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A reappraisal of the Cretaceous non-avian dinosaur faunas from Australia and New Zealand: evidence for their Gondwanan affinities

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It has often been assumed that Australasian Cretaceous dinosaur faunas were for the most part endemic, but with some Laurasian affinities. In this regard, some Australasian dinosaurs have been considered Jurassic relicts, while others were thought to represent typical Laurasian forms or endemic taxa. Furthermore, it has been proposed that some dinosaurian lineages, namely oviraptorosaurians, dromaeosaurids, ornithomimosaurians and protoceratopsians, may have originated in Australia before dispersing to Asia during the Early Cretaceous. Here we provide a detailed review of Cretaceous non-avian dinosaurs from Australia and New Zealand, and compare them with taxa from other Gondwanan landmasses. Our results challenge the traditional view of Australian dinosaur faunas, with the majority of taxa displaying affinities that are concordant with current palaeobiogeographic models of Gondwanan terrestrial vertebrate faunal distribution. We reinterpret putative Australian 'hypsilophodontids' as basal ornithopods (some of them probably related to South American forms), and the recently described protoceratopsian*s* are referred to Genasauria indet. and Ornithopoda indet. Among Theropoda, the Australian pigmy '*Allosaurus*' is referred to the typical Gondwanan clade Abelisauroidea. Similarities are also observed between the enigmatic Australian theropod *Rapator*, *Australovenator* and the South American carcharodontosaurian *Megaraptor*. *Timimus* and putative oviraptorosaurians are referred to Dromaeosauridae. The present revision demonstrates that Australia's non-avian Cretaceous dinosaurian faunas were reminiscent of those found in other, roughly contemporaneous, Gondwanan landmasses, and are suggestive of faunal interchange with these regions via Antarctica.

Keywords: Australia; New Zealand; Cretaceous; Gondwana; Dinosauria

Introduction

The Gondwana Cretaceous vertebrate record has been widely thought to be distinct from that of Laurasia (Bonaparte 1986). The Cretaceous tetrapod fauna of Gondwana is mainly composed of abelisauroid and carcharodontosaurian theropods (Bonaparte 1991; Sereno *et al.* 1996; Novas 1997a; Benson *et al*. 2009), titanosaurian sauropods (Bonaparte 1986; Salgado *et al.* 1997), basal ornithopods (Coria & Salgado 1996a; Coria 1999; Coria & Calvo 2002), notosuchian crocodyliforms, pipoid anurans, pelomedusoid turtles and gondwanatherian mammals (Baez & Gasparini 1979; Bonaparte 1986, 1999). In particular, regarding dinosaurs, the faunistic differences recorded between Laurasia and Gondwana are clear. Specifically, the northern landmasses exhibit a wide array of endemic taxa, including marginocephalian ornithischians, therizinosaurid, ornithomimid, tyrannosaurid, troodontid and oviraptorid coelurosaurian theropods (Bonaparte 1999; Upchurch *et al.* 2002).

The Gondwanan dinosaur record has drastically increased in the last 30 years, mainly in Early and Late Cretaceous assemblages of South America, Africa and Madagascar (Bonaparte 1991, 1999; Novas 1997b; Sereno *et al.* 1996, 1998, 2004; Forster *et al.* 1998; Sampson *et al.* 1998, 2001). Nevertheless, the dinosaur faunas of some Gondwanan regions still remain poorly known, particularly in Australia and New Zealand. The first Australian dinosaur was reported as early as 1906 by the palaeontologist Arthur Smith Woodward (Woodward 1906), who described an isolated theropod ungual phalanx. Later, von Huene (1932) described and illustrated three new species of Australian dinosaurs, namely *Rapator ornitholestoides*, *Fulgurotherium australe* and *Walgettosuchus woodwardi*,

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which he considered as carnivorous dinosaurs; whereas Longman (1933) erected a new genus and species of a basal sauropod that he called *Austrosaurus mckillopi*. Until the early 1980s there was a hiatus in Australian dinosaur discoveries. Since then, several new Australian Cretaceous dinosaur taxa have been described, and new dinosaurian records have been reported from Australasia (e.g. Molnar 1980a, b, c, 1981, 1996a, b, 2001a, b; Molnar & Pledge 1980; Bartholomai & Molnar 1981; Molnar *et al.* 1981; Molnar & Galton 1986; Rich & Rich 1989; Rich & Vickers-Rich 1994, 1997, 1999a, 2003; Wiffen & Molnar 1989; Long 1992, 1995; Molnar & Wiffen 1994, 2007; Long & Cruickshank 1996; Wiffen 1996; Molnar & Salisbury 2005; Salisbury *et al*. 2006b; Stilwell *et al*. 2006; Smith *et al*. 2008; Hocknull *et al*. 2009).

However, the Australian and New Zealand dinosaur record is still very patchy and biased, being restricted to a handful of horizons and localities (Fig. 1). In spite of its incompleteness, significant palaeobiogeographical and palaeoecological implications have been claimed for Australasian dinosaurs. These Cretaceous dinosaur faunas have been considered to be endemic, very different from those of other Gondwanan localities, and indicating a long isolation of this continent during the Cretaceous, probably due to its distant geographical position and sub-polar climate (Rich *et al.* 1988; Rich & Rich 1989; Molnar 1991; Rich 1996; Vickers-Rich 1996; Forster 1999; Rich & Vickers-Rich 1999a, 2003; Rich *et al.* 1999, 2002; Upchurch *et al.* 2002). In this way, an isolated 'sub-polar' Gondwana was thought to have served as both a refuge and birthplace for some dinosaur clades (Molnar 1991; Rich & Vickers-Rich 1994, 2003; Rich 1996; Vickers-Rich 1996). These unusual dinosaurian faunas may be informally split into three different groups. In the first group are taxa with presumed relictual links to taxa from the Triassic and Jurassic, persisting in Australia because of high-latitude climate and possibly geographic barriers to dispersal with adjoining regions–the 'nursery and refugium' model (Molnar 1991;

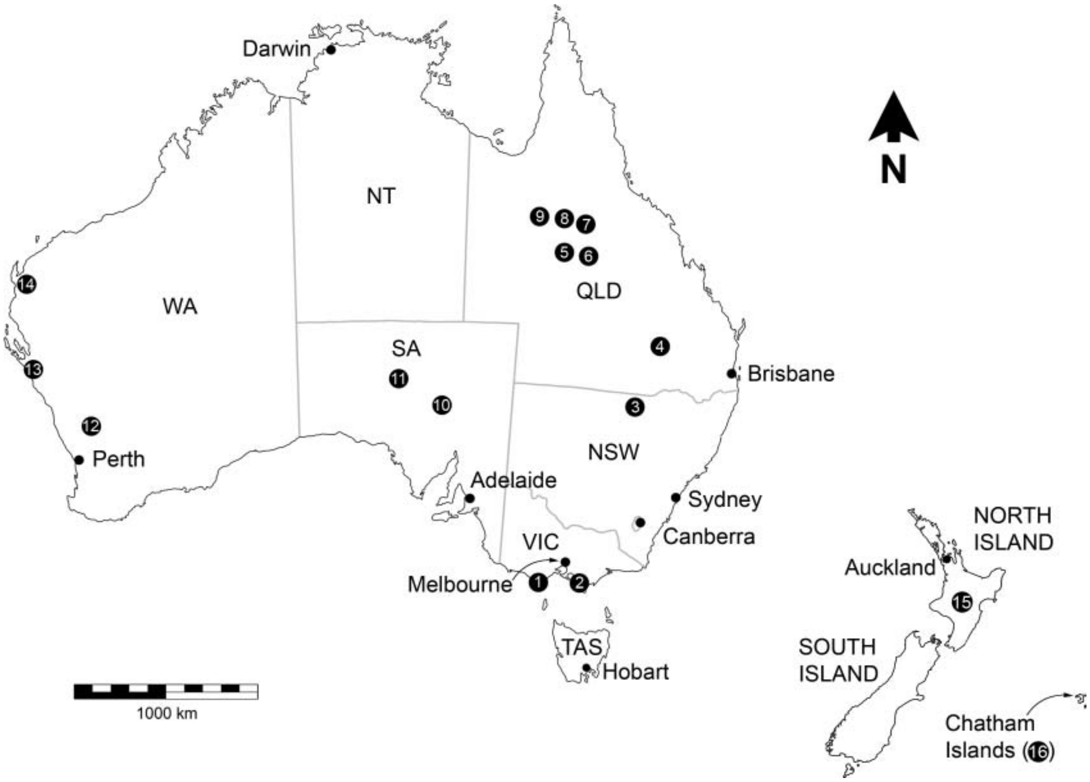

Figure 1. Map showing the geographic position of the main Cretaceous localities of Australia and New Zealand dinosaur body fossils: 1, Otway Basin localities (Eumeralla Formation, late Aptian-early Albian); 2, Gippsland Basin localities (Wonthaggi Formation, early Aptian); 3, Lightning Ridge (Griman Creek Formation, early-middle Albian); 4, Roma (Bungil Formation, Aptian); 5, Winton localities (Winton Formation, latest Albian-earliest Cenomanian; Makunda Formation, late Albian); 6, Muttaburra (Makunda Formation, late Albian); 7, Hughenden localities (Alluru Formation, late Albian; Toolebuc Formation, mid-late Albian); 8, Richmond and Maxwelton localities (Makunda Formation, late Albian; Alluru Formation, late Albian; Toolebuc Formation, mid-late Albian); 9, Julia Creek (Alluru Formation, late Albian); 10, Andamooka, Maree Formation (Aptian); 11, Cooper Pedy (Maree Formation, Aptian); 12, Gingin (Molecap Greensand, Cenomanian-early Turonian); 13, Kalbarri (Birdrong Sandstone, Hauterivian-Barremian); 14, Giralia Range (Maria Formation, late Maastrichtian); 15, Mangahouanga Stream (Maungataniwha Member, Campanian-Maastrichtian); 16, Chatham Islands (Campanian-Maastrichtian).

Rich *et al.* 2002). The presence in the Early Cretaceous of Australia of the theropod *Allosaurus* (Molnar *et al.* 1981, 1985), and 'cetiosaurian' sauropods (Molnar 1980b) were considered indicative of the late survival of Jurassic dinosaur taxa in this continent. Moreover, a New Zealand Late Cretaceous ornithopod ilium showed more resemblance to ilia of the Late Jurassic and Early Cretaceous taxa rather than to ilia of contemporaneous ornithopods (Molnar 1989). In addition to these dinosaur relicts, ausktribosphenid mammals (Rich & Vickers-Rich 1999b; Rich *et al.* 2001), temnospondyl amphibians (Warren *et al.* 1991) and dicynodont synapsids (Thulborn & Turner 2003) have also been interpreted as relictual elements of the peculiar Cretaceous Australian faunas. The presence of these relictual taxa allowed some authors to speculate on the possibility that the factors causing the pre-Cretaceous extinction of these groups elsewhere did not apply in Australia (Molnar 1992).

A second informal group that can be recognized from amongst the currently described Australian and New Zealand non-avian dinosaurs, includes taxa that appear to have diverged to a significantly greater extent than related forms elsewhere, the endemics. These include the peculiar ankylosaur *Minmi paravertebra*, which shows ossified tendons and aponeuroses absent in other ankylosaurians, and the enigmatic iguanodontian *Muttaburrasaurus*, which was unique in having a raised hollow rostral bulla and a peculiar dentition distinct from that of any other ornithopod (Molnar 1980a, c, 1991, 1992, 1996a, b, 2001a; Bartholomai & Molnar 1981).

The third and final group includes Early Cretaceous dinosaurs that, although based on isolated bones, have been interpreted as the oldest representatives of their respective clades (Molnar 1980b; Rich & Vickers-Rich 1994; Currie *et al.* 1996). These include materials that have been referred to ornithomimosaurs, oviraptorosaurs, protoceratopsians, and ankylosaurs, all of which are well known in the rest of the world by the early Late Cretaceous, but not in Gondwana. These identifications allowed Rich & Vickers-Rich (1994, 2003) and Rich and collaborators (Rich *et al.* 1999a, 2001) to propose that Australia may have been the 'center of origin' for these dinosaurian clades. In this regard, the presence of such dinosaur groups in Asia was best explained as a result of either island hopping or 'arking' between Australia and Southeast Asia via a series of micro-continents and terrains in the Meso-Tethys (Rich *et al.* 1999, 2001); a migratory route that also may have been employed by placental mammals (but see Kielan-Jaworoska *et al.* 2004). The hypothesis that Australia was in some way isolated from other Gondwanan landmasses during the Early Cretaceous is, at first sight, clearly contradictory with most palaeogeographical reconstructions (Smith *et al*. 1994; Hay *et al.* 1999; Scotese 2001).

As was pointed out by Molnar (1992), the arrangement of Gondwanan continents during the Cretaceous suggests that Australian terrestrial tetrapods should be similar to those of other Gondwanan landmasses (i.e. Antarctica, South America, Africa, Madagascar, and India), since the oldest estimation time of separation of Australia from Western Gondwana was during the Valanginian (Early Cretaceous) (Upchurch *et al*. 2002). Thus, the apparent distinctiveness of the Australian dinosaur fauna has been explained by the fact that the dinosaurs that occurred in this part of Gondwana were specially adapted to near-polar environmental conditions and were therefore unable to migrate into adjoining regions (Molnar 1992). Some authors have proposed that the effects of this isolation are detectable in Australian terrestrial tetrapod faunas as early as the start of the Triassic (Thulborn 1986), and that isolation probably intensified during the Cretaceous (Thulborn & Turner 2003). Australia, at the extremity of an enormous East Gondwanan peninsula, therefore maintained only a tenuous trans-Antarctic connection to other Gondwanan continents (Thulborn & Turner 2003). Thus, Australia's polar location, coupled with its relative isolation as a peninsula at the eastern extremity of Gondwana, may have favoured the area as both a place of origin for evolutionary novelties and a final haven for groups that had become extinct elsewhere (Rich & Vickers-Rich 1994; Vickers-Rich 1996; Henderson *et al*. 2000). So, although one may expect the Australian dinosaur fauna to show a greater resemblance to South America than to Asia, it has been claimed that the reverse was more likely (Rich & Vickers-Rich 2003).

The palaeobiogeographical setting that has been employed to explain the aforementioned faunal anomalies has a number of distinct stages, each relating to a particular time period for which there is a vertebrate record in Australia. The first stage occurs during the Late Jurassic, when Australia was intimately linked to Antarctica (i.e. Eastern Gondwana), and its dinosaurian faunas were Pangean in origin and composition, being well isolated from Laurasia by a Meso-Tethys sea. The second stage involves Aptian-Albian (Early Cretaceous) faunas. The palaeogeographic position of Australia was far to the southeast from the rest of Gondwana, remote and at high-latitudes. The peculiar climatic and geographical conditions favoured the rise of a very peculiar tetrapod fauna. This fauna included a number of Jurassic relicts, endemics and 'origin taxa'. During the Late Cretaceous, beginning approximately 80 million years ago, Rich and collaborators (Rich *et al.* 1999, 2001; Rich & Vickers-Rich 2003) stated that micro-continents or terranes were splitting off from the northern edge of Australia and drifting north. They hypothesised that such terranes could have served as a 'Noah's Ark', transporting ancestral stocks of protoceratopsians, ornithomimosaurs, oviraptorans and eutherian mammals northwards to Asia during the Late Cretaceous.

In addition to the geographical position of Australia among Gondwanan continents, several authors have also suggested that the unusual composition of the Australian

Cretaceous dinosaur fauna was due to climatic factors (Rich *et al.* 1988; Rich 1996; Constantine *et al.* 1998; Thulborn & Turner 2003). In this regard, the isolation of Australia and New Zealand from remaining Gondwanan continents was not only geographical in nature, but also climatic. These authors cited a number of biological and geological data that supported a cold temperature in parts of Australia, particularly the south-eastern corner, during parts of the Cretaceous. Although palaeoclimatic hypotheses derived from geological evidence is unconsensual, it is clear that Australian palaeoclimatic conditions were far from tropical. Additionally, several lines of evidence (Rich *et al.* 1988; Rich & Rich 1989; Constantine *et al.* 1998) indicate the presence of permafrost and consequently a cool climate with an annual mean temperature between 5°C and 0°C during the Aptian-Albian (Otway and Strzelecki groups; Rich & Rich 1989), indicating that the dinosaur-bearing sediments must have been seasonally frozen. Faunal elements that supported these palaeoclimatological scenarios also include a number of dinosaurs. 'Hypsilophodontid' ornithopods are generally a rare element in most dinosaur assemblages. However, Rich (1996) considered their abundance and apparent high diversity in south-eastern Australia to correlate with the cold climate that prevailed in this region during the Aptian-Albian. As suggested by Rich (1996), no matter what the palaeotemperature was, polar dinosaurs were adapted to prolonged periods of annual darkness each winter. Evidence cited in favour of this hypothesis includes the apparently enlarged optic lobes in the brain of the 'hypsilophodontid' *Leaellynasaura amicagraphica*, which Rich & Rich (1989) interpreted as an adaptation for enhanced visual acuity during the winter darkness, facilitating active foraging at that time. The presence of distinct lines of arrested growth in the femur of the putative ornithomimosaurian *Timimus hermani* has also been linked to regular episodes of rapid growth alternating with ones of little growth; this being considered by Chinsamy *et al.* (1998) as indicative of hibernation.

Nevertheless, Molnar (1992), in a comprehensive study of Australian terrestrial tetrapods, concluded that, in spite of the strong differences, the Australian fauna may have been more similar to that of South America than to other continents. More recently, Bonaparte (1999) suggested that the interpretations of isolated Australian dinosaur elements as belonging to taxa typically found only in Laurasia needed to be carefully reconsidered after comparisons with the new South American basal iguanodontians and African and South American theropods. Recent work by Molnar & Salisbury (2005) and Hocknull *et al.* (2009) has supported the close phylogenetic relationships between Australian Cretaceous sauropods and similarly aged sauropod taxa from South America. In addition, a biogeographic analysis performed through optimized area cladograms found Australia clustered with the Gondwanan territories of Africa and South America (Upchurch *et al*. 2002).

The great increase in the South American Cretaceous dinosaur sample in recent years has resulted in substantial advances in our knowledge of Gondwanan tetrapod communities. Discoveries in areas such as Madagascar, Africa and India have further improved our knowledge of Gondwanan dinosaur faunas during the Cretaceous. Herein, we analyze and compare in detail the Cretaceous non-avian dinosaur specimens of Australia and New Zealand with new material from South America and other Gondwanan landmasses in order to better understand their phylogenetic relationships and palaeobiogeographical affinities.

Institutional abbreviations

AM: Australian Museum, Sydney, Australia; **AMNH**: American Museum of Natural History, New York, USA; **AOD**: Australian Age of Dinosaurs Fossil Museum of Natural History, Winton, Australia; **BMNH**: The Natural History, London, UK; **CD**: New Zealand Geological Survey Collection, Lower Hutt, New Zealand; **MACN**: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; **MCF-PVPH**: Museo Carmen Funes, Paleontología de Vertebrados, Plaza Huincul, Neuquén, Argentina; **MPCA**: Museo Provincial Carlos Ameghino, Río Negro, Argentina; **MPM**: Museo Padre Molina, Santa Cruz, Argentina; **MUCPv**: Museo de la Universidad del Nacional Comahue, Paleontología de Vertebrados, Neuquén, Argentina; **NMV P**: Museum of Victoria, Melbourne, Victoria, Australia, Paleontological collections; **QM**: Queensland Museum, Brisbane, Queensland, Australia; **SAM**: South Australian Museum, Adelaide, South Australia; **SAM-K**: South African Museum, Cape Town, South Africa; **UA**: Université d'Antananarivo, Tananarive, Madagascar; **UCMP**: University of California Museum of Paleontology, Berkeley, USA; **UNPSJB**: Universidad Nacional de la Patagonia San Juan Bosco, Chubut, Argentina; **YPM**: Yale Peabody Museum, Yale University, New Haven, Connecticut, USA.

Material

The following material of non-avian dinosaurs was examined during the course of the present study: *Anabisetia saldiviai* (MCF-PVPH 74, PVPH 75, PVPH 76); *Atlascopcosaurus loadsi* (NMV P166409, P157390, P182967a, P186440); Australian '*Allosaurus*' (NMV P150070); *Australovenator wintonensis* (AOD F604); *Austrosaurus mckillopi* (QM F2316); *Buitreraptor gonzalezorum* (MPCA 245); *Dilophosaurus wetherilli* (UCMP 77270); *Diamantinasaurus maltidae* (AOD F603); *Fulgurotherium australe* (Type cast from QM, NMV P150054, P164 998); *Gasparinisaura cincosaltensis* (MUCPv-208, MUCPv-212); *Heterodontosaurus tucki* (UCMP 129614 cast of SAM-K 1332); Hypsilophodontidae indet. (NMV

P186 047); *Kakuru kujani* (BMNH R9803); *Leaellynasaura amicagraphica* (NMV P185991, P185999, P185990, P185992, P186004); *Liliensternus liliensterni* (MB R.2175); *Megaraptor namunhuaiquii* (MUCPv 341, MCF-PVPH 79); *Minmi paravertebra* (QM F10329); *Minmi* sp. (QM F18101), *Muttaburrasaurus langdoni* (QM F6140); *Muttaburrasaurus* sp. (QM F14921); Neosauropoda indet. (QM F7291); Sauropoda indet. (QM F311, QM L380); *Patagonykus puertai* (MCF-PVPH 37); Protoceratopsia indet. (NMV P186399); *Qantassaurus intrepidus* (NMV P199075, P198962, P199087); *Rapator ornitholestoides* (BMNH R.3718); *Scutellosaurus lawleri* (UCMP 130580, 130581, 170829); *Serendipaceratops arthurcclarkei* (NMV P186385); *Talenkauen santacrucencis* (MPM 10001); *Timimus hermani* (NMV P186303); Titanosauridae indet. (QM F2470, QM F6737); Titanosauria indet. (QM F40347, QM F10916, QM F2470, QM F7880); Titanosauriformes indet. (AM F66769, AM F66770, QM F3390, QM F13712); Titanosauriformes cf. Brachiosauridae (QM F6142); *Velocisaurus unicus* (MUCPv 41); *Wintonotitan wattsi* (QM F7292); *Xenotarsosaurus bonapartei* (UNPSJB-Pv 184/612); *Zupaysaurus rougieri* (PULR 076); an indeterminate ankylosaurian from Patagonia (MPCA-Pv 68/69/70).

Systematic framework

In the discussion of the phylogenetic relationships of basal theropod dinosaurs from Australia and New Zealand we use the systematic nomenclature proposed by Rauhut (2003). This author considered a paraphyletic Ceratosauria (sensu Rowe & Gauthier 1990) as a senior synonym of Neoceratosauria (sensu Novas 1992). Regarding basal tetanurans, we follow the phylogenetic analysis of Smith *et al.* (2008) and Benson *et al*. (2009), in which Spinosauroidea is the sister-taxon of the clade including Allosauroidea and Coelurosauria. Allosauroidea includes the clades Allosauridae, Sinraptoridae and Carcharodontosauria. Within Carcharodontosauria, the families Carcharodontosauridae and Neovenatoridae (inclusive of Megaraptora) are recognized. Among coelurosaurians, Tyrannosauroidea and Ornithomimosauria are considered to be successive sister-groups to Maniraptora. Within Maniraptora, two main lineages are recognised, the first comprising Therizinosauroidea and Oviraptorosauria, and the second comprising Deinonychosauria and Aves. Deinonychosauria comprises Troodontidae and Dromaeosauridae. Recent contributions (Bonaparte 1999; Makovicky *et al.* 2005; Senter 2007) have recognized a Gondwanan dromaeosaurid clade named Unenlagiinae. Regarding the taxonomic nomenclature of the Sauropoda we accept the arrangement proposed by Salgado (2003).

Regarding systematic arrangements of Ornithischia we follow Sereno (1986, 1998), who recognized Thyreophora as including Stegosauria and Ankylosauria. Families defined by Sereno (1986, 1998) nested within the Ankylosauria that we recognise are Nodosauridae and Ankylosauridae. We also follow Sereno's (1986) definition of Marginocephalia as the clade that includes Pachycephalosauria and Ceratopsia. Finally, we follow Butler *et al.*'s (2008) definition of Ornithopoda as all genasaurians more closely related to *Parasaurolophus walkeri* than to *Triceratopos horridus*. For the relationships of basal Ornithopoda we follow Coria and Salgado (1996a; see also Coria & Calvo 2002; Novas *et al.* 2004; Calvo *et al.* 2007). Due to the fluctuating position of *Gasparinisaura* between various phylogenetic analyses of basal ornithopods and the paraphyly of Hypsilophodontidae (Butler *et al*. 2008), we follow Norman's (2004) definition for Iguanodontia as all euornithopods (= ornithopods) closer to *Edmontosaurus* than to *Thescelosaurus*. Relevant major clades that we recognise within Iguanodontia follow Sereno (1998), and include Dryomorpha (*Dryosaurus altus*, *Parasaurolophus walkeri*, their most recent common ancestor and all descendants), Ankylopollexia (*Camptosaurus dispar*, *Parasaurolophus walkeri*, their most recent common ancestor and all descendants), and Styracosterna (all ankylopollexians closer to *Parasaurolophus walkeri* than *Camptosaurus dispar*). We consider Iguanodontoidea as defined by Norman (2002) to be a junior synonym of Styracosterna, as both definitions use *Camptosaurus* as an external specifier and a hadrosaurid as an internal specifier. Following Butler *et al.* (2008) and Varrichio *et al.* (2007), we consider Hypsilophodontidae to be paraphyletic (contra Weishampel & Heinrich 1992).

Similarity indices

In Table 1, the main dinosaur clades recorded for the different continents during the Cretaceous period are compared. Whole dinosaur communities were compared for the entire Cretaceous because the scarce record in particular landmasses for particular time spans (e.g. Early Cretaceous of Madagascar and India, and Late Cretaceous of Australia and Africa) will produce an artificial increase of the differences between each Early and Late Cretaceous dinosaur fauna, respectively. A detailed cladistic biogeographic comparison of each dinosaur-bearing assemblage of the different Cretaceous landmasses goes beyond the scope of the present paper. Nonetheless, the grade of similarity between the compositions of the dinosaur communities of each continent was assessed through a similarity index. In order to perform this index of similarity we applied the formula of Sorensen ($SI = 2a / 2a + b + c$; where 'a' represents the number of common elements in both communities, 'b' the number of elements present in community A but absent in B, and 'c' the number of elements present in community B but absent in A) (Matteucci & Colma 1982). Sorensen's formula was followed because it emphasizes the importance of the common elements in communities over the

Table 1. Table summarizing the original and revised assignments of the taxa discussed here.

Taxon	Original Assignment	Revised Assignment
Serendipaceratops arthurcclarkei	Neoceratopsia (Rich & Vickers-Rich 2003)	Genasauria indet. (*nomen dubium*)
'Protoceratopsia' indet.	Protoceratopsia (Rich & Vickers-Rich 2003)	Ornithischia indet.
Minmi paravertebra	Ankylosauria (Molnar 1980a)	Ankylosauridae
Minmi sp.	Ankylosauria (Molnar 1996a)	Ankylosauridae
Ankylosauria indet.	Ankylosauria (Molnar & Wiffen 1994)	Ankylosauria indet.
Qantassaurus intrepidus	Hypsilophodontidae (Rich & Vickers-Rich 1999a)	Non-dryomorph Ornithopoda
Atlascopcosaurus loadsi	Hypsilophodontidae (Rich & Rich 1989)	Non-dryomorph Ornithopoda indet. (*nomen dubium*)
Leaellynasaura amicagraphica	Hypsilophodontidae (Rich & Rich 1989)	Non-iguanodontian Ornithopoda
Fulgurotherium australe	Coelurosauria (von Huene 1932); Hypsilophodontidae (Molnar & Galton 1986)	Iguanodontia indet. (*nomen dubium*)
Victoria femur type I	Hypsilophodontidae (Rich & Rich 1989)	Ornithopoda indet.
Victoria femur type II	Hypsilophodontidae (Rich & Rich 1989)	Ornithopoda indet.
Muttaburrasaurus langdoni	Iguanodontidae (Bartholomai & Molnar 1981); basal Iguanodontia (Molnar 1996b)	Styracosterna indet.
Muttaburrasaurus sp.	basal Iguanodontia (Molnar 1996b)	Styracosterna indet.
Dryosaurus-like ilium	*Dryosaurus*-like (Wiffen & Molnar 1989)	Ornithopoda indet.
Hypsilophodontid scapula	Hypsilophodontidae (Molnar & Galton 1986)	Ornithopoda indet.
Austrosaurus mckillopi	'Cetiosaurid-like' (Coombs & Molnar 1981)	Titanosauriformes (Salgado *et al*. 1997)
Wintonotitan wattsi	Titanosauriformes (Hocknull *et al*. 2009)	Titanosauriformes (Hocknull *et al*. 2009)
Diamantinasaurus matildae	Titanosauridae (Hocknull *et al*. 2009)	Titanosauridae (Hocknull *et al*. 2009)
Walgettosuchus woodwardi	Coelurosauria (von Huene 1932)	Theropoda indet. (*nomen dubium*)
Allosaurus	*Allosaurus* sp. (Molnar *et al.* 1981, 1985)	Abelisauroidea indet. (*nomen dubium*)
Kakuru kujani	Theropoda (Molnar & Pledge 1980); Abelisauroidea (Rauhut 2005)	Averostra indet.
cf. *Megaraptor*	Theropoda indet. (Rich & Vickers-Rich 2003)	Carcharodontosauria, Megaraptora indet.
Rapator ornitholestoides	Coelurosauria (von Huene 1932); Alvarezsauridae (Holtz *et al.* 2004)	Carcharodontosauria, Megaraptora indet. (*nomen dubium*)
Australovenator wintonensis	Allosauroidea (Hocknull *et al*. 2009)	Carcharodontosauria, Megaraptora (Benson *et al*. 2009)
Timimus hermani	Ornithomimidae (Rich & Vickers-Rich 1994)	Paraves, Dromaeosauridae indet. cf. Unenlagiinae (*nomen dubium*)
Australian oviraptorosaur	Oviraptorosauria (Currie *et al.* 1996)	Theropoda indet. (surangular) and Dromaeosauridae indet. (vertebra)
Theropod pedal phalanx	Theropoda indet. (Molnar & Wiffen 1994)	Theropoda indet.
Theropod pedal ungual phalanx	Theropoda indet. (Woodward 1906)	Theropoda indet.
Theropod pedal phalanx	Theropoda indet. (Scarlett & Molnar 1984)	Theropoda indet.
Theropod pedal phalanx	Carnosauria, related to Allosauridae (Long 1995)	Theropoda indet.
Mid-caudal theropod vertebra	Theropoda indet. (Long & Cruickshank 1996)	Theropoda indet.
Theropod humerus (WAM 90.10.2)	Theropoda indet., possibly coelurosaurian (Long 1992)	Theropoda indet. cf. Coelurosauria
Theropod caudal vertebra	Theropoda indet. (Molnar 1981)	Theropoda indet.
Theropod vertebral centrum	Theropoda indet. (Stilwell *et al.* 2006)	Dinosauria? indet.
Theropod proximal tibia	Theropoda indet. (Stilwell *et al.* 2006)	Indeterminate
Theropod manual ungual	Ornithomimosaurian-like (Stilwell *et al.* 2006)	Non-maniraptoran Coelurosauria
Theropod manual phalanx	Theropoda (Stilwell *et al.* 2006)	Enantiornithes? indet.
Theropod proximal pedal phalanx	Basal Allosauroidea? (Stilwell *et al.* 2006)	Dinosauria indet. cf. Theropoda

differences indicated by the absence of a particular element. This is especially important regarding fossil communities, because the differences indicated by absences can be the cause of a bias in the fossil record rather an actual difference between both communities.

Australasian Cretaceous dinosaur taxa

Ornithischia

Among the best known Cretaceous dinosaurs of Australia and New Zealand are the ornithischians. Until now, nine species of ornithischians have been provisionally recognized: two species of ankylosaurian (*Minmi paravertebra* and *Minmi* sp.), one marginocephalian (*Serendipaceratop*s *arthurcclarkei*), and six species of ornithopods (*Qantassaurus intrepidus*, *Atlascopcosaurus loadsi*, *Leaellynasaura amicagraphica*, *Fulgurotherium australe*, *Muttaburrasaurus langdoni* and *Muttaburrasaurus* sp.). In addition, several isolated bones recovered from Early and Late Cretaceous beds of Australia and New Zealand referred to Ornithischia have also been figured and/or briefly described.

Early Cretaceous ornithischians. The Cretaceous fossil records of Australia and New Zealand contrast with that of other Gondwanan and Laurasian landmasses in having a comparatively much richer sample of Early Cretaceous than Late Cretaceous dinosaurs. This is clearly the case for the described and figured ornithischian specimens. Some of the Early Cretaceous ornithischians are the best known of the Australian and New Zealand dinosaurs, including some forms represented by fragmentary or fairly complete specimens, namely *Minmi* and *Muttaburrasaurus*. The currently described and figured Early Cretaceous record of Australasian ornithischians includes ornithopods, thyreophorans and putative marginocephalians (but see below).

Thyreophora and Marginocephalia. Very few non-ornithopodan ornithischians are known from Australia. Only four specimens have been described and figured: two purported neoceratopsians (Rich & Vickers-Rich 1994, 2003) and two species of the basal ankylosaurid *Minmi* (Molnar 1980a, 1996a; Vickaryous *et al.* 2001; Hill *et al.* 2003). Rich & Vickers-Rich (1994, 2003) and Molnar (1980a, 1996a) regarded these taxa as relicts of clades that once had a worldwide distribution during the Late Jurassic (*Minmi* spp.), or as being closely related to Asian taxa (*Serendipaceratops*). Possible ankylosaurid material has also been described from the Late Cretaceous of New Zealand (Molnar & Wiffen 1994).

Minmi paravertebra Molnar, 1980a

Horizon and locality. Bungil Formation (Barremian-Valanginian: Early Cretaceous; Scheibner & Basden 1998), near Roma, south-eastern Queensland, Australia (Molnar 1980a).

Holotype. QM F10329, fragmentary postcranial skeleton with associated dermal skeleton.

Revised taxonomic assignment. Ankylosauridae.

Remarks. Although fragmentary, this specimen displays a number of unusual features of the axial and dermal skeleton that are unique to *Minmi*, along with a suite of characteristics that demonstrate it is an ankylosaurian. The specimen comprises a series of eleven thoracic vertebrae, several of which are preserved in articulation, along with some associated vertebral rib segments, an incomplete, partly articulated right pes and numerous dermal ossifications. The latter include small, pebble-like ossicles and a series of ossified epaxial aponeuroses and tendon cores that are preserved in close to their natural position alongside the thoracic vertebrae (Molnar & Frey 1987). Apomorphies of this specimen that identify it as an ankylosaur include fusion of the posterior-most thoracic vertebral bodies to form a presacral rod (Coombs 1978), fusion of the ribs to the thoracic vertebrae, laterally constricted amphiplatyan vertebral bodies with expanded articular surfaces that lack notochordal knobs (Makovicky 1997), and dorsally inclined transverse processes (Coombs 1978; Molnar 1980a). At the time that this specimen was described, its dermal ossifications (both the numerous small ossicles–initially interpreted as coming from the belly–and the ossified aponeuroses and associated tendons) were unique among ankylosaurs and formed the basis of the generic diagnosis. These features also occur in the Marathon specimen (QM F18101; see below), and were part of the basis for referring this specimen to *Minmi* (Molnar 1996a). The Marathon specimen, which is considerably more complete than the type of *M. paravertebra*, has been preliminarily referred to *Minmi* sp. (Molnar 1996a), expanding our knowledge of this unique Australian ankylosaur.

We agree with Molnar's (1980a) interpretation of QM F10329, and consider *Minmi paravertebra* a valid species of ankylosaurian thyreophoran. Further details on the precise phylogenetic relationships of *Minmi* are best discussed in relation to the Marathon specimen (Molnar 1996a).

Minmi sp.
(Fig. 2)

Horizon and locality. Allaru Mudstone (late Albian; late Early Cretaceous), Marathon Station, east of Richmond, central western Queensland, Australia (Molnar 1996a).

Material. QM F18101, a nearly complete, articulated skeleton, lacking only the distal parts of the limbs, the terminal part of the tail, and some of the anterior-most parts of the skull, partly described by Molnar (1996a, 2001a), and Molnar & Clifford (2000).

Revised taxonomic assignment. Ankylosauridae.

Remarks. QM F18101 is one of best-known Australian dinosaur specimens (Fig. 2B). Albeit widely considered as a member of Ankylosauria, based on this specimen, *Minmi* has alternatively been interpreted as either a basal member of this clade (Molnar 1996a; Kirkland *et al.* 1998; Carpenter 2001), a basal nodosaurid (Coombs & Maryanska 1990), or a basal ankylosaurid (Hill 1999; Sereno 1999). More recent authors (Vickaryous *et al.* 2001, 2004; Hill *et al.* 2003) have carried out cladistic analyses that supported the position of *Minmi* as a basal ankylosaurid. The latter view is followed here. QM F18101 represents the most complete ankylosaurian dinosaur known from the southern continents, and together with *Minmi paravertebra* and *Antarctopelta oliveroi* from Antarctica (Gasparini *et al.* 1996; Salgado & Gasparini 2006), and an indeterminate ankylosaurian from the latest Cretaceous (Maastrichtian) beds of Patagonia (Salgado & Coria 1996; Coria and Salgado

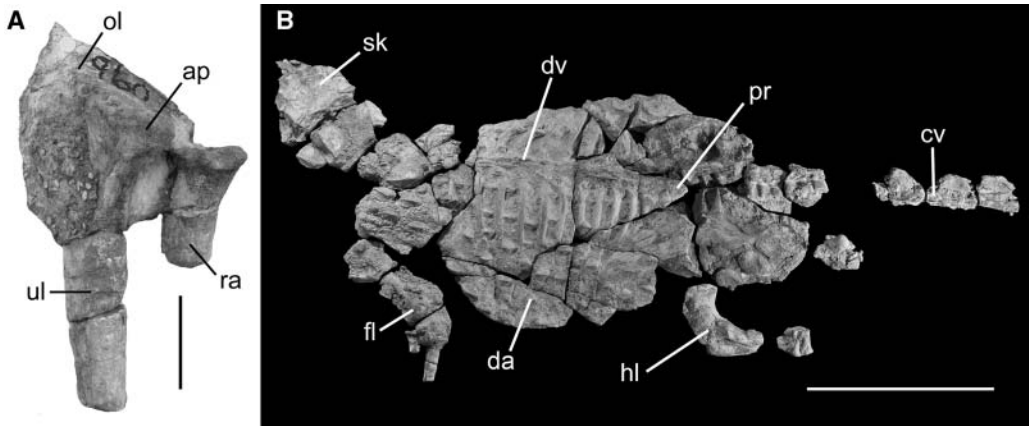

Figure 2. *Minmi* sp. (QM F18101). **A,** proximal left ulna and radius in lateral view; **B,** partial articulated skeleton in dorsal view. Abbreviations: ap, anterior process; cv, caudal vertebrae; da, dorsal armour; dv, dorsal vertebrae; fl, forelimb; hl, hindlimb; ol, olecranon process; pr, presacral rod; ra, radius; sk, skull; ul, ulna. Scale bar for A = 5 cm and for B = 50 cm.

2001), represents one of the few specimens of Cretaceous ankylosaurs from Gondwana.

Minmi sp. is characterized by a melange of plesiomorphies found throughout Ankylosauria. In addition to the characteristics of the axial skeleton outlined above for *Minmi paravertebra*, it also shares a number of features with the Patagonian ankylosaur described by Salgado & Coria (1996) and Coria & Salgado (2001), such as a femur with a proximally positioned fourth trochanter, a medially offset femoral head, and teeth with an asymmetrical cingulum (Molnar 1996a; Salgado & Coria 1996; Coria & Salgado 2001). The latter dental characteristic is also present in *Antarctopelta* (Salgado & Gasparini 2006). *Minmi* also shares with the Patagonian ankylosaur (MPCA Pv68/69/70) two traits that were previously regarded as autapomorphies of *Minmi* by Molnar (1980a): (1) transverse processes of dorsal vertebrae subtriangular in cross-section (rather than T-shaped); and (2) posterior intervertebral notch of dorsal vertebrae shallow (following Molnar 1980a). Further detailed study of QM F18101 and comparisons with the Patagonian ankylosaurs are needed, in order to reach to a clearer understanding of the phylogenetic relationship of these taxa.

In conclusion, we accept that the precise position of *Minmi* sp. within Ankylosauria is yet to be resolved and, as a consequence, its relationships with other Gondwanan ankylosaurs are difficult to assess pending a comprehensive phylogenetic analysis of the entire clade (Leahey *et al.* 2008).

Serendipaceratops arthurcclarkei Rich & Vickers-Rich, 2003
(Fig. 3)

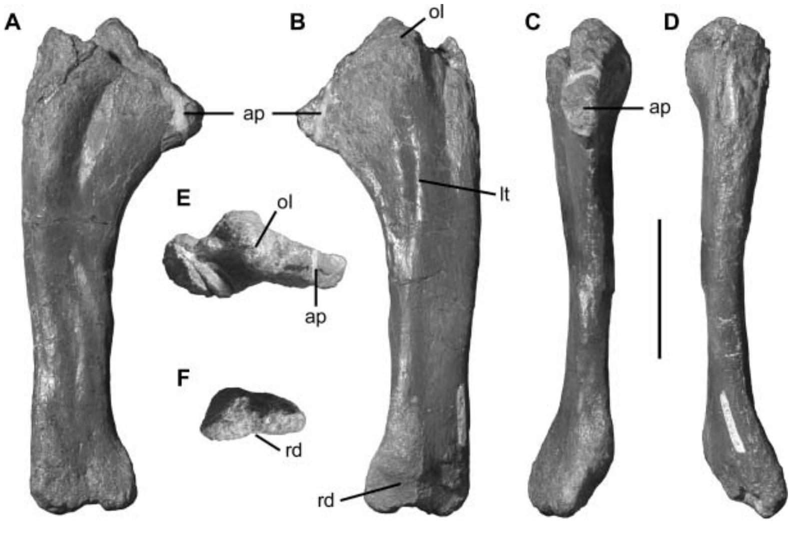

Figure 3. *Serendipaceratops arthurcclarkei* Rich & Vickers-Rich, 2003 (NMV P186385). Left ulna in: **A,** medial; **B,** lateral; **C,** anterior; **D,** posterior; **E,** proximal; and **F,** distal views. Abbreviations: ap, anterior process; lt, lateral process; ol, olecranon process; rd, radial depression. Scale bar = 5 cm.

Horizon and locality. Wonthaggi Formation of the Strzelecki Group (early Aptian: late Early Cretaceous; Wagstaff & McEwen Mason 1989), 'The Arch' on the shore platform near the village of Kilcunda, Victoria, Australia (Rich & Vickers-Rich 2003).

Holotype. NMV P186385, a partial left ulna, lacking portions of the proximal and distal extremities.

Revised taxonomic assignment. Genasauria indet. (*nomen dubium*).

Remarks. This taxon is based on an isolated ulna from the Aptian (Early Cretaceous) of Victoria, originally reported as an unnamed new taxon by Rich & Vickers-Rich (1994), and later named as *Serendipaceratops arthurcclarkei* (Rich & Vickers-Rich 2003) (Fig. 3). These authors suggested that *Serendipaceratops* more closely approaches Thyreophora and Neoceratopsia than other dinosaur clades. They further suggested that this specimen can be referred to Neoceratopsia rather than Ankylosauria because its proximal end is not expanded transversely (Rich & Vickers-Rich 2003). However, the proximal end of the ulna is only slightly expanded transversely in at least some basal nodosaurids (e.g. *Texasetes*; Carpenter *et al.* 1995; Carpenter & Kirkland 1998), contra Rich & Vickers-Rich (2003). Similarly, the proximal end of the ulna of *Minmi* sp. (QM F18101) is also not as transversely expanded relative to the shaft and distal end as it is in more derived ankylosaurians (Molnar 1996a). This condition is clearly different from that in derived ankylosaurids and ceratopsids where the proximal end is markedly expanded transversely (Marsh 1891). *Serendipaceratops* differs from stegosaurians (e.g. *Dacentrurus*, *Stegosaurus*, *Kentrosaurus*, *Chialingosaurus*; Janensch 1924; Dong *et al.* 1983; Galton 1985; Galton & Upchurch 2004) in having a remarkable transversely compressed proximal end and a proximal anterior process (the 'coronoid process' of Rich & Vickers-Rich 2003) that is obliquely oriented with respect to the main axis of the bone.

Serendipaceratops approaches ankylosaurians in having a shallow radial distal depression (Carpenter *et al.* 1995) and a proximodistally extended and mediolaterally inflated lateral tubercle (Rich & Vickers-Rich 2003). Rich & Vickers-Rich (2003) recognized that the ulna of *S. arthurcclarkei* differs from protoceratopsians in having a shorter dorsoventral length of the bone relative to its anteroposterior depth (Rich & Vickers-Rich 2003, p. 1). Indeed, the proportions of the ulna of *Serendipaceratops* are closer to *Minmi* sp. and other ankylosaurians (Kirkland *et al.* 1998; Carpenter *et al.* 1999) than to any neoceratopsian.

Based on the comparisons carried out above, we are not able to recognize any unambiguous synapomorphy present in the ulna of *Serendipaceratops* that would unite it with Neoceratopsia. All characteristics that are apparent in *Serendipaceratops* are also seen in basal thyreophorans, including taxa such as *Minmi*. Thus, in a strict sense *Serendipaceratops* cannot be diagnosed beyond Genasauria, and the taxon should be considered a *nomen dubium*.

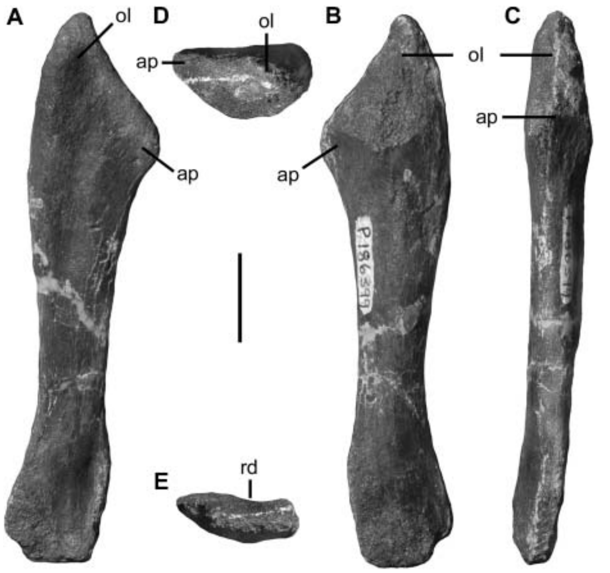

Figure 4. Ornithischia indet. (NMV P186399). Left ulna in: **A,** medial; **B,** lateral; **C,** anterior; **D,** proximal; and **E,** distal views. Abbreviations: ap, anterior process; ol, olecranon process; rd, radial depression. Scale bar = 2 cm.

Protoceratopsia indet. Rich & Vickers-Rich, 2003
(Fig. 4)

Horizon and locality. Eumeralla Formation, Otway Group (late Aptian early Albian: late Early Cretaceous; Wagstaff & McEwen Mason 1989), Dinosaur Cove East, Dinosaur Cove, Victoria, Australia.

Material. NMV P186399, poorly preserved but complete left ulna.

Revised taxonomic assignment. Ornithischia indet.

Remarks. In the same paper in which *Serendipaceratops* was erected, Rich & Vickers-Rich (2003) also described a complete left ulna (NMV P186399), interpreting it as an indeterminate 'protoceratopsian' (Fig. 4). However, this element more closely approaches the morphology of adult ornithopods than ceratopsians, due to a reduced anterior process and a weak, ventrally-developed lateral tubercle. Furthermore, the specimen also displays a proximally tapering olecranon process, as occurs in several ornithopod taxa (e.g. *Ouranosaurus*; Taquet 1976). If, however, as is suggested by Rich & Vickers-Rich (2003), this ulna does belong to a juvenile individual, then any assignment beyond Ornithischia becomes difficult to justify in the absence of more complete material.

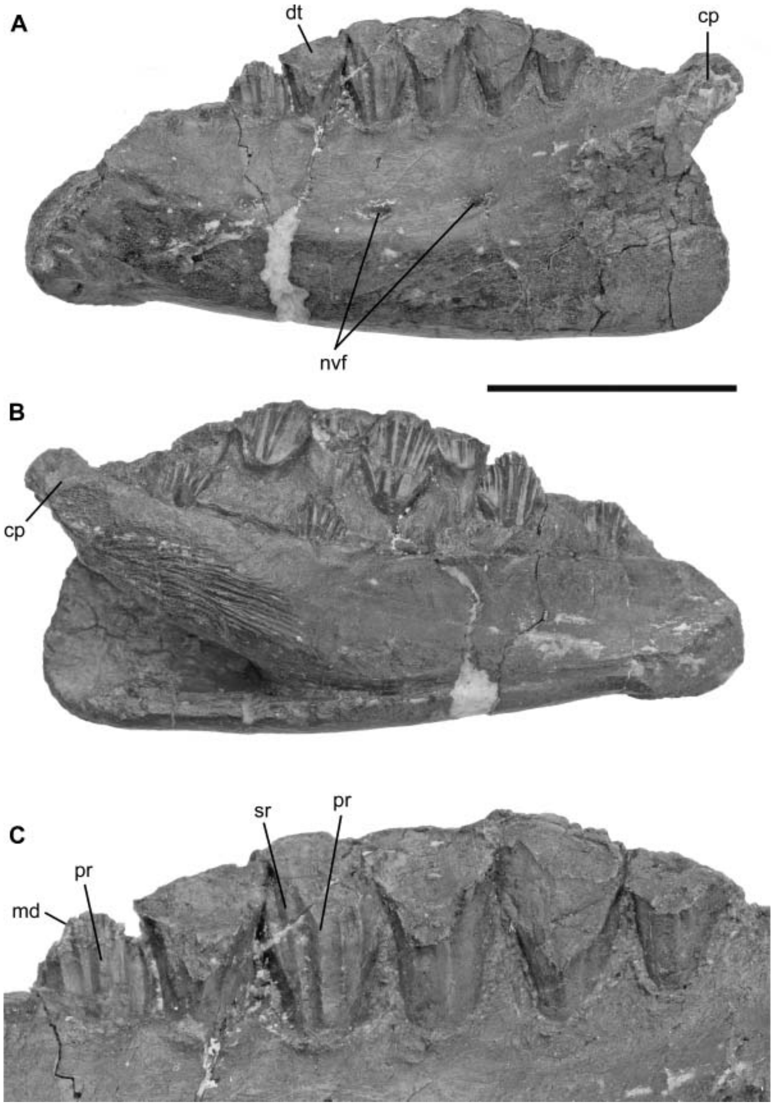

Figure 5. *Qantassaurus intrepidus* Rich & Vickers-Rich, 1999a (NMV P199075). **A, B**, left dentary in lateral and medial views, respectively; **C,** close-up of teeth in labial view. Abbreviations: cp, coronoid process; dt, dentary teeth; md, marginal denticle; nvf, neurovascular foramina; pr, primary ridge; sr, secondary ridge. Scale bar for A and B is 2 cm. Photo courtesy of the Museum of Victoria.

Ornithopoda. The published Australian Cretaceous dinosaur fossil record is dominated by ornithopods (Bartholomai & Molnar 1981; Molnar & Galton 1986; Rich & Rich 1989; Rich & Vickers-Rich 1999a; Molnar 1996b). Described ornithopod taxa include the enigmatic *Muttaburrasaurus langdoni* (Bartholomai & Molnar 1981), a species of *Muttaburrasaurus* (Molnar 1996b), and the putative 'hypsilophodontids' *Leaellynasaura amicagraphica* (Rich & Rich 1989), *Fulgurotherium australe* (von Huene 1932; Molnar & Galton 1986; Rich & Vickers-Rich 1999a), *Qantassaurus intrepidus* (Rich & Vickers-Rich 1999a), *Atlascopcosaurus loadsi* (Rich & Rich 1989) and several unnamed 'hypsilophodontid' remains (Figs 5, 6).

Australian 'hypsilophodontid' taxa have previously been considered Laurasian relicts, specially adapted to subpolar environments (Rich & Rich 1988, 1989; Vickers-Rich & Rich 1993; Rich & Vickers-Rich 1999a). However, Bonaparte (1999) suggested that the Laurasian affinities of Australian 'hypsilophodontids' might need to be reevaluated based on comparisons with basal ornithopod taxa from South America. More recently, Norman *et al*. (2004) considered Australian 'hypsilophodontids' to be basal ornithopods. All the described Australian and New Zealand ornithopods are reviewed below.

Qantassaurus intrepidus Rich & Vickers-Rich, 1999a
(Fig. 5)

Horizon and locality. Wonthaggi Formation, Strzelecki Group (early Aptian: late Early Cretaceous). Flat Rocks

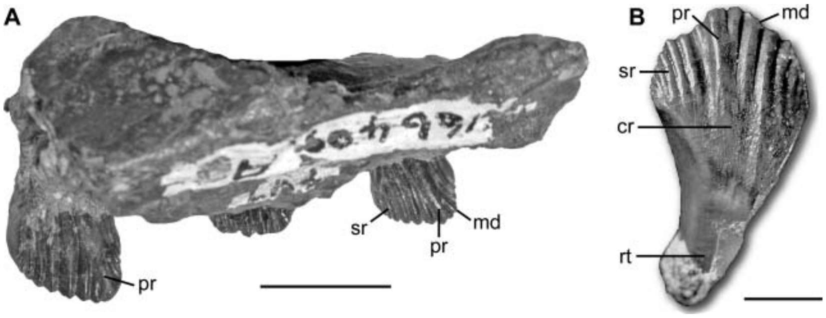

Figure 6. *Atlascopcosaurus loadsi* Rich & Rich, 1989. **A,** lateral view of left maxilla (NMV P166409); **B,** isolated tooth in labial view (NMV P177934); photo courtesy of the Museum of Victoria. Abbreviations: cr, crown; md, marginal denticle; pr, primary ridge; rt, root; sr, secondary ridge. Scale bars: A = 1 cm; B = 5 mm.

fossil vertebrate site, 38° 39′ 40±02″S, 145° 40′52±03″E on the shore platform of the Bunurong Marine Park, Victoria, Australia (Rich & Vickers-Rich 1999a).

Holotype. NMV P199075, almost complete left dentary.

Referred materials. NMV P198962, an almost complete left dentary; P199087, a fragment of right dentary.

Revised taxonomic assignment. Non-dryomorph Ornithopoda.

Remarks. *Qantassaurus* is based on an isolated dentary with complete dentition (Fig. 5) Rich & Vickers-Rich (1999a) considered the presence of a primary ridge on the labial side of the dentary teeth of *Qantassaurus* as grounds for supporting its referral to 'Hypsilophodontidae'. However, this ridge is widely distributed among several ornithopods, including *Thescelosaurus*, *Hypsilophodon*, *Gasparinisaura*, *Talenkauen*, *Zalmoxes*, *Anabisetia*, *Dryosaurus*, and *Iguanodon* (Weishampel *et al.* 2003; Galton 2007). *Qantassaurus* differs from *Hypsilophodon*, but resembles more derived ornithopods (e.g. *Gasparinisaura*, *Anabisetia*, *Talenkauen*, *Zalmoxes*), in having well developed secondary ridges that contact the base of the denticles. Additionally, *Qantasssaurus* differs from *Parksosaurus*, *Thescelosaurus* (Norman *et al.* 2004) and dryomorphs (e.g. *Dryosaurus*, *Camptosaurus*, *Iguanodon*; Norman 2004) in the presence of a low tooth count (i.e. fewer than 12 dentary teeth). Low tooth counts are present in the rhabdodontid *Zalmoxes* (Weishampel *et al.* 2003), *Tenontosaurus* (Sues & Norman 1990) and *Talenkauen* (MPM 10001). Furthermore, the Australian taxon can be distinguished from Dryomorpha by the presence of only two types of ridges (Galton 2007). The latter two characters represent plesiomorphies for Ornithopoda (Norman *et al.* 2004; Galton 2007), suggesting that *Qantassaurus* is more basal than Dryomorpha.

Autapomorphies of *Qantassaurus* listed by Rich & Vickers-Rich (1999a) include: (1) only ten dentary teeth; (2) a shortened dentary; and (3) ventral and dorsal margins of the dentary converging anteriorly. The first feature is more widely distributed among Ornithopoda. Traits (2) and (3) deserve the following comment. Regarding (2), in the basal ornithischians *Pisanosaurus* (Bonaparte 1976), *Heterodontosaurus* (Norman *et al.* 2004; UCMP 129614), *Eocursor* (Butler *et al.* 2008) and *Lesothosaurus* (Sereno 1991), the dentary is elongated, thus representing the plesiomorphic condition of the clade. Otherwise the dentaries of *Tenontosaurus* (Sues & Norman 1990) and *Zalmoxes* (Weishampel *et al.* 2003) are similar to that of *Qantassaurus* in being proportionately short when they are compared with other basal ornithopods (e.g. *Hypsilophodon*, *Agilisaurus*, *Thescelosaurus*, *Talenkauen*, *Gasparinisaura*; Norman *et al.* 2004), as well as dryomorphs (e.g. *Camptosaurus*, *Dryosaurus*, *Iguanodon*, *Ouranosaurus*; Norman 2004). However, both anterior and ventral margins of the dentary of *Qantassaurus* are not preserved, thus the real length of the bone is obscured. With regards to trait (3), the dentary in *Qantassaurus* has anteriorly convergent alveolar (dorsal) and ventral margins where it articulates with the predentary bone (Rich & Vickers-Rich 1999a). The same feature is also present in *Talenkauen* (Novas *et al.* 2004), *Hypsilophodon* (Galton 1974) and *Dryosaurus* (Sues & Norman 1990). On the other hand, the dentary has subparallel alveolar and ventral margins in the basal ornithischians *Pisanosaurus* (Bonaparte 1976), *Heterodontosaurus* (UCMP 129614), *Eocursor* (Butler *et al.* 2008) and *Lesothosaurus* (Sereno 1991), as well as several ornithopods such as *Anabisetia*, *Gasparinisaura*, *Agilisaurus*, *Orodromeus*, *Zalmoxes*, and *Tenontosaurus* (Weishampel & Heinrich 1992; Norman 2004; Norman *et al.* 2004). Thus, we failed to recognise autapomorphies in the available remains of *Qantassaurus*. However, the combination of a shortened dentary with anteriorly convergent alveolar and ventral margins allows us to distinguish *Qantassaurus* from other known ornithopods.

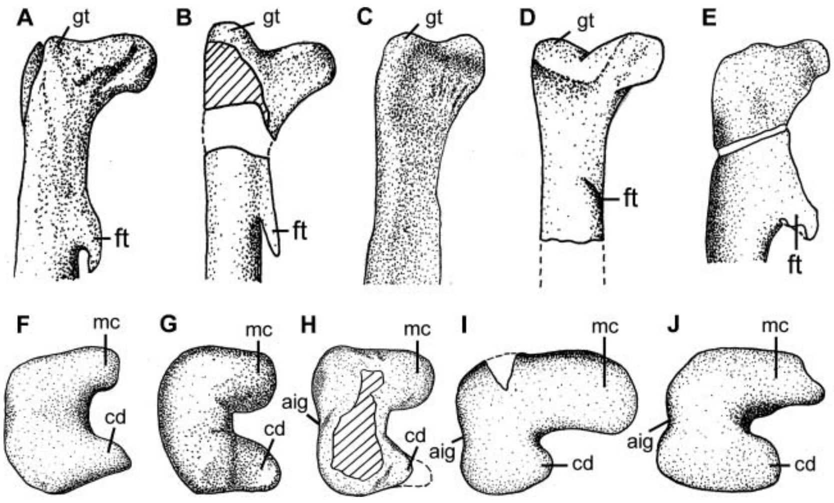

Figure 7. Femora of several basal ornithopods. **A-E,** proximal half of femora in posterior view; **F-J,** distal end of femora in distal view. **A, F,** *Hypsilophodon foxii* (after Galton 1974); **B, G,** *Gasparinisaura cincosaltensis* (after Coria & Salgado 1996a); **C, H,** "*Fulgurotherium australe*" (NMV P 177935); **D, I,** *Notohypsilophodon comodorensis* (after Martínez 1998); **E, J,** Victorian femur type I (NMV P 185999). Abbreviations: aig, anterior intercondylar groove; cd, condylid; ft, fourth trochanter; gt, greater trochanter; mc, medial condyle. Not to scale.

To summarize, the present review of the available material of *Qantassaurus* led us to consider it as a valid species of non-dryomorph ornithopod.

Atlascopcosaurus loadsi Rich & Rich, 1989
(Figs 6, 7A)

Horizon and locality. Eumeralla Formation, Otway Group (late Aptian-early Albian: late Early Cretaceous; Wagstaff & McEwen Mason 1989), Dinosaur Cove East, Dinosaur Cove, Victoria, Australia.

Holotype. NMV P166409, left maxillary fragment with one erupted and three unerupted cheek teeth (Rich & Rich 1989).

Previously referred materials. NMV P157390, left maxilla; NMV P182967a, incomplete mandible (Rich & Rich 1989); NMV P186466, isolated fragmentary dentary (Rich & Vickers-Rich 1999a).

Revised taxonomic assignment. Non-dryomorph Ornithopoda (*nomen dubium*).

Remarks. Rich & Vickers-Rich (1999a) assigned *Atlascopcosaurus* to 'Hypsilophodontidae' on the basis of cheek teeth that have confluent ridges with marginal denticles (Weishampel & Heinrich 1992) (Fig. 6). Along with *Qantassaurus* and *Leaellynasaura*, Rich & Vickers-Rich (1999a) excluded *Atlascopcosaurus* from Dryomorpha (*sensu* Sereno 1986) on the basis of the relatively low crowns of the maxillary teeth. However, Norman *et al.* (2004) suggested that *Atlascopcosaurus* could represent a grade of basal ornithopod similar to *Gasparinisaura*.

Regarding the features mentioned by Rich & Vickers-Rich (1999a) in support of the 'hypsilophodontid' affinities of *Atlascopcosaurus*, several basal ornithopods (e.g. *Zalmoxes*, *Camptosaurus*, *Dryosaurus*; Weishampel & Heinrich 1992; Weishampel *et al.* 2003), including the South American ornithopods *Gasparinisaura* and *Talenkauen*, possess cheek teeth that have confluent ridges with marginal denticles. In this light, the 'hypsilophodontid' affinities of this Australian taxon tend to blur. Regarding the traits supporting the exclusion of *Atlascopcosaurus* from Dryomorpha, the presence of relatively low maxillary tooth crowns was considered by Sereno (1984; see also Weishampel *et al.* 2003) to be symplesiomorphic for Ornithopoda. Indeed, this feature is retained in several basal ornithopods, including *Talenkauen*, *Gasparinisaura*, *Anabisetia*, *Zalmoxes* and *Zephyrosaurus* (Sues 1980; Weishampel *et al.* 2003).

It is worth mentioning that on the basis of Coria & Salgado's (1996a) research, Rich & Vickers-Rich (1999a, p. 174) pointed out that *Atlascopcosaurus* shares with Dryosauridae and Ankylopollexia (i.e. Dryomorpha) the presence of well developed labial primary ridges on the maxillary teeth. They considered this feature as convergently developed in both *Atlascopcosaurus* and Dryomorpha, such that the presence in the former could be considered an autapomorphy. However, a labial primary ridge on the maxillary teeth is also present in non-dryomorph ornithopods, such as *Gasparinisaura* (Coria & Salgado 1996a), *Anabisetia* (Coria & Calvo 2002) and *Talenkauen* (Novas *et al*. 2004) (Galton 2007). Nevertheless, in more

Figure 8. Victorian ornithopod femora in side view. The second specimen from the left is Victoria type II (NMV P 156980) and the first specimen from the left in the lower row is Victoria type I (NMV P 185999). Scale bar = 10 cm. Photo courtesy of the Museum of Victoria.

basal ornithopods (*sensu* Butler *et al*. 2008) such as *Orodromeus*, *Agilisaurus*, *Othnielosaurus*, *Zephyrosaurus* and *Hypsilophodon* (Norman *et al.* 2004), there is no primary ridge on the maxillary teeth. It must be noted that the presence of these labial maxillary primary ridges is not only restricted to *Gasparinisaura* and Dryomorpha, but it is also present in *Talenkauen* (MPM 10001) and *Anabisetia* (MCF-PVPH 74), contrasting with Butler *et al*. (2008) who regarded it as a synapomorphy of Dryomorpha.

Additionally, as was pointed out by Rich & Vickers-Rich (1999a, p. 169), the presence in *Atlascopcosaurus* of a strong primary ridge on both maxillary and dentary teeth (NMV P186466; the partial dentary) and at least eight strong secondary ridges (and subsidiary denticles) that cover the remaining buccal and lingual sides of the upper and lower teeth is also found in the dentition of *Gasparinisaura* and *Thescelosaurus*. The presence of only eight secondary ridges on both upper and lower teeth is a derived feature present in *Thescelosaurus*, *Bugenasaura*, *Gasparinisaura*, *Anabisetia* and *Talenkauen* (Coria & Calvo 2002; Norman *et al.* 2004; Novas *et al.* 2004). In most basal ornithopods the number of ridges and subsidiary denticles varies from ten to more than fifteen (Norman *et al.* 2004). Rich & Rich (1989) considered the distally displaced primary ridge on the maxillary teeth of *Atlascopcosaurus* as diagnostic for the genus. Nevertheless, this feature also occurs in the basal ornithopods *Gasparinisaura* and *Anabisetia* (Fig. 10) and two indeterminate Australian forms (referred by Rich & Vickers-Rich (1999a) to *Qantassaurus* or *Atlascopcosaurus*). Furthermore, this character is also apparent on at least some of the maxillary teeth of *Muttaburrasaurus* sp. (QM F12541; Molnar 1996b; RE Molnar, pers. comm. 2006). Among basal ornithopods, *Atlascopcosaurus* could be excluded from the more derived Dryomorpha (Coria & Salgado 1996a) in lacking a third type of crest on the maxillary teeth (Galton 2007).

The above mentioned similarities between *Atlascopcosaurus*, *Gasparinisaura* and *Anabisetia* may indicate that these three taxa are phylogenetically related. However, the incomplete nature of the available specimens of *Atlascopcosaurus* prevents us from us from determining a more constrained phylogenetic assignment than an indeterminate non-dryomorphan ornithopod.

Leaellynasaura amicagraphica Rich & Rich, 1989
(Fig. 11)

Horizon and locality. Eumeralla Formation, Otway Group (late Aptian-early Albian: late Early Cretaceous; Wagstaff & McEwen Mason 1989), Dinosaur Cove East, Dinosaur Cove, Victoria, Australia.

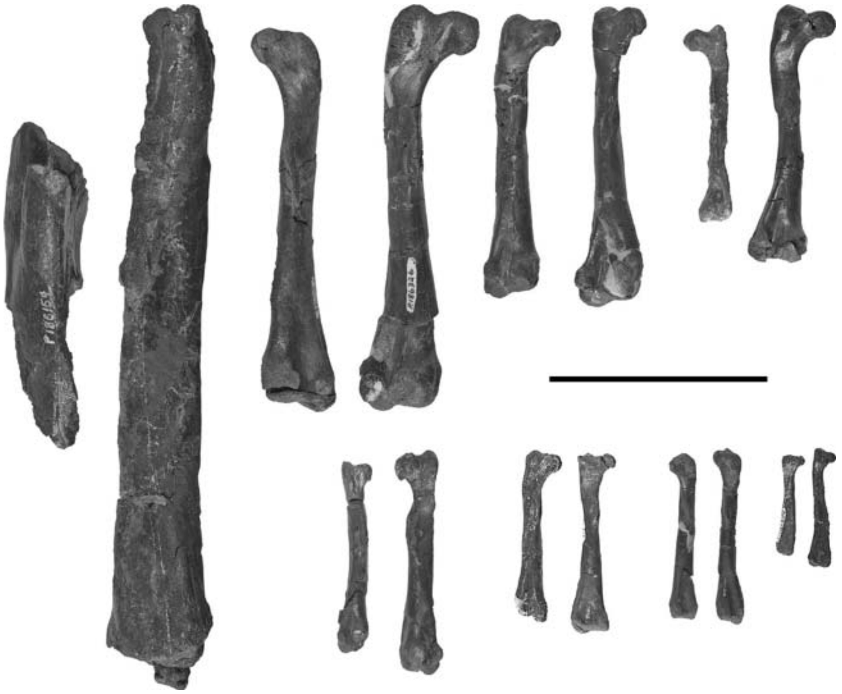

Figure 9. Victorian ornithopod femora in posterior and anterior views. The second specimen from the left is Victoria type II (NMV P 156980) and the first specimen from the left in the lower row is Victoria type I (NMV P 185999). Scale bar = 10 cm. Photo courtesy of the Museum of Victoria.

Holotype. NMV P185991, fragmentary skull that includes portions of the premaxilla, maxilla, ectopterygoid, jugal, quadrate, and a probable vomer from a likely juvenile specimen.

Referred materials. NMV P185990, left and right nasal, frontal, prefrontal and parietals, possibly from the same individual as the holotype; NMV P185992, partially articulated caudal vertebrae and a partial hindlimb, also thought to belong to the same individual as the holotype; NMV P179561, a right femur; NMV P179564, an incomplete left femur; NMV P182968, an incomplete right femur; NMV P185867, an incomplete right femur; NMV P185980, an incomplete right femur; NMV P181681, an incomplete left femur; NMV P186004, a left femur.

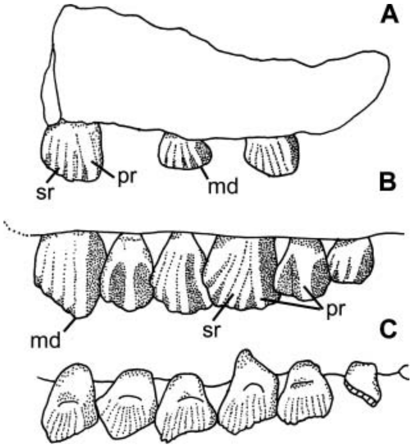

Figure 10. Maxillary teeth of basal ornithopods in labial view. **A,** *Atlascopcosaurus loadsi* (NMV P 166409); **B,** *Gasparinisaura cincosaltensis* (after Coria and Salgado 1996a); **C,** *Zephyrosaurus schaffi* (after Sues, 1980). Abbreviations: md, marginal denticle; pr, primary ridge; sr, secondary ridge. Not to scale.

Revised taxonomic assignment. Non-iguanodontian Ornithopoda.

Remarks. *Leaellynasaura amicagraphica* was erected by Rich & Rich in 1989. Based on a referred specimen, the species was distinguished from other ornithopods known at the time on a single autapomorphy: an anteroposteriorly compressed distal end of the femur (Rich & Vickers-Rich 1999a). Rich & Vickers-Rich (1999a) cited the following traits in order to support the phylogenetic position of *Leaellynasaura* within 'Hypsilophodontidae' sensu Weishampel and Heinrich (1992): (1) combined width of paired frontals less than their length; (2) angle of the femoral head relative to the shaft of the femur greater than 100°; and (3) maxillary teeth with confluent ridges and denticles. Rich and Rich (1989) also made the following comparisons between *Leaellynasaura* and other ornithopods: (4) distinguished from Dryomorpha by relatively low crowns

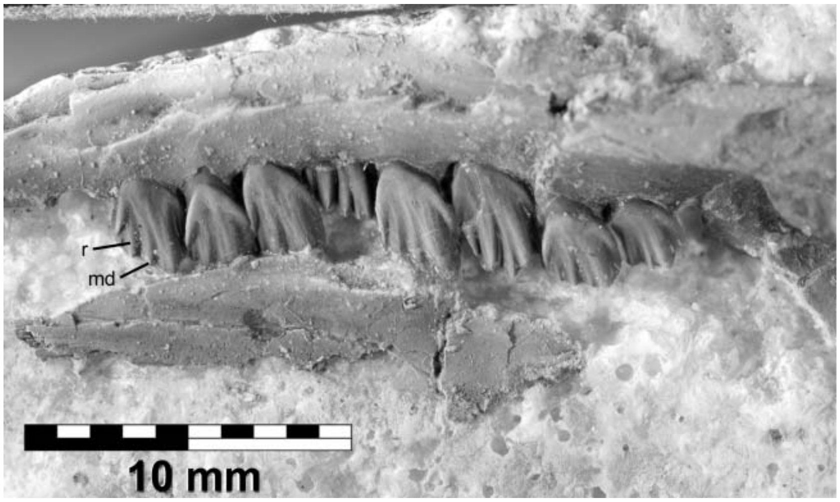

Figure 11. *Leaellynasaura amicagraphica* Rich & Rich, 1989 (NMV P185991). Close up of the maxillary teeth in labial view. Abbreviations: md, marginal denticle; r, ridge. Photograph courtesy of the Museum of Victoria.

on cheek teeth; (5) distinguished from Camptosauridae and Iguanodontidae by the absence of a primary ridge on the maxillary teeth; (6) distinguished from Camptosauridae and Iguanodontidae because the fourth trochanter of the femur is placed proximal to the mid-point of the shaft; and (7) distinguished from Iguanodontoidea by an anterior intercondylar groove on the femur shallow or non-existent. Several of the features listed by Rich & Rich (1989) and Rich & Vickers-Rich (1999a) deserve comment. (1) As was noted by Weishampel & Heinrich (1992), the narrowing of the frontals is a derived condition seen in 'Hypsilophodontidae' (except *Thescelosaurus*) and *Leaellynasaura*. However, this trait is not preserved in any other South American or Australian taxon, precluding any further comparison. (2) An angle of the femoral head with respect to the shaft greater than 100° is also present in *Dryosaurus*, *Gasparinisaura*, *Anabisetia* and '*Loncosaurus*' (Coria & Salgado 1996b; Ruiz-Omeñaca *et al.* 2007). (3 and 4) The presence of ridges confluent with marginal denticles and the relatively low crowns on the cheek teeth were discussed above in the section about *Atlascopcosaurus* (showing that these characters are widely distributed among Iguanodontia and Ornithopoda, respectively; e.g. *Gasparinisaura* and *Talenkauen*). (5) The absence of a primary ridge on maxillary teeth (Fig. 11) is plesiomorphic for basal ornithopods, since the primary ridge is absent in taxa such as *Drinker* and *Othnielosaurus* (Bakker *et al.* 1990). On the other hand, a strong primary ridge is observed in most derived ornithopods, including the South American *Gasparinisaura*, *Talenkauen* and *Anabisetia*, and the Australian *Atlascopcosaurus* and *Muttaburrasaurus* (see above). Thus, *Leaellynasaura* can be excluded from the clade that includes *Gasparinisaura* and more derived taxa (following the phylogenetic scheme of Butler *et al.* 2008) because it lacks a prominent primary ridge on its cheek teeth (Fig. 11; Coria & Salgado 1996a; Novas *et al.* 2004), and enamel deposited homogeneously in both sides of the crown (Norman *et al.* 2004). (7) The anterior intercondylar groove on the distal femur is also shallow or non-existent in the basal ornithopods *Notohypsilophodon* and *Gasparinisaura* (Fig. 7), otherwise being well developed in Dryomorpha (Ruiz-Omeñaca *et al.* 2007; see also Sereno 1986; Novas *et al.* 2004). In spite of the incomplete nature of the specimens referred to *Leaellynasaura*, the presence of a deep pit adjacent to the femoral fourth trochanter allows us to include it within Ornithopoda (Norman *et al.* 2004).

Rich & Rich (1988, 1989) were also of the opinion that enlarged optic lobes and orbits were features unique to *Leaellynasaura*, and were probably an adaptation for enhanced visual acuity. However, given that the specimen in which these features occur probably represents a juvenile individual, we strongly suspect that their expression in *Leallynasaura* most likely relates to ontogenetic stage and is therefore not autapomorphic of the taxon. Thus, pending a detailed phylogenetic analysis of basal ornithopods, and a critical reassessment of the type series (see Herne 2009; Herne & Salisbury 2009), *Leaellynasaura* is here considered a non-iguanodontian Ornithopoda more basal than *Gasparinisaura*.

Fulgurotherium australe von Huene, 1932
(Fig. 7C, H)

Horizon and locality. The holotype of *F. australe* and some of the previously referred specimens come from the Wallangalla Sandstone Member of the Griman Creek Formation (Albian: late Early Cretaceous; Scheibner & Basden 1998), Lightning Ridge, northwestern New South Wales, Australia (Molnar & Galton 1986). Victorian material that has been referred to *F. australe* comes from the middle Valanginian-Aptian Wonthaggi Formation of the Strzelecki Group at The Arch (near Kilkunda), Eagles Nest, Flat Rocks and Cape Paterson (all near Inverloch), and the late Aptian–early Albian Eumeralla Formation of the Otway Group at Dinosaur Cove East and Slippery Rock (also at Dinosaur Cove), Cape Otway (Rich & Rich 1989; Wagstaff & McEwen Mason 1989; Rich & Vickers-Rich 1999a).

Holotype. BMNH R 3719, the natural cast of the distal extremity of a right femur.

Previously referred materials. QM F10220, a cast of an almost complete right femur; QM F10221, a cast of the greater distal part of right femur; QM 12673, a cast of the distal third of a right femur (from the Grawin opal field, 20 km south-west of Lightning Ridge); AM F66764, a natural cast of the proximal part of a right femur; AM F66765, a natural cast of the greater distal part of a right femur; AM F66775, a natural cast of a segment of shaft from a left femur; NMV P150054, a partial right femur (from Eagles Nest); NMV P185948, a partial right femur (from Eagles Nest); NMV P164998, a partial left femur (from The Arch); NMV P177935, the greater proximal part of a right femur (from Dinosaur Cove East; Fig. 7C, H); NMV P185961, the fragmentary proximal end of a left femur (from Dinosaur Cove East). Rich & Vickers-Rich (1999a) also referred the following complete femora to *F. australe*: Cape Paterson (NMV P156980, NMV P186184, 3–4 km east of Cape Paterson), Slippery Rock, Dinosaur Cove (NMV P186102), Dinosaur Cove East (NMV P186326), Eagles Nest (NMV P186403), and Flat Rocks (NMV P186370, P186468, P198888, P198889, P198931, P198963, P198981, P198981a, P198982, P199022, P199091, P199138, P199146, P208159, P208231).

Revised taxonomic assignment. Iguanodontia indet. (*nomen dubium*).

Remarks. *Fulgurotherium australe* was initially described by von Huene (1932), who regarded it as an enigmatic species of coelurosaurian theropod. *Fulgurotherium* remained a theropod until 1986, when Molnar & Galton (1986) reviewed the Lightning Ridge material and placed *F. australe* in the ornithopod group 'Hypsilophodontidae' *sensu* Galton & Jensen (1973) and Galton (1974, 1983). The 'hypsilophodontid' status of the taxon was maintained by Rich & Rich (1989) and Rich & Vickers-Rich (1999a), who referred *Fulgurotherium* (as well as the 'Victoria femur types I and II'; see below) to 'Hypsilophodontidae' (Fig. 12).

As has been outlined by Molnar & Galton (1986), our understanding of the femoral morphology of *F. australe* assumes that the referred material from Lightning Ridge is conspecific with the holotype described by von Huene (1932). The holotype and referred specimens from Lightning Ridge all have a shallow anterior distal intercondylar fossa and a flat medial surface of the tibial condyle (= the 'medial epicondyle' of some authors) (Molnar 1980b; Molnar & Galton 1986). While this may validate the identification of these femora as pertaining to a single taxon within the Lightning Ridge dinosaur sample, both features are now known to occur widely among non-hadrosaurian iguanodontians, often in combination (e.g. *Anabisetia saldiviai*, MCF-PVPH-75). The anterior distal intercondylar fossa is also shallow or non-existent on the femora in the basal ornithopods *Notohypsilophodon* and *Gasparinisaura*, otherwise being well developed in dryomorphans (Ruiz-Omeñaca *et al.* 2007; see also Sereno 1986; Novas *et al.* 2004). It thus becomes difficult to maintain these features as being autapomorphic for *F. australe*. Based on the morphology of the holotype specimen alone, *F. australe* is therefore best considered a *nomen dubium*.

Building on the assumption that more complete ornithopod femora from Lightning Ridge that display the same characteristics as BMNH R 3719, also belong to *F. australe*, other features that Molnar & Galton (1986) and Rich & Rich (1989) and Rich & Vickers-Rich (1999a) have used to diagnose and determine the phylogenetic affinities of this taxon are as follows: (1) *F. australe* can be distinguished from camptosaurids and iguanodontids because the fourth trochanter is proximal to the mid-point of the shaft; and (2) that the angle of the femoral head relative to the shaft is greater than 100°. The position and morphology of the fourth trochanter on the femur varies among basal ornithopods, and appears to be strongly correlated with size and locomotor ability. Larger-bodied taxa such as *Tenontosaurus tilletti* and *Mantellisaurus atherfieldensis* (= *Iguanodon atherfieldensis sensu* Paul 2008) tend to have a straight shaft with a pendent-like fourth trochanter positioned mid-way between the distal and proximal extremities (Forster 1990; Norman 2004). Smaller-bodied taxa with a presumed greater capacity for cursorial locomotor modes tend to have a decidedly more gracile, bowed femur, with a more proximally positioned fourth trochanter, consistent with the condition displayed by material referred to *F. australe*. Although the femur in taxa such as *Zalmoxes* and *Camptosaurus* is decidedly more robust than in other, similarly sized basal ornithopods, it also has a more proximally positioned fourth trochanter compared with the condition in larger-bodied taxa (Weishampel *et al.* 2003; Norman *et al.* 2004; Carpenter & Wilson 2008). Similarly, a greater than 100° angulation of the femoral head relative to the shaft seen in referred material of *F. australe* is also present in *Dryosaurus*, *Gasparinisaura*, *Anabisetia*, and '*Loncosaurus*' (Coria & Salgado 1996b).

Norman *et al.* (2004) considered *Fulgurotherium* to be a non-iguanodontian basal ornithopod on the basis of the absence of an anterior distal intercondylar fossa and a tibial condyle that does not envelop the posterior distal intercondylar fossa. As discussed previously, although only

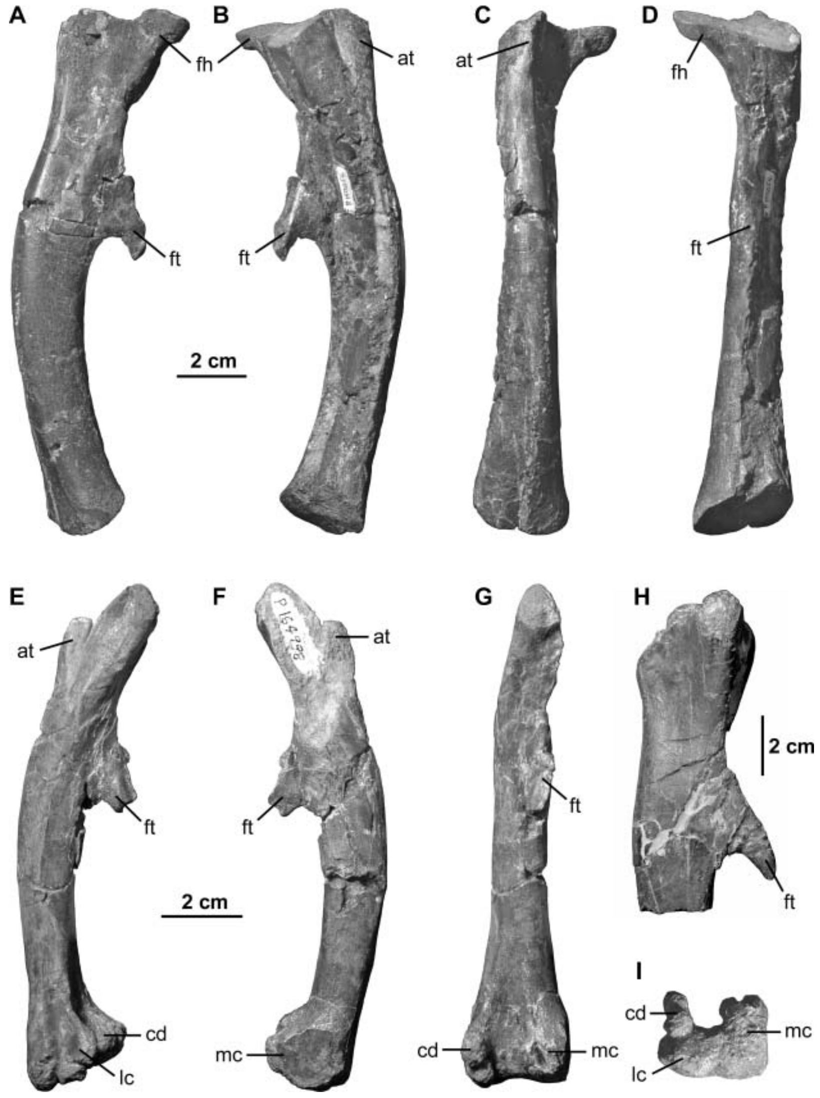

Figure 12. *Fulgurotherium australe* von Huene, 1932. NMV P150054, right femur in: **A,** medial; **B,** lateral; **C,** anterior; and **D,** posterior views. NMV P164998, left femur in: **E,** lateral; **F,** medial; **G,** posterior; and **H,** distal views; **I,** NMV P177935, right femur in medial view. Abbreviations: at, anterior trochanter; cd, condylid; fh, femoral head; ft, fourth trochanter; lc, lateral condyle; mc, medial condyle.

weakly developed, an anterior distal intercondylar fossa is present on the type and referred specimens of *F. australe*. The square, open posterior distal intercondylar fossa on the type and referred specimens of *F. australe* is similar to the condition seen in *Hypsilophodon* and *Gasparinisaura* (Figs. 7, 12). Also in common with *Gasparinisaura*, the type and referred material of *F. australe* has a laterally positioned distal femoral condylid, which is continuous with the external edge of the lateral condyle (Coria & Salgado 1996a; Fig. 7). This condition was previously considered autapomorphic for *Gasparinisaura* by Coria & Salgado (1996a). In clear contrast, in most ornithopods (e.g. *Hypsilophodon*, *Callovosaurus*, *Tenontosaurus*, *Dryosaurus*, *Iguanodon, Anabisetia*; Forster 1990; Coria & Salgado 1996a; Ruiz-Omeñaca 2007) the distal femoral condylid is inset medially (see discussion in Coria & Salgado 1996a).

Finally, referred specimens of *F. australe* show a femoral anterior trochanter that is placed more distally than the greater trochanter, as occurs in most basal ornithischians (e.g. *Lesothosaurus*, *Scutellosaurus*; Thulborn 1971; Colbert 1981; UCMP 130580) and *Notohypsilophodon* (Martínez 1998). On the other hand, in more derived ornithopods (e.g. *Hypsilophodon*, iguanodontids, dryomorphans) the anterior trochanter nearly approaches the level of the greater trochanter (Galton 1974). In the case of *Gasparinisaura*, the fusion of both trochanters means that it is impossible to compare with the condition seen in the femora referred to *F. australe*.

Accordingly, the type material of *Fulgurotherium australe* is undiagnostic. As such, the species should be considered a *nomen dubium*. The previous referral of other specimens to *Fulgurotherium australe* should be considered invalid. Despite this, it is worth noting that the holotype and referred specimens of *Fulgurotherium australe* display a number of characteristics indicating that this material pertains to basal iguanodontians, and a number of characteristics are also shared with *Gasparinisaura* and *Notohypsilophodon*. Pending further study, all specimens previously referrred to *Fulgurotherium australe* are placed in Iguanodontia indet.

Victoria femur type I
(Figs 8, 9)

Horizon and locality. Eumeralla Formation, Otway Group (late Aptian-early Albian: late Early Cretaceous; Wagstaff & McEwen Mason 1989), Dinosaur Cove East and Slippery Rock, Dinosaur Cove, Victoria, Australia.

Material. NMV P185976, an incomplete left femur; NMV P185995, an incomplete left femur; NMV P185999, an incomplete left femur (Fig. 7E, J); NMV P186004, an incomplete right femur; NMV P187115, an incomplete left femur.

Revised taxonomic assignment. Ornithopoda indet.

Remarks. Victoria femur type I (Figs. 8, 9) was originally diagnosed by Rich & Rich (1989) among ornithopods on the basis of two characters: (1) greater and anterior trochanters anteroposteriorly expanded and transversely compressed, forming a blade-like structure on its proximal end; and (2) a transverse compression of the distal end of the femur. As occurs in the available specimens of Victoria femur type I, in *Gasparinisaura* the proximal portion of the femur is also blade-like, unlike the condition of other ornithopods (e.g. *Dryosaurus*, *Anabisetia*, *Othnielosaurus*; see Rich & Rich 1989; Coria & Salgado 1996a; Salgado *et al.* 1997). Furthermore, in the femur of the Victorian form the condylid is laterally placed, as only occurs in '*Fulgurotherium*' specimens, *Gasparinisaura* and *Notohypsilophodon*, contrasting with *Anabisetia* and other ornithopods (see above). Indeed, in *Notohypsilophodon* the distal end of the femur is almost identical to that of the Australian material in distal view, being transversely compressed, and showing a protruding medial condyle and a reduced lateral condylid. These two latter features seem to be unique of the femur type I of Victoria and the South American genus *Notohypsilophodon*. In conclusion, Victoria femur type I would be a basal onithopod that closely resembles the South American genera *Notohypsilophodon* and *Gasparinisaura*.

Victoria femur type II
(Figs 8, 9)

Horizon and locality. Wonthaggi Formation, Strzelecki Group (early Aptian: late Early Cretaceous). Cape Patterson, Victoria, Australia (Rich & Rich 1989).

Material. NMV P 156980, incomplete right femur.

Revised taxonomic assignment. Ornithopoda indet.

Remarks. Rich & Rich (1989) indicated that the Victoria femur type II differs from any other Victorian 'hypsilophodontid' in having a rod-like anterior trochanter. However, more recently Rich & Vickers-Rich (1999a) considered that these specimens may well be combined with *Fulgurotherium australe*.

Muttaburrasaurus langdoni Bartholomai & Molnar, 1981
(Fig. 13)

Muttaburrasaurus sp. Molnar, 1996b

Horizon and locality. The type specimen of *Muttaburrasaurus langdoni* comes from the upper part of the Mackunda Formation (late Albian-early Cenomanian; Gray *et al.* 2002), near Rock Hole, Thomson River, 'Rosebery Downs' Station, southwest of Muttaburra, central-western Queensland, Australia (Bartholomai and Molnar 1981). Specimens referred to *Muttaburrasaurus* sp. (QM F6140 and QM F12541) come from the Allaru Mudstone (late Albian-?early Cenomanian; Gray *et al.* 2002), at localities on Dunluce Station (between Hughenden and Richmond) and Iona Station (southeast of Hughenden), respectively, both in central-western, Queensland, Australia (Molnar 1996a).

Material. Holotype of *M. langdoni*: QM F6140, an incomplete skeleton, including cranial and postcranial material (see Bartholomai & Molnar 1981).

Muttaburrasaurus sp.: QM F14921, an incomplete skull, referred to *Muttaburrasaurus* sp. by Molnar (1996b); QM F12541, part of two dentary teeth and natural moulds of parts of four other teeth, associated with a fragmentary, partial skeleton that has remained in Hughenden (Molnar 1996b).

Revised taxonomic assignment. Styracosterna indet.

Remarks. Bartholomai & Molnar (1981) originally described *Muttaburrasaurus langdoni* as an iguanodontid, using the phylogenetic scheme of Dodson (1980). Molnar (1996a) reevaluated this interpretation following the description of a second skull that he referred to a new, but as yet unnamed species, considering *Muttaburrasaurus* as a non-iguanodontian ornithopod sensu Sereno (1986). More recently, Norman *et al.* (2004), Novas *et al.* (2004) and Calvo *et al.* (2007) placed *Muttaburrasaurus* in a more basal position within Ornithopoda, as a non-dryomorphan basal ornithopod.

Our review of the described material of *Muttaburrasaurus* suggests that there are grounds on which it can be referred to Styracosterna. In the following section we

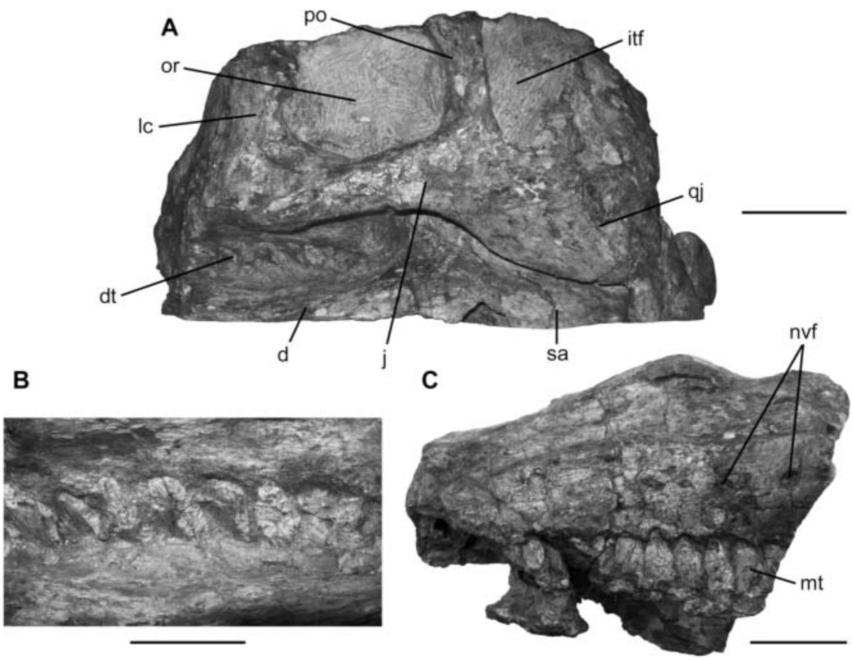

Figure 13. *Muttaburrasaurus langdoni* Bartholomai & Molnar, 1981 (QM F6140). **A,** posterior half of skull in left lateral view; **B,** close-up of distal dentary teeth in labial view; **C,** right maxilla with teeth in lateral view. Abbreviations: d, dentary; dt, dentary teeth; itf, infratemporal fenestra; j, jugal; lc, lacrimal; mt, maxillary teeth; nvf, neurovascular foramina; or, orbit; po, postorbital; qj, quadratojugal; sa, surangular. Scale bars: A = 10 cm; B, C = 2 cm.

discuss features of *Muttaburrasaurus* that support its inclusion in successively more derived iguanondontian clades. Many of these features have either not been scored for *Muttaburrasaurus* in phylogentic analyses of Ornithopoda in which it has been included, or are have been interpreted differently.

The present revision of the available material of *Muttaburrasaurus* allows us to include this taxon within 'Euiguanodontia' (i.e. *Gasparinisaura* and more derived forms; *sensu* Coria & Salgado 1996a), because it exhibits the following derived characters: (1) first primary ridge well developed on maxillary teeth; and (2) reduced quadratojugal, not in contact with all of the anterior margin of the quadrate (Coria & Salgado 1996a; Novas *et al.* 2004; Butler *et al*. 2008). In comparison with most South American basal ornithopods, *Muttaburrasaurus* clearly differs from them in its proximally-placed anterior trochanter, well-defined anterior intercondylar groove on the distal part of the femur, and medially-placed femoral condylid (Bartholomai & Molnar 1981). *Muttaburrasaurus* also possesses the following dryomorphan synapomorphies: (1) maxillary teeth mesiodistally narrower than opposing dentary teeth (Coria & Salgado 1996a); and (2) presence of a space separating the ventral margin of the quadratojugal from the mandibular articulation (Sereno 1986). This taxon could be also included within Ankylopollexia because it shows the following derived traits: (1) cervical neural spines reduced (described for cervical 5 in Bartholomai & Molnar 1981); (2) robust, arching cervical postzygapophyses posterior to the axis (Molnar 1996b); (3) moderate opisthocoely on cervical vertebrae 4–9; and (4) slight opisthocoely on dorsal vertebrae 1–2 (see discussion in Molnar 1996b). Additionally, *Muttaburrasaurus* can be included within Styracosterna because: (1) the humerus has a posteriorly directed head (also present in *Zalmoxes*; Weishampel *et al.* 2003); (2) the femur has a shallow anterior intercondylar groove (Bartholomai & Molnar 1981; Molnar 1996a); (3) manual digit V has at least three phalanges (Bartholomai & Molnar 1981); and (4) a complex peg and socket articulation occurs between jugal and maxilla (Bartholomai & Molnar 1981). Furthermore, the prepubic process has been described as dorsoventrally expanded based on a natural mould of the bone. This feature could be interpreted as another synapomorphy of Styracosterna present in *Muttaburrasaurus*. However, this mould was not found adjoined to the partial pubis and may pertain to a different element (R.E. Molnar, pers. comm., 2009). Moreover, the Australian form resembles some basal iguanodontoids (*sensu* Norman 2004), including *Iguanodon* and *Ouranosaurus*, in the loss of the lateral exposure of the antorbital fenestra. In particular, *Muttaburrasaurus* resembles *Ouranosaurus* and Hadrosauridae (Hadrosauroidea; *sensu* Sereno 1986, 1998) in having a dorsoventral expansion of the jugal in front of the orbit and a dorsoventrally flattened braincase. However, *Muttaburrasaurus* and *Ouranosaurus* are quite different in other details of their anatomy.

There are a number of features of *Muttaburrasaurus* listed by Molnar (1996a) and followed by other authors (e.g. Norman *et al.* 2004) that contradict the revised phylogenetic assignment suggested here. Molnar (1996a) noted that the absence of diamond-shaped maxillary teeth in *Muttaburrasaurus* is not consistent with its inclusion in Dryomorpha. However, at least one specimen referred to *Muttaburrasaurus* sp. (namely, QM F12541) does appear to have diamond-shaped dentary teeth, as is implied in a composite reconstruction that utilises additional information from the holotype of *M. langdoni* (QM F6140; see Molnar 1996a, fig. 8H). The maxillary teeth, on the other hand, are clearly subrectangular in outline, with some apical elongation associated with the primary ridge. Unfortunately, all the maxillary teeth preserved in situ on QM F6140 and QM F14921 appear to be heavily worn apically, so it is difficult to ascertain what their original outline was like. Interestingly, some of the maxillary teeth in the basal-most ankylopollexian *Camptosaurus* (Galton and Powell 1980; Galton 2007) are diamond shaped, whereas others are subrectangular, resembling the condition in *Muttaburrasaurus* (R.E. Molnar, pers. comm., 2006). Thus, the morphology of the maxillary teeth is quite variable and cannot be considered as an unambiguous ankylopollexian synapomorphy (Fig. 13C).

An ankylopollexian synapomorphy not present in *Muttaburrasaurus* that was also noted by Molnar (1996a) relates to the packing of the tooth row. In all aknylopollexians, the functional upper and lower teeth are all closely packed, with the apices from the partially erupted replacement series eliminating spaces between the bases of adjacent crowns (Sereno 1986). Although the maxillary teeth of *Muttaburrasaurus* are closely spaced, no replacement crowns are apparent (Molnar 1996a). On the dentary, however, some replacement teeth are visible between the bases of the functional crowns on QM F12541 (Molnar 1996a, fig. 8C; R.E. Molnar, pers. comm., 2006). Similar variation is apparent in *Iguanodon bernissartensis*, where the morphology of the replacement series varies between the dentary and the maxillary series (Norman 1980, fig. 21). In lateral view, only the rostral-most maxillary teeth of *I. bernissartensis* show the typical ankylopollexian replacement series, whereas the teeth in the middle and at the posterior end of the tooth row are closely packed and there are no spaces between them for functional teeth. Moreover, the dentary and maxilla of both *Muttaburrasaurus* skulls (QM F6140 and QM F14921) are distorted and incompletely prepared (RE Molnar, pers. comm., 2006), thus their exact morphology cannot be ascertained at present.

Molnar (1996a) excluded *Muttaburrasaurus* from Styracosterna because it lacked the following derived features. (1) At least 25 functional 'columns' in the maxillary and dentary tooth rows. In *Muttaburrasaurus*, both maxillary and dentary bones are incomplete, thus this feature cannot be properly observed. We agree with Molnar (1996a) that there were at least 22–23 columns on the maxilla of QM F14921. (2) Lanceolate maxillary teeth. We agree with Molnar (1996a) that *Muttaburrasaurus* does not have lanceolate maxillary teeth. However, pending a detailed phylogenetic analysis, we do not consider the lack of this derived character likely to be sufficient evidence to challenge the inclusion of *Muttaburrasaurus* in Styracosterna. If our interpretation of *Muttaburrasaurus* is correct, then this condition most likely represents a reversal that would consitute an autapomorphy of the taxon. (3) Iliac peduncle of the pubis distinct and stout. As was noted by Bartholomai and Molnar (1981), the proximal portion of the pubis is abraded, hence this feature cannot be properly observed (see Molnar 1996a, fig. 12).

Molnar (1996a) excluded *Muttaburrasaurus* from Iguanodontoidea (essentially a node-based equivalent to Styracosterna) because it lacked the following three derived features: (4) enlarged external nares; (5) a paraoccipital process that is broader proximally than it is distally; and, (6) a slight transverse narrowing of the cranium posterior to the postorbital region in dorsal view. The rostral portion of the skull is not preserved in both of the skulls that are referred to *Muttaburrasaurus*, nor is the lateral part of either paraoccipital process. Hence the respective conditions that related to the aforementioned features cannot be ascertained (Molnar 1996a). Narrowing of the posterior part of the cranium posterior to the postorbital region occurs in *Dryosaurus* (Galton 1983), *Camptosaurus* (Galton & Powell 1980; Brill & Carpenter 2006), and *Zalmoxes* (Weishampel *et al.* 2003), suggesting that this feature is most likely plesiomorphic for styracosternans. Nevertheless, this portion of the skull is badly preserved in both *Muttaburrasaurus* specimens (Bartholomai & Molnar 1981; Molnar 1996a), so the relevance of this character for determining its phylogenetic position is best considered ambiguous.

Pending a detailed analysis of the phylogenetic relatiohships of basal ornithopods, we feel that there is strong evidence to refer *Muttaburrasaurus* to Styracosterna within the context of the phylogenetic schemes of Novas *et al.* (2004), Calvo *et al.* (2007) and Sereno (1998). We follow Molnar (1996a) in considering the material referred to *Muttaburrasaurus langdoni* and *Muttaburrasaurus* sp. as being representative of separate species.

'*Dryosaurus* or *Hypsilophodon*-like scapula'

Horizon and locality. Wallangulla Sandstone Member of the Griman Creek Formation (Albian: late Early Cretaceous; Byrnes 1977), Lightning Ridge, New South Wales, Australia.

Material. An isolated right scapula.

Revised taxonomic assignment. Ornithopoda indet.

Remarks. Molnar & Galton (1986) described a fragmentary isolated scapula from the Early Cretaceous of Australia, which they referred to a *Dryosaurus* or *Hypsilophodon*-like ornithopod. However, this bone differs from those of

Dryosaurus and *Othnielosaurus* in having a wide angle between the posterior border of the scapular blade and the supraglenoid projection, a condition present in most ornithopods (e.g. *Gasparinisaura*, *Anabisetia*). In contrast, this angle in *Dryosaurus* and *Othnielosaurus* is nearly 90°, resulting in a posteriorly-oriented scapular blade when it is compared with the main axis of the scapula. The Australian scapula also exhibits a well-developed, anteriorly-directed acromial process. This condition is absent in some basal ornithischians such as *Heterodontosaurus* and *Gasparinisaura*, as well as in derived members of Iguanodontia (e.g. *Tenontosaurus*, *Iguanodon*). However, as is the case in the Australian material, a well-developed acromial process is present in the basal ornithopods *Anabisetia*, *Talenkauen*, *Dryosaurus* and *Othnielosaurus*. In conclusion, the incomplete nature of this material renders the systematic relationships of this bone inconclusive beyond Ornithopoda.

Late Cretaceous ornithischians

In sharp contrast with the Early Cretaceous record, the available specimens of Late Cretaceous onithischians from Australia and New Zealand are actually very scarce. Indeed, the only recovered remains are a fragmentary ilium of a putative '*Dryosaurus*-like form' ornithopod (Wiffen & Molnar 1989) and an undetermined ankylosaurian (Molnar & Wiffen 1994), both collected from the Late Cretaceous of New Zealand.

Maungataniwha ankylosaur

Horizon and locality. Maungataniwha Member, Tahora Formation (Campanian-Maastrichtian: Late Cretaceous), Mangahouanga Stream, North Island, New Zealand.

Material. CD 545, an incomplete rib; CD 546, two incomplete caudal vertebral centra.

Revised taxonomic assignment. Ankylosauria indet.

Remarks. Molnar & Wiffen (1994) described the Maungataniwha rib (CD 545) and incomplete caudal vertebrae (CD 546) as belonging to an undetermined ankylosaurian with probable nodosaurid affinities. The rib displays a T-shaped cross-section in the proximal half of the shaft, typical of the anterior thoracic ribs of ankylosaurids among thyreophorans, and compares very favourably in size and shape with the anterior thoracic ribs of *Minmi* sp. (QM F18101). As noted by Molnar & Wiffen (1994), in common with ankylosaurians, the caudal vertebrae have low, anteroposteriorly elongated spinal processes (Coombs & Maryanska 1990), and vertebral bodies with a ventral sulcus and hexagonal anterior and posterior articular ends. However, these features are no longer considered unequivocal synapomorphies of Ankylosauria (see Vickaryous *et al.* 2001, 2004; Hill *et al.* 2003; Butler *et al.* 2008), and occur more widely among thyreophorans. Assuming that the rib and caudal vertebrae belong to the same taxon, albeit the identification of the specimen hinges mainly on the rib, we agree with Molnar & Wiffen (1994) and consider the material as belonging to an indeterminate ankylosaurian thyreophoran.

Dryosaurus-like ilium

Horizon and locality. Maungataniwha Member, Tahora Formation (Campanian-Maastrichtian: Late Cretaceous), Mangahouanga Stream, North Island, New Zealand.

Material. CD 529, the posterior portion of a right ilium.

Revised taxonomic assignment. Ornithopoda indet.

Remarks. Wiffen & Molnar (1989) described a posterior portion of an ilium from the Late Cretaceous of New Zealand, which they regarded as representing a *Dryosaurus*-like relictual form. In fact, this fragmentary bone can be referred to Ornithopoda (= Euornithopoda; *sensu* Norman *et al.* 2004) because it possesses a well developed brevis shelf (Coria & Calvo 2002; Norman *et al.* 2004). However, this ilium differs in some aspects from *Dryosaurus* (e.g. it has a less developed brevis shelf and an acute posterior blade to the ilium). The New Zealand specimen cannot be, therefore, diagnosed beyond Ornithopoda indet.

Sauropoda

Until recently, sauropods from Australia and New Zealand were mainly represented by the Early Cretaceous 'cetiosaurid' *Austrosaurus mckillopi* (Longman 1933; Molnar 1980b; Coombs & Molnar 1981) and some isolated bones from several Cretaceous localities (Molnar 1980b; Molnar & Wiffen 1994; see Molnar 2001b). Salgado *et al.* (1997) suggested that *Austrosaurus* may be more nearly related to titanosaurians rather than to 'cetiosaurs' (*sensu* Bonaparte 1986, 1999). Later, Molnar (2001b), Upchurch *et al*. (2004) and Molnar & Salisbury (2005) considered the aforementioned genus to be a titanosaur. In addition, Molnar (2001b), Molnar & Salisbury (2005) and Molnar & Wiffen (2007) also suggested that most sauropod remains from Australia and New Zealand were also titanosaurians or closely related forms, including the bulk of the material later referred to *Wintonotitan wattsi* (QM F 7292) by Hocknull *et al.* (2009; see below), which was described and commented on previously by Coombs and Molnar (1981), Molnar (2001b) and Molnar and Salisbury (2005). For Australian Cretaceous sauropod material described prior to 2005, we follow the taxonomic assignments given in Molnar & Salisbury (2005).

Salisbury *et al.* (2006b) reported at least two new sauropod specimens from the Winton Formation (latest Albian-Cenomanian) of central-western Queensland. These authors pointed out that the new specimens exhibited strong similarities with the non-titanosaurian titanosauriform *Chubutisaurus insignis* from the Albian of Patagonia, but also show more derived features indicating affinities with basal titanosaurians, such as *Argentinosaurus huinculensis* and *Epachthosaurus sciuttoi*. Molnar & Wiffen (2007) also recently described a procoelous mid-caudal titatanosaurian vertebra from the Late Cretaceous Maungataniwha Sandstone of the North Island of New Zealand. In 2009, Hocknull *et al.* described *Wintonotitan wattsi* and *Diamantinasaurus matildae* based on material from the Winton Formation of central-western Queensland. These authors considered *Diamantinasaurus* to be a very derived titanosaurid probably related to saltasaurines, and *Wintonotitan* to be a basal titanosauriform, supporting the earlier interpretations by Molnar (2001b) and Molnar & Salisbury (2005) of most of the material referred to the latter taxon by Hocknull *et al.* (2009). These new discoveries confirm earlier propositions that titanosauriforms were well represented in the Cretaceous of Australia (SWS, pers. obs.). As highlighted by Molnar & Wiffen (2007), palaeobiogeographic considerations suggest that titanosaurians were also present in Antarctica.

Thus, Australia, New Zealand and the remaining Gondwanan landmasses (with the current exception of Antarctica where no Cretaceous sauropods are known) are similar to each other in having their Cretaceous sauropod faunas mainly comprising titanosauriforms, although a similar situation appears to be present in the Asian continent (Salgado *et al.* 1997; Wilson & Sereno 1998).

Theropoda

As is the case with ornithischians, the Australian and New Zealand Early Cretaceous theropod record is much richer than that of the Late Cretaceous. Although the theropod record is based primarily on isolated and fragmentary bones, five species of theropod dinosaurs are recognized (*Walgettosuchus woodwardi*, *Kakuru kujani*, *Rapator ornitholestoides, Timimus hermani* and *Australoventator wintonensis*). Most of these theropods were allied to Laurasian clades, rather than Gondwanan ones. Indeed, no Gondwanan affinities have been recognized among the Australian and New Zealand theropod taxa until recently. Recent studies carried out by Agnolin *et al.* (2005), Rauhut (2005), Salisbury *et al.* (2007, 2009) and Smith *et al.* (2008) have reviewed the phylogenetic position of some Australian and New Zealand theropods, finding some evidence to challenge previous interpretations of the Laurasian affinities of these taxa. In particular, Rauhut (2005) reinterpreted the enigmatic *Ozraptor subotaii* (Long & Molnar 1998) as a small member of Abelisauroidea, showing that this typical Gondwanan clade was in Australia since at least the Middle Jurassic.

Early Cretaceous theropods

Walgettosuchus woodwardi von Huene, 1932

Horizon and locality. Sandstone Member of the Griman Creek Formation (Albian: late Early Cretaceous; Byrnes 1977), Lightning Ridge, New South Wales, Australia.

Holotype. BMNH R 3717, an incomplete caudal vertebra.

Revised taxonomic assignment. Theropoda indet. (*nomen dubium*).

Remarks. Von Huene (1932) described *Walgettosuchus woodwardi* based on an isolated incomplete caudal vertebra from the Griman Creek Formation (Albian), of Lightning Ridge, Australia. He compared this specimen with Ornithomimidae, *Elaphrosaurus* (Ceratosauria; Holtz 1994), and *Allosaurus* (Allosauridae), but did not refer it to any of these theropod groups. Due to the fragmentary nature of this material, it is currently considered to belong to an indeterminate theropod (Molnar 1980b; Norman 1990), and we follow Molnar (1991) in considering it as a *nomen dubium*.

Australian pygmy '*Allosaurus*' Molnar *et al.* 1981
(Fig. 14)

Horizon and locality. Wonthaggi Formation of the Strzelecki Group (early Aptian: late Early Cretaceous; Wagstaff

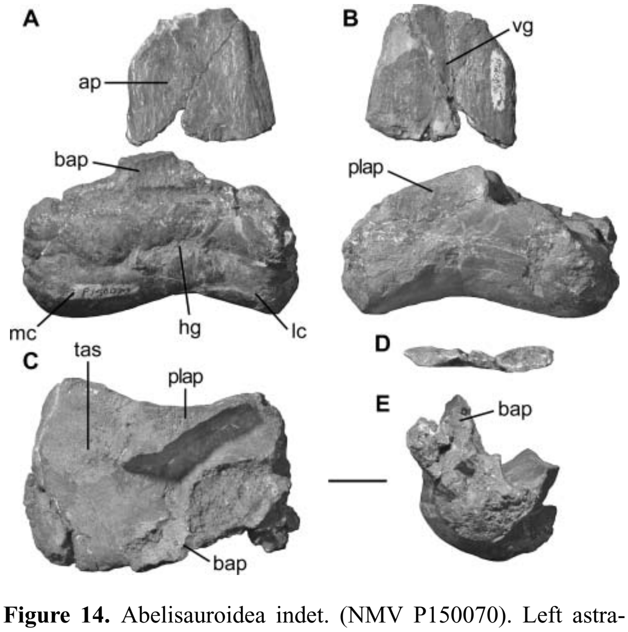

Figure 14. Abelisauroidea indet. (NMV P150070). Left astragalus in: **A,** anterior; **B,** posterior; **C,** proximal; and **E,** lateral views; **D,** cross-section of the base of the ascending process. Abbreviations: ap, ascending process; bap, base of the ascending process; hg, horizontal groove; lc, lateral condyle; mc, medial condyle; plap, accesory posterolateral ascending process; tas, tibial astragalar facet; vg, vertical groove. Scale bar = 2 cm.

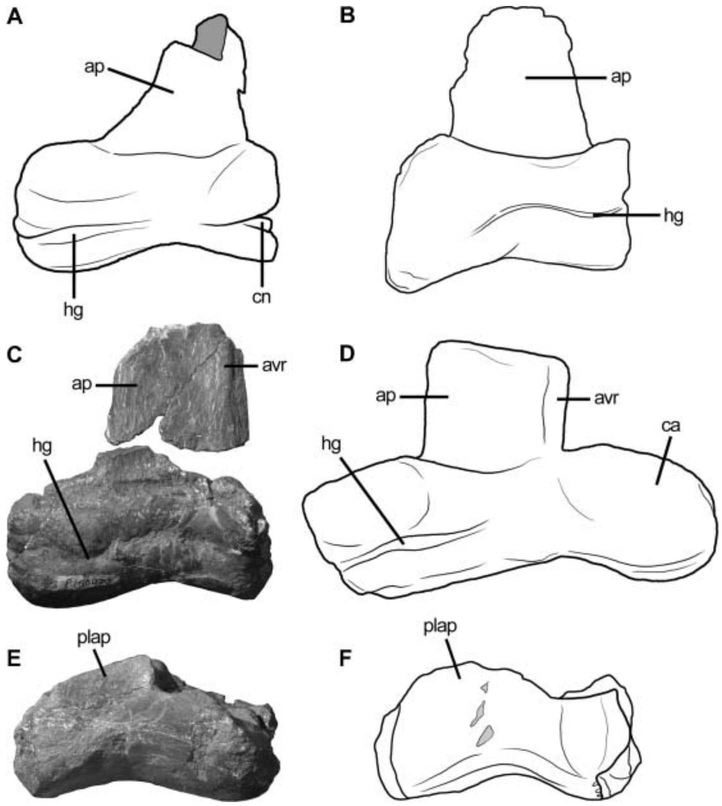

Figure 15. Left astragali of **A,** *Allosaurus fragilis* (YPM 4944); **B,** *Australovenator wintonensis* (modified and reversed from Hocknull *et al*. 2009); **C, E,** Australian abelisauroid (NMV P150070); **D,** *Xenotarsosaurus bonapartei* (UNPSJB-Pv 184/612); and **F,** *Velocisaurus inicus* (MUCPv 41). Anterior (**A-D**) and posterior (**E, F**) views. Note that the ascending process of the Australian abelisauroid has not been included and that of *Velocisaurus* is lacking in E and F, respectively. Abbreviations: ap, ascending process; avr, anterior vertical ridge; ca, calcaneum; cn, calcaneal notch; hg, horizontal groove; plap, accesory posterolateral ascending process. Not to scale.

& McEwen Mason 1989), Eagles Nest Site, Victoria, Australia.

Material. NMV P150070, a left astragalus.

Revised taxonomic assignment. Abelisauroidea indet.

Remarks. Probably one of the most controversial Cretaceous theropod specimens from Australia is an isolated left astragalus from the Early Cretaceous of Victoria, assigned to an undetermined pygmy species of *Allosaurus* by Molnar *et al.* (1981, 1985; Fig. 14). This material was excluded from *Allosaurus* by Welles (1983), but this view was criticized by Molnar *et al.* (1985) who maintained their original assignment. However, Chure (1998) and Azuma & Currie (2000) referred to this taxon as Allosauroidea indet. As a supposed allosaurid, it has been proposed that the specimen represents a Jurassic relict by Molnar *et al.* (1981) and Rich & Rich (1989). Moreover, Rich & Rich (1989) and Vickers-Rich & Rich (1993) suggested that its small size was a consequence of insular dwarfism. The specimen was originally referred to *Allosaurus* on the basis of: (1) the presence of a calcaneal notch in the astragalus; and to Allosauridae on the basis of: (2) restriction of the ascending process to the lateral part of the bone; (3) medial condyle larger than the lateral one; and (4) the presence of a horizontal groove across the faces of the condyles (Molnar *et al.* 1981). These characters deserve the following comments: (1) the lateral part of the astragalar body is broken off and the calcaneal notch is only represented by a poorly developed concavity (Fig. 15A, C); furthermore, a calcaneal notch and sulcus are also present in other theropods such as *Ceratosaurus* (Welles & Long 1974); and (2) an ascending process restricted to the lateral part of the astragalus is widely distributed among Theropoda (e.g. *Xenotarsosaurus*, *Ceratosaurus*, *Masiakasaurus*; Martínez *et al.* 1986; Madsen & Welles 2000; Carrano *et al.* 2002). Features (3) and (4) are also present in Abelisauroidea (e.g. *Xenotarsosaurus*, *Masiakasaurus*) (Fig. 15D). A new revision of this material allows us to recognize the following derived traits, leading us to consider the putative Australian '*Allosaurus*' as a member of Abelisauroidea (Agnolin *et al.* 2005; Salisbury *et al*. 2007, 2009):

1. Ascending process of the astragalus subrectangular in anterior view. The ascending process in most basal theropods (e.g. coelophysoids) is asymmetrical

in anterior view, subtriangular in contour, low and pyramidal-shaped (Welles & Long 1974; Sereno 1997). In basal tetanurans (e.g. *Sinraptor, Allosaurus*; Currie & Zhao 1993) and *Ceratosaurus* the ascending process of the astragalus is moderately low and subtriangular, features that are absent in the Australian material (Fig. 15A). In neovenatorids and coelurosaurians the ascending process is laminar and subtriangular, being taller than in the above mentioned taxa (Novas 1992; Benson *et al*. 2009; Fig. 15B). Otherwise, in abelisauroids, such as *Masiakasaurus* (Carrano *et al.* 2002), *Aucasaurus* (MCF-PVPH 236) and *Xenotarsosaurus* (UNPSJB Pv 184-612) (Fig. 15D), the ascending process is relatively tall and subrectangular in outline, showing subparallel medial and lateral margins at its base, as is the case in the Australian astragalus.

2. Vertical groove on the posterior surface of the ascending process of the astragalus. Rauhut (2005) pointed out that the presence of a distinct and narrow vertical ridge of the articular surface of the tibia that abuts with the ascending process of the astragalus, is a character unique to Abelisauroidea (e.g. *Ozraptor*, *Velocisaurus*; Long & Molnar 1998; MUCPv 41). NMV P150070 shows a narrow and shallow vertical sulcus on the posterior surface of the ascending process that we infer to be correlated with a vertical ridge on the distal end of the tibia, a feature absent in non-abelisauroid theropods (Agnolin *et al*. 2005).
3. Anterior vertical ridge on the lateral edge of the ascending process. This feature was indicated by Molnar *et al.* (1981) as an autapomorphic feature of the Australian '*Allosaurus*'. However, this trait is also present in the abelisauroid *Xenotarsosaurus* (UNPSJB Pv 184-612, FLA and MDE, pers. obs.) (Fig. 15D). In *Masiakasaurus* this feature is unobservable, because the lateral edge of the ascending process is overlapped by the distal end of the fibula. This kind of lateral ridge is not present in any other theropod of which we are aware, suggesting that it may be characteristic of a less inclusive clade of abelisauroids.
4. Accessory posterolateral ascending process. In NMV P150070, the astragalar body presents two distinct ascending processes. The ascending process, which is located on the anterodorsal margin of the astragalar body, is homologous with the anterior ascending process of other dinosaurs (Novas 1989). However, the second ascending process of NMV P150070, which is located laterally on the posterodorsal margin of the astragalar body, seems to be an apomorphy restricted to abelisauroids (Figs. 14B, C, E, 15E, F). Contrasting with NMV P150070, the posteromedial ascending process of 'coelophysoids' (Ezcurra & Novas 2007) is restricted to the posteromedial corner of the astragalar body and fits within a notch opening posteromedially on the distal end of tibia. On the other hand, in NMV P150070 (Fig. 16E) and abelisauroids, such as *Velocisaurus* (MUCPv-41; Fig. 16F) and *Aucasaurus* (MCF-PVPH 236), this accessory ascending process is wide, occupying most of the posterior margin of the astragalar body, but laterally displaced from its mid-width. In tetanuran theropods, including the neovenatorids *Australovenator* and *Fukuiraptor*, this posterolateral ascending process is completely absent (Azuma & Currie 2000; Hocknull *et al*. 2009, fig. 33C).

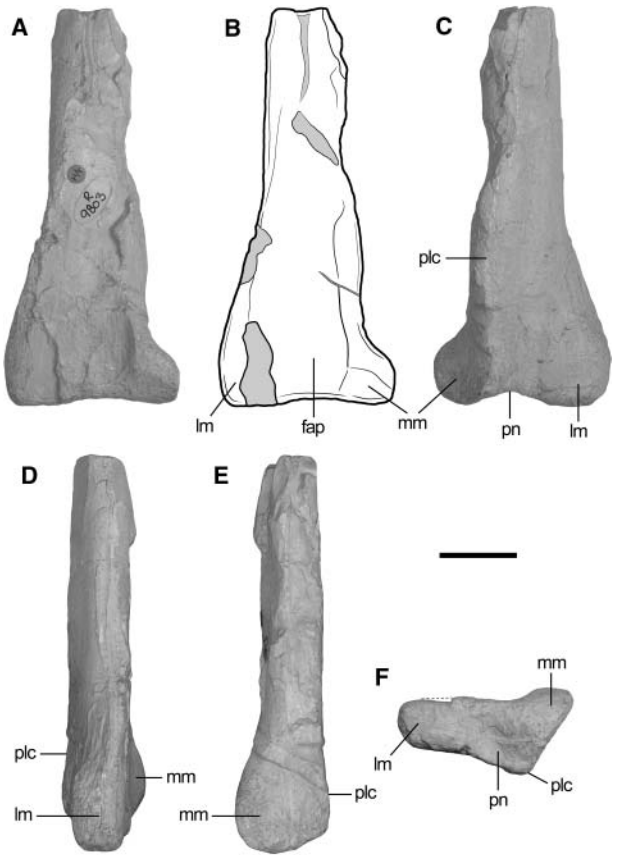

Figure 16. *Kakuru kujani* Molnar & Pledge, 1980 (BMNH R9803, cast of SAM P17926). Right distal end of tibia in: **A, B,** anterior; **C,** posterior; **D,** lateral; **E,** medial; and **F,** ventral views. Abbreviations: lm, lateral malleolous; fap, facet for the reception of the ascending process of astragalus; mm, medial malleolous; plc, posterior longitudinal crest; pn, posterior notch. Scale bar = 2 cm.

More recently, NMV P150070 was considered to compare favourably to *Fukuiraptor* and *Australovenator* by Hocknull *et al*. (2009). This comparison was followed by Benson *et al*. (2009), who referred NMV P150070 to Megaraptora. Hocknull *et al*. (2009) listed the following characteristics as support for these comparisons: a large medial condyle expanded medially and anteroposteriorly (unknown in *Fukuiraptor*), very tall and quadrangular ascending process, 'upper' and 'lower' horizontal grooves, anteroproximal extension of lateral condyle as a rounded triangular process (unknown in NMV P150070), and a crescentic groove on the posterior surface of the ascending process (unknown in *Australovenator*). However, an enlarged medial condyle is also observed in a wide variety of theropods, such as *Liliensternus* (MB R.2175), *Zupaysaurus* (Ezcurra & Novas 2007), *Dilophosaurus* (UCMP 77270), *Ceratosaurus* (Madsen & Welles 2000), *Xenotarsosaurus* (UNPSJB-Pv-184–612) and *Aucasaurus* (MCF-PVPH 236). Regarding the presence of a quadrangular ascending process, this feature has been discussed above (character 1), but *Fukuiraptor* and *Australovenator* actually lack a quadrangular ascending process like that observed in abelisauroids. The medial and lateral margins of the ascending process of the astragalus in *Australovenator* and *Fukuiraptor* converge proximally, resulting in a trapezoideal outline in anterior view (Azuma & Currie 2000; Hocknull *et al*. 2009). The base of the process in of *Fukuiraptor* and *Australovenator* is more transversely extended than in NMV P150070 and abelisauroids (e.g. *Aucasaurus*, *Xenotarsosaurus*, *Masiakasaurus*). The presence of 'upper' and 'lower' grooves on the anterior surface of the astragalus is a more widely distributed condition among theropods than recognized by Hocknull *et al*. (2009) (Rauhut 2003; e.g. *Ceratosaurus*, *Xenotarsosaurus*, *Aucasaurus*). Finally, the presence of a crescentic groove on the posterior surface of the ascending process of *Fukuiraptor* is not followed here (but see comments on character 2). Accordingly, we disagree with the neovenatorid affinities proposed by Benson *et al*. (2009) and Hocknull *et al*. (2009) for NMV P150070.

To conclude, on the basis of the discussions of the characters carried out above we do not agree with the proposed close affinity between NMV P150070 and *Allosaurus* or other allosauroids. In contrast, apomorphic characters presented here allow us to refer with confidence the 'pygmy Australian *Allosaurus*' to Abelisauroidea, supporting earlier interpretations by Agnolin *et al.* (2005) and Salisbury *et al*. (2007, 2009).

Kakuru kujani Molnar & Pledge, 1980
(Fig. 16)

Horizon and locality. Maree Formation (Aptian: late Early Cretaceous), Andamooka, South Australia, Australia.

Holotype. SAM P17926, fragmentary left tibia.

Revised taxonomic assignment. Averostra indet.

Remarks. Another problematic Australian theropod, originally described as a coelurosaur, is *Kakuru kujani* Molnar & Pledge, 1980. This taxon was recently referred to Abelisauroidea by Rauhut (2005) based on the flattened anterior side of the distal end of tibia with a median vertical ridge. This feature is also present in neovenatorid (Benson *et al*. 2009) and coelurosaurian (Rauhut 2003) theropods, but is absent in non-averostran taxa (e.g. *Zupaysaurus*, *Liliensternus*, *Dilophosaurus*; PULR 076; MB. R.2175; UCMP 77270). However, new examinations of the material (BMNH R9803, a cast of the holotype specimen) revealed that the described median vertical ridge is actually an artefact due to a damaged anterior surface of the astragalar articular facet. Moreover, the facet for the ascending process of the astragalus is taller than in any known abelisauroid. Accordingly, we could not recognize unambiguous abelisauroid apomorphies in *Kakuru*, and due to the presence of a flattened anterior side of the distal end of the tibia, we consider this species as an indeterminate averostran.

In distal view, the lateral malleollous (= posterolateral process of other authors) of the tibia of *Kakuru* is subrectangular in outline, constrasting with the laterally tapering lateral malleollous of other theropod dinosaurs. The medial malleollous is anteromedially extended, which constitutes the medial margin of the facet for the reception of the ascending process of the astragalus. This malleollous is posteriorly curved, resulting in a concave medial surface of the distal end of the tibia. In posterior view, the longitudinal crest of the distal end of the tibia is medially displaced, being alligned with the medial border of the shaft above the distal end of the bone, a condition not seen in other theropods. Considering the peculiar morphology of the distal end of the tibia, we here consider *Kakuru kujani* as a valid species of an averostran theropod.

Rapator ornitholestoides von Huene, 1932
(Fig. 17)

Horizon and locality. Sandstone Member of the Griman Creek Formation (Albian: late Early Cretaceous; Byrnes 1977), Lightning Ridge, New South Wales, Australia.

Holotype. BMNH R 3718, left metacarpal I.

Revised taxonomic assignment. Carcharodontosauria, Megaraptora indet. (*nomen dubium*).

Remarks. Von Huene (1932) erected *Rapator ornitholestoides* based on a peculiar left metacarpal I (Fig. 17) (not a right element; contra Molnar 1980b) from the Lower Cretaceous of Lightning Ridge. This author compared *Rapator* with the North American Jurassic coelurosaur *Ornitholestes hermanni* (AMNH 619, a hand referred to *Ornitholestes* which is now considered as belonging to *Tanycolagreus sensu* Carpenter *et al.* 2005). This view was followed by subsequent authors, claiming the presence of a distinct posterolateral process exclusive to both taxa, but less developed in AMNH 619 (Molnar 1980b).

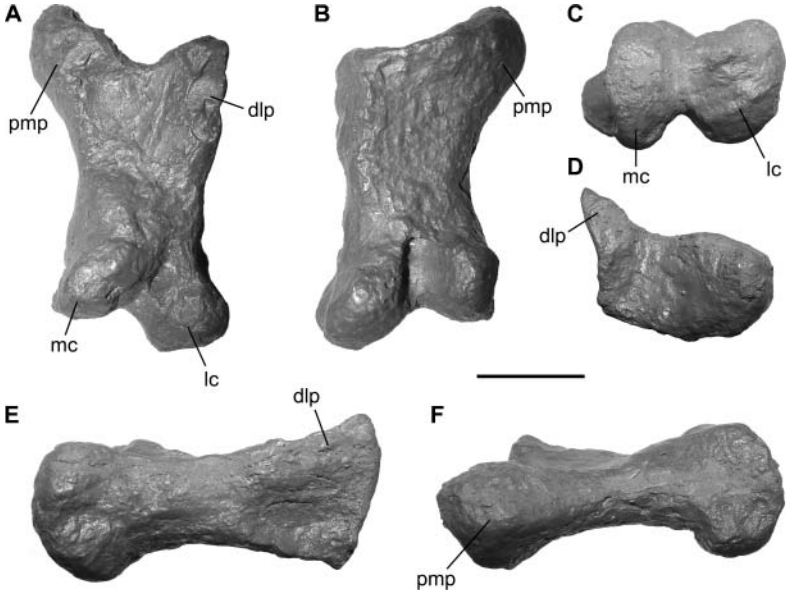

Figure 17. *Rapator ornitholestoides* von Huene, 1932 (cast of BMNH R3718). Left metacarpal I in: **A,** dorsal; **B,** ventral; **C,** distal; **D,** proximal; **E,** medial; and **F,** lateral views. Abbreviations: dlp, dorsolateral process; lc, lateral condyle; mc, medial condyle; pmp, proximomedial process. Scale bar = 2 cm.

More recently, Holtz *et al.* (2004) suggested that *Rapator* may be based on a basal phalanx of the first manual digit of an alvarezsaurid theropod. Regarding the latter interpretation, the distal morphology of the available bone of *Rapator* suggests that it belongs to the metacarpus. Indeed, *Rapator* differs from the phalanges of all other dinosaurs, including alvarezsaurids (Novas 1996) (Fig. 18C–F), in the presence of strongly proximodistally asymmetric distal trochlea and small dorsal ligament pit. These features support von Huene's original interpretation of this bone as a metacarpal I. Furthermore, the posterolateral process of the phalanx I-1 of alvarezsaurids (e.g. *Patagonykus*; Novas 1996) greatly differs from the proximal process present in *Rapator* in both shape and position. Contrasting with *Rapator*, in *Patagonykus* the proximal posterolateral process is ventrally directed (rather than dorsomedially as in *Rapator*), it is much more ventrally developed and posteriorly extended, proximally curved, and the ventral half of the process is transversely flattened (Novas 1996). These differences lead us to dismiss the previous interpretation of Holtz *et al.* (2004), but the bone actually matches better with the morphology of a metacarpal I from a medium-sized dinosaur.

Molnar (1980b) reported that a posterolateral process is unknown in other theropods with the exception of *Tanycolagreus* (AMNH 619) and *Rapator*, but it is much less developed in the former. Nevertheless, in the referred specimen of the neovenatorid *Megaraptor namunhuaiquii* (MUCPv 341; Smith *et al.* 2008) a prominent posterolateral process is also present, but its proximal-most portion is broken off, obscuring its real development (Fig. 18A, B). The

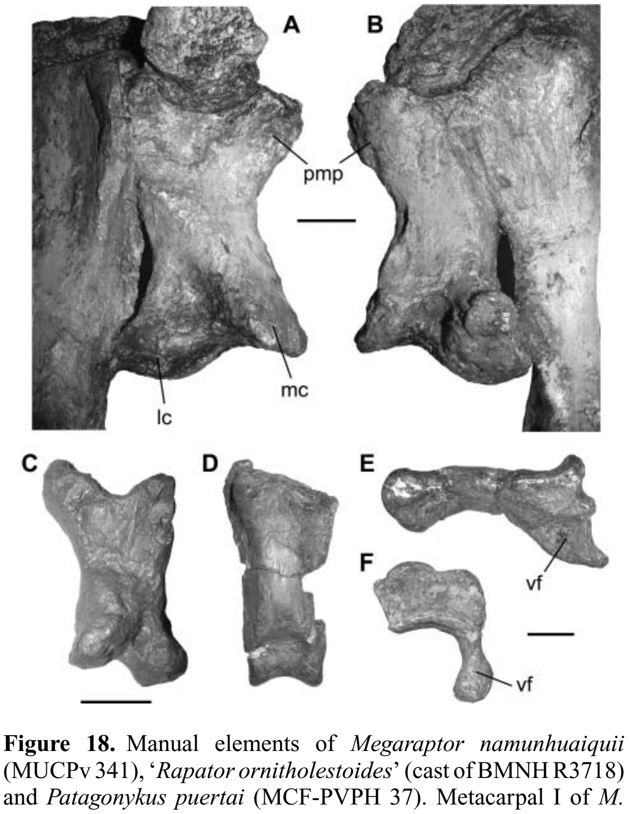

Figure 18. Manual elements of *Megaraptor namunhuaiquii* (MUCPv 341), '*Rapator ornitholestoides*' (cast of BMNH R3718) and *Patagonykus puertai* (MCF-PVPH 37). Metacarpal I of *M. namunhuaiquii* in: **A,** dorsal; and **B,** ventral views; **C,** metacarpal I of *Rapator ornitholestoides* in dorsal view. Phalanx I-1 of *P. puertai* in: **D,** dorsal; **E,** medial; and **F,** proximal views. Abbreviations: lc, lateral condyle; mc, medial condyle; pmp, proximomedial process; vf, ventral flange. Scale bars = 2 cm.

metacarpal of *Rapator* differs from that of *Ornitholestes* in the greater transverse expansions of both proximal and distal ends.

Salisbury *et al.* (2007) suggested, on the basis of the well-developed posterolateral process, that *Rapator* compares favourably with the basal coelurosaurian *Nqwebasaurus thwazi* De Klerk *et al.*, 2000. However, as pointed out here, the presence of a well developed posterolateral process is also present in *Megaraptor* (Calvo *et al*. 2004) and *Australovenator* (Hocknull *et al*. 2009), among other theropods (e.g. *Sinosauropteryx, Tugulusaurus*; Currie & Chen 2001; Rauhut & Xu 2005). Additionally, *Rapator* lacks the hypertrophied and highly modified distal lateral condyle present in *Nqwebasaurus* (De Klerk *et al.* 2000).

The proximal articular surface of the metacarpal of *Rapator*, for articulation with the medialmost distal carpal, is very concave, as is the case in tetanuran theropods, but not in more basal dinosaurs (e.g. *Dilophosaurus*, *Coelophysis*; UCMP 37302; QG 1). As occurs in tetanurans, the proximolateral articular surface of *Rapator*, for attachment with the metacarpal II, is extended well proximodistally, suggesting that both elements were closely appressed along the proximal half of the metacarpal I (Gauthier 1986; Currie & Carpenter 2000; Rauhut 2003). This character supports the tetanuran affinities of *Rapator*. Furthermore, *Rapator* can be excluded from Coelurosauria due to the absence of a medial side of metacarpal I forming a sharp edge (Rauhut & Xu 2005, character 87), otherwise present in coelurosaurians such as Ornithomimosauria, *Tugulusaurus*, *Tanycolagreus* and Dromaeosauridae (Rauhut & Xu 2005). The articular facet of metacarpal II of *Rapator* is dorsoventrally low due to the absence of a ventral development of the posterolateral process. In contrast, a ventral component of this process is present in most tetanurans, including *Tugulusaurus*, *Allosaurus, Acrocanthosaurus, Szechuanosaurus* and *Torvosaurus* (Madsen 1976; Gao 1993; Currie & Carpenter 2000; Rauhut & Xu 2005). On the other hand, a dorsoventrally low articular facet for metacarpal II (due to absence of a ventral component) is also present in the referred material of *Megaraptor* (MUCPv 341) and probably *Tanycolagreus* (Carpenter *et al.* 2005).

In particular, the morphology of metacarpal I in *Rapator*, *Australovenator* and *Megaraptor* is almost identical. In this regard, based on the combination of a proximally well-developed posterolateral process and a dorsoventrally low articular facet for metacarpal II (due to the absence of a ventral component), *Rapator* can be distinguished from all other theropods with the exception of the above mentioned taxa. As such, we consider *Rapator* to be a member of Megaraptora (*sensu* Benson *et al*. 2009). *Rapator* and *Australovenator* differ from *Megaraptor* in the presence of a more dorsoventrally developed mediodistal condyle and a lateral facet for articulation with the metacarpal II lying in almost the same plane as the lateral margin of the shaft. Thus, albeit being very similar in morphology, *Rapator* and *Australovenator* are clearly distinct from *Megaraptor*. Hocknull *et al*. (2009) recognized subtle differences between *Rapator* and *Australovenator* (e.g. more subequal distal condyles, flat proximal articular surface, straight lateral distal condyle) and we add here the presence of a distal medial condyle ventrally extended in *Rapator*. However, due to the fragmentary condition of *Rapator* and the absence of autapomorphies and clear differences with *Australovenator*, we consider the taxon to be a *nomen dubium*.

cf. ***Megaraptor*** Smith *et al.* 2008

Horizon and locality. Dinosaur Cove, near Cape Otway, Eumeralla Formation (early Albian: late Early Cretaceous), Victoria, Australia (38°46′53+1″ S, 143°24′ 14+1″E, World Geodetic Standard 1984) (see Smith *et al.* 2008).

Material. NMV P186076, a nearly complete left ulna (Rich & Vickers-Rich 2003; Smith *et al.* 2008).

Revised taxonomic assignment. Carcharodontosauria, Megaraptora indet. (Benson *et al*. 2009).

Remarks. Among the remains collected from Dinosaur Cove, Rich & Vickers-Rich (2003, fig. 8) figured an isolated left theropod ulna. This ulna shares unique apomorphies with the carcharodontosaurian theropods *Megaraptor* (Novas 1998; Calvo *et al.* 2004) and *Australovenator* (Hocknull *et al*. 2009) (Salisbury *et al.* 2007; Smith *et al*. 2008; Benson *et al*. 2009) (Fig. 19). These taxa show the following unique traits: (1) a posterodorsally expanded, blade-like olecranon process; and (2) a pronounced lateral tuberosity that is continuous with a distinct lateral crest (contra Hocknull *et al*. 2009). Unlike remaining specimens of *Megaraptor*, the distal articular surface of NMV P186076 and *Australovenator* lack a distinct triangular outline (Smith *et al.* 2008). This difference and its smaller size indicate that NMV P186076 is different from *Megaraptor namunhuaiquii*, as defined by Novas (1998) and Calvo *et al.* (2004), and therefore Smith *et al.* (2008) considered it as cf. *Megaraptor* sp. However, it is now clear that in addition to *Megaraptor*, NMV P186076 is also very similar to *Australovenator*. Accordingly, the identification of NMV P186076 as cf. *Megaraptor* can be reassessed. We agree with Hocknull *et al*. (2009) in distinguishing *Australovenator* from NMV P186076 by the presence of a straight posterior margin of the olecranon process and a longitudinal groove on the lateral surface of the shaft. However, it was not until the analysis of Benson *et al*. (2009) that *Australovenator* was considered a related form to *Megaraptor* and NMV P186076, all these forms belonging to the recently recognized clade Megaraptora.

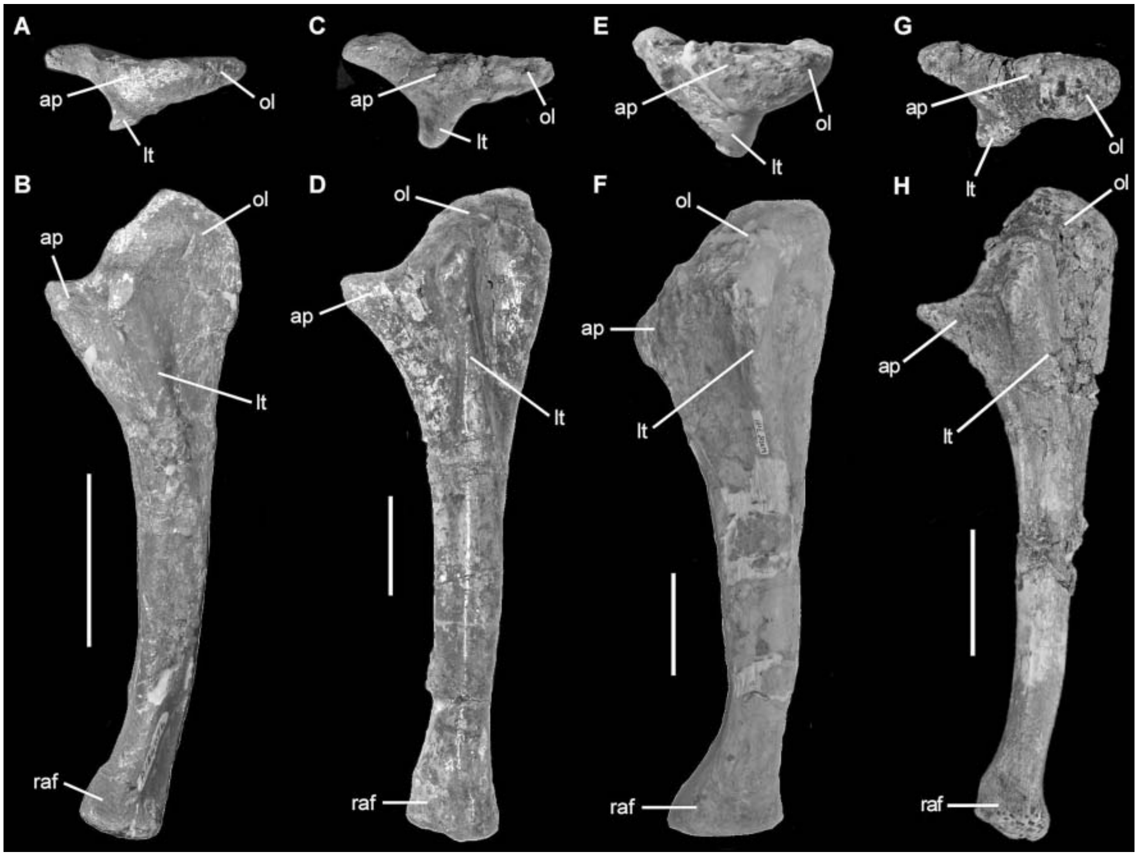

Figure 19. The left ulna of selected megaraptorans in proximal (**A, C, E, G**) and lateral (**B, D, F, H**) views. **A, B,** Megaraptora indet. (NMV P186076); **C, D,** *Megaraptor namunhuaiquii* (MCF-PVPH 79); **E, F,** *Megaraptor namunhuaiquii* (MUCPv 341; right ulnae reversed); **G, H,** *Australovenator wintonensis* (modified from Hocknull *et al.* 2009). Abbreviations: ap, anterior process; lt, lateral tuberosity; ol, olecranon process; raf, radial articular facet. Scale bars = 5 cm.

Australovenator wintonensis Hocknull *et al.* 2009

(Fig. 19E, F)

Horizon and locality. Winton Formation (latest Albian: late Early Cretaceous; Wagstaff & McEwen Mason 1989), 'Matilda Site', Elderslie Station, Central Queensland, Australia.

Holotype. AODF 604, partial skeleton (Hocknull *et al.* 2009).

Revised taxonomic assignment. Carcharodontosauria, Megaraptora (*sensu* Benson *et al.* 2009).

Remarks. This theropod is the most complete predatory dinosaur recovered from the Cretaceous of Australasia. The animal was originally identified as a basal allosauroid more closely related to carcharodontosaurids than to allosaurids and sinraptorids (Hocknull *et al.* 2009). Some months later, Benson *et al.* (2009) reconsidered the phylogenetic position of several Cretaceous theropods and recognized *Australovenator* as a megaraptoran carcharodontosaurian. It is worth mentioning that the phylogenetic position of *Australovenator* in both analyses is almost the same (i.e. as the sister-taxon of Carcharodontosauridae). In the present contribution we follow the interpretation provided by Benson *et al.* (2009).

Timimus hermani Rich & Vickers-Rich, 1994

(Figs 20, 21)

Horizon and locality. Eumeralla Formation, Otway Group (late Aptian-early Albian: late Early Cretaceous; Wagstaff & McEwen Mason 1989), Dinosaur Cove East, Dinosaur Cove, Victoria, Australia.

Holotype. NMV P186303, complete left femur.

Referred materials. NMV P186323, complete left femur.

Revised taxonomic assignment. Paraves, Dromaeosauridae? indet. cf. Unenlagiinae (*nomen dubium*).

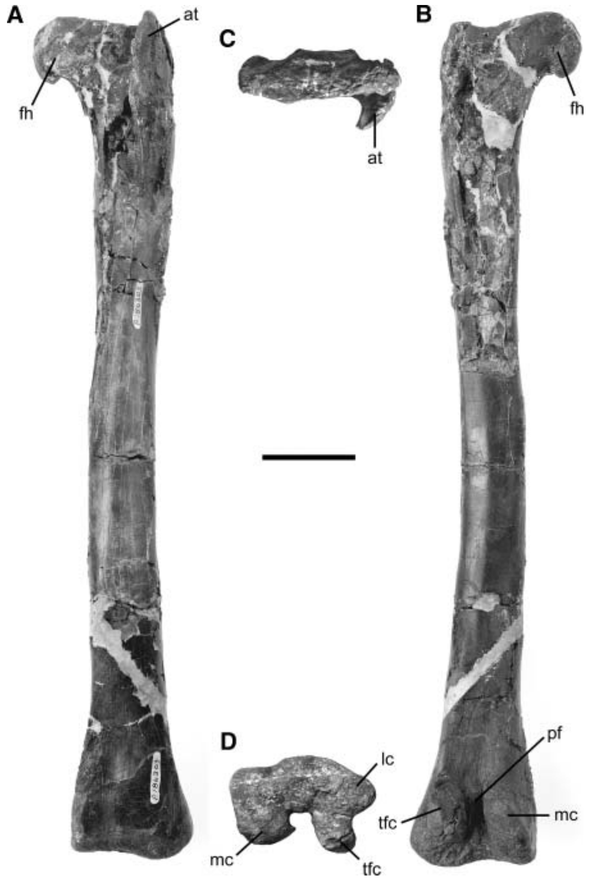

Figure 20. *Timimus hermani* Rich & Vickers-Rich, 1994 (NMV P186303). Left femur in: **A,** anterior; **B,** posterior; **C,** proximal; and **D,** distal views. Abbreviations: at, anterior trochanter; fh, femoral head; lc, lateral condyle; mc, medial condyle; pf, popliteal fossa; tfc, tibiofibular crest. Scale bar = 5 cm.

Remarks. *Timimus hermani* was originally erected on the basis of an isolated femur from the Strzelecki Group (Aptian) of Victoria (Rich & Vickers-Rich 1994; Fig. 20). In the same paper, these authors also referred a second isolated femur, thought to represent a juvenile individual, to *Timimus hermani* (Rich & Vickers-Rich 1994; Fig. 21). Rich & Vickers-Rich (1994), considered *Timimus* to be a basal ornithomimid, and this assignment was not challenged by other authors until recently. Bonaparte (1999) suggested that due to the general proportions of the femur, *Timimus* may be related to the South American maniraptoran *Unenlagia* (see discussion of the status of *Unenlagia* in Novas & Puerta 1997; Makovicky *et al.* 2005) from the Turonian of Argentina. The femur of *Timimus* displays the following plesiomorphies, also seen in Maniraptora and Tyrannosauroidea, allowing us to exclude it from Ornithomimosauria (contra Rich & Vickers-Rich 1994): (1) a proximal tip of the anterior trochanter positioned well above the level of the femoral head; and (2) a non-aliform anterior trochanter (Holtz 2000). In ornithomimosaurians the anterior trochanter is aliform and does not surpass the proximal level of the femoral head. *Timimus* also exhibits the following maniraptoran synapomorphies: (1) anterior trochanter appressed to the greater trochanter (Holtz 2000); and (2) absence of a fourth trochanter (Rauhut 2003). In ornithomimosaurians the anterior trochanter is well separated from the greater trochanter and the fourth trochanter is well developed, as is the case in Tyrannosauridae, and more basal theropods.

Both *Timimus* specimens resemble Paraves (Dromaeosauridae, Troodontidae and Avialae) in lacking a distal anterior extensor groove (originally considered as an autapomorphy of *Timimus* by Rich & Vickers-Rich 1994) and the presence of a reduced mediodistal crest (Holtz 1994; Novas & Puerta 1997). The holotype of *T. hermani* differs from Troodontidae in the presence of an anterior trochanter separated from the greater trochanter by a groove, and absence of a large posterior trochanter on the posterolateral surface of the femur (Currie & Peng 1993; Makovicky & Norell 2004). On the other hand, the femur of *Timimus* is reminiscent of Dromaeosauridae in having a slightly lateromedially bowed (laterally convex) femoral shaft, a femoral head almost perpendicular to the main axis of the bone in proximal view, and an anterior trochanter that is robust and slightly extended anteriorly (Currie & Peng 1993; Makovicky & Norell 2004). Among Dromaeosauridae, *Timimus* shows a fibular condyle that is plesiomorphically proximally positioned, and medially placed, well separated from the lateral margin of the shaft, as occurs in the unenlagiine theropods *Rahonavis*, *Unenlagia* and *Buitreraptor* (Novas & Puerta 1997; Forster *et al.* 1998; Makovicky *et al.* 2005). Unfortunately, the femur of basal members of Microraptoria is poorly known, and thus the morphology of the fibular condyle cannot be determined. In addition, *Timimus* shows an anteroposteriorly bowed (anteriorly convex) femoral shaft, a condition reminiscent of Troodontidae (Norell & Makovicky 2004) and Unenlagiinae (e.g. *Buitreraptor*, *Unenlagia*; Makovicky *et al.* 2005; Novas & Pol 2005), contrasting with the straight shaft present in other dromaeosaurids.

In conclusion, *Timimus* is here excluded from Ornithomimosauria and is considered a paravian probably related to Unenlagiinae (Bonaparte 1999; Makovicky *et al.* 2005; Senter 2007). No autapomorphies or unique combinations of features allow us to differentiate *Timimus* from other paravian theropods, and thus we consider this taxon a *nomen dubium*.

Australian oviraptorosaurian
(Figs 22, 23)

Horizon and locality. Eumeralla Formation, Otway Group (late Aptian-early Albian: late Early Cretaceous; Wagstaff & McEwen Mason 1989), Dinosaur Cove, Victoria, Australia.

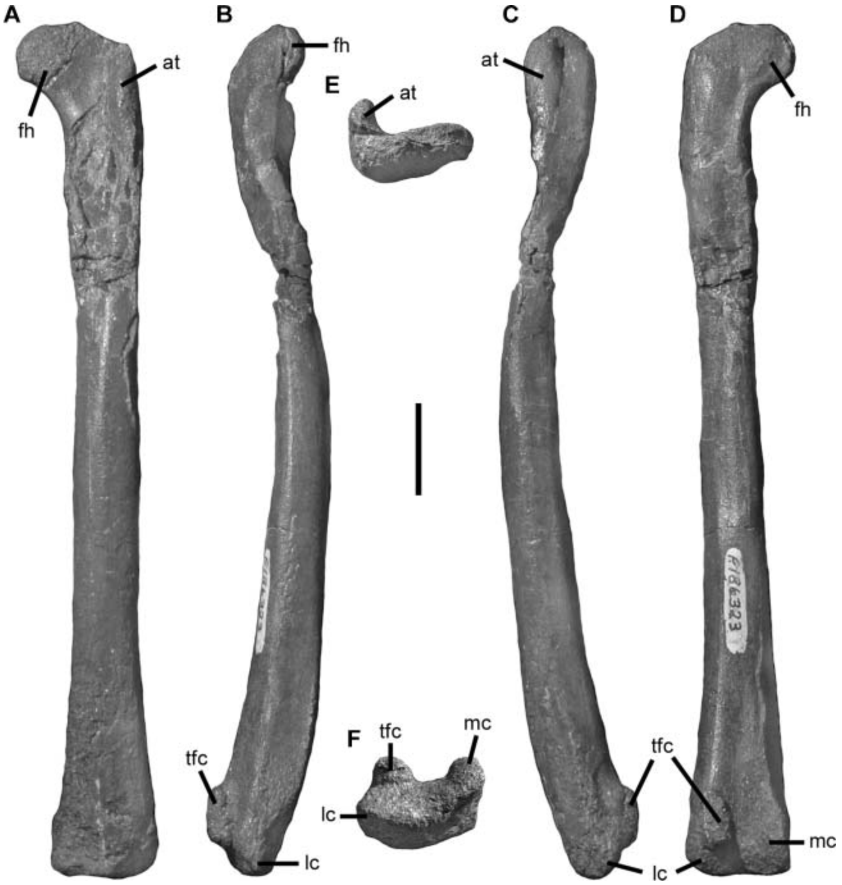

Figure 21. Referred material of *Timimus hermani* (NMV P186323, juvenile). Left femur in: **A,** anterior; **B,** lateral; **C,** medial; **D,** posterior; **E,** proximal; and **F,** distal views. Abbreviations: at, anterior trochanter; fh, femoral head; lc, lateral condyle; mc, medial condyle; tfc, tibiofibular crest. Scale bar = 2 cm.

Material. NMV P186302, a dorsal vertebra; NMV P186386, a probable right surangular.

Revised taxonomic assignment. Theropoda indet. (surangular) and Dromaeosauridae indet. (vertebra).

Remarks. Currie *et al.* (1996) described isolated remains from the Early Cretaceous Otway Group of Dinosaur Cove (Australia) that they referred, with doubts, to Oviraptorosauria (Figs. 22, 23). The remains consist of a possible surangular (NMV P186386) and an isolated dorsal vertebra (NMV P186302). The putative surangular is badly broken, lacking both anterior and posterior ends. It resembles that of oviraptorosaurians in having a medial inflection of the coronoid process (Currie *et al.* 1996) (Fig. 22A, B). However, as pointed out by Currie *et al.* (1996), the surangular also resembles that of dromaeosaurids (especially *Dromaeosaurus*; Colbert & Russell 1964) in having a convex ventral margin and an anteriorly pinched contact with the angular. Moreover, there is no indication of the

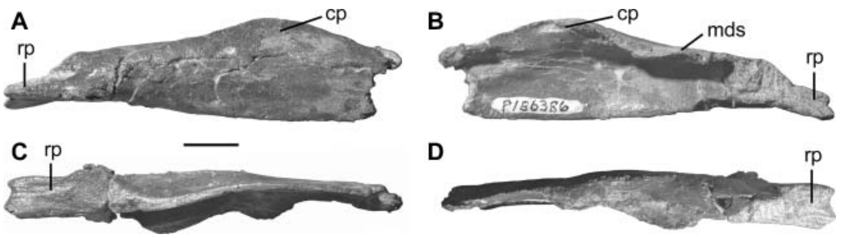

Figure 22. Theropoda indet. (Dinosaur Cove ‘oviraptorosaur’, NMV P186386). Right surangular in: **A,** lateral; **B,** medial; **C,** ventral; and **D,** dorsal views. Abbreviations: cp, coronoid process; mds, mediodorsal shelf; rp, retroarticular process. Scale bar = 1 cm.

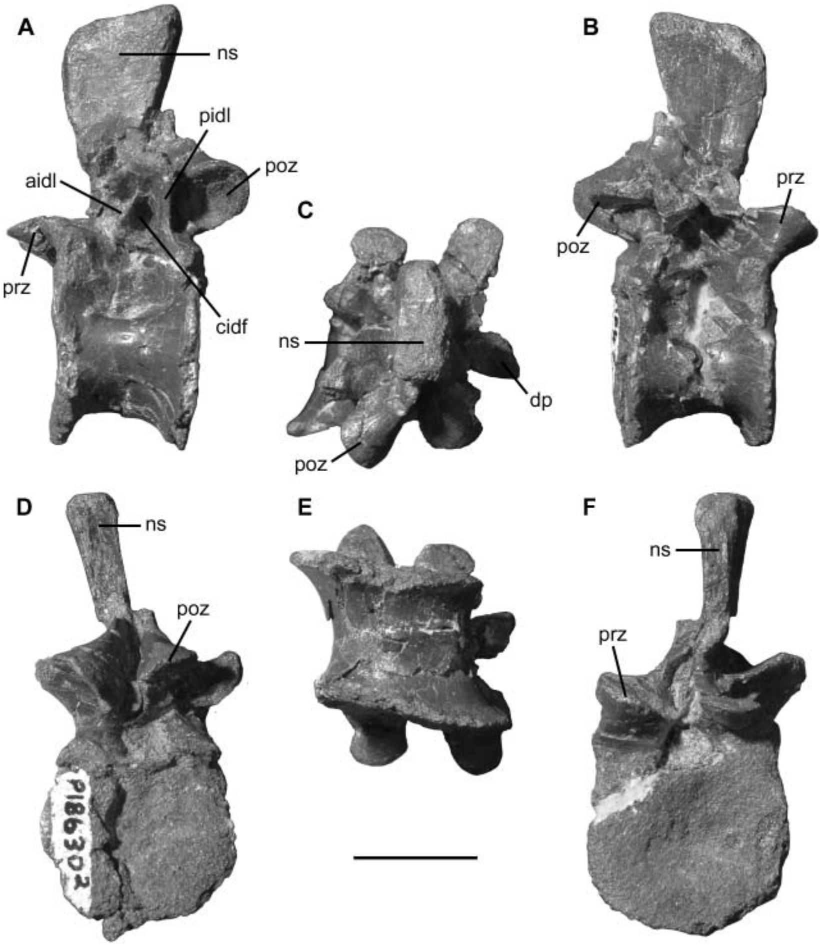

Figure 23. Dromaeosaurid vertebra (Dinosaur Cove 'oviraptorosaur', NMV P186302) in: **A,** left lateral; **B,** right lateral; **C,** dorsal; **D,** posterior; **E,** ventral; and **F,** anterior views. Abbreviations: aidl, anterior infradiapophyseal lamina; cidf, central infradiapophyseal fossa; dp, diapophysis; ns, neural spine; pidl, posterior infradiapophyseal lamina; prz, prezygapophysis; poz, postzygapophysis. Scale bar = 2 cm.

presence of a mandibular fenestra anterior to the angular facet. Additionally, the surangular is not fused to the articular, also contrasting with the condition present in oviraptorosaurians (Barsbold 1981; Currie *et al.* 1996). On the basis of the strong differences between NMV P186386 and known oviraptorosaurians and the absence of further informative characters, we suggest that the Australian specimen is regarded as Theropoda indet.

The isolated vertebra described by Currie *et al.* (1996; see Makovicky & Sues 1998) resembles Dromaeosauridae and Oviraptorosauria in possessing a single internal cavity divided by a medial septum (Britt 1993), and the presence of a single pleurocoel (Currie *et al.* 1996). The Australian vertebra was originally assigned to Oviraptorosauria by Currie *et al.* (1996) because of: (1) the presence of a low neural spine; and (2) the poorly developed lamina between the parapophysis and diapophysis. However, regarding the first trait, we think that the neural spine does not differ from the condition seen in dromaeosaurids (e.g. *Rahonavis*, *Deinonychus*, *Microraptor*; Forster *et al.* 1998; Hwang *et al.* 2002) or basal birds (e.g. *Archaeopteryx*). In fact, in dromaeosaurids and NMV P186302 the height of the neural spine represents more than 70% of the total height of the neural arch (e.g. NMV P186302: 78%; *Deinonychus*: 73%; *Buitreraptor*: 75%; Ostrom 1969; Makovicky *et al.* 2005), whereas in Oviraptorosauria, it is usually less than 60% (e.g. *Microvenator*: 60%; *Nemegtomaia*: 57%; Makovicky & Sues 1998; Lü *et al.* 2004).

With respect to the lamina that connects the parapophysis with the diapophysis, in contrast with the opinion of Currie *et al.* (1996), the morphology of NMV P186302 does not resemble that of oviraptorosaurians but is reminiscent of that of dromaeosaurids. Indeed, the lamina of NMV P186302 is acute, very well developed, and widely contacts the parapophysis, as occurs in several dromaeosaurids (e.g. *Deinonychus*, *Unenlagia, Buitreraptor*; Ostrom 1969; Novas & Puerta 1997; Makovicky *et al.* 2005). In contrast, in other coelurosaurians including Troodontidae (Norell & Makovicky 2004) and Oviraptorosauria (Makovicky & Sues 1998), this lamina is very thin and never contacts the parapophysis. Furthermore, NMV P186302 and dromaeosaurids, such as *Deinonychus* (Ostrom 1969), differ from oviraptorosaurians in that the pleurocoels are placed in a large lateral depression. In addition to the above mentioned features, the presence of stalked parapophyses in NMV P186302 represents an apomorphy of Dromaeosauridae (Hwang *et al.* 2002; Norell & Makovicky 2004; Makovicky *et al.* 2005). In conclusion, we suggest that NMV P186302 represents the dorsal vertebra of an indeterminate dromaeosaurid theropod.

Other theropod remains from the Early Cretaceous of Australia and New Zealand

Several isolated theropod bones from different Early Cretaceous localities of Australia and New Zealand have been described in the last century, and they are reviewed in this section.

Woodward (1906) described an isolated pedal ungual phalanx from the Wonthaggi Formation (Valanginian-Aptian), Cape Patterson, Australia (NMV P10058, Fig. 24). This element differs from the phalanges of *Allosaurus* in being more strongly arched along its ventral margin and more laterally compressed (Molnar *et al.* 1981). Moreover, this phalanx superficially resembles phalanges described by Lapparent (1960) from the Early Cretaceous of Saharan Africa in having a ventral depression on the posteroventral end of the lateral groove. However, with the evidence at hand, it cannot be diagnosed here beyond Theropoda indet.

Long and Cruickshank (1996) documented a fragmentary theropod mid-caudal vertebra from the Lower Cretaceous Birdsong Sandstone (Hauterivian-Barremian) of Western Australia. We agree with Long and Cruickshank in considering this material as an indeterminate theropod.

Late Cretaceous theropods

Molnar (1981) reported an isolated mid-caudal vertebra of an indeterminate theropod, from the Tahora Formation (Campanian) of North Island, New Zealand. This material is phylogenetically uninformative and is considered here as Theropoda indet. following Molnar (1981).

Scarlett & Molnar (1984) reported a theropod pedal phalanx from the Tahora Formation (Campanian) of North Island, New Zealand. They did not refer this element to any specific theropod group, and we follow them in considering it as Theropoda indet.

From the Miria Formation (Maastrichtian) of Western Australia, Long (1992) reported a partial proximal humerus (WAM 90.10.2) considered to represent a gracile theropod dinosaur, probably related to Coelurosauria. This theropod humerus can be included within Neotheropoda due to the presence of a biconvex humeral head in proximal view (Rauhut 2003). However, there are no apomorphies allowing us to diagnose this bone beyond Neotheropoda, and among the hitherto described Cretaceous theropods this specimen seems not to be a ceratosaurian. Indeed, WAM 90.10.2 contrasts with abelisauroids in lacking both a proximally inflated humeral head and a reduced deltopectoral crest (Novas *et al.* 2006). Furthermore, the Australian specimen seems not to be allied with Spinosauroidea or Allosauroidea due to its very slender shaft (Rauhut 2003). Its original assignment to Coelurosauria is likely correct.

A pedal phalanx I of digit III coming from the Tahora Formation (Campanian) of North Island, New Zealand, was assigned by Molnar & Wiffen (1994) to an indeterminate theropod similar in size to *Allosaurus*. This phalanx shows anteroposteriorly shortened distal flexor pits and a thickened proximodorsal lip of the proximal articular surface. Both characters are also present in Gondwanan carcharodontosaurids (e.g. *Mapusaurus*; Coria & Currie

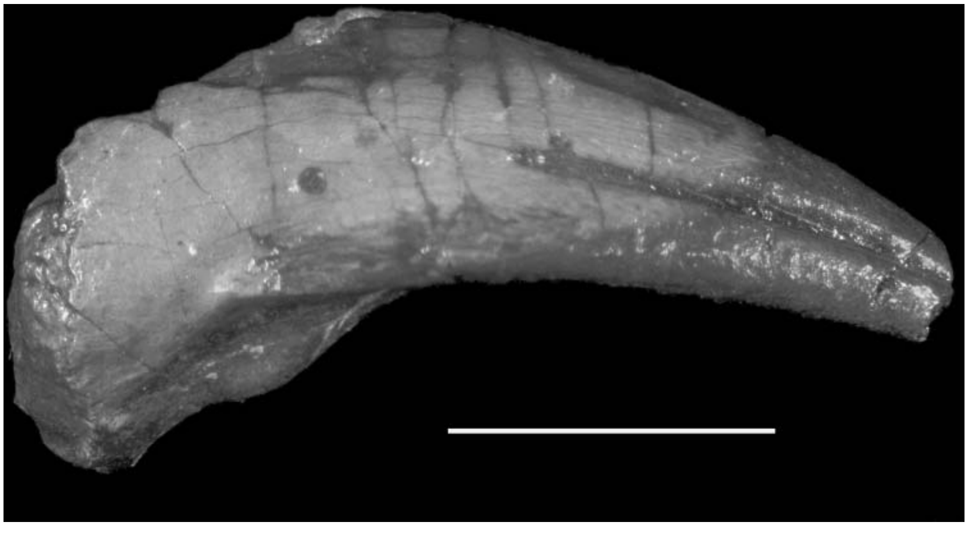

Figure 24. Pedal ungual of Theropoda indet. (‘Cape Patterson claw’ NMV P10058) in lateral view. Scale bar = 2 cm.

2006; MPCA unnumbered). However, we follow Molnar & Wiffen's (1994) original interpretation, being cautious and considering this pedal phalanx as belonging to an indeterminate theropod.

From the Molecap Greensand (Cenomanian-Santonian?) of Western Australia, Long (1995) described an isolated pedal phalanx that he referred to Carnosauria, noting similarities with Allosauridae. However, this phalanx differs from those of allosaurids in having a relatively larger flexor fossa and a more reduced proximomedial ventral tuberosity; both features are present in Abelisauroidea and Carcharodontosauridae, at least. We conclude that this material represents an indeterminate non-allosaurid theropod.

Stilwell *et al.* (2006) described several fragmentary and isolated remains of theropods from the Takatika Grit (K-T boundary) of Chatham Island, southwest Pacific. These specimens deserve the following comments:

1. Partial theropod vertebral centrum. Stilwell *et al.* (2006) pointed out that this element could not be from a marine reptile because of its lateral constriction at midlength. However, they did not cite any feature that may indicate that this specimen belongs to Theropoda, and not to Ornithopoda or Sauropoda. Thus we suggest that this element is best considered Dinosauria indet.
2. Proximal end of theropod tibia. This material is too incomplete and badly preserved to permit a clear systematic assignment and we suggest that the element should be considered Dinosauria indet.
3. Theropod manual ungual. The absence of a proximodorsal lip excludes this ungual from Oviraptorosauria, Dromaeosauridae, Troodontidae and Aves (Rauhut 2003). As Stilwell *et al.* (2006) noted, it is reminiscent of ornithomimids in the presence of a weak flexor tubercle and poor curvature. Nevertheless, the uninformative nature of the specimen precludes any assignment beyond non-maniraptoran Coelurosauria.
4. Theropod manual phalanx. This element is quite well preserved. Stilwell *et al.* (2006, p. 247) indicated that 'the phalanx is comparable to those of many theropods (e.g. troodontids, oviraptorosaurids, ornithomimids)', and also pointed out its similarity to a pedal phalanx of a bird. The features that Stilwell *et al.* (2006) used in order to support the identification of this element as a manual phalanx are also present in the pedal phalanges of basal birds. Furthermore, this phalanx possesses a proximoventral sulcus that is shared with pedal phalanges of Enantiornithes (Sereno *et al.* 2002) and could belong to a closely related form.
5. Theropod proximal pedal phalanx II-1 or III-1. Stilwell *et al.* (2006) tentatively assigned this isolated material to Allosauroidea, but they did not mention any feature supporting this interpretation. Thus, because of the incomplete nature of the specimen, we reinterpret this material as Theropoda indet.

Discussion

Through the years, different assignments of fossil specimens from Cretaceous dinosaur faunas of Australia and New Zealand have indicated the presence of ornithomimosaurians, oviraptorosaurians, allosaurids and 'cetiosaurids' among saurischians, and 'hypsilophodontids', iguanodontians, protoceratopsians and ankylosaurians among ornithischians. In the case of the putative 'hypsilophodontids' and allosaurids, their presence in Australia led Rich & Rich (1989) to postulate the existence of Jurassic relicts, an idea followed by most subsequent authors. Some taxa were also considered as endemic components of the Australian Cretaceous dinosaur faunas, such as the indeterminate theropod *Kakuru* (Molnar 1992), the ornithopod *Muttaburrasaurus* and the sauropod *Austrosaurus* (Molnar 1980b, c, 1989). The assignment of theropod specimens from the ECA (Early Cretaceous of Australia) to clades such as Ornithomimosauria and Oviraptorosauria and ornithischian specimens to Neoceratopsia, by Rich & Vickers-Rich (1994) led these authors to state that the Australian faunas were reminiscent of Asiamerica but distinct from central and western Gondwana, necessitating a connection of some sort during the Early Cretaceous between Australia and Asia. Indeed, Rich (1996), Rich & Vickers-Rich (1996) and Vickers-Rich (1996) proposed on the basis of this evidence the origin of ornithomimosaurians, oviraptorosaurians, dromaeosaurids and neoceratopsians in Australia and then their subsequent migration to Asia.

In contrast, the present study has arrived at radically different systematic interpretations for most of these specimens. Based on these new assignments, Cretaceous theropod faunas in Australia comprised abelisauroids, megaraptorans and paravians. In the case of ornithischians, ankylosaurians, basal non-iguanodontian, iguanodontian and styracosternan ornithopods were present. Previous interpretations of the available Australian sauropod material as titanosauriforms are followed (Salgado *et al.* 1997), but recent discoveries indicate that sauropods were a common component of these faunas and not diminished numerically in comparison with ornithopods (Salisbury *et al.* 2006b; Hocknull *et al.* 2009). Although many of the major clades of Australian dinosaurs recognized in the present revision are not completely endemic to Gondwana (see below), the overall faunistic composition is clearly reminiscent of other Gondwanan landmasses (Table 2). In this regard, the presence of Jurassic relicts among dinosaurs in the ECA is not supported. On the other hand, no endemic Laurasian taxon is present in the Cretaceous of Australia or New

Table 2. Geographical distribution of the main dinosaur clades from the Cretaceous and similarity indexes between the dinosaur communities of different landmasses and those of Australia. The closer the similarity indexes are to 1, the more similar are the compositions of the dinosaur communities. Basal Ornithopoda refers to non-ankylopollexian ornithopods.

	North America	Asia	Europe	South America	Antarctica	Africa	Madagascar	India	Australia
Tyrannosauridae	X	X	X	—	—	—	—	—	—
Ornithomimosauria	X	X	X	—	—	—	—	—	—
Therizinosauroidea	X	X	—	—	—	—	—	—	—
Oviraptorosauria	X	X	—	—	—	—	—	—	—
Alvarezsauridae	X	X	X	X	—	—	—	—	—
Troodontidae	X	X	X	—	—	—	—	—	—
Dromaeosauridae	X	X	X	X	X	X	X	—	X
Abelisauroidea	—	—	X	X	—	X	X	X	X
Spinosauroidea	—	—	X	X	—	X	—	—	—
Neovenatoridae	—	X	X	X	—	—	—	—	X
Carcharodontosauridae	X	X	—	X	—	X	—	—	—
Diplodocidae	X	—	X	—	—	X	—	—	—
Rebbachisauridae	—	—	X	X	—	X	—	—	—
Dicraeosauridae	—	—	—	X	—	X	—	—	—
Titanosauria	X	X	X	X	—	X	X	X	X
Stegosauria	X	X	X	X	—	X	—	—	—
Ankylosauria	X	X	X	X	X	X	—	X	X
Basal Ornithopoda	X	X	X	X	X	X	—	—	X
Styracosterna	X	X	X	X	X	—	—	—	X
Pachycephalosauria	X	X	X	—	—	—	—	—	—
Ceratopsia	X	X	X	—	—	—	—	—	—
Similarity index	0.43	0.52	0.58	0.70	0.72	0.55	0.60	0.60	—

Zealand. Furthermore, the reinterpretations of the putative ornithomimosaurian '*Timimus*' and oviraptorosaurians as paravians (Dromaeosauridae) and the neoceratopsian '*Serendipaceratops*' as an indeterminate genasaurian go against previous interpretations for the origin of these dinosaur clades in Australia (Rich 1996; Rich & Vickers-Rich 1996; Vickers-Rich 1996). Regarding the Australian origin of dromaeosaurids and oviraptorosaurians (in part reinterpreted as dromaeosaurids), the cosmopolitan distribution of dromaeosaurids in the Late Cretaceous of Laurasia and Gondwana and their presence in the Early Cretaceous of Asia, led several authors to propose their origin by, at least, the Late Jurassic (Xu *et al.* 1999, 2002; Novas & Pol 2005). Thus, the Australian origin of dromaeosaurids is not supported by the evidence at hand. In the context of the present reappraisal, the Cretaceous Australian and New Zealand dinosaur faunas must be analyzed within a more refined palaeobiogeographic framework. The lack of an eloquent Early Cretaceous dinosaur record from Gondwana constituted a strong bias on previous palaeobiogeographic analyses. The latter problem has hampered a clear view about the understanding of the distribution of the main dinosaur clades during this time span. Therefore, the revised ECA record constitutes a valuable source of information for elucidating the distribution of dinosaur species and the timing of the breakup of Gondwana (Smith *et al.* 2008).

Three main hypotheses for the fragmentation of Gondwana have been proposed (see Upchurch 2008). The 'traditional model' implies the separation of western (South America, Africa) and eastern (Antarctica, India, Madagascar, Australia) Gondwana in the latest Jurassic or Early Cretaceous (Smith *et al.* 1994; Scotese 2001). The second hypothesis is the so-called 'Africa-first' model, in which Africa was isolated from the remaining Gondwanan landmasses before the beginning of the Late Cretaceous, and South America, Antarctica and Australia remained connected until the Early Tertiary (Hay *et al.* 1999; Krause *et al.* 2007). Finally, the third hypothesis is the 'Pan-Gondwana' model, in which all the southern continents remained connected by three land-bridges through the Early Cretaceous and were severed during a relatively brief interval at the beginning of the Late Cretaceous (Sereno *et al.* 2004).

The presence of abelisauroids, paravians (including cf. unenlagiines), allosauroids, ankylosaurids, titanosauriforms, and non-iguanodontian, iguanodontian and styracosternan ornithopods in the Early to mid-Cretaceous of Australia, and ankylosaurids, titanosauriforms and non-maniraptoran coelurosaurs in the Late Cretaceous of New Zealand, shows that a typical Gondwanan dinosaur fauna, characteristic of other southern Late Cretaceous basins (Bonaparte 1999), was well established in this part of East Gondwana during the Early Cretaceous. This is also supported by the other well-known Early Cretaceous Gondwanan faunas, namely those from Niger (Sereno *et al.* 1998, 2004; Brusatte & Sereno 2007; Sereno & Brusatte 2008) and Patagonia (Bonaparte 1996, 1999; Novas *et al.* 2005), and the Late Jurassic of Tanzania

(Bonaparte 1999; Rauhut 2005). Previous authors stated that exclusive common elements shared between Australia and South America, i.e. the presence of *Megaraptor* and closely related forms, indicated that faunal exchange was present across South America and Australia via Antarctica during the late Early Cretaceous (Smith *et al.* 2008). However, new available information indicates that *Megaraptor* and closely related forms (i.e. Megaraptora) achieved a more wide geographic distribution than supposed by Smith *et al*. (2008) (Benson *et al*. 2009). Furthermore, no dinosaur clade that is exclusive to South America and Australasia is recognized here. Accordingly, we cannot dismiss the traditional model of fragmentation of the Gondwanan supercontinent. In a broader context, the presence of Gondwanan dinosaur clades (e.g. titanosauriforms, abelisauroids, dromaeosaurids, spinosauroids, allosauroids, alvarezsaurids) in the Cretaceous of Europe (Le Loeuff 1991; Buffetaut 1997; Benson *et al*. 2009) and Asia (Wilson 2005; Brusatte *et al*. 2009) supports the idea that the origin of major 'Gondwanan dinosaur clades' occurred prior to the final separation of Pangea (e.g. abelisauroids; Allain *et al.* 2007), most likely during the Late Jurassic-earliest Cretaceous. Nevertheless, this scenario may not hold true for several Laurasian dinosaur clades (e.g. troodontids, therizinosauroids, oviraptorosaurians, ornithomimosaurians, tyrannosauroids, pachycephalosaurians, ceratopsians), which are abundantly recorded in northern Cretaceous beds but are currently unknown from Gondwana. Indeed, the present refutation of the occurrence of ornithomimosaurians and neoceratopsians in Australia leads us to dismiss any possible palaeogeographic connection between this landmass and Asia during the Early Cretaceous (cf. Rich & Vickers-Rich 1996, 2003; Vickers-Rich 1996).

The Cretaceous Australian and New Zealand dinosaur record provides some new information about the palaeobiogeography of the clades present in these landmasses and their distribution across the rest of Gondwana. Ankylosauria is scarcely represented in the Late Cretaceous of South America, Africa, India and Antarctica (Lapparent 1960; Chatterjee & Rudra 1996; Coria & Salgado 2001; Salgado & Gasparini 2006). However, basal ankylosaurians are well represented in the Early and Late Cretaceous of Australia and New Zealand respectively (Molnar 1980a, b, 1996a; Molnar & Wiffen 1994), which may suggest a wider distribution of this clade around Gondwana. On the basis of a terrestrial connection between South America and Australia via Antarctica during the Early Cretaceous, the presence of basal members of Ankylosauria during this time in Australia suggests that the group may also have occurred in South America and Antarctica during the Early Cretaceous, and that their Late Cretaceous Gondwanan representatives are not latest Cretaceous immigrants from North America, as previously proposed by other authors (Gasparini *et al.* 1987, 1996).

Basal ornithopods were traditionally considered as the most diverse and abundant group of dinosaurs in the ECA (Rich & Rich 1989; Rich & Vickers-Rich 1999a). Indeed, six different species of 'hypsilophodontids' were recognized in the Aptian-Albian time span. This high basal ornithopod diversity was considered as a peculiar trait related to near-polar climatic conditions, which would prompt a high abundance of the group during the ECA (Rich 1996). Nevertheless, the current paraphyletic condition of 'Hypsilophodontidae' (e.g. Norman *et al.* 2004; Butler *et al*. 2008) and more recent discoveries in South American and Antarctic outcrops indicate that a high diversity of basal ornithopods was not unique to the ECA but also present in the Late Cretaceous of the former landmasses (Novas *et al.* 2004). Furthermore, three of the six taxa of basal ornithopods (i.e. *Qantassaurus*, '*Atlascopcosaurus*' and *Leaellynasaura*) are represented primarily by cranial material, whereas the remaining three (i.e. other '*Fulgurotherium*' materal; Victoria femur types I and II) are only known from isolated femora. Regarding the cranial material, three distinct morphotypes can be discerned: *Qantassaurus* with a short and anteriorly tapering dentary, '*Atlascopcosaurus*' with a low and long dentary, and *Leaellynasaura* with a primitive dental morphology lacking a primary ridge. In the same way, three distinct basal ornithopod femoral morphologies are recognized in the ECA (see above). Nonetheless, no clearly overlapping materials exist between those taxa known from cranial and, on the other hand, femoral material, with the possible exception of *Leaellynasaura*. Thus, we do not have any evidence to consider taxa represented by isolated femora to be distinct from those known from cranial remains. As a consequence, in a conservative approach, it is possible that only three distinct species of basal ornithopods can be recognized in the ECA, indicating that the diversity of this group may be lower than previously thought. Moreover, recent findings of abundant sauropod dinosaurs in Australia indicate that they were not underrepresented in comparison with ornithopods (Molnar 2001b; Molnar & Salisbury 2005; Salisbury *et al.* 2006b; Hocknull *et al*. 2009).

In addition, it is important to note that some basal ornithopod remains from the ECA exhibit common derived traits with South American forms. For instance, '*Fulgurotherium*' and Victoria type I femur are reminiscent of the Argentinian genera *Gasparinisaura* and *Notohypsilophodon*, respectively, suggesting close phylogenetic relationships.

Regarding styracosternan ornithopods, their occurrence in the Early Cretaceous of Australia (e.g. *Muttaburrasaurus*) and Africa (e.g. *Ouranosaurus*, *Lurdusaurus*; Taquet 1976; Taquet & Russell 1999) indicates that at least some derived ornithopods were present in Gondwana at this time. In fact, their presence, together with the appearance in the South American record of Hadrosauriformes indicates that derived ornithopods underwent a complex, but poorly known radiation in the southern continents.

Abelisauroids were a diverse group of theropods, represented in the Jurassic of Africa and Australia (Rauhut 2005; Allain *et al.* 2007), and were the dominant predatory dinosaurs in the Cretaceous of most Gondwanan assemblages (Bonaparte 1991). In Australia, the group was thought to be absent until recently, when Rauhut (2005) suggested that the Middle Jurassic *Ozraptor* and the Early Cretaceous *Kakuru* were abelisauroid theropods. In the present contribution, the enigmatic pygmy '*Allosaurus*' is confidently referred to Abelisauroidea, providing further evidence of the presence of this group in the ECA. However, the abelisauroid affinities of *Kakuru* are not followed here.

The recent discovery of dromaeosaurid theropods in the Late Cretaceous of Patagonia demonstrated the presence of the group in the Late Cretaceous of Gondwana (Novas & Puerta 1997; Makovicky *et al.* 2005; Novas & Pol 2005). More recently, cladistic analyses depicted Gondwanan dromaeosaurids (*Buitreraptor*, *Rahonavis*, *Austroraptor*, *Unenlagia*, *Neuquenraptor*) as more closely related to each other than to northern forms, being classified in the subfamily Unenlagiinae (Makovicky *et al.* 2005; Senter 2007; Novas *et al*. 2009). In this regard, unenlagiine dromaeosaurids are currently recorded in South America, Madagascar, and Africa (Makovicky *et al.* 2005). Consequently, the presence of a monophyletic clade of Gondwanan dromaeosaurids suggested a vicariant distribution of this group after the Late Jurassic breakup between the northern and southern landmasses (Makovicky *et al.* 2005). More recently, fragmentary remains of a dromaeosaurid theropod were briefly reported from the Maastrichtian of the James Ross Island, northwestern Antarctica (Case *et al.* 2007). The assignment of this material to Dromaeosauridae was based on the following suite of pedal apomorphies: metatarsal II with a lateral expansion posterior to metatarsal III, metatarsal III proximally narrow and distally wide, distal end of metatarsal III incipiently ginglymoidal, and pedal digit II with trenchant ungual phalanx (Case *et al.* 2007, p. 3). Nevertheless, all these characters were employed by Novas & Pol (2005) as a unique combination of features diagnostic of the unenlagiine *Neuquenraptor argentinus*. Furthermore, these characters are also present in *Buitreraptor*, thus they seems to be synapomorphies of Unenlagiinae. In this regard, the Antarctic dromaeosaurid can be assigned to this clade. Thus unenlagiines were also present in the Late Cretaceous of Antarctica.

Until now, no unequivocal dromaeosaurid remains have been described from the Early Cretaceous of Gondwana. The assignment of *Timimus* and an isolated vertebra to Dromaeosauridae constitutes the first evidence of this group in the ECA and the oldest record for Gondwana. The presence of a paravian (cf. Unenlagiinae) in the Early Cretaceous of Australia is congruent with a Jurassic origin of Dromaeosauridae. Furthermore, some features of *Timimus* resemble those of unenlagiines (e.g. *Unenlagia*). If further information reinforces the similarities between *Timimus* and unenlagiines in the future, the group would be widely distributed across southern landmasses, namely South America, Africa, Madagascar, Antarctica and Australia.

The present overview of the Cretaceous non-avian dinosaur faunas from Australia and New Zealand led us to revaluate the similarities between this fauna and those from other landmasses. In order to perform such comparisons a statistical analysis was carried out (see Materials and Methods) (Table 2). Including the present systematic reinterpretations in the data set, Sorensen's similarity indexes indicate that the Cretaceous dinosaur faunas from Australia (and, by inference, New Zealand) are actually more similar to those from other Gondwanan landmasses (i.e. South America, Antarctica, India, Madagascar and Africa) than to Asia, Europe and North America (contra Rich & Rich 1989; Rich & Vickers-Rich 1999a, 2003; Rich 1996; Vickers-Rich 1996). Europe shows an intermediate condition to that depicted between Asiamerica and Gondwana. Indeed, common elements shared between Australia and Europe include dromaeosaurid, abelisauroid and neovenatorid theropods, titanosaurian sauropods and ankylosaurian thyreophorans.

Regarding the Cretaceous non-dinosaurian tetrapod faunas it is important to note that the putative Australian endemic ausktribosphenan mammals have also been reported in other parts of Gondwana (Rauhut *et al.* 2001; Rougier *et al.* 2001; Martin & Rauhut 2005). In the same way, most Cretaceous Australian dipnoan fishes are closely related to Patagonian taxa (Kemp 1997; Apesteguía & Agnolin 2002; Apesteguia *et al.* 2007). With respect to crocodyliforms, some Cretaceous South American neosuchian taxa have also been shown to be closely related to basal eusuchians from Australia (Salisbury *et al.* 2003a, b, 2006a). In the case of turtles it is noteworthy that some basal cryptodirans have been described that are probably related to meiolaniid Gondwanan terrestrial tortoises (Gaffney *et al.* 1998). On the other hand, some typical Gondwanan clades are currently unknown in the Cretaceous fossil record of Australia and New Zealand, namely chelid turtles, notosuchian crocodyliforms and pipid anurans. However, regarding the last two groups we must note that they are thus far also totally absent from the Early Cretaceous of South America, Africa and other Gondwanan landmasses, contrasting with the Late Cretaceous record. As claimed previously, the Australian and New Zealand Late Cretaceous record is extremely patchy and poor, so the absence of notosuchians and pipids could be related to taphonomic issues.

In this context, the only differences currently recorded between the Cretaceous tetrapod faunas of Australia and the other Gondwanan landmasses are the presence of chigutisaurid temnospondyls (Warren *et al.* 1991) and dicynodont synapsids (Thulborn & Turner 2003), and the absence of chelid turtles. Nevertheless, temnospondyls and dicynodonts are also absent in the Cretaceous of Laurasian continents, suggesting that both are actually Australian endemics. Temnospondyl amphibians were thought to have become extinct at the end of the Triassic; however, they have also been recently described from the Middle Jurassic of Australia and China, as well as from the Late Jurassic of Asia. Several cranial and postcranial elements from the Early Cretaceous of Australia clearly belong to this peculiar group of amphibians (Warren *et al.* 1991). Rich (1996) indicated that these specimens constitute the latest record for the group and clearly represent an endemic and relictual Australian clade that extends the range of temnospondyls another 50 million years forward in time. Regarding the Cretaceous dicynodont, Thulborn & Turner (2003) indicated that with this record the biochron of this group expanded more than 100 million years after their supposed extinction. Although a thorough revaluation of the Australian Cretaceous dicynodont goes beyond the scope of the present paper, similarities with some baurusuchian crocodyliforms (e.g. *Baurusuchus pachecoi*; Riff & Kellner 2001) are striking. Among these traits are the presence of an anterolateral fossa, a large canine-tooth, and very small postcanine tooth. Thus, in light of the similarities between the Alderley dicynodont and baurusuchian crocodyliforms, a re-evaluation of the affinities of this fragmentary specimen is warranted.

In conclusion, the present study presents a new interpretation of the Cretaceous dinosaur faunas of Australia and New Zealand, as well as their affinities to other continental landmasses. With the exception of temnospondyls and possibly dicynodonts, no Jurassic relicts are recognized here. No exclusively Asiatic or North American dinosaur clade occurs in Australia or New Zealand, but a number of typically Gondwanan dinosaur clades are present. Indeed, statistical analysis supports a closer faunistic relationship of Australia to other Gondwanan landmasses than to Asia and North America, at least as far as dinosaurs are concerned. In this regard, contrasting with previous authors, typical Gondwanan dinosaur assemblages are recorded in the Cretaceous of Australia and New Zealand.

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