & Smith, 2019a (see also Devereaux *et al.* 2024).

Despite the relative abundance of isolated small ornithopod remains in the GCF (Bell *et al.* 2018, 2019a), associated or articulated remains are exceedingly rare. In fact, only two associated dinosaurs, or accumulations, have been described from this interval after more than a century of collecting (Bell *et al.* 2016, Bell *et al.* 2019a). Two further undescribed specimens, AM F106298 (a partial ornithopod crus) and AM F127930 (a partial ornithopod hindlimb) are also known but have yet to be described. Here, we describe the best of these two specimens, AM F127930, a well-preserved left femur, tibia and astragalus of a small-bodied ornithopod, which was discovered in an open-cut mine on the 'Wyoming' or 'Ten Mile' opal field, approximately 10 km to the northwest of Lightning Ridge, by miners Bill and Yudi Kotru probably sometime during the 1990s. Importantly, the specimen was identified *in situ* and excavated by hand by miners (as opposed to being haphazardly exhumed by mining machinery, which is the typical mode of recovery at Lightning Ridge), during which process the femur and tibia were inadvertently broken. Whether or not the now-missing fibula was originally present is unknown. The specimen was acquired in 1999 by one of us (E.S.) and donated to the Australian Museum where it is now curated. As with all vertebrate remains from the GCF, AM F127930 is preserved in opal (SiO_2-nH_2O), which, in the present specimen, has obliterated details of the bone microstructure and obviates histological analysis.

The relative age/maturity of the individual is therefore unknown. Nevertheless, as the only articulated remains of a small-bodied ornithopod yet known from the GCF (the crus AM F106298 notwithstanding), the new material offers important insights into the anatomy and possible diversity of these animals, which dominated the high-paleolatitude faunas of southeastern Australia during the mid-Cretaceous.

Institutional abbreviations

AM, Australian Museum, Sydney, Australia; LRF, Australian Opal Centre, Lightning Ridge, Australia; NHMUK, Natural History Museum, London, England; MCF-PVPH, Museo Municipal 'Carmen Funes', Plaza Huincul, Neuquén, Argentina; MUCP, Museo de la Universidad Nacional del Comahue, Lago Barreales, Neuquén Province, Argentina; QM, Queensland Museum, Brisbane, Australia.

Geological setting

The GCF (Rolling Downs Group, Surat Basin) is an up to 345 m thick sedimentary package that crops out between the towns of Lightning Ridge (New South Wales) and Surat (Queensland) to the north (Reiser 1970, Exon 1976, Green *et al.* 1997, Price 1997) (Fig. 1A, B). Exon (1976) and Green *et al.* (1997) interpreted these deposits as a relatively complex succession of initially regressive beach or nearshore marine deposits, followed by paralic to deltaic conditions and finally floodplain deposits in the upper part of the sequence, that accumulated at or near the southeastern margin of the epeiric Eromanga Sea (Bell *et al.* 2019b).

In the Lightning Ridge area, which exclusively consists of the upper, terrestrial part of the succession, the GCF is divided into two informal members, the Wallangulla Sandstone Member and the overlying Coocoran Claystone Member (Moore 2002). Commercial opals and opalized fossils, including AM F127930, derive from the Wallangulla Sandstone Member (up to 19 m thick), which comprises fine- to medium-grained, locally cross-bedded kaolinitic sandstone and interbedded montmorillonite-rich claystone lenses. These sediments were deposited at a palaeolatitude of ∼60°S (Hay *et al.* 1999, Matthews *et al.* 2016) and are therefore considered as high latitude.

The GCF at Lightning Ridge has been recently reinterpreted as lower Cenomanian (100.2–96.6 Ma) based on radiometric dates obtained from a reworked ash horizon (Bell *et al.* 2019b). Outcrops of the lower,
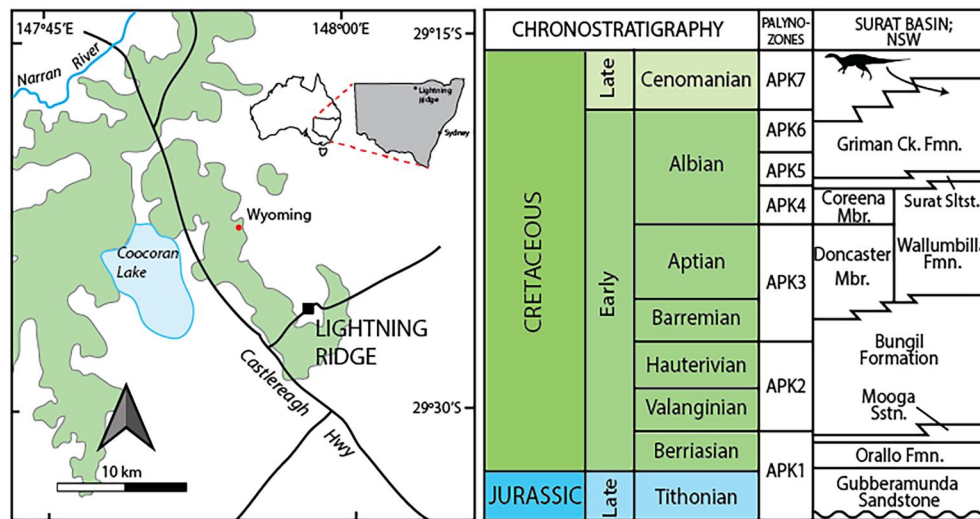
Fig. 1. Geographic and stratigraphic context of AM F127930. Map of the Lightning Ridge area in northern New South Wales (left) showing the subsurface extent of the Griman Creek Formation (green) and the locality of 'Wyoming' where AM F127930 was found. Chronostratigraphy of the Surat Basin (right). AM F127930 comes from the Cenomanian part of the Griman Creek Formation (arrow). Geological map based on Meakin (2011). Dinosaur silhouette created by Caleb M. Brown and used under the Creative Commons Attribution-ShareAlike 3.0 Unported licence made available through Phylopic. Chronostratigraphy based on Bell *et al.* (2019b).

more marine-influenced section of the GCF, which are exposed further to the north at Surat, were likely considerably older, possibly upper Albian in age (Raza *et al.* 2009). Exposures of the GCF at Lightning Ridge (and, hence the fossils described here) are therefore younger than the Eumeralla and Wonthaggi formations (upper Barremian–lower Albian) in Victoria to the south but temporally straddled by the Winton Formation (upper Albian–Turonian) in Queensland to the north.

Materials and methods

AM F127930 was surface scanned using a hand-held Artec Space Spider and converted to .stl files in MeshLab v.2020 (https://www.meshlab.net/). These 3D files are available from the authors. Descriptions of the distal tibia and proximal astragalus were aided by video footage taken by R.M. prior to the astragalus being glued in place by museum technicians sometime after 2000. Measurements of each element are provided in Supplementary Data 1.

Description

Femur

The left femur consists of two non-contiguous pieces, missing a section of the mid-shaft (Fig. 2). The overall length of the femur is therefore unknown. Despite this break, the femur is clearly bowed in lateral view

(Fig. 2G, H) as in other small-bodied ornithopods (Norman *et al.* 2004). When the femoral shaft is oriented vertically, the proximal end of the femur is medially inclined (Fig. 2A, B), unlike the straight (in anterior view) proximal femur of most other neornithischians (e.g., *Anabisetia saldiviai* Coria & Calvo, 2002 [MCF-PVPH-074], *Haya griva* Makovicky, Kilbourne, Sadleir & Norell, 2011, *Jeholosaurus shangyuanensis* Xu, Wang & You, 2000 [Han *et al.* 2012]; *Notohypsilophodon comodorensis* Martínez, 1998, *Orodromeus makelai* Horner & Weishampel, 1988 [Scheetz 1999]) and more derived iguanodontians. A similar medially inclined proximal femoral shaft is present in NMV P186326 (originally referred to *Fulgurotherium australe* by Rich & Vickers-Rich 1999) and possibly *Changchunsaurus parvus* Zan, Chen, Jin & Li, 2005 (Butler *et al.* 2011, Fig. 6), although the femur of that taxon is incompletely preserved. Viewed anteriorly, the proximal surface of the greater trochanter is higher than the femoral head. The lateral surface of the greater trochanter is markedly convex in proximal view (Fig. 2I, J), similar to another femur from the GCF (QMF10220), some Victorian femora (e.g., NMV P186326, NMV P199146) and *Dysalotosaurus lettowvorbecki* Virchow, 1919 (BMNH R6861). In other taxa, this surface is flat (e.g., *Hypsilophodon foxii* Huxley 1870 [Galton 1974]; *O. makelai* [Scheetz 1999]; *Parksosaurus warreni* Parks, 1926 [Brown *et al.* 2013, Sues *et al.* 2023]; *Thescelosaurus* spp. [Brown *et al.* 2013]; *Zalmoxes*
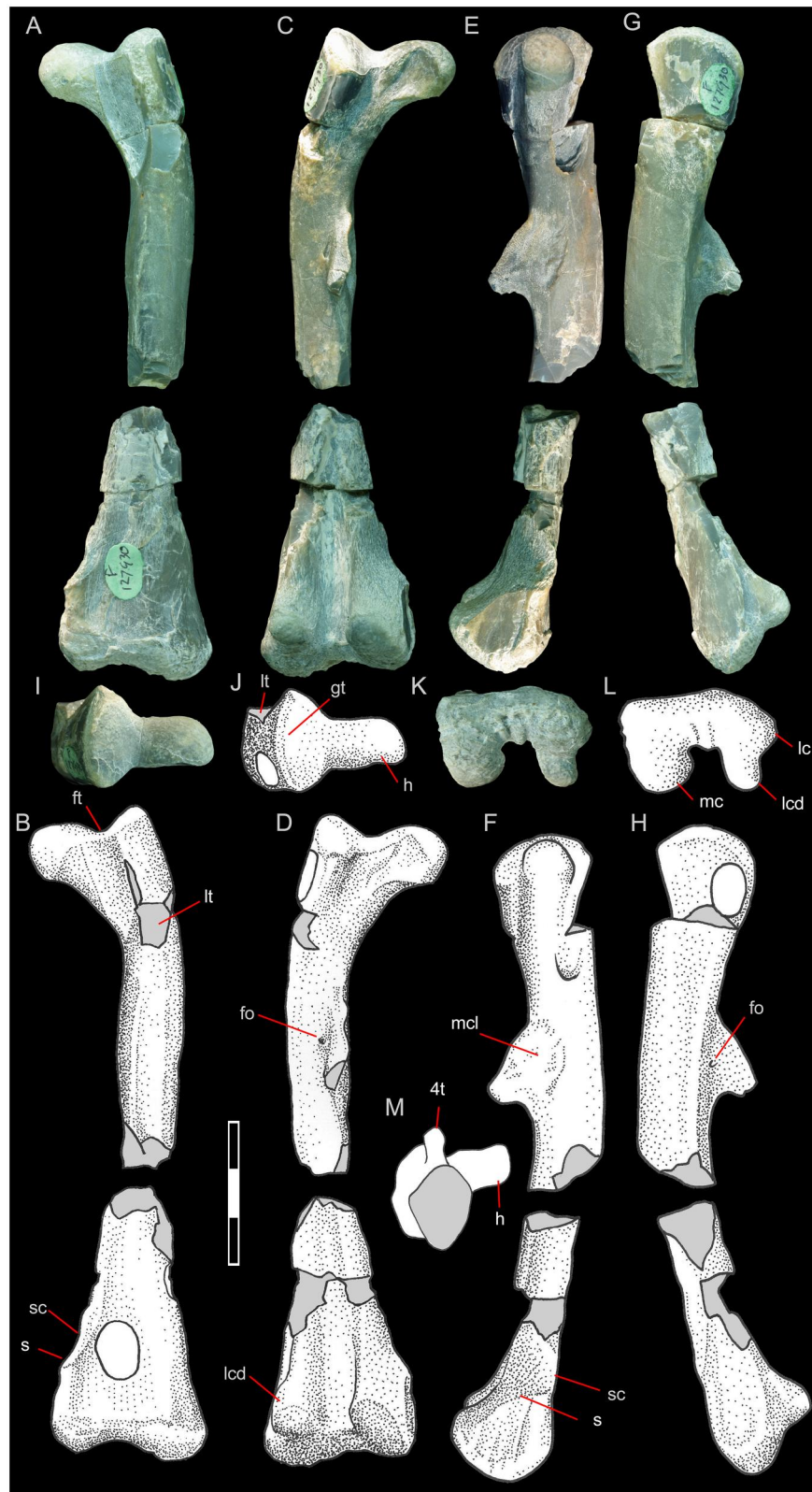
Fig. 2. Left femur of AM F127930. Photographs and interpretive illustrations in **A**, **B**, anterior, **C**, **D**, posterior, **E**, **F**, medial, **G**, **H**, lateral, **I**, **J**, proximal and **K**, **L**, distal views. Scale bar increments equal 1 cm. Abbreviations: 4t, fourth trochanter; fo, foramen; ft, fossa trochanteris, gt, greater trochanter; h, femoral head; lc, lateral condyle; lcd, lateral condylid; lt, lesser trochanter; mc, medial condyle; mcl, scar for m. caudofemoralis longus; s, shelf; sc, arcing ridge (=supracondylar ridge).

robustus Nopcsa, 1900 [BMNH R3834]; *N. comodorensis*) or sinuous (e.g., *A. saldiviai* [Coria & Calvo 2002]; *Gasparinisaura cincosaltensis,* [Coria & Salgado 1996]; *Morrosaurus antarcticus* Rozadilla, Agnolin, Novas, Rolando, Motta, Lirio & Isasi, 2016). Only the broken base of the lesser trochanter is preserved, therefore its overall shape can not be determined. The anterolateral edge of the greater trochanter (i.e., where the lesser trochanter would have been) is smooth and unbroken, suggesting that it was completely separated from the lesser trochanter and not fused to it as it is in *G. cincosaltensis, O. makelai* and *P. warreni* (Norman *et al.* 2004). At the broken base of the lesser trochanter, a strong anterolaterally situated ridge extends the length of the shaft, twisting to a more anterior position distally (Fig. 2B), as in Victorian Hypsilophodontid Femur Type 2 (Herne 2013, fig. E6.1). The femoral head forms a ~110° angle with the femoral shaft, similar to *A. saldiviai, G. cincosaltensis, O. makelai, N. comodorensis* and some Victorian femora (e.g., NMV P186326) but unlike other basally branching ornithopods (e.g., *H. foxii*) in which the femoral head is oriented at ~90° (Norman *et al.* 2004). In proximal view (Fig. 2I, J), the femoral head is centrally located with respect to the greater trochanter as in many Victorian femora (e.g., NMV P186326), QM F10220, *D. lettowvorbecki* (BMNH R6861) and *H. foxii* (BMNH R196), but differing from *A. saldiviai* (Coria & Calvo 2002), *M. antarcticus* (Rozadilla *et al.* 2016), *N. comodorensis* (Martínez 1998), *G. cincosaltensis* (Salgado *et al.* 1997) and *Kangnasaurus coetzeei* Haughton, 1915 (Cooper 1985) in which the femoral head is posteriorly offset. A deep, angular fossa trochanteris separates the femoral head from the lateral trochanters in anterior/posterior view. The posterior surface of the femoral head is excavated by an inverted teardrop-shaped depression that marks the insertion for the *M. iliotrochantericus* (Maidment & Barrett, 2011).

The fourth trochanter is placed posteromedially on the shaft and, although the femur is broken, clearly proximally situated (Fig. 2C, D), as is characteristic of non-styracosternan ornithopods (Norman *et al.* 2004). The fourth trochanter is mediolaterally compressed and triangular in lateral outline. The dorsal margin is sinuous in posterior and, to a lesser extent, medial/lateral views and the ventral margin is oriented nearly perpendicular to the long axis of the shaft (Fig. 2C–H). A pendant morphology (typical of non-iguanodontian ornithopods; Norman *et al.* 2004) can not be confirmed, as the distal tip of the trochanter is broken; however, it was clearly better developed than the low,

triangular fourth trochanter seen in *Iguanodon bernissartensis* Boulenger, 1881 and more derived Hadrosauriformes (Norman 2004). Laterally, at the base of the fourth trochanter, the femoral shaft is pierced by a small elliptical foramen (Fig. 2C, D). A similar foramen, albeit more proximally situated, has been figured for a variety of ornithopods (e.g., Gilmore 1915, Han *et al.* 2012, Brown *et al.* 2013) and probably represents the femoral nutrient foramen (Seymour *et al.* 2012). A large ovoid depression at the base of the fourth trochanter (Fig. 2E, F) on the medial side marks the attachment for *M. caudofemoralis longus* (Galton 1974). Unlike dryosaurids and *A. saldiviai*, the scar is not separated from the base of the fourth trochanter. The length of this scar is approximately equal to the proximodistal length of the fourth trochanter.

The distal end of the femur is mediolaterally and anteroposteriorly expanded into two condyles (Fig. 2K, L). The medial condyle is approximately twice as mediolaterally wide as the lateral condylid. The medial condyle and lateral condylid extend posteriorly to approximately the same level (in distal view), which differs from *O. makelai* (Scheetz, 1999) where they are unequal in length. The lateral condylid is incompletely preserved in NHMUK PV R3719 (holotype of 'Fulgurotherium australe'), *M. antarcticus, N. comodorensis* (Cambiaso 2007). It also differs from some specimens of *D. lettowvorbecki* (NHMUK PV R12277), *Trinisaura santamartaensis* Coria, Moly, Reguero, Santillana & Marenssi, 2013 and orodromines (Brown *et al.* 2013) in which the medial condyle and lateral condylid form relatively low eminences. The medial condyle is approximately hemispherical in distal aspect and slightly expanded laterally to partially enclose the posterior intercondylar groove, similar to *A. saldiviai* and *G. cincosaltensis*, but contrasting with *Fostoria dhimbangunmal* (LRF 3050), *Muttaburrasaurus langdoni* Bartholomai & Molnar, 1981 (QM F6140) and many Dryomorpha where the medial expansion of the medial condyle is more strongly developed (see also Dieudonné *et al.* 2016). The medial surface of the medial condyle is flat, proximal to which the femoral shaft forms a distinct obliquely sloping shelf in anteroposterior view (Fig. 2A, B). This shelf is separated from the medial condyle by an arcing ridge (supracondylar ridge of Molnar 1980) that becomes vertically inclined and sharp-edged on the anteromedial part of the distal femoral shaft (Fig. 2A, B, E, F). This ridge and its associated surfaces can not be confidently associated with any musculature (e.g., Maidment & Barrett 2011), nor is the ridge the result of diagenetic crushing. Molnar (1980) identified a weak supracondylar ridge in NHMUK PV

R3719 (holotype of '*F. australe*') and several other isolated femora from the GCF (accession numbers not given by Molnar [1980] but present in QM F10220 based on plate 1 in Molnar and Galton [1986]). A similar ridge appears in *J. shangyuanensis* (Han *et al.* 2012); however, in all cases, these ridges are best described as incipient in comparison with AM F127930. This ridge is absent in other neornithischians, including *A. saldiviai* (MCF-PVPH-74); *G. cincosaltensis* (MUCPv 208); *H. griva* (Makovicky *et al.* 2011, fig. 5); *O. makelai* (MOR 1692) and *Thescelosaurus assiniboiensis* Brown, Boyd & Russell, 2011 (Brown *et al.* 2011, fig. 20) and therefore appears unique to AM F127930. The lateral condylid is only slightly inset from the lateral margin of the lateral condyle, forming a shallow groove for attachment of the *M. iliofibularis*, similar to some non-iguanodontian ornithopods (e.g., *A. saldiviai, O. makelai, J. shangyuanensis*). In contrast, most iguanodontians (except rhabdodontids; Dieudonné *et al.* 2016), including *F. dhimbangunmal*, have a strongly inset lateral condylid forming a deep L-shaped notch in distal aspect for the m. iliofibularis. The anterior intercondylar groove is shallow, similar to NHM R3719, *Thescelosaurus* spp. (Brown *et al.* 2013) and *T. santamartaensis* (Coria *et al.* 2013) but unlike the relatively deep groove in iguanodontians.

Tibia

The left tibia is broken into three non-contiguous pieces (Fig. 3). The proximal end is mediolaterally and anteroposteriorly expanded, and forms a horizontal proximal articular surface, as in *Orodromeus makelai* (Scheetz 1999), *Talenkauen santacrucensis* Novas, Cambiaso & Ambrosio, 2004 (Cambiaso 2007, fig. 35) and NMVUK PV P186047 (Herne 2013, p. 221), but contrasting with the posteroventrally sloping proximal surface in *Albertadromeus syntarsus* Brown, Evans, Ryan & Russell, 2013, *Gasparinisaura cincosaltensis* and some specimens of *Hypsilophodon foxii* (Brown *et al.* 2013). The cnemial crest projects anterolaterally, exceeding the length of the medial condyle (in proximal view; Fig. 3E, M), similar to *Anabisetia saldiviai*, *A. syntarsus* and *Thescelosaurus assiniboiensis*, but differing from *G. cincosaltensis* and *O. makelai* in which the cnemial crest is shorter than the medial condyle, and *Jeholosaurus shangyuanensis* (Han *et al.* 2012) in which the cnemial crest and medial condyles are subequal in length. The lateral condyle is bilobed as in most basally branching ornithopods (Brown *et al.* 2013), forming a posterior condylid and an anterolaterally directed epicondyle separated by a well-developed popliteal groove (Fig. 3E, M). The posterior

condylid is larger and more bulbous than the epicondyle, as in *A. saldiviai*. The epicondyle is relatively narrow, forming a deep groove between it and the cnemial crest. This contrasts with basally branching ornithopods such as *G. cincosaltensis, H. foxii* and non-ornithopodan neornithischians, such as *A. syntarsus, J. shangyuanensis, Thescelosaurus neglectus* Gilmore, 1913 in which this groove is comparatively shallow and open. The medial and lateral condyles are separated by a deep groove, which forms an acute angle in proximal view, similar to *A. syntarsus, G. cincosaltensis* and *T. neglectus*. This differs from *H. foxii* and *O. makelai*, in which this angle approaches 90° (Galton 1974, fig. 56; Scheetz 1999, fig. 29).

Extending from the proximal end, the shaft becomes roughly teardrop shaped in cross-section for the first third of its (preserved) length, becoming triangular near the mid-shaft (Fig. 3O). Much of the distal portion of the tibia is reniform in cross-section, the concavity corresponding to a broad and proximodistally extensive fossa on the anterior surface of the distal tibia. The distal end is transversely expanded and mediolaterally concave on its anterior surface. The posterior inter-malleolar ridge is centrally positioned and strongly developed (more so than in *Diluvicursor pickeringi*: Herne *et al.* 2018), terminating in a distinct, distally projecting spur (Fig. 3B, J). Salgado *et al.* (1997, p. 937) commented on a 'protuberance' at the distal tip of the posterior inter-malleolar ridge in *G. cincosaltensis*; however, first-hand observations of these specimens (MUCPv 212, MUCPv 213) show that this protuberance does not extend distally beyond the posterodistal margin of the tibia and can not be considered equivalent to that of AM F127930. This spur therefore appears to be a unique feature of AM F127930, but its function is unknown. Medial to the inter-malleolar ridge, the posterior surface of the tibia is mediolaterally convex, whereas lateral to it, the surface is concave. The lateral and medial malleoli are subequal in mediolateral width and have gently rounded terminations, although the lateral malleolus extends further distally. In distal aspect, the two malleoli are linked by a transverse ridge, posterior to which the distal articular surface for the astragalus is gently concave and rises posterodorsally towards the inter-malleolar ridge.

Astragalus

The astragalus of AM F127930 is distinctive. Unlike, *Orodromeus makelai* (Scheetz 1999), *Zephyrosaurus schaffi* Sues, 1980 (Scheetz 1999), possibly *Muttaburrasaurus langdoni* (Molnar 1980) and some
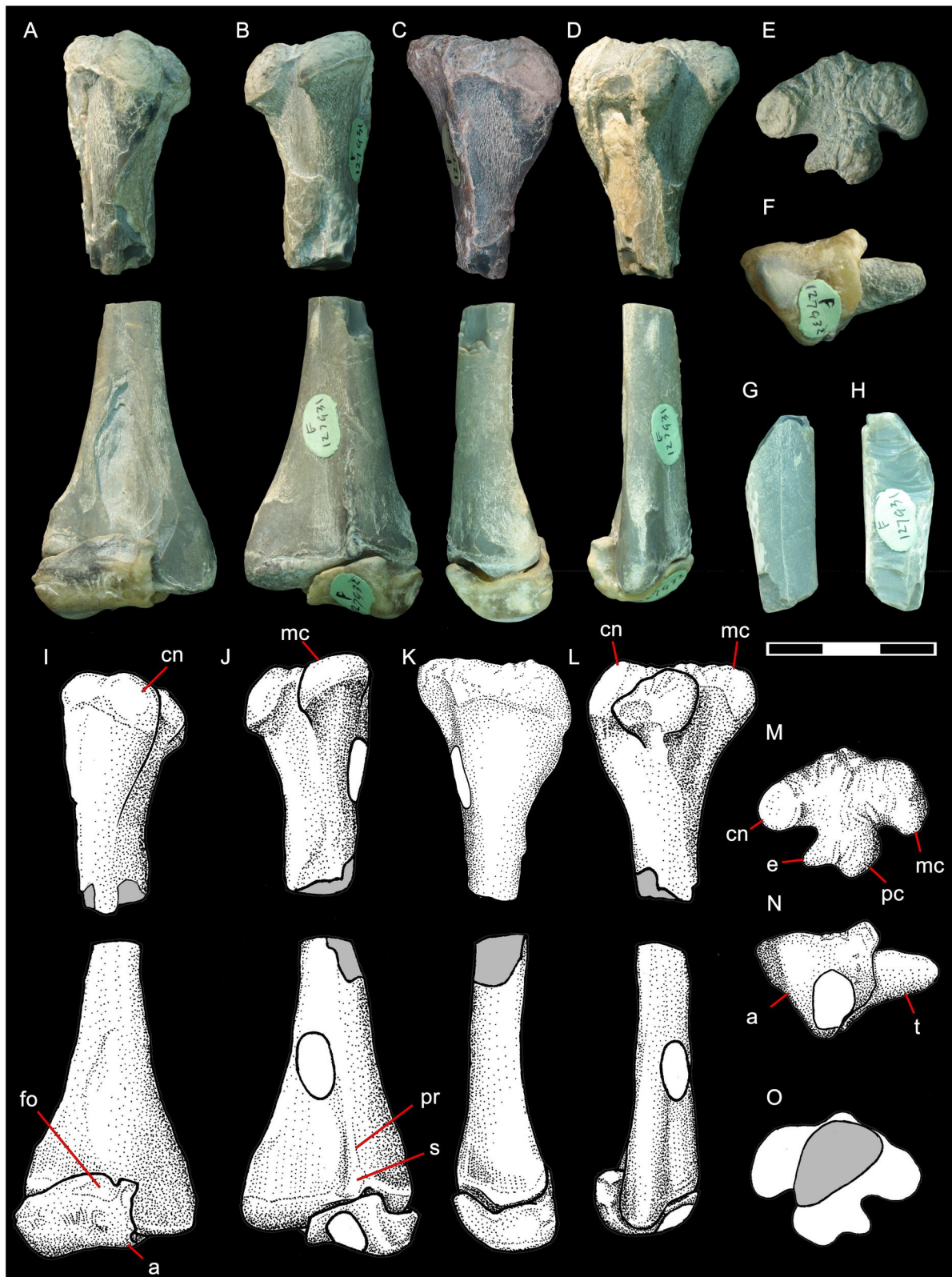
Fig. 3. Left tibia and astragalus of AM F127930. Photographs and interpretive illustrations in **A, I**, anterior, **B, J**, posterior, **C, K**, medial, **D, L**, lateral, **E, M**, proximal and **F, A**, distal views. **G, H**, two views of the intervening tibial shaft fragment. **O**, distal view of the proximal portion of the tibia showing cross-section (grey) of the shaft. Scale-bar increments equal 1 cm. Abbreviations: a, astragalus; cn, cnemial crest; e, epicondyle; fo, fossa; mc, medial condyle; pc, posterior condyle; pr, posterior medial malleolar ridge; s, 'spur'; t, tibia.

(but not all) specimens of *Anabisetia saldiviai*, it is not fused to the calcaneum. Anteriorly, the ascending process is low, mediolaterally broad and asymmetrical (the apex is laterally offset). Lateral to the ascending process is a distinct notch in the dorsal margin (Fig. 3A, 1; 4 A). As a result of this notch, the dorsolateral corner of the astragalus (in anterior view) is tabular and well separated from the ascending process. The presence of a notch that separates the ascending process from the dorsolateral 'process' (described as a 'forked' ascending process by Scheetz 1999, p. 70) occurs in *O. makelai* (Scheetz 1999) and some specimens of *Dryosaurus altus* (Galton 1981, fig. 18), but not in *Diluvicursor pickeringi* (Fig. 4). Anteriorly, this notch is associated with a broad, well-developed fossa that extends across the base of the ascending process for nearly half the width of the astragalus (Fig. 3A, 1). This broad fossa is widely found among ornithopods, including *A. saldiviai, D. altus, Jeholsaurus shangyuanensis* and *M. langdoni*, but is lacking in *D. pickeringi* (Herne *et al.* 2018; Fig. 4). There is no transverse groove on the anterior surface of the astragalus as occurs in *Haya griva* (Makovicky *et al.* 2011) and *J. shangyuanensis* (Han *et al.* 2012). The proximal surface of the astragalus is anteroposteriorly concave to receive the distal end of the tibia. On this proximal surface, roughly in line with the fossa on the anterior surface, a low ridge extends posteriorly from the anterior margin and becomes less pronounced

posteriorly. This ridge separates the contact surfaces for the medial and lateral malleoli of the tibia, respectively. In distal view, the astragalus is roughly trapezoidal and slightly rugose, suggesting the presence of a cartilaginous bursa (Fig. 3F, N). The medial surface is crescentic. The posterior part of this crescent corresponds to the posterior ascending process, which forms a low spur in posterior view. In contrast, the low posterior ascending process in *D. pickeringi* is broadly rounded. The spur-like posterior ascending process locates in a notch on the distal tibia, medial to the inter-malleolar ridge. Medial offset of the posterior ascending process relative to the inter-malleolar ridge appears to be natural rather than caused by post-mortem displacement and differs from other ornithopods where the process typically aligns with the inter-malleolar ridge (Fig. 3B, J). The proximal height of the posterior ascending process is similar to a range of basally branching neornithischians (*A. saldiviai, Agilisaurus louderbacki* Peng, 1990, *O. makelai*, *G. cincosaltensis, J. shangyuanensis, Thescelosaurus* spp.) and some basally branching iguanodontians (*M. langdoni, Tenontosaurus tilletti* Ostrom, 1970), but unlike that of *Talenkauen santacrucensis* in which the posterior ascending process is particularly tall, or *Hypsilophodon foxii, Notohypsilophodon comodorensis* and *Parksosaurus warreni* in which it is virtually absent (Cambiaso 2007).
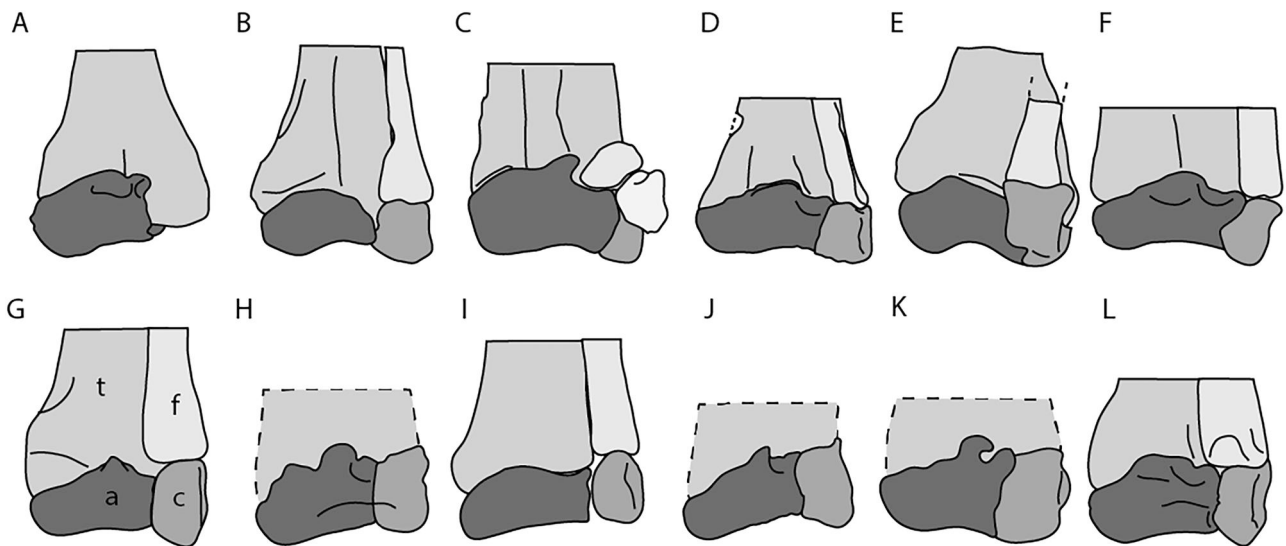

Fig. 4. Comparison of ornithopod crura. **A**, AM F127930; **B**, *Diluvicursor pickeringi* (redrawn and reversed from Herne *et al.* 2018); **C**, NMV P186047 (redrawn and reversed from Herne *et al.* 2018); **D**, *Muttaburrasaurus langdoni* (redrawn from Herne *et al.* 2018); **E**, *Gasparinisaura cincosaltensis* (redrawn and reversed from Salgado *et al.* 1997); **F**, *Anabisetia saldiviai* (redrawn from Herne *et al.* 2018); **G**, *Hypsilophodon foxii* (redrawn from Galton 1974); **H**, *Jeholosaurus shangyuanensis* (redrawn from Han *et al.* 2012); **I**, *Thescelosaurus neglectus* (redrawn and reversed from Gilmore 1915); **J**, 'Nanosaurus agilis' (=*Drinker nisti*) (redrawn from Bakker *et al.* 1990); **K**, *Orodromeus makelai* (redrawn from Scheetz 1999); **L**, *Dryosaurus altus* (redrawn from Herne *et al.* 2018). Abbreviations: a, astragalus; ap, ascending process; c, calcaneum; f, fibula; n, notch; t, tibia.

Phylogenetic analysis

The phylogenetic position of AM F127930 was evaluated by including it in the phylogenetic matrix of Fonseca *et al.* (2024). The resulting matrix consisted of 173 taxa and 943 characters (Supplementary Data 2). The matrix was subjected to a parsimony analysis under both equal and implied weighting strategies using TNT 1.6 (Goloboff & Morales 2023). Following the analyses of Fonseca *et al.* (2024), 55 characters were treated as ordered (12, 63, 99, 160, 177, 197, 202, 203, 238, 258, 261, 331, 375, 410, 414, 427, 439, 446, 452, 462, 481, 500, 502, 503, 506, 513, 528, 536, 537, 539, 558, 560, 586, 588, 608, 612, 621, 622, 642, 678, 686, 688, 708, 724, 742, 744, 752, 762, 785, 795, 833, 838, 849, 866 and 909). Tree searching used a driven search strategy consisting of three replicates, each with 10 rounds of ratcheting, fusing and drifting. Searching was stopped when the same result was obtained three times. A further round of branch swapping with tree-bisection and reconnection was performed on the most parsimonious trees (MPTs) returned from the driven search to find more trees of equal length. Preliminary analyses under equal weighting found that the consensus topology contained a large polytomy of early branching ornithopods including AM F127930. Therefore, iterative PCR was applied to the MPTs to identify taxa that could be excluded from consensus calculations to improve resolution. This was also applied to the implied weighting strategies. Implied weighting was performed with four different values for the concavity parameter k ($k = 3$, 6, 10 and 20) to assess the effects of downweighting homoplasy to different extents. Support statistics for the summary reduced consensus trees with the exclusion of taxa identified by iterative PCR from each search were calculated by symmetric resampling (Goloboff *et al.* 2003) and branch supports (Bremer 1994). Symmetric resampling analyses were calculated using 1000 random resamples of the original character-taxon matrix, which were subjected to the aforementioned driven search strategy to obtain a set of MPTs. Node supports were reported in terms of both absolute frequencies (i.e., the proportion of times a group from the summary tree appeared in a resampled tree set) and relative frequencies (i.e., the difference in frequency between a group and the most common contradictory group, Goloboff *et al.* 2003). Branch supports were calculated by using branch swapping to sample suboptimal trees up to 10 steps longer from each set of MPTs. The mean resampling values for both relative and absolute frequencies were calculated for all reduced consensus trees as a proxy for the strength of support for each topology.

All summary statistics for the strict consensus trees obtained from both equal and implied weighting searches, lists of taxa identified for exclusion by iterative PCR and complete phylogenetic topologies of the reduced consensus topologies are provided in Supplementary Data 2. The results of the phylogenetic analyses show AM F127930 nesting with other early branching Gondwanan ornithopods to form a monophyletic Elasmaria (Fonseca *et al.* 2024) regardless of character weighting (Fig. 5; Supplementary Data 3). In all reduced consensus topologies, AM F127930 is identified as a member of Elasmaria and forms successive clades with the South American species *Isasicursor santacrucensis* Novas, Agnolin, Rozadilla, Aranciaga-Rolando, Brissón-Eli, Motta, Cerroni, Ezcurra, Martinelli, D'Angelo, Álvarez-Herrera, Gentil, Bogan, Chimento, García-Marsà, Lo Coco, Miquel, Brito, Vera, Loinaze, Fernandez & Salgado 2019 and either *Trinisaura santamartaensis* or *Morrosaurus antarcticus*, both from Antarctica, under equal and implied weighting respectively.

The composition and topology of Elasmaria are identical among the implied weighting reduced consensus trees where the concavity parameter for the analysis is 6, 10 and 20. In these, four Australian taxa were selected for removal from the consensus topology: *Atlascopcosaurus loadsi*, *Galleonosaurus dorisae*, *Leaellynasaura amicagraphica* and *Qantassaurus intrepidus* (Supplementary Data 3). The remaining implied weighting tree differs only in the additional exclusion of *Sektensaurus sanjuanboscoi*; otherwise, the topology resembles the results from the other implied weighting analyses (Supplementary Data 3). In comparison, most taxa identified as elasmarians under implied weighting were selected for exclusion by iterative PCR under equal weighting, leaving only six elasmarian taxa (Supplementary Data 3).

The phylogenetic hypothesis resulting from the three implied weighting analysis where the concavity parameter for the analysis is 6, 10 and 20 (Fig. 5) is favoured for assessing the position of AM F127930 over any of those from the remaining analyses because of the stability of Elasmaria in the reduced strict consensus trees (Supplementary Data 3) and the comparatively higher mean resampling support (Supplementary Data 3). Resampling support values for nodes in Elasmaria are low compared with other ornithopod clades, regardless of weighting strategy. This is likely an artefact of the incompleteness of many elasmarian specimens, which complicates efforts
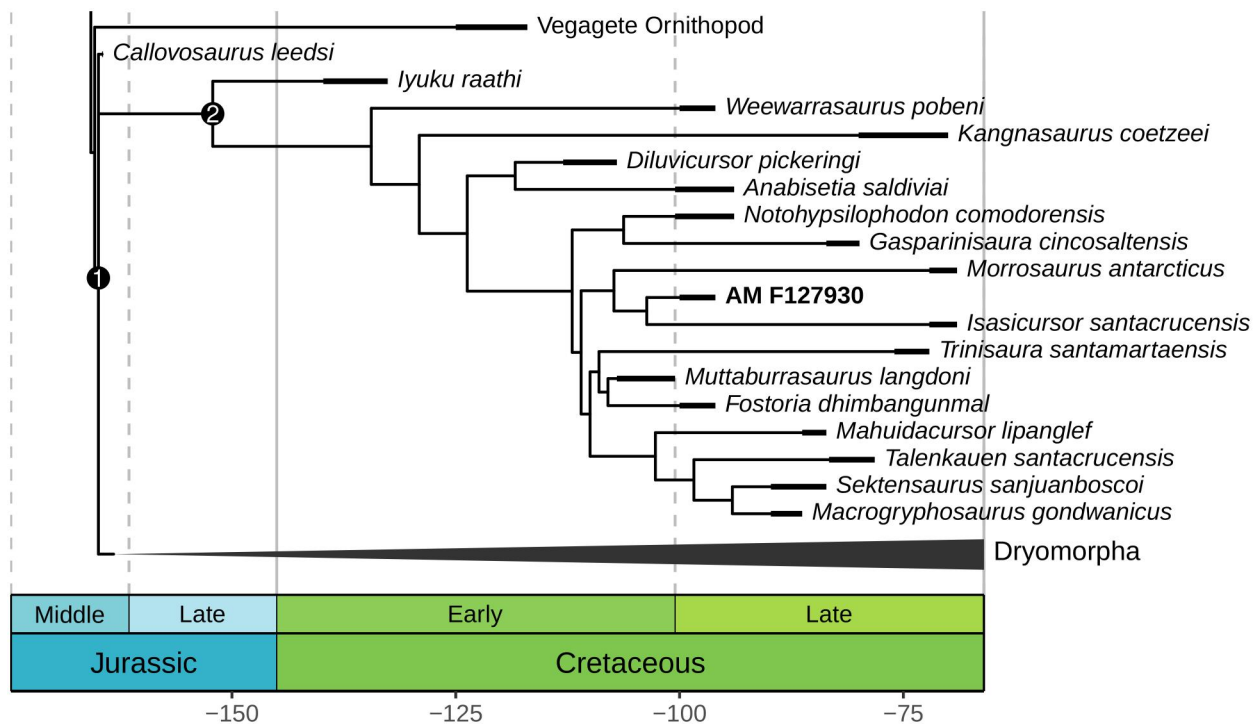
Fig. 5. Time-calibrated reduced strict consensus tree resulting from the analysis of the modified Fonseca *et al.* (2024) matrix under implied weighting, where the concavity parameter *k* was 6, 10 and 20. The position of AM F127930 within Elasmaria is highlighted. Node labels represent (1) Euiguanodontia and (2) Elasmaria. The complete trees are provided in Supplementary Data 2.

to resolve the ingroup relationships of the clade as demonstrated in recent studies (e.g., Herne *et al.* 2019, Fonseca *et al.* 2024).

There is a single apomorphy diagnosing the clade consisting of AM F127930 and *I. santacrucensis*: the absence of an anterior (extensor) intercondylar groove on distal end of the femur (824:0).

Discussion

A number of small-bodied ornithopods are known from southeastern Australia, most of which come from the Eumeralla (upper Aptian–upper Albian; Otway Group) and the Wonthaggi (upper Barremian–lower Aptian, upper Strzelecki Group) formations, which crop out along the Victorian coastline. Although articulated material in these deposits is rare (Herne *et al.* 2018; Poropat *et al.* 2018), a diversity of jaw morphotypes—with corresponding dentition—have led to the formalization of several taxa, including *Atlascopcosaurus loadsi*, *Leaellynasaura amicagraphica*, originally from the Eumeralla Formation, and *Galleonosaurus dorisae* and *Qantassaurus intrepidus* originally from the Wonthaggi Formation, but nearly all of which (except *L. amicagraphica*) are now known from both formations (Duncan *et al.* 2021, Poropat *et al.* 2023). Two of these taxa (*A. loadsi*,

L. amicagraphica) were named, in part, on the basis of maxillae—although additional cranial material pertains to the holotype of *L. amicagraphica*—whereas *Q. intrepidus* was erected on the basis of an isolated dentary. The original assignment of a partial postcranial skeleton (NMV P185992/P185993) to the holotype individual of *L. amicagraphica* and a second partial skeleton (NMV P186047) to the same taxon (Rich & Vickers-Rich 1989, Rich *et al.* 2010) has been questioned (Herne *et al.* 2016) and currently all postcranial materials previously referred to *L. amicagraphica* are considered inconclusive (Herne *et al.* 2016; for a detailed summary, see Poropat *et al.* 2023).

A fifth taxon, *Diluvicursor pickeringi*, was described from articulated postcranial remains from the Eumeralla Formation (Herne *et al.* 2018), but whether or not this material in fact pertains to one of the named or unnamed jaw morphotypes from Victoria has been questioned (Duncan *et al.* 2021, Poropat *et al.* 2023). Although the precise stratigraphic relationships between the Victorian taxa are yet to be determined, *D. pickeringi* and *A. loadsi* are roughly coeval and stratigraphically lower/older than the holotype of *L. amicagraphica* within the Eumeralla Formation (Herne *et al.* 2018). However, a recently referred specimen of *L. amicagraphica* from close to the *D. pickeringi* holotype locality hints at a wider

stratigraphic range for the former (Duncan *et al.* 2021).

Within the GCF, there are only two named ornithopods (both recovered as elasmarians by Fonseca *et al.* 2024) currently considered as valid: *Weewarrasaurus pobeni,* based on a partial dentary and a second referred specimen (also a dentary; Bell *et al.* 2018), and the relatively large-bodied form *Fostoria dhimbangunmal* based on associated bonebed material (Bell *et al.* 2019a). 'Fulgurotherium australe' is widely considered an indeterminate non-iguanodontian ornithopod (e.g., Agnolin *et al.* 2010; Bell *et al.* 2018; Duncan *et al.* 2021; Poropat *et al.* 2023). Whether or not the present specimen (AM F127930) pertains to *W. pobeni* must await the discovery of more complete, overlapping specimens. Further complicating this is the recognition of at least two (possibly three) small-bodied forms from the GCF based on craniodental remains (Bell *et al.* 2018) that can not be compared with AM F127930.

In summary, only the postcranial skeleton of *D. pickeringi* (NMV P221080) can be confidently compared with AM F127930 among the named Australian taxa, although the two Victorian postcrania (NMV P185992/P185993 and NMV P186047) and NHMUK PV R3719 (holotype of '*F. australe*') are also considered here. Herne (2013) regarded NMV P185992/P185993 and NMV P186047 as closely related but separate morphotypes/taxa, which he assigned as Victorian Ornithopod Postcranium Type [VOPC] I and VOPC II, respectively. Subsequently, Poropat *et al.* (2018) suggested that they might both pertain to *L. amicagraphica* based largely on their close association with the holotype cranium (NMV P185991). Brief comparisons with the Australian iguanodontians, *Muttaburrasaurus langdoni* and *F. dhimbangunmal*, are also warranted.

AM F127930 displays at least one feature that is unique: a distal femur with an obliquely sloping, channel-like shelf proximal to the medial condyle, bordered anteriorly by an anteroposteriorly compressed supracondylar ridge. This prominent ridge is also absent from all previously described ornithopod femora from the GCF, including the holotype of '*F. australe*' (NHMUK PV R3719; Molnar 1980, Molnar & Galton 1986). The shape of the astragalus—particularly the combination of a low, laterally offset anterior ascending process and a tabular dorsolateral 'process'—is also unusual, although variations of this condition are more widely occurring among early branching ornithopods. In addition to these characteristics, AM F127930 can be distinguished from *D. pickeringi* in having a tibia with a strongly developed posterior medial malleolar ridge with a prominent distal 'spur'. With regard to the astragalus, the notched proximal margin of the anterior ascending process and the presence of a deep fossa at the base of the ascending process in AM F127930 are unlike the symmetrical, arched proximal margin of the anterior ascending process and shallow fossa in *D. pickeringi*.

The proximal femur of NMV P185992/P185993 is obscured by matrix; however, it is visible in a referred specimen, NMV P186326 (Herne 2013). The fossa trochanteris in AM F127930 is distinctly deeper and more angular in anterior view compared with the relatively shallow, saddle-shaped fossa in NMV P186326. The tibia and astragalus are too poorly preserved in NMV P185992/P185993 to permit comparisons. The other Victorian postcranial skeleton, NMV P186047, is most obviously distinguished from AM F127930 in having a distal tibia that is only weakly mediolaterally expanded (a peculiar feature of NMV P186047) and in having a hook-shaped anterior ascending process of the astragalus. The femur of NMV P186047 is diagenetically deformed (mediolaterally compressed and longitudinally sheared between left and right sides), although it too appears to differ from AM F127930 in having an anteriorly expanded medial condyle and a more proximally positioned depression for the *m. caudofemoralis longus*.

AM F127930 clearly differs from NHMUK PV R3719 (holotype of '*F. australe*') in having a distal femur with a much larger lateral condylid that is medially inset and a medial condyle that is laterally expanded to partially enclose the posterior intercondylar groove. Molnar (1980) indicated the presence of a supracondylar crest—such as that described here for AM F127930—on NHMUK PV R3719; however, re-inspection of the specimen shows it to be poorly developed compared with AM F127930. The latter also differs from 'typical' large-bodied iguanodontians, including *M. langdoni* (QM F6140) and *F. dhimbangunmal* (LRF 3050), in having a proximally positioned fourth trochanter (not observable in *F. dhimbangunmal*) and distal femur with a relatively shallow anterior intercondylar groove and a less well inset lateral condylid. In distal view, the lateral condylid of AM F127930 forms a concave depression for the attachment of the *m. iliofibularis*, whereas it is deep and L-shaped in *M. langdoni* and *F. dhimbangunmal*. The shape of the medial edge of the medial condyle in the

latter two taxa is strongly convex in distal aspect, whereas it is nearly straight in AM F127930. The distal tibiae of *M. langdoni* and *F. dhimbangunmal* lack the deep anterior concavity and a the 'spur' on the posterior medial malleolar ridge, both of which are present in AM F127930. Bartholomai & Molnar (1981) also indicated that the astragalus and calcaneum of *M. langdoni* are fused, whereas they were clearly separate in AM F127930. To what extent fusion between the astragalus and calcaneum is ontogenetically controlled has yet to be tested. The proximal tarsals of *F. dhimbangunmal* are unknown.

The GCF at Lightning Ridge represents a freshwater lowland floodplain environment that was situated at a palaeolatitude of ∼60°S (Matthews *et al.* 2016) close to the southeastern margin of the Eromanga Sea (Bell *et al.* 2019b). This differs from the volcaniclastic river floodplains within the Australian–Antarctic rift valley where the majority of named Australian ornithopods (*A. loadsi, D. pickeringi, G. dorisae, L. amicagraphica, Q. intrepidus*) would have lived at a palaeolatitude of ∼68°S (Matthews *et al.* 2016) in present-day Victoria (Rich & Vickers-Rich 1989, Dettmann *et al.* 1992, Herne *et al.* 2018). Small-bodied ornithopods from penecontemporaneous strata in Queensland, to the north, are exceedingly rare (Hocknull & Cook 2008, White *et al.,* 2022) although trackways in the Winton Formation hint at the hidden abundance of these animals (Thulborn & Wade 1979, 1984, Romilio *et al.* 2013, Poropat *et al.* 2021). The diversity and abundance of small-bodied ornithopods in the southeastern part of the country have been well established largely on the basis of the Victorian sample (Rich *et al.* 1988, Rich & Vickers-Rich 1989, 1999, Vickers-Rich & Rich 1997) and have been postulated to be the result of their preadaptation to high-latitude conditions (Vickers-Rich & Rich 1997). With an estimated height at the hip of ∼30 cm and a body mass of approximately 10–11 kg (based on a femoral circumference of ∼50 mm and the equation for body mass estimates in bipeds given by Campione *et al.* 2014), AM F127930 would have been incapable of long-distance migration (Bell & Snively, 2008) and was likely a year-round resident. Although ontogeny and taphonomic filters must also be considered (Vickers-Rich & Rich 1997), the distinctiveness of AM F127930 underscores the diversity of small-bodied ornithopods in mid-Cretaceous Australia and lends further support to the notion that both the GCF and Victorian localities harboured diverse, yet distinct ornithopod faunas (Bell *et al.* 2018).

Conclusions

Articulated dinosaur remains, especially those of small-bodied forms, are exceedingly rare in the Cretaceous of Australia. AM F127930, an articulated hindlimb (femur, tibia, astragalus), represents the first articulated postcranial remains and the best-represented small ornithopod currently known from the GCF of New South Wales. AM F127930 can not be compared with most of the named (craniodental-based) ornithopods from the Australian Cretaceous but is distinguishable from those for which hindlimb material is confidently known (*Diluvicursor pickeringi, Fostoria dhimbangunmal, Muttaburrasaurus langdoni*). Whether AM F127930 represents a new taxon or pertains to *Weewarrasaurus pobeni* or any of the unnamed morphotypes currently recognized from the GCF is uncertain. Although size-related differences can not be accounted for, particularly between AM F127930, *F. dhimbangunmal* and *M. langdoni*, several features appear to be unique to AM F127930. The new specimen highlights the ongoing challenges faced especially in Australia where fragmentary craniodental remains have often been used as the basis for establishing taxonomic diversity. Although rarer, more complete postcranial remains (such as AM F127930 and the Victorian specimens NMV P186047, NMV P185992/P185993, NMV P221080 [holotype of *D. pickeringi*]) are potentially more anatomically informative, unless more complete 'Rosetta Stone' specimens are recovered, they are unlikely to help resolve the phylogenetic relationships of named taxa because of the lack of overlapping elements. Nevertheless, the new material contributes novel information on the distinctiveness of the ornithopods from southeastern Australia and further supports their elasmarian affinities.

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References

AGNOLIN, F.L., EZCURRA, M.D., PAIS, D.F. & SALISBURY, S.W., 2010. A reappraisal of the Cretaceous non-avian dinosaur faunas from Australia and New Zealand: evidence for their Gondwanan affinities. *Journal of Systematic Palaeontology 8*, 257–300.

BAKKER, R.T., GALTON, P., SIEGWARTH, J. & FILLA, J., 1990. A new latest Jurassic vertebrate fauna, from the highest levels of the Morrison Formation at Como Bluff, Wyoming. Part IV. The dinosaurs: a new *Othnielia*-like hypsilophodontid. *Hunteria 2*, 8–19.

BARTHOLOMAI, A. & MOLNAR, R.E., 1981. *Muttaburrasaurus*, a new iguanodontid (Ornithischia: Ornithopoda) dinosaur from the Lower Cretaceous of Queensland. *Memoirs of the Queensland Museum 20*, 319–349.

BELL, P.R. & SNIVELY, E., 2008. Polar dinosaurs on parade: a review of dinosaur migration. *Alcheringa 32*, 271–284.

BELL, P.R., CAU, A., FANTI, F. & SMITH, E.T., 2016. A large-clawed theropod (Dinosauria: Tetanurae) from the Lower Cretaceous of Australia and the Gondwanan origin of megaraptorid theropods. *Gondwana Research 36*, 473–487.

BELL, P.R., HERNE, M., BROUGHAM, T. & SMITH, E., 2018. Ornithopod diversity in the Griman Creek Formation (Cenomanian), New South Wales, Australia. *PeerJ.6*, e6008.

BELL, P.R., BROUGHAM, T., HERNE, M., FRAUENFELDER, T. & SMITH, E., 2019a. *Fostoria dhimbangunmal* gen. et sp. nov., a new iguanodontian (Dinosauria, Ornithopoda) from the mid-Cretaceous of Lightning Ridge, NSW, Australia. *Journal of Vertebrate Paleontology 39*, e1564757.

BELL, P.R., FANTI, F., HART, L.J., MILAN, L.A., CRAVEN, S.J., BIRCH, S.A. & SMITH, E., 2019b. Revised geology, age, and vertebrate diversity of the dinosaur-bearing Griman Creek Formation (Cenomanian), Lightning Ridge, New South Wales, Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology 514*, 655–671.

BOULENGER, G.A., 1881. Sur l'arc pelvien chez les dinosauriens de Bernissart [On the pelvic arch in the dinosaurs of Bernissart]. *Bulletins de L'Académie royale de Belgique, 3eme série 1*, 1–11.

BREMER, K., 1994. Branch support and tree stability. *Cladistics 10*, 295–304.

BROWN, C.M., BOYD, C.A. & RUSSELL, A., 2011. A new basal ornithopod dinosaur (Frenchman Formation, Saskatchewan, Canada), and implications for late Maastrichtian ornithischian diversity in North America. *Zoological Journal of the Linnean Society 163*, 1157–1198.

BROWN, C.M., EVANS, D.C., RYAN, M.J. & RUSSELL, A.P., 2013. New data on the diversity and abundance of small-bodied ornithopods (Dinosauria, Ornithischia) from the Belly River Group (Campanian) of Alberta. *Journal of Vertebrate Paleontology 33*, 495–520.

BUTLER, R.J., LIYONG, J., JUN, C. & GODEFROIT, P., 2011. The postcranial osteology and phylogenetic position of the small ornithischian dinosaur *Changchunsaurus parvus* from the Quantou Formation (Cretaceous: Aptian–Cenomanian) of Jilin Province, north-eastern China. *Palaeontology 54*, 667–683.

CAMBIASO, A.V., 2007. *Los ornitópodos e iguanodontes basales (Dinosauria, Ornithischia) del Cretácico de Argentina y Antártida.* PhD thesis, Universidad de Buenos Aires, Buenos Aires, 412 pp. (unpublished)

CAMPIONE, N.E., EVANS, D.C., BROWN, C.M. & CARRANO, M.T., 2014. Body mass estimation in non-avian bipeds using a theoretical conversion to quadruped stylopodial proportions. *Methods in Ecology and Evolution 5*, 913–923.

COOPER, M.R., 1985. A revision of the ornithischian dinosaur *Kangnasaurus coetzeei* Haughton, with a classification of the Ornithischia. *Annals of the South African Museum 95*, 281–317.

CORIA, R.A. & CALVO, J.O., 2002. A new iguanodontian ornithopod from Neuquen Basin, Patagonia. *Journal of Vertebrate Paleontology 22*, 503–509.

CORIA, R.A. & SALGADO, L., 1996. A basal iguanodontian (Ornithischia: Ornithopoda) from the Late Cretaceous of South America. *Journal of Vertebrate Paleontology 16*, 445–457.

CORIA, R.A., MOLY, J.J., REGUERO, M., SANTILLANA, S. & MARENSSI, S., 2013. A new ornithopod (Dinosauria; Ornithischia) from Antarctica. *Cretaceous Research 41*, 186–193.

DETTMANN, M.E., MOLNAR, R.E., DOUGLAS, J.G., BURGER, D., FIELDING, C., CLIFFORD, H.T., FRANCIS, J., JELL, P., RICH, T., WADE, M., RICH, P.V., PLEDGE, N., KEMP, A. & ROZEFELDS, A., 1992. Australian Cretaceous terrestrial faunas and floras: biostratigraphic and biogeographic implications. *Cretaceous Research 13*, 207–262.

DEVEREAUX, O., HERNE, M.C., CAMPIONE, N.E. & BELL, P.R., 2024. Paleoneurology of the iguanodontian *Fostoria*

dhimbangunmal from the mid-Cretaceous of Australia. *Journal of Paleontology* 98, 1098–1106.

DIEUDONNÉ, P.-E., TORTOSA, T., TORCIDA FERNÁNDEZ-BALDOR, F., CANUDO, J.I. & DÍAZ-MARTÍNEZ, I., 2016. An unexpected early rhabdodontid from Europe (Lower Cretaceous of Salas de los Infantes, Burgos Province, Spain) and a re-examination of basal iguanodontian relationships. *PLoS One* 11, e0156251.

DUNCAN, R.J., EVANS, A.R., VICKERS-RICH, P., RICH, T.H. & POROPAT, S.F., 2021. Ornithopod jaws from the Lower Cretaceous Eumeralla Formation, Victoria, Australia, and their implications for polar neornithischian dinosaur diversity. *Journal of Vertebrate Paleontology* 41, e1946551.

EXON, N.F., 1976. Geology of the Surat Basin in Queensland. *Bureau of Mineral Resources. Geology and Geophysics Bulletin* 166, 1–235.

FONSECA, A.O., REID, I.J., VENNER, A., DUNCAN, R.J., GARCIA, M.S. & MÜLLER, R.T., 2024. A comprehensive phylogenetic analysis on early ornithischian evolution. *Journal of Systematic Palaeontology* 22, 2346577.

GALTON, P.M., 1974. The ornithischian dinosaur *Hypsilophodon* from the Wealden of the Isle of Wight. Bulletin of the British Museum (Natural History). *Bulletin of the British Museum (Natural History) Geology* 25, 1–152.

GALTON, P.M., 1981. *Dryosaurus*, a hypsilophodontid dinosaur from the Upper Jurassic of North America and Africa postcranial skeleton. *Paläontologische Zeitschrift* 55, 271–312.

GILMORE, C.W., 1913. A new dinosaur from the Lance Formation of Wyoming. *Smithsonian Miscellaneous Publications* 61, 1–5.

GILMORE, C.W., 1915. Osteology of *Thescelosaurus*, an orthopodous dinosaur from the Lance Formation of Wyoming. *Proceedings of the United States National Museum* 49, 591–616.

GOLOBOFF, P.A., FARRIS, J.S., KÄLLERSJÖ, M., OXELMAN, B., RAMIACUTEREZ, M.J. & SZUMIK, C.A., 2003. Improvements to resampling measures of group support. *Cladistics* 19, 324–332.

GOLOBOFF, P.A. & MORALES, M.E., 2023. TNT version 1.6, with a graphical interface for MacOS and Linux, including new routines in parallel. *Cladistics: The International Journal of the Willi Hennig Society* 39, 144–153.

GREEN, P.M., CARMICHAEL, D.C., BRAIN, T.J., MURRAY, C.G., MCKELLAR, J.L., BEESTON, J.W. & GRAY, A.R.G., 1997. Lithostratigraphic units in the Bowen and Surat basins, Queensland. In *The Surat and Bowen Basins, Southeast Queensland*. GREEN, P.M., ed., Queensland Minerals and Energy Review Series, Queensland Department of Mines and Energy, Brisbane, Australia, 41–108.

HAN, F.–L., BARRETT, P.M., BUTLER, R.J. & XU, X., 2012. Postcranial anatomy of *Jeholosaurus shangyuanensis* (Dinosauria, Ornithischia) from the Lower Cretaceous Yixian Formation of China. *Journal of Vertebrate Paleontology* 32, 1370–1395.

HAUGHTON, S.H., 1915. On some dinosaur remains from Bushmanland. *Transactions of the Royal Society of South Africa* 5, 259–264.

HAY, W.W., DECONTO, R., WOLD, C.N., WILSON, K.M., VOIGT, S., SCHULZ, M., WOLD-ROSSBY, A., DULLO, W.-C., RONOV, A.B., BALUKHOVSKY, A.N. & SOEDING, E., 1999. Alternative global Cretaceous paleogeography. In *The Evolution of Cretaceous Ocean/Climate Systems*. BARRERA E. & JOHNSON, C., eds, *Geological Society of America Special Paper*, Boulder Colorado, USA, 332, 1–47.

HERNE, M.C., 2013. *Anatomy, systematics and phylogenetic relationships of the Early Cretaceous ornithopod dinosaurs of the Australian-Antarctic rift system*. PhD Thesis, University of Queensland, Brisbane, Australia, 464 pp. (unpublished)

HERNE, M.C. & SALISBURY, S.W., 2009. The status of *Leaellynasaura amicagraphica* (Dinosauria: Ornithischia) from the Early Cretaceous of south-eastern Australia. *Geological Society of Australia Abstracts* 93, 35.

HERNE, M.C., TAIT, A.M. & SALISBURY, S.W., 2016. Sedimentological reappraisal of the *Leallynasaura amicagraphica* (Dinosauria, Ornithopoda) holotype locality in the Lower Cretaceous of Victoria, Australia with taphonomic implications for the taxon. *New Mexico Museum of Natural History and Science Bulletin* 71, 121–148.

HERNE, M.C., TAIT, A.M., WEISBECKER, V., HALL, M., NAIR, J.P., CLEELAND, M. & SALISBURY, S.W., 2018. A new small-bodied ornithopod (Dinosauria, Ornithischia) from a deep, high-energy Early Cretaceous river of the Australian-Antarctic rift system. *PeerJ.5*, e4113.

HERNE, M.C., NAIR, J.P., EVANS, A.R. & TAIT, A.M., 2019. New small-bodied ornithopods (Dinosauria, Neornithischia) from the Early Cretaceous Wonthaggi Formation (Strzelecki Group) of the Australian-Antarctic rift system, with revision of *Qantassaurus intrepidus* Rich and Vickers-Rich, 1999. *Journal of Paleontology* 93, 543–584.

HOCKNULL, S.A. & COOK, A.G., 2008. Hypsilophodontid (Dinosauria: Ornithischia) from the latest Albian, Winton Formation, central Queensland. *Memoirs of the Queensland Museum* 52, 212.

HORNER, J.R. & WEISHAMPEL, D.B., 1988. A comparative embryological study of two ornithischian dinosaurs. *Nature* 332, 256–257.

HUXLEY, T.H., 1870. On *Hypsilophodon foxii*, a new dinosaurian from the Wealden of the Isle of Wight. *Quarterly Journal of the Geological Society of London* 26, 3–12.

MADZIA, D., ARBOUR, V.M., BOYD, C.A., FARKE, A.A., CRUZADO-CABALLERO, P. & EVANS, D.C., 2021. The phylogenetic nomenclature of ornithischian dinosaurs. *PeerJ.9*, e12362.

MAIDMENT, S.C. & BARRETT, P.M., 2011. The locomotor musculature of basal ornithischian dinosaurs. *Journal of Vertebrate Paleontology* 31, 1265–1291.

MAKOVICKY, P.J., KILBOURNE, B.M., SADLEIR, R.W. & NORELL, M.A., 2011. A new basal ornithopod (Dinosauria, Ornithischia) from the Late Cretaceous of Mongolia. *Journal of Vertebrate Paleontology* 31, 626–640.

MARTÍNEZ, R.D., 1998. *Notohypsilophodon comodorensis* gen. et sp. nov. un Hypsilophodontidae (Ornitischia: Ornithopoda) del Cretácico Superior de Chubut, Patagonia central, Argentina [*Notohypsilophodon comodorensis* gen. et sp. nov., a Hypsilophodontidae (Ornithischia: Ornithopoda) from the Upper Cretaceous of Chubut, central Patagonia, Argentina]. *Acta Geologica Leopoldensia* 21, 119–135.

MATTHEWS, K.J., MALONEY, K.T., ZAHIROVIC, S., WILLIAMS, S.E., SETON, M. & MÜLLER, R.D., 2016. Global plate

boundary evolution and kinematics since the late Paleozoic. *Global and Planetary Change 146*, 226–250.

MEAKIN, S., 2011. Geodiversity in the Lightning Ridge area and implications for geotourism. *Proceedings of the Linnean Society of New South Wales 132*, 71–82.

MOLNAR, R.E., 1980. Australian late Mesozoic terrestrial tetrapods: some implications. *Memoirs de les Société Géologique de France 139*, 131–143.

MOLNAR, R.E., 1996. Observations on the Australian ornithopod dinosaur. *Muttaburrasaurus. Memoirs of the Queensland Museum 39*, 639–652.

MOLNAR, R.E. & GALTON, P.M., 1986. Hypsilophodontid dinosaurs from Lightning Ridge, New South Wales, Australia. *Geobios 19*, 231–243.

MOORE, M., 2002. Geophysical ground surveys over Lightning Ridge opal prospects. *Geological Survey of New South Wales Department of Mineral Resources, Geological Survey Report No. GS2002/442*, 43 pp.

NOPCSA, B.F., 1900. Dinosaurierreste aus Siebenbürgen (Schädel von *Limnosaurus transsylvanicus* nov. gen. et spec.) [Dinosaur remains from Transylvania (skull of *Limnosaurus transsylvanicus* nov. gen. et spec.)]. *Denkschriften der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe 68*, 555–591.

NORMAN, D.B., 2004. Basal Iguanodontia. In *The Dinosauria*, second edition. WEISHAMPEL, D. B., DODSON, P. & OSMÓLSKA, H., eds, University of California Press, Bloomington and Indianapolis, 413–437.

NORMAN, D.B., SUES, H.-D., WITMER, L.M. & CORIA, R.A., 2004. Basal Ornithopoda. In *The Dinosauria*., second edition. WEISHAMPEL, D. B., DODSON, P. & OSMÓLSKA, H., eds, University of California Press, Bloomington and Indianapolis, 393–412.

NOVAS, F.E., CAMBIASO, A.V. & AMBROSIO, A., 2004. A new basal iguanodontian (Dinosauria, Ornithischia) from the Upper Cretaceous of Patagonia. *Ameghiniana 41*, 75–82.

OSTROM, J.H., 1970. Stratigraphy and paleontology of the Cloverly Formation (Lower Cretaceous) of the Bighorn Basin area, Wyoming and Montana. *Peabody Museum Bulletin 35*, 1–234.

PARKS, W.A., 1926. *Thescelosaurus warreni*, a new species of ornithopodous dinosaur from the Edmonton Formation of Alberta. *University of Toronto Studies. Geology Series 21*, 1–42.

PENG, G., 1990. A new small ornithopod (*Agilisaurus louderbacki* gen. et sp. nov.) from Zigong. *China. Newsletter of the Zigong Dinosaur Museum 2*, 19–27.

POROPAT, S.F., MARTIN, S.K., TOSOLINI, A.M.P., WAGSTAFF, B.E., BEAN, L.B., KEAR, B.P., VICKERS-RICH, P. & RICH, T.H., 2018. Early Cretaceous polar biotas of Victoria, southeastern Australia—an overview of research to date. *Alcheringa 42*, 157–229.

POROPAT, S.F., WHITE, M.A., ZIEGLER, T., PENTLAND, A.H., RIGBY, S.L., DUNCAN, R.J., SLOAN, T. & ELLIOTT, D.A., 2021. A diverse Late Cretaceous vertebrate tracksite from the Winton Formation of Queensland, Australia. *PeerJ.9*, e11544.

POROPAT, S.F., BELL, P.R., HART, L.J., SALISBURY, S.W. & KEAR, B.P., 2023. An annotated checklist of Australian Mesozoic tetrapods. *Alcheringa 47*, 129–205.

PRICE, P.L., 1997. Permian to Jurassic palynostratigraphic nomenclature of the Bowen and Surat Basins. In *The Surat and Bowen Basins, Southeast Queensland*. GREEN, P.M., ed., Queensland Minerals and Energy Review Series, Queensland Department of Mines and Energy, Brisbane, Australia, 137–148.

RAZA, A., HILL, K.C. & KORSCH, R.J., 2009. Mid-Cretaceous uplift and denudation of the Bowen and Surat Basins, eastern Australia: relationship to Tasman Sea rifting from apatite fission-track and vitrinite-reflectance data. *Australian Journal of Earth Sciences 56*, 501–531.

REISER, R.F., 1970. Stratigraphic nomenclature of the upper part of the Rolling Downs Group in the Surat area. *Queensland Government Mining Journal 71*, 301–303.

RICH, T.H. & VICKERS-RICH, P., 1989. Polar dinosaurs and biotas of the Early Cretaceous of southeastern Australia. *National Geographic Research and Exploration 5*, 15–53.

RICH, T.H. & VICKERS-RICH, P., 1999. The Hypsilophodontidae from southeastern Australia. *National Science Museum Monographs 15*, 167–180.

RICH, P.V., RICH, T.H., WAGSTAFF, B.E., MASON, J.M., DOUTHITT, C.B., GREGORY, R.T. & FELTON, E.A., 1988. Evidence for low temperatures and biologic diversity in Cretaceous high latitudes of Australia. *Science 242*, 1403–1406.

RICH, T.H., GALTON, P.M. & VICKERS-RICH, P., 2010. The holotype individual of the ornithopod dinosaur *Leaellynasaura amicagraphica* Rich & Rich, 1989 (late Early Cretaceous, Victoria, Australia). *Alcheringa 34*, 385–396.

ROMILIO, A., TUCKER, R.T. & SALISBURY, S.W., 2013. Reevaluation of the Lark Quarry dinosaur tracksite (late Albian–Cenomanian Winton Formation, Central-Western Queensland, Australia): no longer a stampede? *Journal of Vertebrate Paleontology 33*, 102–120.

ROZADILLA, S., AGNOLIN, F.L., NOVAS, F.E., ROLANDO, A.M.A., MOTTA, M.J., LIRIO, J.M. & ISASI, M.P., 2016. A new ornithopod (Dinosauria, Ornithischia) from the Upper Cretaceous of Antarctica and its palaeobiogeographical implications. *Cretaceous Research 57*, 311–324.

SALGADO, L., CORIA, R.A. & HEREDIA, S.E., 1997. New materials of *Gasparinisaura cincosaltensis* (Ornithischia, Ornithopoda) from the Upper Cretaceous of Argentina. *Journal of Paleontology 71*, 933–940.

SCHEETZ, R.D., 1999. *Osteology of Orodromeus makelai and the phylogeny of basal ornithopod dinosaurs*. PhD Thesis, Montana State University, Bozeman, 186 pp. (unpublished)

SUES, H.-D., 1980. Anatomy and relationships of a new hypsilophodontid dinosaur from the Lower Cretaceous of North America. *Palaeontographica Abteilung A 169*, 51–72.

SUES, H.-D., EVANS, D.C., GALTON, P.M. & BROWN, C.M., 2023. Anatomy of the neornithischian dinosaur *Parksosaurus warreni* (Parks, 1926) from the Upper Cretaceous (lower Maastrichtian) Horseshoe Canyon Formation of Alberta, Canada. *Cretaceous Research 141*, 105369.

THULBORN, R.A. & WADE, M., 1979. Dinosaur stampede in the Cretaceous of Queensland. *Lethaia 12*, 275–279.

THULBORN, R.A. & WADE, M., 1984. Dinosaur trackways in the Winton Formation (mid-Cretaceous) of Queensland. *Memoirs of the Queensland Museum 21*, 413–517.

WHITE, M.A., BELL, P.R., CAMPIONE, N.E., SANSALONE, G., BIRCH, S.A., BEVITT, J.J., MOLNAR, R.E., COOK, A.G., WROE, S. & ELLIOTT, D.A., 2022. Abdominal contents reveal Cretaceous crocodyliforms ate dinosaurs. *Gondwana Research 106*, 281–302.

VICKERS-RICH, P. & RICH, T.H., 1997. The polar dinosaurs of southeastern Australia. *Dinofest International Proceedings.* WOLBERG, D. L., STUMP, E. & ROSENBERG, G. D., eds, Academy of Natural Science Philadelphia, Philadelphia, 253–257.

VIRCHOW, H., 1919. Atlas und epistropheus bei den schildkröten [Atlas and axis in the turtles]. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin 1919*, 303–332.

VON HUENE, F., 1932. Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte [The fossil reptile order Saurischia, their development and history]. *Monographien zur Geologie und Palaeontologie, serie 1 4*, 1–361.

XU, X., WANG, X.-L. & YOU, H.-L., 2000. A primitive ornithopod from the Early Cretaceous Yixian Formation of Liaoning. *Vertebrata PalAsiatica 38*, 318–325.

ZAN, S.-Q., CHEN, J., JIN, L.-Y. & LI, T., 2005. A primitive ornithopod from the Early Cretaceous Quantou Formation of central Jilin, China. *Vertebrata PalAsiatica 43*, 182–193.