A megaraptorid (Dinosauria: Theropoda) frontal from the upper Strzelecki Group (Lower Cretaceous) of Victoria, Australia

Jake Kotevski [a, f, *], Ruairidh J. Duncan [a, f], Adele H. Pentland [b, c], James P. Rule [a, d], Patricia Vickers-Rich [c, e], Thomas H. Rich [f], Erich M.G. Fitzgerald [a, d, f], Alistair R. Evans [a, f], Stephen F. Poropat [a, c]

[a] School of Biological Sciences, Faculty of Science, Monash University, Clayton, Victoria 3800, Australia
[b] Australian Age of Dinosaurs Museum of Natural History, The Jump-Up, Winton, Queensland 4735, Australia
[c] Western Australian Organic & Isotope Geochemistry Centre, School of Earth and Planetary Science, Curtin University, Bentley, Western Australia 6102, Australia
[d] Science Group, Natural History Museum, Cromwell Rd, South Kensington, London SW7 5BD, United Kingdom
[e] School of Earth, Atmosphere and Environment, Faculty of Science, Monash University, Melbourne, Victoria 3800, Australia
[f] Museums Victoria Research Institute, GPO Box 666, Melbourne, Victoria 3001, Australia

A B S T R A C T

Cretaceous (non-avian) theropod dinosaurs from Australia are poorly understood, primarily because almost all specimens described thus far comprise isolated postcranial elements. In Australia, only three non-dental cranial elements pertaining to Theropoda have been reported: the left and right dentaries of *Australovenator wintonensis* from the Winton Formation (Cenomanian–lowermost Turonian) of Queensland, and an isolated surangular from the Eumeralla Formation (lower Albian) of Victoria. Herein, we report the first evidence of non-mandibular cranial material of a non-avian theropod from Australia: a left frontal and fused parietal fragment from the Lower Cretaceous (lower Aptian) upper Strzelecki Group of Victoria. The specimen shares several synapomorphies with the frontals assigned to Megaraptoridae, including an anteroposteriorly elongate postorbital articulation and a truncated nasal articular surface. Accordingly, we regard this frontal as Megaraptoridae gen. et sp. indet. We performed both parsimony-based and Bayesian-based phylogenetic analyses to support our assignment, and both analyses support a placement within Megaraptoridae. However, this specimen appears to possess plesiomorphic characters relative to other megaraptorid frontals, lacking dorsoventrally high walls of bone that emarginate the nasal and prefrontal articular surfaces. The plesiomorphies of this specimen have implications for the evolution of the megaraptoran skull roof, suggesting the acquisition of specialised adaptations for longirostry over time. This specimen improves the limited record of Cretaceous Australian theropod cranial remains, and provides limited support for the hypothesis that Megaraptoridae might have originated in Australia.

1. Introduction

THE Australian Cretaceous non-avian theropod record is poorly understood when compared with that of most other continents, as it almost exclusively comprises isolated postcranial remains (Molnar and Pledge, 1980; Hocknull et al., 2009; Benson et al., 2012; Fitzgerald et al., 2012; Poropat et al., 2018, 2019, 2020; Brougham et al., 2019). Only four specimens described to date comprise associations of multiple elements: a pair of theropod pubic bones from the lower Albian Eumeralla Formation (NMV P186046: Benson et al., 2010a, 2010c, 2012; Herne et al., 2010; Wagstaff et al., 2020); the megaraptorid dubbed 'Lightning Claw' (LRF 100–106) from the Cenomanian Griman Creek Formation (Bell et al., 2016, 2019); and an unnamed megaraptorid (AODF 967–968, 972, 977–979: White et al., 2020) and the holotype specimen of *Australovenator wintonensis* Hocknull et al., 2009 (AODF 604) from the

* Corresponding author. School of Biological Sciences, Faculty of Science, Monash University, Clayton, Victoria 3800, Australia.

E-mail addresses: kotevskij2401@outlook.com.au (J. Kotevski), ruairidhjohnduncan@gmail.com (R.J. Duncan), pentlandadele@gmail.com (A.H. Pentland), jrule.palaeo@gmail.com (J.P. Rule), pat.rich@monash.edu (P. Vickers-Rich), trich@museum.vic.gov.au (T.H. Rich), efitzgerald@museum.vic.gov.au (E.M.G. Fitzgerald), alistair.evans@monash.edu (A.R. Evans), steve.poropat@curtin.edu.au (S.F. Poropat).

Cenomanian Winton Formation (Hocknull et al., 2009; White et al., 2012, 2013, 2015b; Tucker et al., 2013). Three of these four specimens have been referred to the Megaraptoridae, the group of theropods to which the vast majority of diagnostic theropod remains in Australian mid-Cretaceous dinosaur assemblages can be referred (Benson et al., 2010b, 2012; White et al., 2015b, 2020; Poropat et al., 2019; Kotevski and Poropat, 2022).

Although fewer than 50 isolated postcranial specimens have been described, the record of theropods from the Lower Cretaceous (Barremian–Albian: Wagstaff et al., 2020) of Victoria is the most taxonomically rich of any Australian state (Benson et al., 2012; Poropat et al., 2018). Previous research has suggested the presence of several clades, including indeterminate members of Cerato-sauria, Tetanurae, Avetheropoda, Neovenatoridae, Coelurosauria, Megaraptora, possibly Tyrannosauroidea and Ornithomimosauria, Maniraptora and Unenlagiinae (Benson et al., 2010a, 2012; Barrett et al., 2011; Fitzgerald et al., 2012; Novas et al., 2013; Delcourt and Grillo, 2018). Additional isolated specimens are known and classified to more inclusive theropod groups (e.g. Tetanurae, Avetheropoda, Coelurosauria), but no further owing to their incompleteness (Benson et al., 2012). The presence of Neovenatoridae is possibly symptomatic of a previous nesting of Megaraptora within Neovenatoridae coupled with a cautious approach by the authors on these isolated remains (Benson et al., 2010b, 2012). More recently described specimens indicate the presence of the Mega-raptoridae (Poropat et al., 2019), Noasauridae (Brougham et al., 2020) and Elaphrosaurinae (Poropat et al., 2020) in the Victorian Cretaceous. Nevertheless, there is a notable dearth of cranial material (excluding teeth) from Australian non-avian theropods. Only a single non-dental cranial fossil has been reported from Victoria thus far: an isolated surangular referred to Oviraptorosauria (NMV P186386: Currie et al., 1996), but now considered Theropoda indet. (Poropat et al., 2018). Outside Victoria, the only other reported Australian theropod cranial fossils are the left and right dentaries of the *Australovenator wintonensis* holotype (Hocknull et al., 2009; White et al., 2015b). Thus, all known Australian theropod cranial fossils comprise mandibular elements.

The frontal bone of theropods is particularly diagnostic, containing a suite of characters facilitating referral to more exclusive clades (Currie, 1987; Averianov, 2016). Herein we describe NMV P229038, an isolated non-avian theropod frontal from the Early Cretaceous (upper Strzelecki Group, lower Aptian) of Victoria, southeast Australia, which represents the first theropod non-mandibular cranial fossil from the Mesozoic of Australia. Herein, we follow the phylogenetic position of Megaraptora as an early-branching clade within Tyrannosauroidea (Novas et al., 2013; Porfiri et al., 2014; Aranciaga Rolando et al., 2019, 2022; Ding et al., 2020; Naish and Cau, 2022), and relate our taxonomic descriptions to this.

1.1. Institutional abbreviations

AMNH, American Museum of Natural History, New York, USA; AODF, Australian Age of Dinosaurs Museum of Natural History Fossil, Winton, Queensland, Australia; BHI, Black Hills Institute of Geological Research, Hill City, South Dakota, USA; FPDM, Fukui Prefectural Dinosaur Museum, Fukui, Japan; GIN/IGM, Institute of Geology, Mongolian Academy of Sciences, Ulaan Baatar, Mongolia; GM, Ganzhou Museum, Ganzhou, China; IVPP, Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China; LACM, Natural History Museum of Los Angeles County, Los Angeles, California, USA; MCF-PVPH, Museo Carmen Funes, Paleontologia de Vertebrados, Plaza Huincul, Neuquén, Argentina; MCNA, Museo de Ciencias Naturales y Antropológicas J.C. Moyano, Mendoza, Argentina; MOR, Museum of the Rockies, Bozeman, Montana, USA;

MPC, Mongolian Paleontological Center, Ulaan Baatar, Mongolia; MPM-Pv, Museo Padre Molina Paleontologia de Vertebrados, Rio Gallegos, Santa Cruz, Argentina; MUCPv, Museo de la Universidad Nacional del Comahue, Paleontologia de Vertebrados, Neuquén, Argentina; NMC, Canadian Museum of Nature, Ottawa, Canada; NMV, Museums Victoria (formerly National Museum of Victoria), Melbourne, Australia; ROM, Royal Ontario Museum, Toronto, Canada; SDNH, San Diego Museum of Natural History, San Diego, California, USA; TMP, Royal Tyrell Museum of Palaeontology, Drumheller, Alberta, Canada; UA, University of Alberta, Edmonton, Alberta, Canada; UNPSJB-PV, Universidad Nacional de la Patagonia San Juan Bosco, Comodoro Rivadavia, Argentina; ZPAL, Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, Poland.

2. Methods

2.1. Material

The nearly complete frontal and fused parietal fragment described herein (NMV P229038) were collected from the Shack Bay locality by Michael Cleeland of the volunteer organisation Dinosaur Dreaming in 2007. The specimen was then prepared by David Pickering using air scribes and tungsten carbide scrapers and reposited into the Palaeontology Collection of Museums Victoria, Melbourne, Australia.

2.2. Computed tomography

NMV P229038 was scanned using micro-computed tomography (μCT) performed by a Zeiss Xradia 520 Versa CT facility located at Monash University, Clayton, Victoria, Australia, at 140 kV, HE1 filter, 1601 projections and 52.86 μm voxel size. The data were visualised using AVIZO 2022.1. The 3D dataset used in this work is archived at and available from Museums Victoria, Melbourne, Australia, and MorphoSource (media ID 000533313; doi.org/10.17602/M2/M533313).

2.3. Phylogenetic analyses

2.3.1. Morphological and stratigraphic data

For our phylogenetic analyses, we utilised the data matrix of Aranciaga Rolando et al. (2022). Although these authors utilised two matrices, one including and one excluding fragmentary taxa (*Aoniraptor libertatem* and UNPSJB PV-944/958), we only utilised the matrix excluding the fragmentary taxa. The analysis included 357 characters coded for 57 taxa, and 35 of these characters were ordered. We retained the characters and original scores provided, but added all possible scores for NMV P229038. Stratigraphic data were obtained for each taxon (Supplementary Information; references therein), consisting of geologic age ranges (maximum to minimum).

2.3.2. Parsimony analysis

Our parsimony phylogenetic analysis includes a single outgroup: *Ceratosaurus nasicornis*. The data matrix was analysed with implied-weighting parsimony using TNT v1.5 to run a heuristic tree search (Goloboff et al., 2008). We ran a traditional search of 1500 Wagner tree replicates (saving 10 trees per replicate) and with one random seed. This was followed by a TBR branch-swapping algorithm that generated the most parsimonious trees, with bootstrap values calculated for these. The resulting consensus tree and the stratigraphic age ranges for tip values were used along with the R package *strap* (R v.4.2.2, *strap* v.1.6-0) to calculate idealised divergence times for visualisation.

2.3.3. Bayesian analysis

Our Bayesian phylogenetic analysis included one outgroup (*Ceratosaurus nasicornis*) and three ingroups (Carnosauria, Coelurosauria and Paraves). We utilised MrBayes v.3.2.7a (Ronquist et al., 2012) via the CIPRES Science Gateway (Miller et al., 2011) to run a fossilized birth-death analysis (Gavryushkina et al., 2017). This analysis used simultaneous tip and node dating (O'Reilly and Donoghue, 2016; Barido-Sottani et al., 2019), with stratigraphic ranges for tips and an offset exponential distribution for Paraves. We also included Avialae (with morphology coded as unknowns), constrained with *Velociraptor* in the Paraves clade to help anchor the age estimation of the nodes (Bapst et al., 2016). The sampling strategy parameter "SampleStrat" was set to 'fossiltip', allowing all fossils to be resolved as tips on the tree. We ran 20 million MCMC generations (four runs and four chains), with sampling every 2000 generations. Convergence was set at 0.01 standard deviation of split frequencies. Consensus tree and clade credibility values were estimated using median node depths.

2.4. Geologic setting

The upper Strzelecki Group (Fig. 1), informally referred to as the 'Wonthaggi Formation' (Poropat et al., 2018; Herne et al., 2019), is hosted within the Gippsland Basin. It overlies the Tyers River Subgroup (lower Strzelecki Group (Tosolini et al., 1999; Duddy, 2003)), and underlies the Latrobe Group (Duddy, 2003). The unit comprises volcaniclastic sandstones, mudstones, conglomerates and thin coals that were deposited in a low to high-energy non-marine fluvial palaeoenvironment in a wide river valley that lay between Australia and Antarctica (Tosolini et al., 1999; Duddy, 2003; Aghaei et al., 2015; Wagstaff et al., 2020). These sediments were sourced from an active volcanic system along the east side of Australia (Bryan et al., 1997) and deposited along the developing rift valley of the Australian-Antarctic rift. The sediments were originally assigned to the Middle Jurassic (Ferguson, 1909), but are now interpreted as being Barremian−Aptian (Seegets-Villiers, 2012; Wagstaff et al., 2020).

Shack Bay is situated approximately 1 km west of Eagles Nest (Benson et al., 2012; Poropat et al., 2018), and lies within the upper Strzelecki Group (Fig. 1). Although this site has never been excavated, vertebrate fossil specimens have been discovered in three separate layers at this locality. The lowest, Layer 1, forms the shore platform at the site, and is comprised of coarse-grained conglomerates bearing fossilised vegetation and a small selection of vertebrate bones. Layer 2 overlies Layer 1 and consists of an approximately 30 cm-thick conglomerate containing carbonaceous material. Layer 3 is an approximately 1 m thick, coarse-grained conglomerate containing pebbles and rip-up clasts. Palynological studies indicate that the Shack Bay sediments fall within the lower Aptian portion of the *Pilosisporites notensis* Palynomorph Zone (Wagstaff et al., 2020).

Relatively few vertebrate fossils have been collected from Shack Bay, and none have yet been formally described. Nevertheless, the following clades are represented: Theropoda (NMV P228851, incomplete metatarsal), Ornithopoda (NMV P256478, femur; NMV P256996, vertebra) and Dipnoi (NMV P230785, right lower tooth plate) (Fig. 2). The theropod frontal described herein, NMV P229038, was retrieved from Layer 3, and the associated matrix that held the specimen was retained and registered under the same specimen number in the NMV collections. The associated matrix is comprised of rounded rip-up clasts (ranging between 3.7 and 12.5 mm in diameter) overlying a very fine-grained grey sandstone.
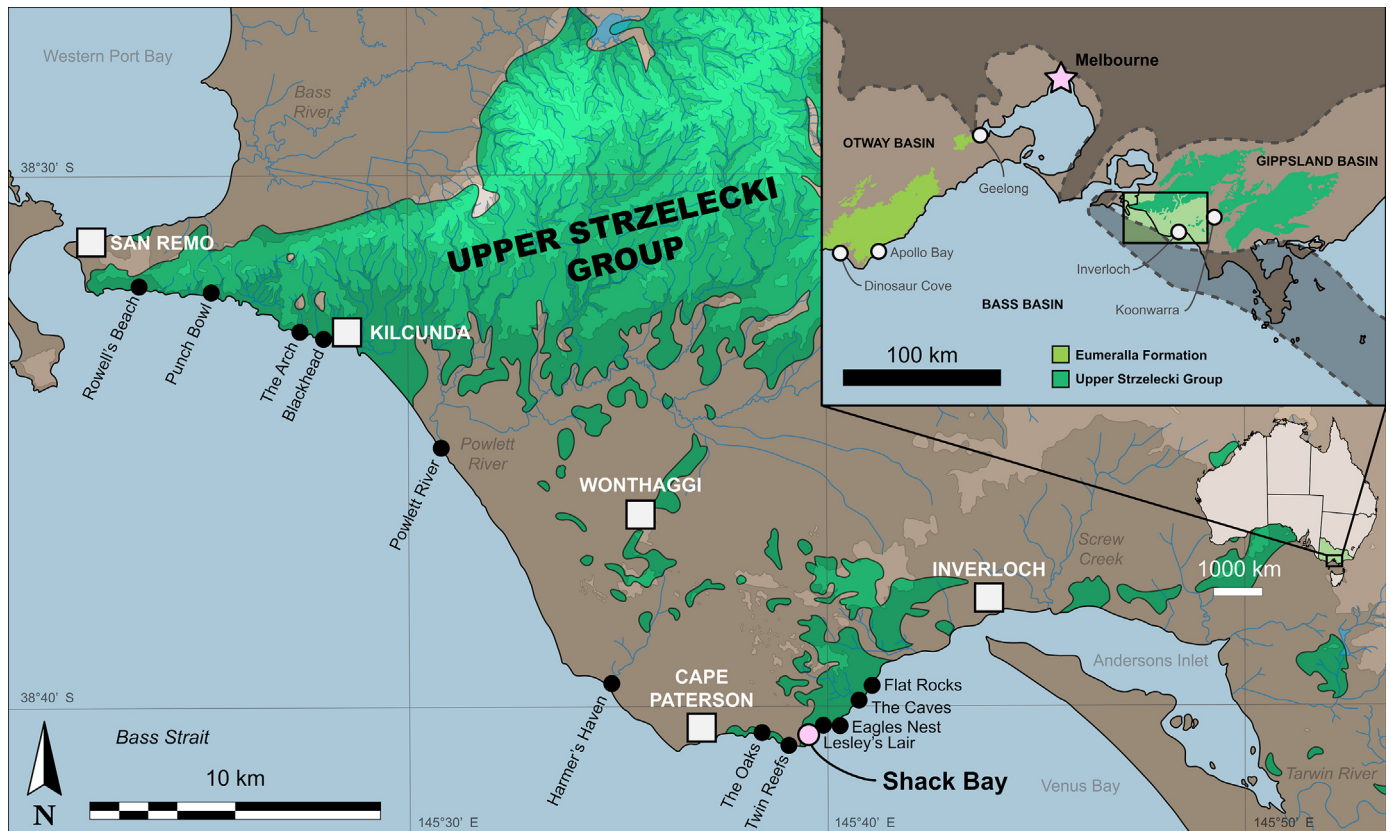

Fig. 1. Map of the Bass Coast, Victoria, Australia, showing the location of the Shack Bay locality from which NMV P229038 was collected. Geological data derived and adapted from Early Cretaceous fossil locality map by M. Cleeland, VandenBerg (1997a, 1997b), Korasidis and Wagstaff (2020), Wagstaff et al. (2020), Vicmap and (VSDL) (2021), and Google Earth.
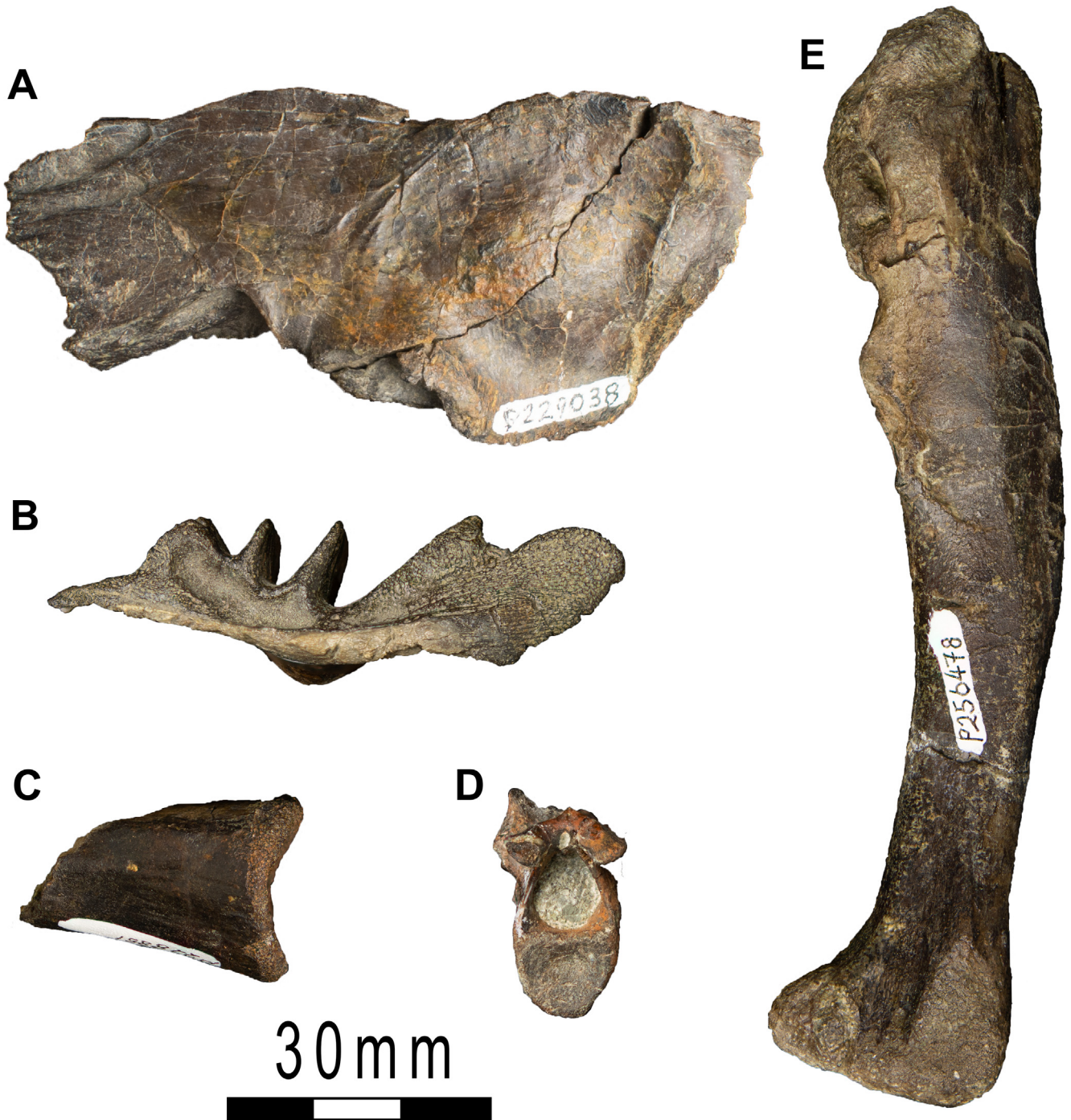
Fig. 2. Vertebrate fossils collected from the Shack Bay locality, upper Strzelecki Group, Victoria, Australia. **A.** NMV P229038 Megaraptoridae left frontal and fused parietal fragment in dorsal view; **B.** NMV P230785 Dipnoi right lower tooth plate in abocclusal view; **C.** NMV P228851 Theropoda incomplete proximal metatarsal in lateral view; **D.** NMV P256996 Ornithopoda vertebra in anterior view; and **E.** NMV P256478 Ornithopoda left femur in anterior view.

3. Systematic palaeontology

THEROPODA Marsh, 1881
TETANURAE Gauthier, 1986
COELUROSAURIA Huene, 1914
MEGARAPTORA Benson et al. 2010
MEGARAPTORIDAE Novas et al., 2013

Megaraptoridae gen. et sp. indet.

3.1. Referred material

NMV P229038: An isolated, almost complete left frontal, fused to a fragment of the left parietal (Fig. 3).

3.2. Locality and litho-chronostratigraphic horizon

Shack Bay, near Inverloch, Victoria, Australia. Upper Strzelecki Group, lower Aptian ~121.4—118 Ma (Wagstaff et al., 2020).
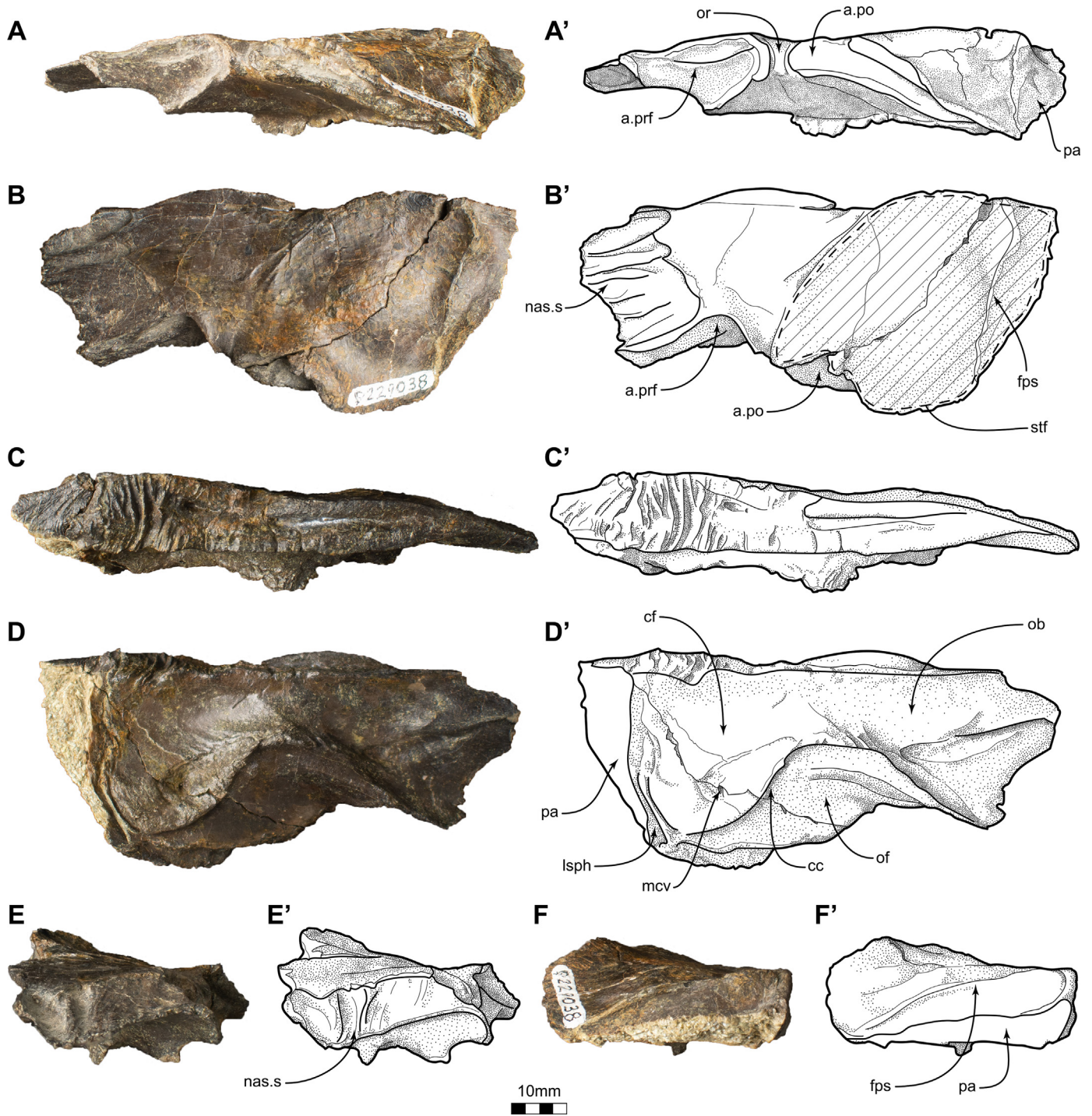
Fig. 3. Megaraptorid left frontal and fused parietal fragment (NMV P229038) from the upper Strzelecki Group of Victoria, Australia. Photographs of frontoparietal in **A.** lateral; **B.** dorsal; **C.** medial; **D.** ventral; **E.** anterior; and, **F.** posterior views. Interpretive drawings of frontoparietal in **A'.** lateral; **B'.** dorsal; **C'.** medial; **D'.** ventral; **E'.** anterior; and, **F'.** posterior views. Abbreviations: **a.po:** articular surface for the postorbital; **a.prf:** articular surface for the prefrontal; **cc:** crista cranii; **cf:** cerebral hemisphere fossa; **fps:** frontoparietal suture; **lsph:** articular surface for the laterosphenoid; **mcv:** passage for the mesencephalic vein; **nas.s:** articular surface for the nasal; **ob:** olfactory bulb; **of:** orbital fossa; **or:** contribution to the orbital rim; **pa;** parietal; **stf:** supratemporal fossa.

4. Description and comparisons

NMV P229038 is a well-preserved, almost complete left frontal, fused to a fragmentary portion of the left parietal (Fig. 3). In life, the frontal would have articulated with the nasal anterodorsally, the prefrontal anterolaterally (inferred from *Murusraptor barrosaensis*, wherein the prefrontal precludes the lacrimal from articulating with the frontal: Coria and Currie, 2016, Fig. 5), the postorbital posterolaterally, the parietal posteriorly, and the opposing frontal medially. In both medial and lateral views, the frontal is dorsoventrally thin anteriorly but thickens posteriorly (Table 1). Its overall shape (in dorsal view) is an anteroposteriorly elongate trapezoid that increases in mediolateral width toward the posterior end. NMV P229038 is not fused to the right frontal, indicating that the individual to which it pertained was skeletally immature perimortem.

Table 1
Measurements for the frontal and partially fused parietal NMV P229038.

Measurement (mm)	Frontal and partial parietal (NMV P229038)
Total Anteroposterior Length	83.6
Dorsally Exposed Frontal Anteroposterior Length	63.1
Maximum Mediolateral Width	36.8
Midpoint Mediolateral Width	28.6
Maximum Dorsoventral Height	11.6

There are several distinguishing features that allow us to exclude NMV P229038 from most higher order theropod clades. The extension of temporal musculature on to a large portion of the dorsal surface of the frontal is characteristic of Theropoda (Currie, 1997; Wilson and Sereno, 1998). The contribution of the frontal to the orbital rim is strongly reduced, contrasting with the more anteroposteriorly elongate contributions of the frontal to the orbital rim seen in herrerasaurids (Sereno and Novas, 1993), coelophysoids (Rauhut, 2003), dilophosaurids (Rauhut, 2003), ceratosaurids (Rauhut, 2003; Pol and Rauhut, 2012), noasaurids (Xu et al., 2009; Carrano et al., 2011), early-branching coelurosaurs (*e.g. Zuolong salleei*: Choiniere et al., 2010; Rauhut et al., 2012), some tyrannosauroids (*e.g. Guanlong wucaii and Dilong paradoxus*: Xu et al., 2004, 2006; Choiniere et al., 2010), compsognathids (Hwang et al., 2004) and maniraptoriforms (Osmólska et al., 1972; Rauhut, 2003; Novas et al., 2009). The dorsally exposed surface of the frontal is narrow mediolaterally and subquadrangular in shape, contrasting with the mediolaterally broad frontals of abelisaurids and carcharodontosaurids (Brusatte and Sereno, 2007; Sampson and Witmer, 2007; Sereno and Brusatte, 2008; Cau et al., 2012), spinosaurines (Arden et al., 2019), adult tyrannosaurids (Currie,

1987; Hurum and Sabath, 2003; Tsuihiji et al., 2011) and maniraptoriforms (Osmólska et al., 1972; Currie, 1987). NMV P229038 also lacks the ornamentation characteristic of abelisaurid frontals (Wilson et al., 2003; Sampson and Witmer, 2007; Cerroni et al., 2020). The supratemporal fossa of NMV P229038 is anteroposteriorly long, contrasting with the much shorter supratemporal fossae of abelisaurids (Wilson et al., 2003; Sereno and Brusatte, 2008), allosaurids (Madsen Jr, 1976; Brusatte and Sereno, 2008; Eddy and Clarke, 2011), and some basal tyrannosauroids (*e.g. Guanlong* and *Dilong*: Xu et al., 2004, 2006; Choiniere, 2010). The slightly-raised ridge of the sagittal crest strongly contrasts with the transversely broad sagittal crests of allosauroids (Madsen Jr, 1976; Currie and Zhao, 1993), and the dorsoventrally tall sagittal crests of spinosaurids (Sues et al., 2002; Arden et al., 2019). Considering all the above features, we are able to constrain NMV P229038 to a position within Coelurosauria, outside Maniraptoriformes and Compsognathidae. Thus, the frontal is most likely referable to Tyrannosauroidea or Megaraptora, and we largely restrict our comparisons below to taxa within those clades.

4.1. Dorsal view

The dorsally exposed region of the frontal is subquadrangular in shape, similar to the condition in *Xiongguanlong baimoensis* (Li et al., 2010), *Megaraptor namunhuaiquii* (Porfiri et al., 2014), *Murusraptor barrosaensis* (Coria and Currie, 2016) and *Albertosaurus sarcophagus* (Currie, 2003). This is in contrast to the subtriangular frontals present in most other members of the Tyrannosauridae (Brochu, 2003; Currie, 2003; Bever et al., 2013; Foster et al., 2022; Voris et al., 2021). The width: length ratio of the dorsally exposed portion of the frontal, calculated from the maximum anteroposterior length in dorsal view to the mediolateral length at the

Table 2
Width: length ratio of dorsally exposed region of the frontal bone in various Coelurosauria. Unless otherwise indicated, the data in this table derives from Currie (2003: Table 2).

Theropod species	Width: Length ratio	Measured specimen	Reference
Zuolong salleei	0.27	IVPP V15912	Choiniere et al. (2010): Fig. 5
Megaraptora indet.	0.45	NMV P229038	This paper: Table 1
Megaraptor namunhuaiquii	0.55	MUPCv 595	Porfiri et al. (2014): Fig. 6A
Murusraptor barrosaensis	0.58	MCF-PVPH-411	Paulina-Carabajal and Currie (2017): Fig. 1.1
Tyrannosauroidea indet.	0.27	MPC-D 102/4	Tsuihiji et al. (2012): Fig. 3
Dilong paradoxus	0.40	IVPP V14242	Xu et al. (2004): Fig. 1
Gorgosaurus libratus	0.37	ROM 1247	
	0.40	TMP 80.16.485	
	0.44	AMNH 5664	
	0.53	TMP 91.36.500, TMP 81.39.8	
	0.55	TMP 67.14.3	
	0.56	TMP 82.16.181, UA 10	
	0.57	ROM 3520	
	0.66	UA 10	
Albertosaurus sarcophagus	0.58	TMP 85.98.1	
	0.59	TMP 81.9.1	
	0.61	TMP 81.10.1	
Qianzhousaurus sinensis	0.47	GM F10004-1	Foster et al. (2022): Fig. 3
Alioramus altai	0.42	IGM 100/1844	Bever et al. (2013): Fig. 2
Daspletosaurus torosus	0.39	NMC 8506	
Daspletosaurus sp.	0.40	TMP 94.143.1	
	0.48	TMP 85.62.1	
	0.53	SDNH 32701	
Tarbosaurus bataar	0.23	MPC-D 107/7	Tsuihiji et al. (2011): Fig. 5
	0.40	MPC-D 107/14	
	0.54	GIN Jap-Mong	
	0.61	GIN PJC.2000.25, GIN PJC.2000.26	
	0.71	GIN PJC.2000.8	
	0.76	ZPAL MgD-I/4	Hurum and Sabath (2003): Table 1
Tyrannosaurus rex	0.31	BHI 116	
	0.42	LACM 23845	
	0.68	MOR 008	
	0.84	BHI 3033	Hurum and Sabath (2003): Table 1

orbital rim in dorsal view, is 0.45 for NMV P229038 (Table 2). This ratio is higher than that observed in some coelurosaurs and tyrannosauroids, lower than the values present in megaraptorids, and lies in the mid-range condition occurring between juvenile and adult tyrannosaurid frontals (Table 2).

The medial margin is effectively anteroposteriorly straight and bears subtle interdigitation, similar to *Xiongguanlong* (Li et al., 2010), *Megaraptor* (Porfiri et al., 2014), *Murusraptor* (Coria and Currie, 2016) and Tyrannosauridae (Currie, 2003; Bever et al., 2013; Foster et al., 2022; Voris et al., 2021). The lateral margin

undulates and flares slightly laterally toward the posterior end, similar to *Megaraptor*, *Murusraptor* and tyrannosaurids (Currie, 1987, 2003; Bever et al., 2013; Porfiri et al., 2014; Coria and Currie, 2016).

The anterior end of the frontal is sheet-like, forming the articular surface for the nasal (Fig. 3, Fig. 4). At its lateral margin, the articular surface for the nasal is separated from the prefrontal by an anterolaterally-projecting slight ridge, a condition somewhat similar to that in *Murusraptor* (Paulina-Carabajal and Currie, 2017), but not in *Megaraptor* (Porfiri et al., 2014). In *Alioramus altai*, and an
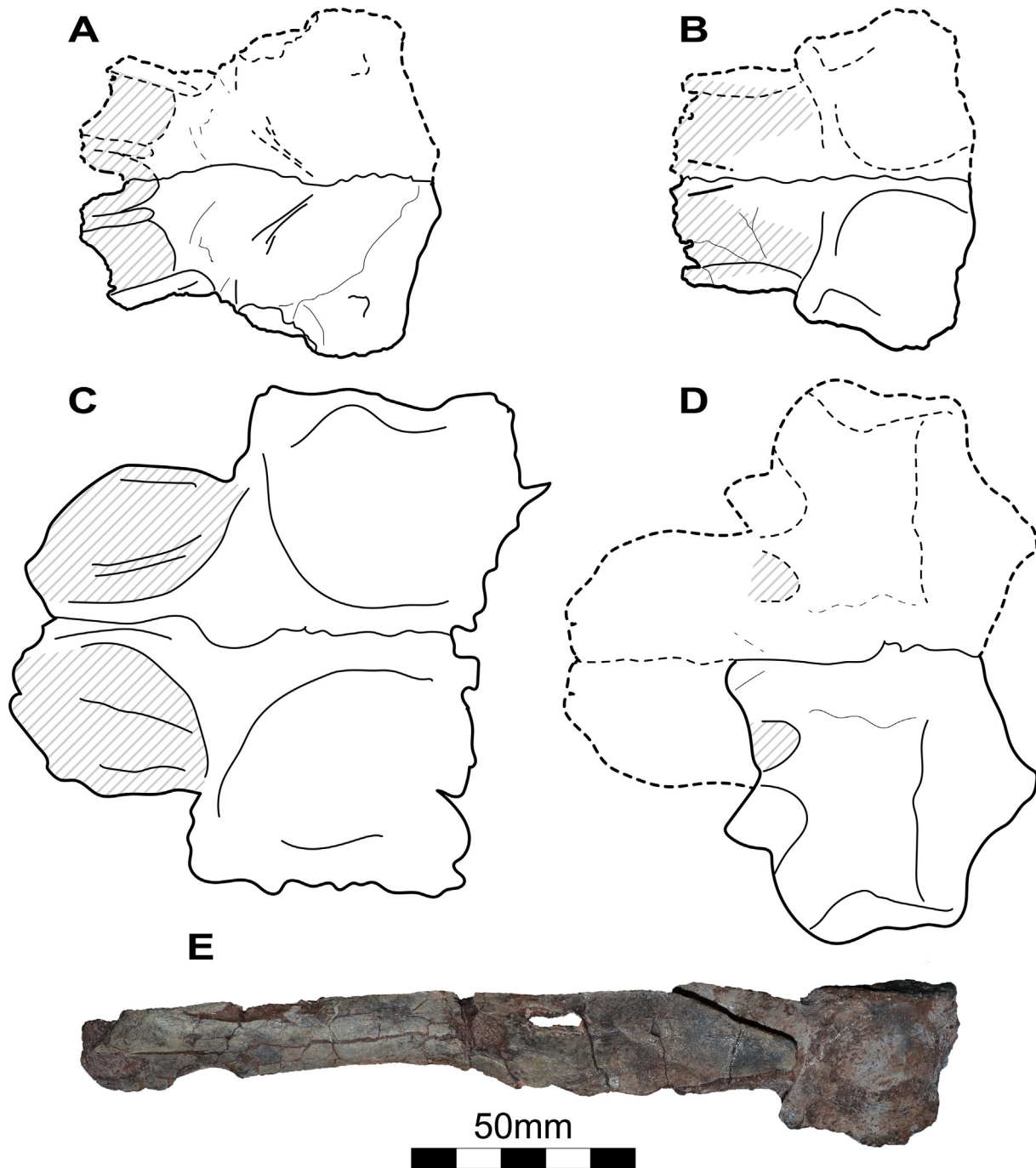

Fig. 4. Dorsal view interpretive drawings of reconstructed frontals of **A.** Megaraptoridae *indet.* (NMV P229038); **B.** *Megaraptor namunhuaiquii* (MUCPv 595); **C.** *Murusraptor barrosaensis* (MCF-PVPH-411); and **D.** Megaraptoridae *indet.* (MCF-PVPH-320). **E.** *Megaraptor namunhuaiquii* (MUCPv 595) left frontal and nasal in dorsal view. Shaded regions indicate nasal articular surface of the frontal, and dashed lines indicated inferred material. Image of MUCPv 595 provided by Alexis M. Aranciaga Rolando. C derived from Paulina-Carabajal and Currie (2017), D derived from Paulina-Carabajal and Coria (2015). Scale bar applies to A-E.

isolated tyrannosauroid frontal from the Late Cretaceous of Mongolia (MPC-D 102/4), a similar, albeit better defined, ridge separates the articular surface of the prefrontal from the articular surface of the lacrimal (Tsuihiji et al., 2012; Bever et al., 2013).

The nasal articular surface is approximately 13 mm long anteroposteriorly, and is thin dorsoventrally relative to the rest of the frontal. It is undamaged, subquadrangular in shape and exhibits slight anterolateral undulation, similar to both *Megaraptor* and *Murusraptor* (Porfiri et al., 2014; Coria and Currie, 2016), and in contrast to the triangular projections of the frontal in all tyrannosauroids other than *Bistahieversor sealeyi*, wherein the frontal is also subquadrangular (Brochu, 2003; Currie, 2003; Carr et al., 2005; Carr and Williamson, 2010; Choiniere, 2010; Bever et al., 2013; Voris et al., 2021).

The lateral region of the nasal articular surface is covered with fine, anteroposteriorly-extending striations that indicate the position of the overlap of the nasal, as in MPC-D 102/4 and some tyrannosaurids (Currie, 1987; Tsuihiji et al., 2012; Bever et al., 2013). These striations are also present in the megaraptorids *Megaraptor* and *Murusraptor* (Porfiri et al., 2014; Coria and Currie, 2016). The striations in NMV P229038 are more pronounced than those of *Megaraptor*, but less pronounced than in *Murusraptor* (Porfiri et al., 2014; Coria and Currie, 2016). Medially, the dorsal surface of the nasal suture undulates, forming two furrowed concavities with anteriorly-facing pits at their posterior margins that would have articulated with the posterior processes of the nasal. The medial-most furrow is deeper than the lateral one. Similar furrows are present in some tyrannosaurids (*e.g. Alioramus altai* and *Tyrannosaurus rex*: Brochu, 2003; Bever et al., 2013). In MPC-D 102/4, a small mediolateral furrow is present for articulation with a posterior prong of the nasal, while the lateral furrow is deeper (Tsuihiji et al., 2012). The medial-most furrow is similarly present in *Murusraptor* and *Megaraptor*, although in these two taxa this structure is bounded posteriorly by a dorsoventrally high wall of bone (Porfiri et al., 2014; Coria and Currie, 2016). In immature specimens of *Gorgosaurus libratus* and *Tyrannosaurus rex*, the medial margin of the nasal suture remains flat (Bever et al., 2013), a condition contrasting with that of NMV P229038.

On the anterior half, the part of the dorsal surface that would have been exposed is essentially flat, with a subtle convexity located towards the posteromedial margin of the midpoint. This convexity is bounded posteriorly by a subtle ridge, which also emarginates the supratemporal fossa anteriorly. The ridge extends posteromedially−anterolaterally, terminating at the anterior edge of the postorbital articulation laterally and the anterior-most region of the gently convex sagittal crest medially. Curiously, this ridge is nearly identical to the ridge emarginating the supratemporal fossa observed in a juvenile *Tarbosaurus bataar* (MPC-D 107/7: Tsuihiji et al., 2011) and *Gorgosaurus libratus* (TMP 2009.12.14: Voris et al., 2021). In adult tyrannosaurids and in the megaraptorids *Murusraptor* and *Megaraptor*, the delineating ridge is present, but more strongly pronounced (Currie, 1987, 2003; Porfiri et al., 2014; Coria and Currie, 2016). Posterior to this ridge lies the supratemporal fossa, which is anteroposteriorly elongate (approximately 54% of the exposed dorsal surface of the frontal), broadly convex anteroposteriorly, and undulates laterally — similar to *Megaraptor* (Porfiri et al., 2014), *Murusraptor* (Coria and Currie, 2016) and tyrannosaurids (Currie, 2003; Carr and Williamson, 2010; Brusatte and Carr, 2016). However, the supratemporal fossa in *Tarbosaurus* and *Tyrannosaurus* is more anteroposteriorly elongate than in other tyrannosaurids (Brochu, 2003; Currie, 2003).

The posterior margin of the frontal is marked by a distinct frontoparietal suture, which is oriented effectively mediolaterally in dorsal view. This distinguishes NMV P229038 from members of the Tyrannosauridae, in which the dorsal view of the frontoparietal suture is characteristically V-shaped with each sutural line oriented anteromedially−posterolaterally (Currie, 2003; Paulina-Carabajal and Coria, 2015; Voris et al., 2021). In dorsal view, the medial region of the suture is slightly convex posteriorly, and the lateral region is slightly concave posteriorly. This suture divides the supratemporal fossa across the frontal and parietal, as in *Murusraptor* (Paulina-Carabajal and Currie, 2017), and might indicate a point of separation between the muscles *m. pseudotemporalis superficialis* (anterior) and *m. adductor mandibulae profundus* (posterior: *sensu* Holliday, 2009; Paulina-Carabajal and Currie, 2017).

4.2. Medial view

In medial view, the frontal is dorsoventrally thin anteriorly but thickens posteriorly (Table 1). Anteriorly, the interfrontal suture is divided into a dorsal and ventral region by an anteroposteriorly elongate groove, which might have accepted a projection from the unfused right frontal. The absence of fusion of the interfrontal suture indicates that this theropod was skeletally immature at the time of its death (Rauhut, 2004; Sereno et al., 2009). The dorsal region of the interfrontal suture projects slightly over the groove as a shelf, and thus would have overlain the right frontal. The ventral region hosts numerous subtle dorsoventral ridges and grooves that would have interdigitated with complementary sutures on the right frontal. Posterior to the overhanging dorsal shelf lies an anteroposteriorly short groove, which would have accepted another projection of the right frontal. Dorsal to the anterior-most point of this groove, the medial contact of the frontal begins to slightly rise posterodorsally, forming the low, poorly defined ridge of the mediolaterally narrow sagittal crest. Transversely narrow sagittal crests are a characteristic of *Megaraptor, Murusraptor* and Tyrannosauroidea (Brochu, 2003; Currie, 2003; Xu et al., 2004; Choiniere, 2010; Porfiri et al., 2014; Coria and Currie, 2016). At the posterior end of the frontal, the frontoparietal suture is visible medially, and is dorsally elevated above the sagittal crest, clearly emarginating the frontal from the parietal, similar to *Murusraptor* (Paulina-Carabajal and Currie, 2017) some Tyrannosauroidea (*e.g.* MPC-D 102/4: Tsuihiji et al., 2012) and Tyrannosauridae (Brochu, 2003; Currie, 2003).

4.3. Ventral view

In ventral view, the frontal is divided into three distinct, shallowly concave regions by the semilunate longitudinal ridge of the crista cranii: these are anterior, lateral and posterior (Fig. 3). The overall morphology of the ventral surface of the frontal is strikingly similar to the ventral surface of the frontal of *Murusraptor*, predominantly the shape of the crista cranii and the position of the small nutrient foramen immediately anterior to its longitudinal ridge (Paulina-Carabajal and Currie, 2017).

The anterior concavity marks the shallow depression for the olfactory bulb. Within this depression, immediately anterior to the edge of the crista cranii, lies a small nutrient foramen that is approximately 3.5 mm in anteroposterior diameter; *Murusraptor* has a similarly-shaped foramen in almost exactly the same position (Paulina-Carabajal and Currie, 2017). Anterior to the foramen lies an anteroposteriorly extending ridge that underlies the anterior process (which hosts the articular surface for the nasal on its dorsal surface). Lateral to this ridge is a region bearing slight longitudinal striations, which might represent an attachment point for the ethmoid complex *sensu* Ali et al. (2008), similar to the condition in *Murusraptor*, MPC-D 102/4 and Tyrannosauridae (Tsuihiji et al., 2012; Brusatte and Carr, 2016; Paulina-Carabajal and Currie, 2017). The olfactory bulb depression is bounded laterally by the

articulation for the prefrontal, posterolaterally by the longitudinal ridge of the crista cranii, and posteriorly by a shallow convexity, in a strikingly similar configuration to *Murusraptor* (Paulina-Carabajal and Currie, 2017).

The laterally-situated orbital fossa is emarginated by the articulation of the prefrontal anterolaterally, the articulation of the postorbital posterolaterally, and the crista cranii medially. The crista cranii projects ventrally and forms a semilunate longitudinal ridge that extends anteroposteriorly and distinctly separates the ventral surface. Posterior to the crista cranii lies the anterior roof of the cerebrum; immediately medial to the longitudinal ridge, a small foramen (approximately 3 mm in diameter) is present that might represent the passage of the mesencephalic vein (Fig. 3). At the posterior end of the frontal lies the mediolaterally-extending frontoparietal suture, which is bounded laterally by the articulation point of the laterosphenoid and medially by the interfrontal suture, contrasting with the condition in *Murusraptor* and Tyrannosauridae, wherein the frontoparietal suture is anteromedially-posterolaterally 'V-shaped' (Paulina-Carabajal and Currie, 2017).

4.4. Lateral view

The articular surface for the prefrontal is situated anteriorly on the lateral surface, whereas that for the postorbital is situated posteriorly (Fig. 3). Each of these articular surfaces is emarginated by a strong ridge, with the small section of bone between them representing a tiny contribution of the frontal to the orbital rim. As inferred from the morphology in *Murusraptor* (Coria and Currie, 2016: Fig. 5), there appears to be no articulation point for the lacrimal; however, the lacrimal may have contacted the frontal anteriorly (between the nasal and prefrontal), as in *Murusraptor* and Tyrannosauridae (Currie, 2003; Paulina-Carabajal and Currie, 2017).

The prefrontal articulation is divided into dorsal and ventral regions by an anteroposteriorly-oriented slight ridge. At the posterior margin, the prefrontal groove curves slightly dorsally, terminating in a slight ridge at the border of the orbital rim, such that the dorsal surface of the frontal posteriorly overlaps the prefrontal, as in MPC-D 102/4 (Tsuihiji et al., 2012), *Gorgosaurus* (Currie, 1987; Voris et al., 2021) and *Alioramus* (Bever et al., 2013), but in contrast to *Murusraptor*, wherein the prefrontal articulation terminates posteriorly with a dorsoventrally tall face (Coria and Currie, 2016). The slight ridge emarginating the prefrontal articulation forms an anteriorly-facing socket, also observed in *Murusraptor* and Tyrannosauridae (Currie, 2003; Coria and Currie, 2016; Voris et al., 2021). This socket would have accepted a projection from the prefrontal, as in tetanurans generally (Carrano et al., 2012). Ventrally, the prefrontal groove meets the anterolateral edge of the crista cranii, producing a vertical contact with the prefrontal.

Posterior to the articulation for the prefrontal lies the small concave notch that represents a possible frontal contribution to the orbital rim (Fig. 3), similarly observed in some members of the Tyrannosauroidea (including most tyrannosaurids) (Currie, 1987, 2003; Li et al., 2010; Bever et al., 2013; Paulina-Carabajal and Currie, 2017; Voris et al., 2021). In the derived tyrannosaurids *Tarbosaurus* and *Tyrannosaurus*, the frontal is completely excluded from the orbital rim by increased ornamentation of the lacrimal (Brochu, 2003; Currie, 2003). However, we note that the frontal of juvenile *Tarbosaurus* still makes a contribution to the orbital rim, as the lacrimal and postorbital have not developed to contact each other (Tsuihiji et al., 2012). The frontal of *Murusraptor* is almost excluded from the orbital rim by the prefrontal and postorbital (Coria and Currie, 2016), and we infer a similar configuration for NMV P229038.

Posterior to the orbital rim contribution lies the articulation for the postorbital, which is overlain by a dorsal alar projection (Paulina-Carabajal and Currie, 2017). The postorbital articulation is dorsally raised at its anterior end and extends posteroventrally from this point. The articulation for the postorbital is anteroposteriorly elongate (34.5 mm), similar to the condition in *Megaraptor* (Porfiri et al., 2014), *Murusraptor* (Coria and Currie, 2016), some non-tyrannosaurid tyrannosauroids (Xu et al., 2004; Choiniere, 2010) and most tyrannosaurids (Brochu, 2003; Currie, 2003; Carr et al., 2005; Fiorillo and Tykoski, 2014; Voris et al., 2021). The anteroposterior length of the postorbital articulation is almost equal to half of the anteroposterior length of the frontal, as in both *Murusraptor* and *Megaraptor* (Porfiri et al., 2014; Aranciaga Rolando et al., 2019) and some tyrannosaurids (*e.g. Qianzhousaurus sinensis* and *Tyrannosaurus rex*: Brochu, 2003; Lu et al., 2014).

5. Phylogenetic analysis

5.1. Parsimony phylogenetic analysis

The results of our parsimony phylogenetic analysis support our referral of NMV P229038 to Megaraptoridae, having resolved five most parsimonious trees (MPTs) of 1388 steps (consistency index: 0.311; retention index 0.598). The strict consensus (Fig. 5) positions Megaraptora within Tyrannosauroidea, thus lending support to the hypothesis originally expressed by Novas et al. (2013) and more recently supported by Aranciaga Rolando et al. (2019, 2022). *Phuwiangvenator yaemniyomi* is the earliest-branching member of Megaraptora, and sister to a clade including *Vayuraptor nongbualamphuensis* and *Fukuiraptor kitadaniensis*: these three taxa comprise the only non-megaraptorid megaraptorans. The indeterminate Australian megaraptorid known as 'Lightning Claw' (LRF 100−106) was resolved as the earliest-branching megaraptorid, followed by *Australovenator*. The remaining megaraptorids (NMV P229038 and all South American taxa) form a polytomy, contrasting with the well-resolved topology returned by Aranciaga Rolando et al. (2022). However, the relationships of and within Megaraptora have weak support from bootstrap values (Supplementary Information).

5.2. Bayesian phylogenetic analysis

The topology of the posterior consensus tree resulting from our fossilised birth-death Bayesian phylogenetic analysis (Fig. 6) resolves Megaraptora within Tyrannosauroidea, and displays improved resolution within Megaraptora and Megaraptoridae. Interestingly, and in contrast to the parsimony results, the Compsognathidae (*Compsognathus* + *Sinosauropteryx*) is resolved as the earliest-branching clade within Megaraptora, followed by *Phuwiangvenator*, and then *Vayuraptor*, which does not form a clade with *Fukuiraptor* (unlike the parsimony analysis). NMV P229038 remains within Megaraptoridae, now representing the earliest-branching megaraptorid. Resolution within Megaraptoridae is seemingly stabilised, relative to the parsimony analysis, and broadly follows the trends outlined in the previous work to use this matrix (Aranciaga Rolando et al., 2022).

Posterior probabilities (PP) are broadly weak across the analysis, although some reasonable support is noted. There is weak support for resolution within Megaraptora, including the position of Compsognathidae within the clade (PP = 40%), and the position of NMV P229038 (PP = 39%) within Megaraptoridae. Support for the remaining Megaraptoridae is strong (PP = 96%), including the position of *Murusraptor* as the earliest-branching non-Australian megaraptorid (PP = 82%). Following this, the remainder of clades within Megaraptoridae have weak support (Supplementary
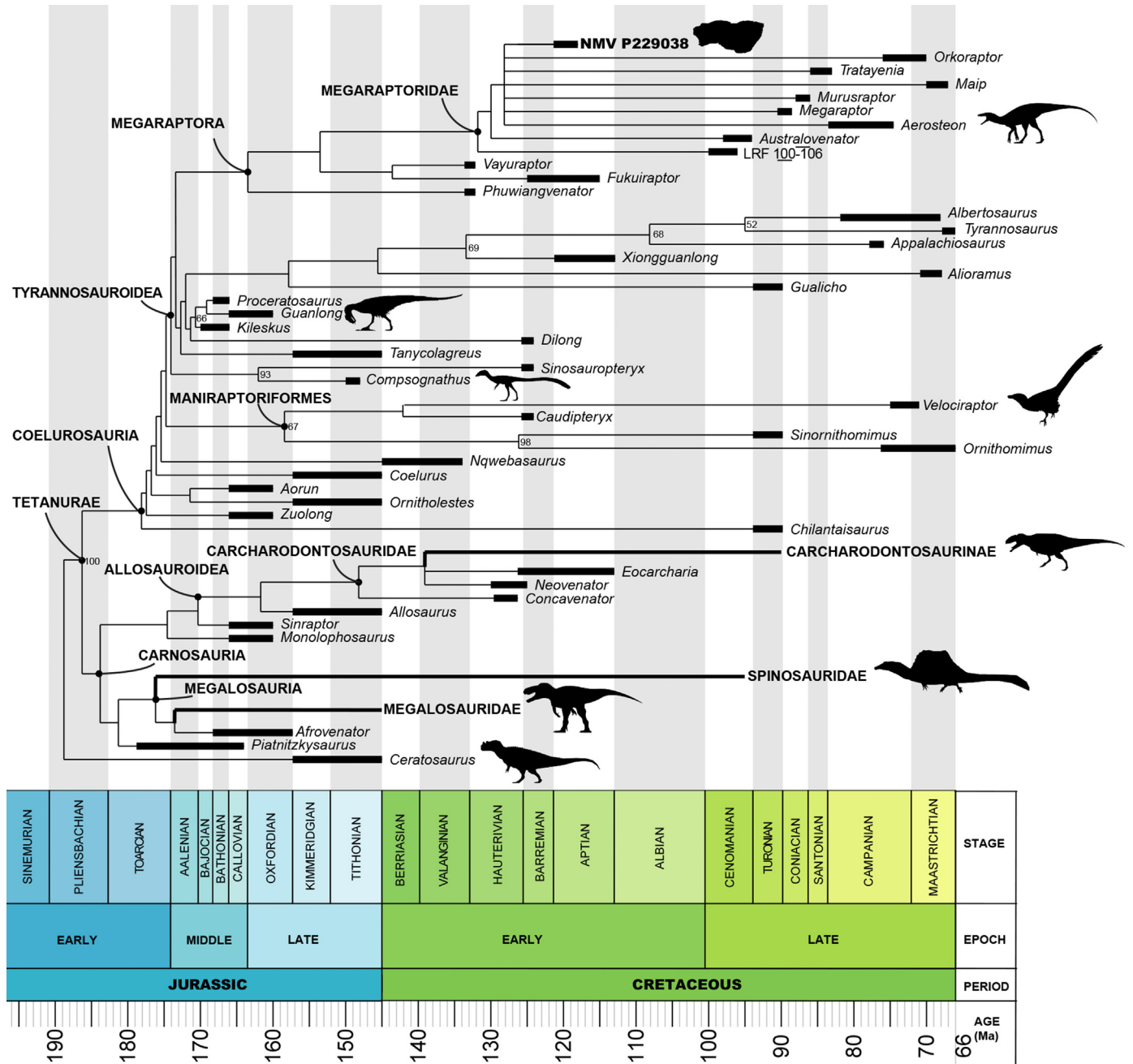
Fig. 5. Time-calibrated parsimony phylogenetic analysis of Tetanurae, showing the position of NMV P229038 within Megaraptoridae. Numbers at nodes represent bootstrap values >50.

Information). Considering the above noted strong support for Megaraptoridae as shown in the Bayesian tree (Fig. 6), our analysis indicates that NMV P229038 is strongly supported as the earliest-branching megaraptorid.

6. Discussion

6.1. NMV P229038 as a megaraptorid

The frontal (NMV P229038) described herein has been shown to share similarities with both Megaraptoridae and members of Tyrannosauroidea, including: the supratemporal fossa covering more than 50% of the dorsally exposed anteroposterior length (Currie, 2003; Carr and Williamson, 2010; Porfiri et al., 2014;

Brusatte and Carr, 2016; Coria and Currie, 2016); the transversely narrow sagittal crest (Brochu, 2003; Currie, 2003; Xu et al., 2004; Choiniere, 2010; Porfiri et al., 2014; Coria and Currie, 2016); the reduced contribution of the frontal to the orbital rim (Currie, 1987, 2003; Li et al., 2010; Bever et al., 2013; Coria and Currie, 2016; Voris et al., 2021); and the anteroposteriorly-elongate articular facet for the postorbital (Brochu, 2003; Currie, 2003; Xu et al., 2004; Carr et al., 2005; Choiniere, 2010; Fiorillo and Tykoski, 2014; Coria and Currie, 2016; Voris et al., 2021). However, we note that the following features distinguish NMV P229038 from non-megaraptoran Tyrannosauroidea: the subquadrangular shape of the exposed dorsal surface (Porfiri et al., 2014; Aranciaga Rolando et al., 2019); the mediolateral frontoparietal suture on the dorsal surface (Paulina-Carabajal and Currie, 2017); the truncated nasal
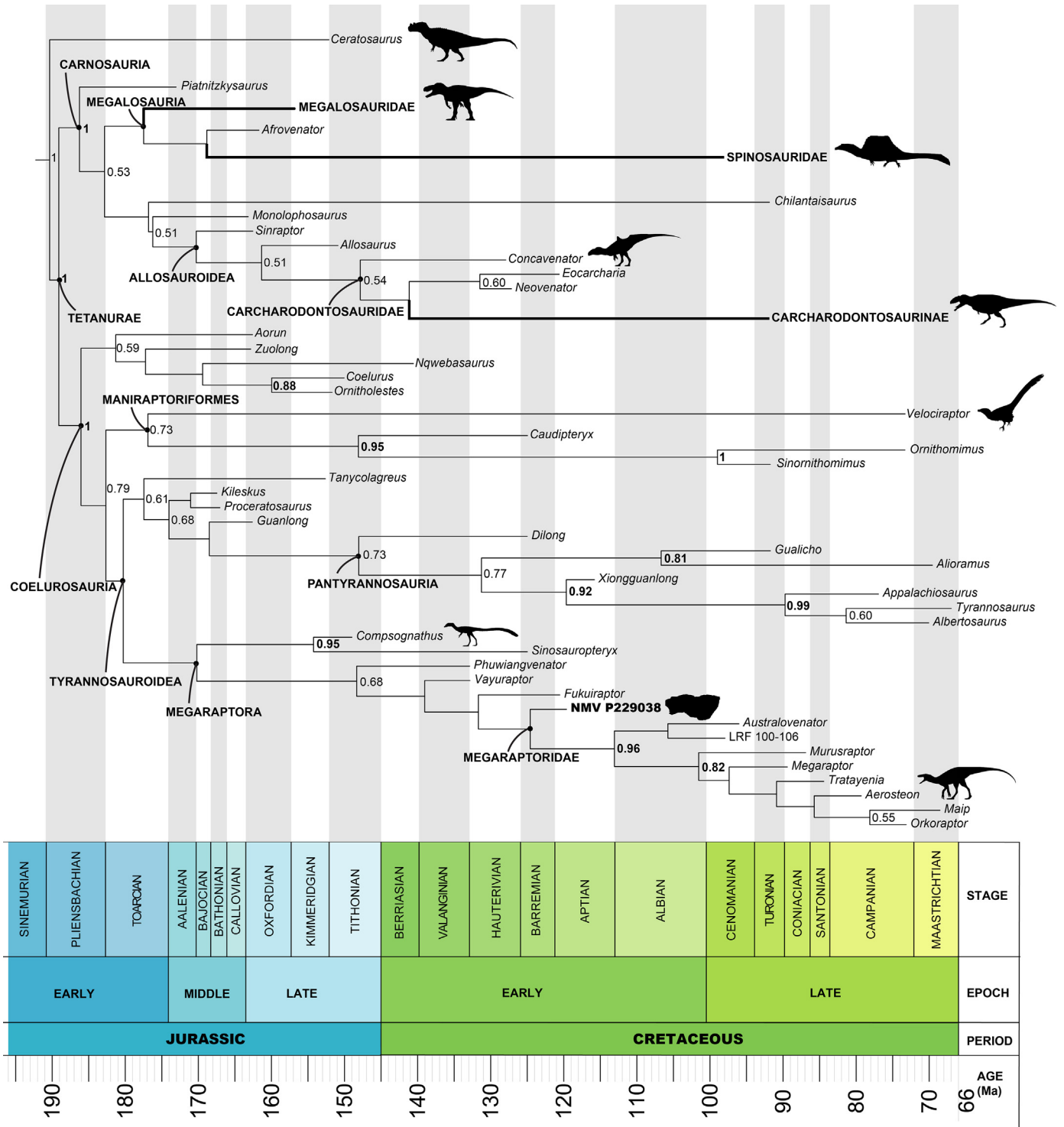
Fig. 6. Posterior consensus tree of tip and node dated fossilised birth-death Bayesian phylogenetic analysis of Tetanurae, showing the position of NMV P229038 within Megaraptoridae. Numbers at nodes represent posterior probabilities of clades >0.50. Tip ages estimated from analysis.

articular surface (we interpret this as truncated relative to most theropod clades: Aranciaga Rolando et al., 2019); the absence of an articulation for the lacrimal on the frontal (Coria and Currie, 2016: Fig. 5); and the presence of a ridge that delineates the supra-temporal fossa anteriorly (although this ridge is less pronounced than in either *Megaraptor* or *Murusraptor*: Porfiri et al., 2014; Paulina-Carabajal and Currie, 2017).

NMV P229038 is the first theropod frontal to be described from Australia; consequently, there are no local analogues available for comparison. Similarly, all non-megaraptorid megaraptorans (*Phuwiangvenator* and *Fukuiraptor*, and possibly *Vayuraptor*) lack frontals (Azuma and Currie, 2000; Samathi et al., 2019). Thus, our comparisons are restricted to megaraptorid frontals from the Late Cretaceous of South America: those of *Megaraptor* (MUCPv 595:

Porfiri et al., 2014) and *Murusraptor* (MCF-PVPH-411: Coria and Currie, 2016). Both of these are derived megaraptorids, and the only known frontals for each pertain to subadult individuals; moreover, they are temporally separated from NMV P229038 by at least 30 million years (Garrido, 2011). Because no non-megaraptorid megaraptoran frontals are known, we cannot determine which features of the frontal define Megaraptoridae to the exclusion of earlier-diverging megaraptorans.

Our parsimony-based phylogenetic analysis resolved NMV P229038 within Megaraptoridae, forming a polytomy with all included South American megaraptorid taxa. Of the six characters we were able to score for NMV P229038, the greatest overlap was observed within megaraptorids: four characters were scored the same as in *Megaraptor* and *Murusraptor* (state 0 for C42; state 1 for C260, C341 and C342: Aranciaga Rolando et al., 2022 Supplementary Information A); one character score was shared with only *Murusraptor* (state 1 for C41); and one character score contrasted with those of other megaraptorids (state 1 for C43). The inclusion of NMV P229038 within Megaraptoridae, and destabilisation of the clade, might be a consequence of the incompleteness of NMV P229038, causing it to act as a 'wildcard' taxon owing to missing data. Aranciaga Rolando et al. (2022) suggested that the exclusion of specimens less than 15% complete led to better resolution within Megaraptoridae (Aranciaga Rolando et al., 2022: Fig. 15B); thus, it is perhaps unsurprising that the inclusion of NMV P229038 in this parsimony analysis had a destabilising effect.

Our Bayesian-based phylogenetic analyses also resolved NMV P229038 within Megaraptoridae, thereby reinforcing the results of our parsimony analysis. It also provided strong support for NMV P229038 as the earliest-branching megaraptorid. This analysis incorporated stratigraphic data for all taxa, which might have the greatest direct impact on a Bayesian-based topology for palaeontological analysis (King, 2021). Furthermore, Bayesian analyses may be biased against taxa with incompletely-coded characters (King, 2019). Consequently, we refer NMV P229038 to Megaraptoridae. It must be considered, however, that all megaraptorids are represented by incomplete skeletons, and the small degree of anatomical overlap between these might confound understanding of their true interrelationships.

Both of our phylogenetic analyses supported a position of Megaraptora within Tyrannosauroidea (Novas et al., 2013; Aranciaga Rolando et al., 2019, 2022), in contrast to previous analyses that exclude this clade from Tyrannosauroidea (Delcourt and Grillo, 2018; Porfiri et al., 2018). Of particular interest was the position of Compsognathidae within Megaraptora in our Bayesian analysis, although this is not supported by our parsimony analysis. We regard these findings as tentative, as a phylogenetic reassessment of Tetanurae was beyond the scope of this paper; as such, we continue to regard Megaraptora as an early-branching clade within Tyrannosauroidea (Novas et al., 2013; Porfiri et al., 2014; Aranciaga Rolando et al., 2019, 2022).

NMV P229038 has several features that appear to be plesiomorphic for Megaraptoridae, including: the slight ridge separating the articular surfaces of the nasal and prefrontal (although, a somewhat similar feature is observed in *Murusraptor*: Paulina-Carabajal and Currie, 2017); the absence of a dorsoventrally high-wall of bone separating the medial-most furrow of the nasal articular surface (Porfiri et al., 2014; Coria and Currie, 2016); a transverse frontoparietal suture on the ventral surface (Porfiri et al., 2014; Coria and Currie, 2016); and the absence of an anteriorly-facing dorsoventrally high wall of bone to emarginate the articular point of the prefrontal (Porfiri et al., 2014; Coria and Currie, 2016). Although there is evidence to suggest that Australian megaraptorans had already developed trenchant manual unguals as early as the late Barremian (NMV P186153: Poropat et al., 2018;

White and Campione, 2021), the plesiomorphic condition of NMV P229038 implies that the skulls of early-branching megaraptorans were much less specialised than those of more derived megaraptorids (Porfiri et al., 2014; Coria and Currie, 2016).

It is difficult to determine which, if any, of the characters seen in megaraptorid frontals are ontogenetically variable. We have identified two phylogenetic characters in the dataset that might vary with ontogenetic stage: C42 (whether or not the frontals are fused), and C260 (the ratio of anteroposterior length to the mediolateral width of the dorsally exposed portion of the frontal). The degree of fusion between cranial elements has long been considered a reliable indicator of the ontogenetic stage in specimens of Dinosauria (Rauhut, 2004; Sereno et al., 2009; Hone et al., 2016). Recently, it was proposed that sutural fusion in archosaur crania as an indicator of ontogenetic stage might be more ambiguous than previously thought (Bailleul et al., 2016), but extant archosaurs might not be representative of the basal archosaur condition (Cullen et al., 2023). Herein, we suggest that the unfused nature of NMV P229038 is indicative of skeletal immaturity (Rauhut, 2004; Sereno et al., 2009). Although frontal fusion is considered a phylogenetic character in the matrix utilised by this study (Aranciaga Rolando et al., 2022), we speculate this character might be more influenced by ontogenetic stage, especially for taxa represented only by a single individual of unclear or sub-adult maturity.

The ratio of the dorsally-exposed anteroposterior length to mediolateral width at the midpoint in theropod frontals is also considered a diagnostic character among Theropoda (Brusatte and Carr, 2016; Aranciaga Rolando et al., 2022). However, this value is also flagged as an indicator of ontogenetic stage in most amniote clades, as the frontal becomes relatively wider through ontogeny (Carr, 1999; Abdala et al., 2001; Currie, 2003; Bhullar, 2012; Bever et al., 2013; Voris et al., 2021). The width: length ratio of NMV P229038 is 0.45, higher than the values seen in some early-branching coelurosaurs (*e.g. Zuolong*: Choiniere et al., 2010) and tyrannosauroids (*e.g.* MPC-D 102/4, *Dilong*: Xu et al., 2004; Tsuihiji et al., 2012), but in the mid-range between juvenile and adult tyrannosaurid frontals (Table 2). Strangely, the width: length ratio of NMV P229038 is closer to those of the alioramine tyrannosaurids *Alioramus* (0.42) and *Qianzhousaurus* (0.47) than it is to those of *Megaraptor* (0.55) or *Murusraptor* (0.58).

Although several recent studies have supported the idea that Megaraptora occupies an early-branching position within Coelurosauria, often as sister to Tyrannosauroidea (Delcourt and Grillo, 2018; Porfiri et al., 2018), megaraptorans have alternatively been resolved within Tyrannosauroidea, basal to Tyrannosauridae (Novas et al., 2013; Porfiri et al., 2014; Aranciaga Rolando et al., 2019, 2022; Ding et al., 2020; Naish and Cau, 2022). Considering that the width: length ratio of NMV P229038 is higher than in Coelurosauria and Tyrannosauroidea (excluding Tyrannosauridae), within the range of juvenile to adult Tyrannosauridae, and less so than in Megaraptoridae, widening of the frontal might have both ontogenetic and phylogenetic significance within Megaraptora.

6.2. MCF-PVPH 320 as a megaraptorid

An isolated theropod frontal from the Portezuelo Formation (Turonian−Coniacian: Garrido, 2011) of Patagonia (MCF-PVPH 320) was first described in 2015 and referred to the clade Allosauroidea (outside Carcharodontosauria: Paulina-Carabajal and Coria, 2015). Following the description of *Murusraptor*, this specimen was subsequently referred to Megaraptoridae, but as a species distinct from *Megaraptor*, which also derives from the Portezuelo Formation (Novas, 1998; Paulina-Carabajal and Currie, 2017). The only non-avian theropod clades other than Megaraptoridae known from the Portezuelo Formation are Abelisauroidea (Novas et al., 2006;

Baiano et al., 2022), Alvarezsauridae (Novas and Puerta, 1996) and Unenlagiinae (Novas and Puerta, 1997; Novas and Pol, 2005; Porfiri et al., 2011).

Several synapomorphies of Megaraptoridae were shown to be present in MCF-PVPH 320, including a dorsal alar projection over the postorbital articulation (Paulina-Carabajal and Currie, 2017), which we also observe in NMV P229038. Although we agree with the synapomorphies outlined by Paulina-Carabajal and Currie (2017), we note that this specimen was suggested to be distinct from *Megaraptor* on the basis of comparisons with the juvenile frontal (MUCPv 595: Porfiri et al., 2014; Paulina-Carabajal and Currie, 2017).

A number of features observed in NMV P229038 support the referral of MCF-PVPH 320 to Megaraptoridae, including: an effectively mediolateral frontoparietal suture in ventral view (Paulina-Carabajal and Coria, 2015); a dorsal alar projection over the postorbital articulation (Paulina-Carabajal and Currie, 2017); absence of an articulation point on the frontal for the lacrimal (Paulina-Carabajal and Coria, 2015); a reduced contribution to the orbital rim (Paulina-Carabajal and Coria, 2015; Paulina-Carabajal and Currie, 2017); and an anteroposteriorly long supratemporal fossa that covers more than 50% of the dorsally exposed region of the frontal (Paulina-Carabajal and Coria, 2015; Paulina-Carabajal and Currie, 2017). We note that the frontoparietal suture in dorsal view of NMV P229038 is transverse, but V-shaped in MCF-PVPH 320; this might be an apomorphic trait of the specimen, as it also differs in this respect from *Murusraptor* (Paulina-Carabajal and Coria, 2015; Paulina-Carabajal and Currie, 2017). The frontal of *Megaraptor* does not preserve the parietal suture, and thus we cannot determine if the orientation in MCF-PVPH 320 is similar (Porfiri et al., 2014). These features seemingly support a referral of MCF-PVPH 320 to at least Megaraptoridae, but whether or not it pertains to *Megaraptor* remains an open question that will only be resolvable once megaraptorid frontal ontogeny is better understood.

6.3. On Australian Megaraptora

Recently, Aranciaga Rolando et al. (2022: Supplementary Information B) proposed the presence of different "megaraptoran forms" in the Cretaceous of Australia. They suggested that only early-branching megaraptorans were present in the upper Strzelecki Group, as evidenced by an isolated partial astragalus (NMV P150070) and four teeth (NMV P186353, NMV P210084, NMV P212859 and NMV P230871), whereas more derived megaraptorids were present in the Eumeralla, Griman Creek and Winton formations. The plesiomorphic morphology of NMV P229038 suggests that this specimen represents an early-branching megaraptorid, contrasting with the contention of Aranciaga Rolando et al. (2022: Supplementary Information B) and supporting the presence of Megaraptoridae in the upper Barremian–lower Aptian upper Strzelecki Group (Fig. 7). We also note that one previously described theropod specimen from the upper Strzelecki Group has been referred to Megaraptoridae: NMV 186153 (the "Punchbowl Claw"), which is considered to represent Australia's largest theropod (Benson et al., 2012; Poropat et al., 2019). This specimen was originally referred to Neovenatoridae (Benson et al., 2012), but was recently reappraised and found to represent a member of Megaraptoridae (Poropat et al., 2019; White and Campione, 2021) based on its morphological congruence with manual ungual II-3 in *Australovenator* (White et al., 2012; Poropat et al., 2019). This suggests that the trenchant manual claws of megaraptorids appeared relatively early in their evolutionary history (Poropat et al., 2019; White and Campione, 2021).

Aranciaga Rolando et al. (2022: Supplementary Information B) also suggested that four teeth from the upper Strzelecki Group

(Benson et al., 2012) belonged to non-megaraptorid megaraptorans (NMV P186353, NMV P210084, NMV P212859 and NMV P230871). The mesial carinae of these teeth reportedly bear denticles all the way to the base of the crown, as in *Fukuiraptor* (Azuma and Currie 2000; Currie and Azuma 2006), but in contrast to *Australovenator*, in which the mesial denticles are restricted to the apex of the crown (Hocknull et al., 2009; White et al., 2015b). The inclusion of the isolated tooth NMV P186353 by Aranciaga Rolando et al. (2022: Supplementary Information B) in a sample derived from the upper Strzelecki Group perpetuates an error made by Benson et al. (2012) and corrected by Poropat et al. (2018): this specimen is in fact from the lower Albian portion of the Eumeralla Formation at Dinosaur Cove. If the argument that a denticulate mesial carina characterises non-megaraptorid megaraptorans, then NMV P186353 — which displays this condition (Benson et al., 2012: Fig. 24A-C) — would therefore provide evidence that non-megaraptorid megaraptorans persisted into the early Albian in southeast Australia at least.

The remaining three teeth to which Aranciaga Rolando et al. (2022: Supplementary Information B) refer all derive from the Flat Rocks site of the upper Strzelecki Group (Fig. 1; Fig. 7), which has yielded more than 90 megaraptorid teeth in total (Benson et al., 2012; Kotevski and Poropat, 2022). Although we agree that at least one tooth from Flat Rocks (NMV P212859: Benson et al., 2012) hosts denticles on the mesial surface, we note that most sufficiently complete exemplars present either no denticles or denticles restricted to a very small region of the mesial carina (Benson et al., 2012; Kotevski and Poropat, 2022). This is in contrast to the condition in *Fukuiraptor*, where denticles persist along most of the mesial carina (Azuma and Currie, 2000; Currie and Azuma, 2006). Non- or incompletely-denticulate mesial carinae are observed in several megaraptorids, including *Megaraptor* (Porfiri et al., 2014), *Murusraptor* (Coria and Currie, 2016) and *Orkoraptor* (Novas et al., 2008). All *in situ* teeth from *Australovenator* are heavily worn or damaged on the mesial surface, and the isolated teeth associated with the holotype (Hocknull et al., 2009) have been considered shed, and not pertaining to the same individual (White et al., 2015b). Thus, we cannot reasonably state whether or not the mesial carinae of *Australovenator* were incompletely denticulate to the base of the crown. Although some isolated megaraptorid teeth from the Winton Formation display mesial denticles restricted to the apex of the crown (White et al., 2015b), there may be variability between Australian megaraptorid taxa, as at least one additional species is known (White et al., 2020).

All known megaraptoran specimens are <15% complete, and there is often little to no anatomical overlap in preserved material (Samathi et al., 2019; Aranciaga Rolando et al., 2022). Additionally, there is significant temporal (Legrand et al., 2013; Bell et al., 2019; Foley et al., 2022; Tucker et al., 2022) and geographic (Samathi et al., 2019) separation between the non-megaraptorid megaraptorans and basalmost Megaraptoridae. The consequence of these combined factors is a poor understanding of the evolution and palaeobiogeographic distribution of megaraptorans (Bell et al., 2016; Lamanna et al., 2020). In the upper Strzelecki Group, megaraptorans appear to display a mixture of putatively basal megaraptoran (NMV P229038, NMV P212859, NMV P150070: Benson et al., 2012; Poropat et al., 2018) and derived megaraptorid (Fig. 7; NMV P186153, isolated teeth from Flat Rocks: Benson et al., 2012; Poropat et al., 2018; White et al., 2015b; Kotevski and Poropat, 2022) characteristics, which provide meagre evidence to support the hypothesis of an Australian origin of Megaraptoridae (Bell et al., 2016; Lamanna et al., 2020). However, as there is no record of Gondwanan megaraptorans before the Barremian (Aranciaga Rolando et al., 2018; Poropat et al., 2018), such claims must remain tentative. Regardless, it appears that theropods bearing megaraptorid features were present in the upper Strzelecki
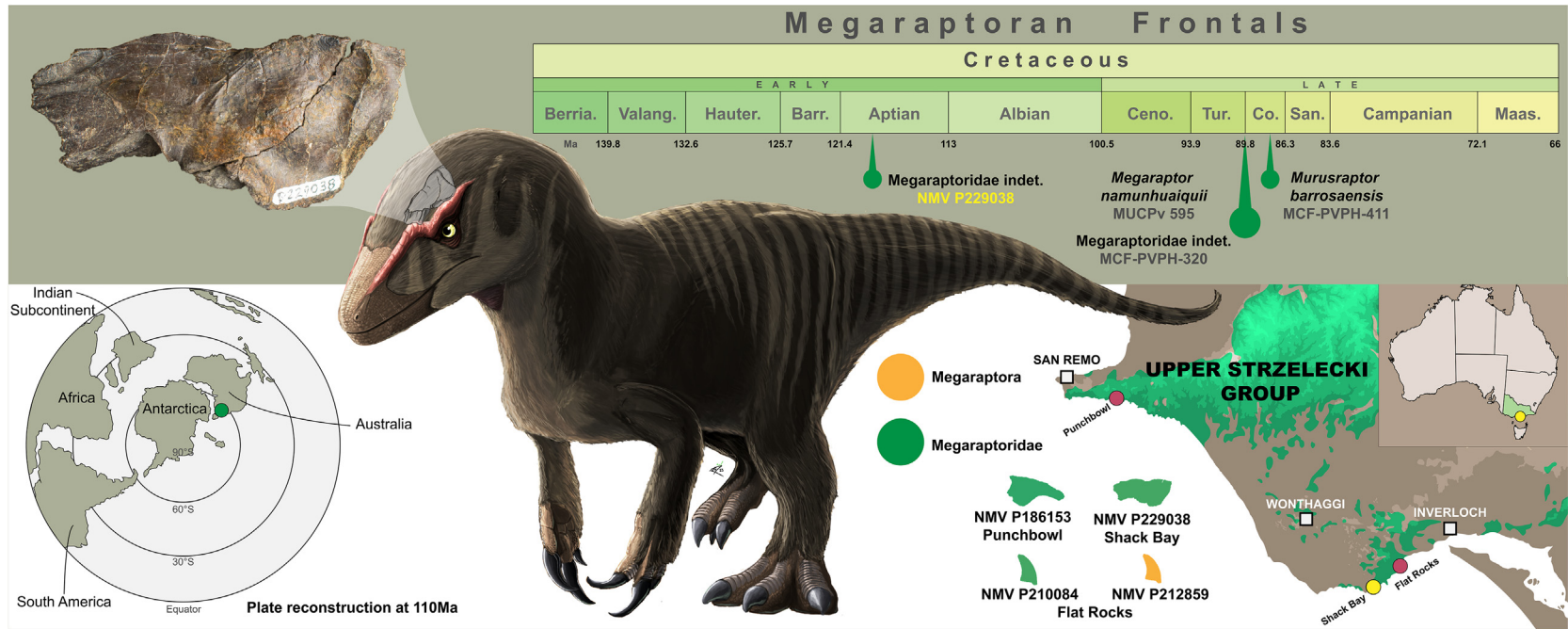
Fig. 7. Graphical abstract depicting major research findings of this report. Clockwise from top: Geological scale indicating ages of known megaraptoran frontals; Locality map of the upper Strzelecki Group portraying localities yielding Megaraptora and Megaraptoridae fossils (map data cited in Fig. 1); Life reconstruction of Victorian megaraptorid with approximate life position of NMV P229038 shown in silhouette and in dorsal view (illustration by Ruairidh J. Duncan); Map of southern hemisphere with modern geographic borders showing approximate location of constituent Gondwanan continents and fossil locality at ~110 Ma. Southern hemisphere map derived and adapted from Rich et al. (2002). Chronostratigraphic data derived from Cohen et al. (2013; updated).

Group, and therefore as early as the late Barremian in southeast Australia (Poropat et al., 2018; Aranciaga Rolando et al., 2022).

6.4. Gracile snouts in Megaraptora

Few megaraptoran specimens preserve associated non-dental cranial material, and no complete or nearly complete megaraptoran skulls are known. Currently, our understanding of the megaraptoran skull is restricted to: an isolated left frontal (MCF-PVPH 320: Paulina-Carabajal and Currie, 2017); fragments of the left maxilla and right dentary of *Fukuiraptor kitadaniensis* (FPDM-V97122: Azuma and Currie, 2000); both dentaries of *Australovenator wintonensis* (AODF 604: Hocknull et al., 2009; White et al., 2015b); both premaxillae, maxillae, nasals, the left frontal, and partial braincase of a juvenile *Megaraptor namunhuaiquii* (MUCPv 595: Porfiri et al., 2014); the right lacrimal, right postorbital, right prefrontal, partial right epipterygoid, both pterygoids, right ectopterygoid, both sphenethmoids, and braincase (MCF-PVPH-411: Coria and Currie 2016) of *Murusraptor barrosaensis*; the right prefrontal, right postorbital, left quadrate, and right prearticular of *Aerosteon riocoloradensis* (MCNA-PV-3137: Aranciaga Rolando et al., 2019); the right postorbital, right quadratojugal and possible right coronoid of *Orkoraptor burkei* (MPM-Pv 3457: Novas et al., 2008); and the isolated frontal NMV P229038 described herein. These combined materials have permitted an interpretation of the composite megaraptoran skull, which is suggested to be gracile and elongate (Porfiri et al., 2014; Coria and Currie, 2016; Aranciaga Rolando et al., 2019). The longirostry of the megaraptoran snout is solely inferred from the juvenile *Megaraptor* specimen (MUCPv 595: Porfiri et al., 2014), in which the nasal bones are flattened, relatively elongate and almost straight (Fig. 4).

Although the only megaraptoran nasal known is that of the juvenile *Megaraptor* (MUCPv 595), the presence of a frontal in NMV P229038 and *Murusraptor* enables comparisons of the nasal articulation on this element (Fig. 4); the indeterminate megaraptorid MCF-PVPH 320 is not informative in this regard, because the nasal articular surface is missing (Paulina-Carabajal and Coria, 2015). NMV P229038, *Megaraptor* and *Murusraptor* all display anteroposteriorly-extending striations on the nasal articular surface (Porfiri et al., 2014; Coria and Currie, 2016). Aranciaga Rolando et al. (2019) state that the nasal articular surface of the frontal in *Megaraptor* and *Murusraptor* is truncated relative to other theropod taxa; this is also the case in NMV P229038, supporting the notion that this feature might be a synapomorphy of Megaraptora or Megaraptoridae. The nasal articular surface in NMV P229038 is anteroposteriorly short compared to *Megaraptor* (Fig. 4); this suggests that through megaraptoran evolution, the frontal articular surface for the nasal extended further posteriorly to cover a greater dorsal surface of the frontal, which is also inferred for *Murusraptor* (Coria and Currie, 2016).

Several taxa within Tyrannosauroidea evolved a longirostrine snout somewhat reminiscent of the snout of *Megaraptor*. These include the non-tyrannosaurid tyrannosauroid *Xiongguanlong baimoensis* (Li et al., 2010), and the alioramine tyrannosaurids *Alioramus remotus* (Kurzanov, 1976), *Alioramus altai* (Brusatte et al., 2009, 2012), and *Qianzhousaurus sinensis* (Lu et al., 2014; Foster et al., 2022). In *Alioramus altai*, the nasals vary in width along their length, with their greatest width immediately posterior to the external naris (Brusatte et al., 2012); this contrasts with *Megaraptor*, wherein the width of the nasals remains essentially uniform along their length (Porfiri et al., 2014). The truncated morphology of the nasal articular surface of the frontal in Megaraptora differs from that seen in all tyrannosauroids (excluding *Bistahieversor*), wherein the nasal articular surface is manifested as a triangular projection (Brochu, 2003; Currie, 2003; Carr et al., 2005; Carr and Williamson, 2010; Choiniere, 2010; Bever et al., 2013; Voris et al., 2021). Additionally, tyrannosauroid nasal bones fuse early in ontogeny to form a single vaulted element (Carr, 1999; Xu et al., 2004, 2006; Snively et al., 2006; Li et al., 2010; Brusatte et al., 2012; Foster et al., 2022), which is inferred to increase skull strength for the puncture and pull feeding style characteristic of the clade (Rayfield, 2004; Snively et al., 2006; Brusatte et al., 2012). There is no sign of fusion between the nasal bones of juvenile *Megaraptor* (Porfiri et al., 2014); however, this does not exclude the possibility of fusion through ontogeny. In dorsal view, the nasals in *Megaraptor* suggest separation by a triangular gap posteriorly (Fig. 4); a similar configuration is evident in some tyrannosaurids (*e.g. Qianzhousaurus, Tyrannosaurus*: Brochu 2003; Foster et al., 2022).

The features of the nasal and naso-frontal articulation in Megaraptora imply that longirostrine snouts developed independently at least twice within Tyrannosauroidea (Brusatte et al., 2012; Porfiri et al., 2014; Delcourt and Grillo, 2018; Aranciaga Rolando et al., 2022). It has been suggested that the elongation of the snout in *Alioramus* and *Qianzhousaurus* was a consequence of niche partitioning within Tyrannosauridae, as they were sympatric with non-longirostrine members of the clade (Foster et al., 2022). In *Alioramus* and *Qianzhousaurus*, the nasals remain fused and vaulted, and the forelimbs are truncated (Carpenter and Smith, 2001; Lipkin and Carpenter, 2008); thus, it is likely that their skulls remained their primary means of prey acquisition, with longirostry possibly an ecological adaptation toward hunting smaller prey (Foster et al., 2022). Although the feeding ecology of megaraptorans remains unclear, the retention of enlarged forelimbs and trenchant manual unguals within the clade suggest a successful adaptation for prey capture (Porfiri et al., 2007; White et al., 2015a; Novas et al., 2016; Poropat et al., 2019; Aranciaga Rolando et al., 2023). Megaraptorans comprise the vast majority of diagnostic theropod remains in both the upper Strzelecki Group and Eumeralla Formation, where it appears that only small-to medium-sized prey were available (Poropat et al., 2018); this suggests that, at least in southeast Australia, the megaraptoran forelimb was an adaptation for acquiring smaller prey. It appears that, in contrast to non-megaraptoran tyrannosauroids, the acquisition of a longirostrine snout in *Megaraptor* was likely not an adaptation for prey capture, and a secondary effect drove this evolutionary change (Porfiri et al., 2014). However, the overall scarcity of both basal coelurosaur and megaraptoran cranial material, especially that related to the snout, necessitates that such claims remain tentative until further material is collected (Porfiri et al., 2014; Lamanna et al., 2020).

7. Conclusion

The frontal and fused parietal fragment described herein (NMV P229038) constitutes the first non-mandibular cranial element from a non-avian theropod to be reported from Australia. This frontal represents the geologically oldest megaraptorid skull element worldwide, and emphasises the prevalence of this theropod group in the mid-Cretaceous of Australia. The results of both parsimony-based and Bayesian phylogenetic analyses support referral of this specimen to the clade Megaraptoridae. However, additional megaraptoran cranial remains will be required to clarify both the phylogenetic position of the taxon represented by NMV P229038 and the interrelationships within Megaraptora.

The fact that the NMV P229038 frontal seems to represent an early-deriving megaraptorid implies that the skulls of these theropods became increasingly elongate and gracile through their evolution. Later-diverging megaraptorids appear to have evolved a dorsoventrally high wall of bone to separate the nasal articular surface from the remainder of the frontal, realigned the frontoparietal suture ventrally from transverse to V-shaped anteromedially-

posterolaterally, and increased the extent of the nasal–frontal overlap. All of these features can be interpreted as modifications in response to increasing longirostry. The megaraptorids in the upper Barremian–lower Aptian upper Strzelecki Group are the oldest worldwide, which provides some support in favour of the hypothesis that Megaraptoridae had an Australian origin.

Funding statement

Data availability

Datasets related to this article can be found at doi.org/10.17602/M2/M533313, hosted at MorphoSource, and doi.org/10.6084/m9.figshare.23787303, hosted at Figshare.

Acknowledgements

References

Abdala, F., Flores, D.A., Giannini, N.P., 2001. Postweaning ontogeny of the skull of *Didelphis albiventris*. Journal of Mammalogy 82 (1), 190–200.

Aghaei, H., Gurba, L.W., Ward, C.R., Hall, M., Mahmud, S.A., 2015. Effects of igneous intrusions on thermal maturity of carbonaceous fluvial sediments: a case study of the Early Cretaceous Strzelecki Group in west Gippsland, Victoria, Australia.

International Journal of Coal Geology 152, 68–77. https://doi.org/10.1016/j.coal.2015.10.002.

Ali, F., Zelenitsky, D.K., Therrien, F., Weishampel, D.B., 2008. Homology of the "ethmoid complex" of tyrannosaurids and its implications for the reconstruction of the olfactory apparatus of non-avian theropods. Journal of Vertebrate Paleontology 28 (1), 123–133.

Aranciaga Rolando, A.M., Brissón Egli, F., Sales, M.A.F., Martinelli, A.G., Canale, J.I., Ezcurra, M.D., 2018. A supposed Gondwanan oviraptorosaur from the Albian of Brazil represents the oldest South American megaraptoran. Cretaceous Research 84, 107–119. https://doi.org/10.1016/j.cretres.2017.10.019.

Aranciaga Rolando, A.M., Novas, F.E., Agnolín, F.L., 2019. A reanalysis of *Murusraptor barrosaensis* Coria & Currie (2016) affords new evidence about the phylogenetic relationships of Megaraptora. Cretaceous Research 99, 104–127. https://doi.org/10.1016/j.cretres.2019.02.021.

Aranciaga Rolando, A.M., Motta, M.J., Agnolín, F.L., Manabe, M., Tsuihiji, T., Novas, F.E., 2022. A large Megaraptoridae (Theropoda: Coelurosauria) from Upper Cretaceous (Maastrichtian) of Patagonia, Argentina. Scientific Reports 12 (1), 1–29.

Aranciaga Rolando, A.M., Novas, F.E., Calvo, J.O., Porfiri, J.D., Dos Santos, D.D., Lamanna, M.C., 2023. Reconstruction of the pectoral girdle and forelimb musculature of Megaraptora (Dinosauria: Theropoda). Anatomical Record. https://doi.org/10.1002/ar.25128.

Arden, T.M.S., Klein, C.G., Zouhri, S., Longrich, N.R., 2019. Aquatic adaptation in the skull of carnivorous dinosaurs (Theropoda: Spinosauridae) and the evolution of aquatic habits in spinosaurids. Cretaceous Research 93, 275–284.

Averianov, A., 2016. Frontal bones of non-avian theropod dinosaurs from the Upper Cretaceous (Santonian–? Campanian) Bostobe Formation of the northeastern Aral Sea region, Kazakhstan. Canadian Journal of Earth Sciences 53 (2), 168–175.

Azuma, Y., Currie, P.J., 2000. A new carnosaur (Dinosauria: Theropoda) from the Lower Cretaceous of Japan. Canadian Journal of Earth Sciences 37 (12), 1735–1753.

Baiano, M.A., Pol, D., Bellardini, F., Windholz, G.J., Cerda, I.A., Garrido, A.C., Coria, R.A., 2022. *Elemgasem nubilus*: a new brachyrostran abelisaurid (Theropoda, Ceratosauria) from the Portezuelo Formation (Upper Cretaceous) of Patagonia, Argentina. Papers in Palaeontology 8 (5), e1462.

Bailleul, A.M., Scannella, J.B., Horner, J.R., Evans, D.C., 2016. Fusion patterns in the skulls of modern archosaurs reveal that sutures are ambiguous maturity indicators for the Dinosauria. PLoS One 11 (2), e0147687.

Bapst, D.W., Wright, A.M., Matzke, N.J., Lloyd, G.T., 2016. Topology, divergence dates, and macroevolutionary inferences vary between different tip-dating approaches applied to fossil theropods (Dinosauria). Biology Letters 12 (7), 465–470. https://doi.org/10.1098/rsbl.2016.0237.

Barido-Sottani, J., Aguirre-Fernández, G., Hopkins, M.J., Stadler, T., Warnock, R., 2019. Ignoring stratigraphic age uncertainty leads to erroneous estimates of species divergence times under the fossilized birth–death process. Proceedings of the Royal Society B: Biological Sciences 286 (1902), 20190685.

Barrett, P.M., Benson, R.B.J., Rich, T.H., Vickers-Rich, P., 2011. First spinosaurid dinosaur from Australia and the cosmopolitanism of Cretaceous dinosaur faunas. Biology Letters 7 (6), 933–936.

Bell, P.R., Cau, A., Fanti, F., Smith, E.T., 2016. A large-clawed theropod (Dinosauria: Tetanurae) from the Lower Cretaceous of Australia and the Gondwanan origin of megaraptorid theropods. Gondwana Research 36, 473–487. https://doi.org/10.1016/j.gr.2015.08.004.

Bell, P.R., Fanti, F., Hart, L.J., Milan, L.A., Craven, S.J., Brougham, T., Smith, E., 2019. Revised geology, age, and vertebrate diversity of the dinosaur-bearing Griman Creek Formation (Cenomanian), Lightning Ridge, New South Wales, Australia. Palaeogeography, Palaeoclimatology, Palaeoecology 514, 655–671. https://doi.org/10.1016/j.palaeo.2018.11.020.

Benson, R.B., Barrett, P.M., Rich, T.H., Vickers-Rich, P., 2010a. A southern tyrant reptile. Science 327 (5973), 1613. https://doi.org/10.1126/science.1187456.

Benson, R.B., Carrano, M.T., Brusatte, S.L., 2010b. A new clade of archaic large-bodied predatory dinosaurs (Theropoda: Allosauroidea) that survived to the latest Mesozoic. Naturwissenschaften 97 (1), 71–78. https://doi.org/10.1007/s00114-009-0614-x.

Benson, R.B.J., Barrett, P.M., Rich, T.H., Vickers-Rich, P., Pickering, D., Holland, T., 2010c. Response to comment on "A southern tyrant reptile". Science 329 (5995). https://doi.org/10.1126/science.1190195, 1013–1013.

Benson, R.B., Rich, T.H., Vickers-Rich, P., Hall, M., 2012. Theropod fauna from southern Australia indicates high polar diversity and climate-driven dinosaur provinciality. PLoS One 7 (5), e37122. https://doi.org/10.1371/journal.pone.0037122.

Bever, G.S., Brusatte, S.L., Carr, T.D., Xu, X., Balanoff, A.M., Norell, M.A., 2013. The braincase anatomy of the Late Cretaceous dinosaur *Alioramus* (Theropoda: Tyrannosauroidea). Bulletin of the American Museum of Natural History 2013 (376), 1–72.

Bhullar, B.A.S., 2012. A phylogenetic approach to ontogeny and heterochrony in the fossil record: cranial evolution and development in anguimorphan lizards (Reptilia: Squamata). Journal of Experimental Zoology. Part B, Molecular and Developmental Evolution 318 (7), 521–530.

Brochu, C.A., 2003. Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. Journal of Vertebrate Paleontology 22, 1–138.

Brougham, T., Smith, E.T., Bell, P.R., 2019. New theropod (Tetanurae: Avetheropoda) material from the 'mid'-Cretaceous Griman Creek Formation at Lightning Ridge, New South Wales, Australia [sic]. Royal Society Open Science 6 (1), 180826. https://doi.org/10.1098/rsos.180826.

Brougham, T., Smith, E.T., Bell, P.R., 2020. Noasaurids are a component of the Australian 'mid'-Cretaceous theropod fauna. Scientific Reports 10 (1), 1428. https://doi.org/10.1038/s41598-020-57667-7.

Brusatte, S.L., Sereno, P.C., 2007. A new species of *Carcharodontosaurus* (Dinosauria: Theropoda) from the Cenomanian of Niger and a revision of the genus. Journal of Vertebrate Paleontology 27 (4), 902–916.

Brusatte, S.L., Sereno, P.C., 2008. Phylogeny of Allosauroidea (Dinosauria: Theropoda): comparative analysis and resolution. Journal of Systematic Palaeontology 6 (2), 155–182. https://doi.org/10.1017/s1477201907002404.

Brusatte, S.L., Carr, T.D., 2016. The phylogeny and evolutionary history of tyrannosauroid dinosaurs. Scientific Reports 6, 20252. https://doi.org/10.1038/srep20252.

Brusatte, S.L., Carr, T.D., Erickson, G.M., Bever, G.S., Norell, M.A., 2009. A long-snouted, multihorned tyrannosaurid from the Late Cretaceous of Mongolia. Proceedings of the National Academy of Sciences of the United States of America 106 (41), 17261–17266.

Brusatte, S.L., Carr, T.D., Norell, M.A., 2012. The osteology of *Alioramus*, a gracile and long-snouted tyrannosaurid (Dinosauria: Theropoda) from the Late Cretaceous of Mongolia. Bulletin of the American Museum of Natural History 2012 (366), 1–197.

Bryan, S.E., Constantine, A.E., Stephens, C.J., Ewart, A., Schön, R.W., Parianos, J., 1997. Early Cretaceous volcano-sedimentary successions along the eastern Australian continental margin: implications for the break-up of eastern Gondwana. Earth and Planetary Science Letters 153 (1–2), 85–102.

Carpenter, K., Smith, M., 2001. Forelimb osteology and biomechanics of Tyrannosaurus rex. In: Tanke, D.H., Carpenter, K. (Eds.). Indiana University Press, Indiana, pp. 90–116.

Carr, T.D., 1999. Craniofacial ontogeny in tyrannosauridae (Dinosauria, Coelurosauria). Journal of Vertebrate Paleontology 19 (3), 497–520.

Carr, T.D., Williamson, T.E., 2010. *Bistahieversor sealeyi*, gen. et sp. nov., a new tyrannosauroid from New Mexico and the origin of deep snouts in Tyrannosauroidea. Journal of Vertebrate Paleontology 30 (1), 1–16.

Carr, T.D., Williamson, T.E., Schwimmer, D.R., 2005. A new genus and species of tyrannosauroid from the Late Cretaceous (Middle Campanian) Demopolis Formation of Alabama. Journal of Vertebrate Paleontology 25 (1), 119–143.

Carrano, M.T., Loewen, M.A., Sertich, J.J.W., 2011. New materials of *Masiakasaurus knopfleri* Sampson, Carrano, and Forster, 2001, and implications for the morphology of the Noasauridae (Theropoda: Ceratosauria). Smithsonian Contributions to Paleobiology 95 (95), 1–53.

Carrano, M.T., Benson, R.B.J., Sampson, S.D., 2012. The phylogeny of Tetanurae (Dinosauria: Theropoda). Journal of Systematic Palaeontology 10 (2), 211–300. https://doi.org/10.1080/14772019.2011.630927.

Cau, A., Dalla Vecchia, F.M., Fabbri, M., 2012. Evidence of a new carcharodontosaurid from the Upper Cretaceous of Morocco. Acta Palaeontologica Polonica 57 (3), 661–665.

Cerroni, M.A., Canale, J.I., Novas, F.E., 2020. The skull of *Carnotaurus sastrei* Bonaparte 1985 revisited: insights from craniofacial bones, palate and lower jaw. Historical Biology 33 (10), 2444–2485. https://doi.org/10.1080/08912963.2020.1802445.

Choiniere, J.N., 2010. Anatomy and systematics of coelurosaurian theropods from the Late Jurassic of Xinjiang, China, with comments on forelimb evolution in Theropoda (PhD thesis). The George Washington University.

Choiniere, J.N., Clark, J.M., Forster, C.A., Xu, X., 2010. A basal coelurosaur (Dinosauria: Theropoda) from the Late Jurassic (Oxfordian) of the Shishugou Formation in Wucaiwan, People's Republic of China. Journal of Vertebrate Paleontology 30 (6), 1773–1796.

Cohen, K.M., Finney, S.C., Gibbard, P.L., Fan, J.X., 2013; updated. The ICS international chronostratigraphic chart. Episodes 36 (3), 199–204.

Coria, R.A., Currie, P.J., 2016. A new megaraptoran dinosaur (Dinosauria, Theropoda, Megaraptoridae) from the Late Cretaceous of Patagonia. PLoS One 11 (7), e0157973. https://doi.org/10.1371/journal.pone.0157973.

Cullen, T.M., Larson, D.W., Witton, M.P., Scott, D., Maho, T., Brink, K.S., Evans, D.C., Reisz, R., 2023. Theropod dinosaur facial reconstruction and the importance of soft tissues in paleobiology. Science 379 (6639), 1348–1352.

Currie, P.J., 1987. Theropods of the Judith River Formation of Dinosaur Provincial Park, Alberta, Canada. In: Currie, P.J., Koster, E.H. (Eds.), Fourth Symposium on Mesozoic Terrestrial Ecosystems, Occasional Paper of the Tyrrell Museum of Palaeontology, vol. 3. Tyrrell Museum of Palaeontology, Drumheller, pp. 52–60.

Currie, P.J., 1997. Braincase anatomy. In: Currie, P.J., Padian, K. (Eds.), Encyclopedia of Dinosaurs. Academic Press, New York, pp. 81–85.

Currie, P.J., 2003. Cranial anatomy of tyrannosaurid dinosaurs from the Late Cretaceous of Alberta, Canada. Acta Palaeontologica Polonica 48 (2).

Currie, P.J., Zhao, X., 1993. A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People's Republic of China. Canadian Journal of Earth Sciences 30 (10), 2037–2081.

Currie, P.J., Azuma, Y., 2006. New specimens, including a growth series, of *Fukuiraptor* (Dinosauria, Theropoda) from the Lower Cretaceous Kitadani Quarry of Japan. Journal of the Paleontological Society of Korea 22 (1), 173–193.

Currie, P.J., Vickers-Rich, P., Rich, T.H., 1996. Possible oviraptorosaur (Theropoda, Dinosauria) specimens from the Early Cretaceous Otway Group of Dinosaur Cove, Australia. Alcheringa: An Australasian Journal of Palaeontology 20 (1), 73–79. https://doi.org/10.1080/03115519608619225.

Delcourt, R., Grillo, O.N., 2018. Tyrannosauroids from the Southern Hemisphere: implications for biogeography, evolution, and taxonomy. Palaeogeography, Palaeoclimatology, Palaeoecology 511, 379–387. https://doi.org/10.1016/j.palaeo.2018.09.003.

Ding, A., Pittman, M., Upchurch, P., O'Connor, J., Field, D.J., Xu, X., 2020. The biogeography of coelurosaurian theropods and its impact on their evolutionary history. Bulletin of the American Museum of Natural History 40 (440), 117–157.

Duddy, I.R., 2003. Mesozoic. In: Birch, W.D. (Ed.), Geology of Victoria, third ed. Geological Society of Australia (Victoria Division), pp. 239–286.

Eddy, D.R., Clarke, J.A., 2011. New information on the cranial anatomy of *Acrocanthosaurus atokensis* and its implications for the phylogeny of Allosauroidea (Dinosauria: Theropoda). PLoS One 6 (3), e17932.

Ferguson, W.H., 1909. Report on the Lower Powlett, Cape Paterson, and Inverloch Quarter Sheets, with Maps and Plates. Memoirs of the Geological Survey of Victoria 8, 1–14.

Fiorillo, A.R., Tykoski, R.S., 2014. A diminutive new tyrannosaur from the top of the world. PLoS One 9 (3), e91287. https://doi.org/10.1371/journal.pone.0091287.

Fitzgerald, E.M., Carrano, M.T., Holland, T., Wagstaff, B.E., Pickering, D., Rich, T.H., Vickers-Rich, P., 2012. First ceratosaurian dinosaur from Australia. Naturwissenschaften 99 (5), 397–405.

Foley, E.K., Roberts, E.M., Henderson, R.A., Todd, C.N., Knutsen, E.M., Spandler, C., 2022. Middle Jurassic–Lower Cretaceous stratigraphy of the northern Great Australian Superbasin: insights from maximum depositional age constraints from the U–Pb detrital zircon record. Australian Journal of Earth Sciences 1–24.

Foster, W., Brusatte, S.L., Carr, T.D., Williamson, T.E., Yi, L., Lü, J., 2022. The cranial anatomy of the long-snouted tyrannosaurid dinosaur *Qianzhousaurus sinensis* from the Upper Cretaceous of China. Journal of Vertebrate Paleontology 41 (4). https://doi.org/10.1080/02724634.2021.1999251.

Garrido, A.C., 2011. El Grupo Neuquén (Cretácico Tardío) en la Cuenca Neuquina. Relatorio del 18 Congreso Geológico Argentino.

Gauthier, J., 1986. Saurischian monophyly and the origin of birds. Memoirs of the California Academy of Sciences 8, 1–55.

Gavryushkina, A., Heath, T.A., Ksepka, D.T., Stadler, T., Welch, D., Drummond, A.J., 2017. Bayesian total-evidence dating reveals the recent crown radiation of penguins. Systematic Biology 66 (1), 57–73.

Goloboff, P.A., Farris, J.S., Nixon, K.C., 2008. TNT, a free program for phylogenetic analysis. Cladistics 24 (5), 774–786. https://doi.org/10.1111/j.1096-0031.2008.00217.x.

Herne, M.C., Nair, J.P., Salisbury, S.W., 2010. Comment on "A southern tyrant reptile". Science 329 (5995), 1013.

Herne, M.C., Nair, J.P., Evans, A.R., Tait, A.M., 2019. New small-bodied ornithopods (Dinosauria, Neornithischia) from the early cretaceous Wonthaggi Formation (Strzelecki Group) of the Australian-Antarctic rift system, with revision of *Qantassaurus intrepidus* Rich and Vickers-Rich, 1999. Journal of Paleontology 93 (3), 543–584.

Hocknull, S.A., White, M.A., Tischler, T.R., Cook, A.G., Calleja, N.D., Sloan, T., Elliott, D.A., 2009. New Mid-Cretaceous (latest Albian) dinosaurs from Winton, Queensland, Australia. PLoS One 4 (7), e6190. https://doi.org/10.1371/journal.pone.0006190.

Holliday, C.M., 2009. New insights into dinosaur jaw muscle anatomy. Anatomical Record 292 (9), 1246–1265.

Hone, D.W.E., Farke, A.A., Wedel, M.J., 2016. Ontogeny and the fossil record: what, if anything, is an adult dinosaur? Biology Letters 12 (2), 20150947.

Huene, F.v., 1914. Das natürliche System der Saurischia. Centralblatt für Mineralogie. Geologie und Paläontologie 1914, 154–158.

Hurum, J.H., Sabath, K., 2003. Giant theropod dinosaurs from Asia and North America: skulls of *Tarbosaurus bataar* and *Tyrannosaurus rex* compared. Acta Palaeontologica Polonica 48 (2).

Hwang, S.H., Norell, M.A., Qiang, J., Keqin, G., 2004. A large Compsognathid from the early cretaceous Yixian formation of China. Journal of Systematic Palaeontology 2 (1), 13–30. https://doi.org/10.1017/s1477201903001081.

King, B., 2019. Which morphological characters are influential in a Bayesian phylogenetic analysis? Examples from the earliest osteichthyans. Biology Letters 15 (7), 20190288.

King, B., 2021. Bayesian tip-dated phylogenetics in paleontology: topological effects and stratigraphic fit. Systematic Biology 70 (2), 283–294.

Korasidis, V.A., Wagstaff, B.E., 2020. The rise of flowering plants in the high southern latitudes of Australia. Review of Palaeobotany and Palynology 272, 104126.

Kotevski, J., Poropat, S.F., 2022. On the first dinosaur tooth reported from Australia (Theropoda: Megaraptoridae). Alcheringa: An Australasian Journal of Palaeontology 46 (2), 174–179. https://doi.org/10.1080/03115518.2022.2071463.

Kurzanov, S.M., 1976. New carnosaur from the Late Cretaceous of Nogon– Tsav, Mongolia. The Joint Soviet-Mongolian Paleontological Expedition Transactions 3, 93–104.

Lamanna, M.C., Casal, G.A., Martínez, R.D., Ibiricu, L.M., 2020. Megaraptorid (Theropoda: Tetanurae) partial skeletons from the Upper Cretaceous Bajo Barreal Formation of central Patagonia, Argentina: implications for the evolution of large body size in Gondwanan megaraptorans. Annals of Carnegie Museum 86 (3), 255–294.

Legrand, J., Pons, D., Terada, K., Yabe, A., Nishida, H., 2013. Lower Cretaceous (upper Barremian-lower Aptian?) palynoflora from the Kitadani Formation (Tetori Group, Inner Zone of central Japan). Paleontological Research 17 (3), 201–229.

Li, D., Norell, M.A., Gao, K.Q., Smith, N.D., Makovicky, P.J., 2010. A longirostrine tyrannosauroid from the Early Cretaceous of China. Proceedings of the Royal Society B: Biological Sciences 277 (1679), 183–190. https://doi.org/10.1098/rspb.2009.0249.

Lipkin, C., Carpenter, K., 2008. Looking again at the forelimb of Tyrannosaurus rex. In: Carpenter, K. (Ed.). Indiana University Press, Indiana, pp. 167–190.

Lu, J., Yi, L., Brusatte, S.L., Yang, L., Li, H., Chen, L., 2014. A new clade of Asian late Cretaceous long-snouted tyrannosaurids. Nature Communications 5, 3788. https://doi.org/10.1038/ncomms4788.

Madsen Jr., J.H., 1976. *Allosaurus fragilis*: a revised osteology. In: Utah Geol. Min. Surv. Bull., 109, pp. 1–163.

Marsh, O.C., 1881. Principal characters of American Jurassic dinosaurs. Part V. American Journal of Science and Arts 3 (125), 417–423.

Miller, M.A., Pfeiffer, W., Schwartz, T., 2011. The CIPRES science gateway: a community resource for phylogenetic analyses. In: Proceedings of the 2011 TeraGrid Conference: Extreme Digital Discovery, pp. 1–8.

Molnar, R.E., Pledge, N.S., 1980. A new theropod dinosaur from South Australia. Alcheringa: An Australasian Journal of Palaeontology 4 (4), 281–287. https://doi.org/10.1080/03115518008558972.

Naish, D., Cau, A., 2022. The osteology and affinities of *Eotyrannus lengi*, a tyrannosauroid theropod from the Wealden Supergroup of southern England. PeerJ 10. https://doi.org/10.7717/peerj.12727.

Novas, F.E., 1998. *Megaraptor namunhuaiquii*, gen. et sp. nov., a large-clawed, Late Cretaceous theropod from Patagonia. Journal of Vertebrate Paleontology 18 (1), 4–9. https://doi.org/10.1080/02724634.1998.10011030.

Novas, F.E., Puerta, P.F., 1996. Alvarezsauridae, Cretaceous basal birds from Patagonia and Mongolia. Memoirs of the Queensland Museum 39, 675–702.

Novas, F.E., Puerta, P.F., 1997. New evidence concerning avian origins from the Late Cretaceous of Patagonia. Nature 387 (6631), 390–392.

Novas, F.E., Pol, D., 2005. New evidence on deinonychosaurian dinosaurs from the Late Cretaceous of Patagonia. Nature 433 (7028), 858–861.

Novas, F., Ezcurra, M.D., Agnolin, F., 2006. Humerus of a basal abelisauroid theropod from the Late Cretaceous of Patagonia. Revista del Museo Argentino de Ciencias Naturales, Nueva Serie 8 (1), 63–68.

Novas, F.E., Ezcurra, M.D., Lecuona, A., 2008. *Orkoraptor burkei* nov. gen. et sp., a large theropod from the Maastrichtian Pari Aike Formation, Southern Patagonia, Argentina. Cretaceous Research 29 (3), 468–480. https://doi.org/10.1016/j.cretres.2008.01.001.

Novas, F.E., Pol, D., Canale, J.I., Porfiri, J.D., Calvo, J.O., 2009. A bizarre Cretaceous theropod dinosaur from Patagonia and the evolution of Gondwanan dromaeosaurids. Proceedings of the Royal Society B: Biological Sciences 276 (1659), 1101–1107. https://doi.org/10.1098/rspb.2008.1554.

Novas, F.E., Agnolín, F.L., Ezcurra, M.D., Porfiri, J.D., Canale, J.I., 2013. Evolution of the carnivorous dinosaurs during the Cretaceous: the evidence from Patagonia. Cretaceous Research 45, 174–215. https://doi.org/10.1016/j.cretres.2013.04.001.

Novas, F.E., Aranciaga Rolando, A.M., Agnolín, F.L., 2016. Phylogenetic relationships of the Cretaceous Gondwanan theropods *Megaraptor* and *Australovenator*: the evidence afforded by their manual anatomy. Memoirs of Museum Victoria 74, 49–61.

O'Reilly, J.E., Donoghue, P.C.J., 2016. Tips and nodes are complementary not competing approaches to the calibration of molecular clocks. Biology Letters 12 (4), 20150975.

Osmólska, H., Roniewicz, E., Barsbold, R., 1972. A new dinosaur, *Gallimimus bullatus* n. gen., n. sp. (Ornithomimidae) from the Upper Cretaceous of Mongolia. Palaeontologia Polonica 27, 103–143.

Paulina-Carabajal, A., Coria, R.A., 2015. An unusual theropod frontal from the Upper Cretaceous of north Patagonia. Alcheringa: An Australasian Journal of Palaeontology 39 (4), 514–518. https://doi.org/10.1080/03115518.2015.1042275.

Paulina-Carabajal, A., Currie, P.J., 2017. The braincase of the Theropod Dinosaur *Murusraptor*: osteology, neuroanatomy and comments on the paleobiological implications of certain endocranial features. Ameghiniana 54 (5), 617–640. https://doi.org/10.5710/amgh.25.03.2017.3062.

Pol, D., Rauhut, O.W., 2012. A Middle Jurassic abelisaurid from Patagonia and the early diversification of theropod dinosaurs. Proceedings of the Royal Society B: Biological Sciences 279 (1741), 3170–3175. https://doi.org/10.1098/rspb.2012.0660.

Porfiri, J.D., Dos Santos, D., Calvo, J.O., 2007. New information on *Megaraptor namunhuaiquii* (Theropoda: Tetanurae), Patagonia: considerations on paleoecological aspects. Archivos do Museu Nacional do Rio de Janeiro 65, 545–550.

Porfiri, J.D., Calvo, J.O., Santos, D.d., 2011. A new small deinonychosaur (Dinosauria: Theropoda) from the Late Cretaceous of Patagonia, Argentina. Anais da Academia Brasileira de Ciencias 83, 109–116.

Porfiri, J.D., Novas, F.E., Calvo, J.O., Agnolín, F.L., Ezcurra, M.D., Cerda, I.A., 2014. Juvenile specimen of *Megaraptor* (Dinosauria, Theropoda) sheds light about tyrannosauroid radiation. Cretaceous Research 51, 35–55. https://doi.org/10.1016/j.cretres.2014.04.007.

Porfiri, J.D., Juárez Valieri, R.D., Santos, D.D.D., Lamanna, M.C., 2018. A new megaraptoran theropod dinosaur from the Upper Cretaceous Bajo de la Carpa Formation of northwestern Patagonia. Cretaceous Research 89, 302–319. https://doi.org/10.1016/j.cretres.2018.03.014.

Poropat, S.F., Martin, S.K., Tosolini, A.M.P., Wagstaff, B.E., Bean, L.B., Kear, B.P., Vickers-Rich, P., Rich, T.H., 2018. Early Cretaceous polar biotas of Victoria, southeastern Australia—an overview of research to date. Alcheringa: An Australasian Journal of Palaeontology 42 (2), 157–229. https://doi.org/10.1080/03115518.2018.1453085.

Poropat, S.F., White, M.A., Vickers-Rich, P., Rich, T.H., 2019. New megaraptorid (Dinosauria: Theropoda) remains from the Lower Cretaceous Eumeralla Formation of Cape Otway, Victoria, Australia. Journal of Vertebrate Paleontology 39 (4). https://doi.org/10.1080/02724634.2019.1666273.

Poropat, S.F., Pentland, A.H., Duncan, R.J., Bevitt, J.J., Vickers-Rich, P., Rich, T.H., 2020. First elaphrosaurine theropod dinosaur (Ceratosauria: Noasauridae) from Australia — a cervical vertebra from the Early Cretaceous of Victoria. Gondwana Research 84, 284–295. https://doi.org/10.1016/j.gr.2020.03.009.

Rauhut, O.W.M., 2003. The interrelationships and evolution of basal theropod dinosaurs. Special Papers in Palaeontology 69, 1–213.

Rauhut, O.W.M., 2004. Braincase structure of the Middle Jurassic theropod dinosaur *Piatnitzkysaurus*. Canadian Journal of Earth Sciences 41 (9), 1109–1122.

Rauhut, O.W.M., Foth, C., Tischlinger, H., Norell, M.A., 2012. Exceptionally preserved juvenile megalosauroid theropod dinosaur with filamentous integument from the Late Jurassic of Germany. Proceedings of the National Academy of Sciences of the United States of America 109 (29), 11746–11751.

Rayfield, E.J., 2004. Cranial mechanics and feeding in *Tyrannosaurus rex*. Proceedings of the Royal Society B: Biological Sciences 271 (1547), 1451–1459.

Rich, T.H., Vickers-Rich, P., Gangloff, R.A., 2002. Polar dinosaurs. Science 295 (5557), 979–980.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Hohna, S., Larget, B., Liu, L., Suchard, M.A., Huelsenbeck, J.P., 2012, May. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61 (3), 539–542. https://doi.org/10.1093/sysbio/sys029.

Samathi, A., Chanthasit, P., Sander, P.M., 2019. Two new basal coelurosaurian theropod dinosaurs from the Lower Cretaceous Sao Khua Formation of Thailand. Acta Palaeontologica Polonica 64 (2), 239–260.

Sampson, S.D., Witmer, L.M., 2007. Craniofacial anatomy of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology 27 (S2), 32–104.

Seegets-Villiers, D., 2012. Palynology, taphonomy and geology of the Early Cretaceous Dinosaur Dreaming Fossil Site, Inverloch, Victoria, Australia (PhD thesis). Monash University.

Sereno, P.C., Novas, F.E., 1993. The skull and neck of the basal theropod *Herrerasaurus ischigualastensis*. Journal of Vertebrate Paleontology 13 (4), 451–476.

Sereno, P.C., Brusatte, S.L., 2008. Basal abelisaurid and carcharodontosaurid theropods from the Lower Cretaceous Elrhaz Formation of Niger. Acta Palaeontologica Polonica 53 (1), 15–46.

Sereno, P.C., Tan, L., Brusatte, S.L., Kriegstein, H.J., Zhao, X., Cloward, K., 2009. Tyrannosaurid skeletal design first evolved at small body size. Science 326 (5951), 418–422.

Snively, E., Henderson, D.M., Phillips, D.S., 2006. Fused and vaulted nasals of tyrannosaurid dinosaurs: implications for cranial strength and feeding mechanics. Acta Palaeontologica Polonica 51 (3).

Sues, H.D., Frey, E., Martill, D.M., Scott, D.M., 2002. *Irritator challengeri*, a spinosaurid (Dinosauria: Theropoda) from the Lower Cretaceous of Brazil. Journal of Vertebrate Paleontology 22 (3), 535–547.

Tosolini, A.M.P., McLoughlin, S., Drinnan, A.N., 1999. Stratigraphy and fluvial sedimentary facies of the Neocomian lower Strzelecki Group, Gippsland Basin, Victoria. Australian Journal of Earth Sciences 46 (6), 951–970. https://doi.org/10.1046/j.1440-0952.1999.00757.x.

Tsuihiji, T., Watabe, M., Tsogtbaatar, K., Tsubamoto, T., Barsbold, R., Suzuki, S., Lee, A.H., Ridgely, R.C., Kawahara, Y., Witmer, L.M., 2011. Cranial osteology of a juvenile specimen of *Tarbosaurus bataar* (Theropoda, Tyrannosauridae) from the Nemegt Formation (Upper Cretaceous) of Bugin Tsav, Mongolia. Journal of Vertebrate Paleontology 31, 1–21.

Tsuihiji, T., Watabe, M., Tsogtbaatar, K., Barsbold, R., Suzuki, S., Palasiatica, V., 2012. A tyrannosauroid frontal from the Upper Cretaceous (Cenomanian–Santonian) of the Gobi Desert, Mongolia. Vertebrata PalAsiatica 50, 102–110.

Tucker, R.T., Roberts, E.M., Hu, Y., Kemp, A.I.S., Salisbury, S.W., 2013. Detrital zircon age constraints for the Winton Formation, Queensland: contextualizing Australia's Late Cretaceous dinosaur faunas. Gondwana Research 24 (2), 767–779.

Tucker, R.T., Hyland, E.G., Gates, T.A., King, M.R., Roberts, E.M., Foley, E.K., Berndt, D., Hanta, R., Khansubha, S., Aswasereelert, W., 2022. Age, depositional history, and paleoclimatic setting of Early Cretaceous dinosaur assemblages from the Sao Khua Formation (Khorat Group), Thailand. Palaeogeography, Palaeoclimatology, Palaeoecology 601, 111107.

Vandenberg, A., 1997a. Queenscliff 1:250,000 Geological Map SJ 55-9. Geological Survey of Victoria, Department of Natural Resources and Environment, Victoria.

Vandenberg, A., 1997b. Warragul 1:250,000 Geological Map SJ 55-10. Geological Survey of Victoria, Department of Natural Resources and Environment, Victoria.

Vicmap, D., V. S. D. L. (VSDL), 2021. Woolamai-Wonthaggi 7920-8020, 1:100000 Topographoc Map Series. Victoria State Government Department of Environment, Land, Water and Planning, Melbourne, Victoria.

Voris, J.T., Zelenitsky, D.K., Therrien, F., Ridgely, R.C., Currie, P.J., Witmer, L.M., 2021. Two exceptionally preserved juvenile specimens of *Gorgosaurus libratus* (Tyrannosauridae, Albertosaurinae) provide new insight into the timing of ontogenetic changes in tyrannosaurids. Journal of Vertebrate Paleontology 46, e2041651.

Wagstaff, B.E., Gallagher, S.J., Hall, W.M., Korasidis, V.A., Rich, T.H., Seegets-Villiers, D.E., Vickers-Rich, P.A., 2020. Palynological-age determination of Early Cretaceous vertebrate-bearing beds along the south Victorian coast of Australia, with implications for the spore-pollen biostratigraphy of the region. Alcheringa: An Australasian Journal of Palaeontology 44 (3), 460–474. https://doi.org/10.1080/03115518.2020.1754464.

White, M.A., Cook, A.G., Hocknull, S.A., Sloan, T., Sinapius, G.H., Elliott, D.A., 2012. New forearm elements discovered of holotype specimen *Australovenator*

wintonensis from Winton, Queensland, Australia. PLoS One 7 (6), e39364. https://doi.org/10.1371/journal.pone.0039364.

White, M.A., Benson, R.B., Tischler, T.R., Hocknull, S.A., Cook, A.G., Barnes, D.G., Poropat, S.F., Wooldridge, S.J., Sloan, T., Sinapius, G.H., Elliott, D.A., 2013. New *Australovenator* hind limb elements pertaining to the holotype reveal the most complete Neovenatorid leg. PLoS One 8 (7), e68649. https://doi.org/10.1371/journal.pone.0068649.

White, M.A., Bell, P.R., Cook, A.G., Barnes, D.G., Tischler, T.R., Bassam, B.J., Elliott, D.A., 2015a. Forearm range of motion in *Australovenator wintonensis* (Theropoda, Megaraptoridae). PLoS One 10 (9), e0137709. https://doi.org/10.1371/journal.pone.0137709.

White, M.A., Bell, P.R., Cook, A.G., Poropat, S.F., Elliott, D.A., 2015b. The dentary of *Australovenator wintonensis* (Theropoda, Megaraptoridae); implications for megaraptorid dentition. PeerJ 3, e1512. https://doi.org/10.7717/peerj.1512.

White, M.A., Bell, P.R., Poropat, S.F., Pentland, A.H., Rigby, S.L., Cook, A.G., Sloan, T., Elliott, D.A., 2020. New theropod remains and implications for megaraptorid diversity in the Winton Formation (lower Upper Cretaceous), Queensland, Australia. Royal Society Open Science 7 (1), 191462. https://doi.org/10.1098/rsos.191462.

White, M.A., Campione, N.E., 2021. A three-dimensional approach to visualize pairwise morphological variation and its application to fragmentary palaeontological specimens. PeerJ 9, e10545. https://doi.org/10.7717/peerj.10545.

Wilson, J.A., Sereno, P.C., 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. Society of Vertebrate Palaeontology Memoir 5. Journal of Vertebrate Paleontology 18, 1–68. https://doi.org/10.1080/02724634.1998.10011115.

Wilson, J.A., Sereno, P.C., Srivastava, S., Bhatt, D.K., Khosla, A., Shani, A., 2003. A new abelisaurid (Dinosauria, Theropoda) from the Lameta formation (Cretaceous, Maastrichtian) of India. Contributions from the Museum of Paleontology, University of Michigan 31, 1–42.

Xu, X., Norell, M.A., Kuang, X., Wang, X., Zhao, Q., Jia, C., 2004. Basal tyrannosauroids from China and evidence for protofeathers in tyrannosauroids. Nature 431 (7009), 680–684.

Xu, X., Clark, J.M., Forster, C.A., Norell, M.A., Erickson, G.M., Eberth, D.A., Jia, C., Zhao, Q., 2006. A basal tyrannosauroid dinosaur from the Late Jurassic of China. Nature 439 (7077), 715–718. https://doi.org/10.1038/nature04511.

Xu, X., Clark, J.M., Mo, J., Choiniere, J., Forster, C.A., Erickson, G.M., Hone, D.W., Sullivan, C., Eberth, D.A., Nesbitt, S., Zhao, Q., Hernandez, R., Jia, C.K., Han, F.L., Guo, Y., 2009. A Jurassic ceratosaur from China helps clarify avian digital homologies. Nature 459 (7249), 940–944. https://doi.org/10.1038/nature08124.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2023.105769.