New theropod remains and implications for megaraptorid diversity in the Winton Formation (lower Upper Cretaceous), Queensland, Australia

Matt A. White, Phil R. Bell, Stephen F. Poropat, Adele H. Pentland, Samantha L. Rigby, Alex G. Cook, Trish Sloan and David A. Elliott

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Final acceptance: 28 November 2019

Note: Reports are unedited and appear as submitted by the referee. The review history appears in chronological order.

Review History
RSOS-191462.R0 (Original submission)

Review form: Reviewer 1 (Fernando Novas)

Is the manuscript scientifically sound in its present form?
Yes

Are the interpretations and conclusions justified by the results?
No

Is the language acceptable?
Yes

Do you have any ethical concerns with this paper?
No
Have you any concerns about statistical analyses in this paper?
No

Recommendation?
Accept with minor revision (please list in comments)

Comments to the Author(s)
REVIEW of “New theropod remains and implications for megaraptorid diversity in the Winton Formation (lower Upper Cretaceous), Queensland, Australia”, by Matt White and co-authors.

Let me suggest the following corrections:

ABSTRACT
Line 50. Title and abstract refer to "megaraptorid" (derived from family name Megaraptoridae). Moreover, authors offer anatomical basis to refer the new specimen to this family. Then, it is required to be consistent with this, replacing "Megarapora" for "Megaraptoridae". Lines 51-58. I highly recommend to change this last paragraph for a more cautious one. See comments below on this same aspect.

INTRODUCTION
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PAGE 3 - Line 58. I recommend remove this comment, because Orkoraptor was originally thought as Maastrichtian, which is now considered wrong.

PAGE 4 - Authors say that "These discoveries have provided a much-improved understanding of megaraptoran skeletal anatomy, thereby facilitating the identification of isolated megaraptorid material". No doubt Australian (i.e., Australovenator), Patagonian (different megaraptorid species) and Japanese (Fukuiraptor) specimens conform the best (and probably the only one) source of information about megaraptoran anatomy and evolution. However, the remaining taxa cited here as “Asian and North American megaraptorans”, are not members of this clade. As extensively discussed in previous papers (e.g., Novas et al., 2013, 2016; Porfiri et al., 2014; Aranciaga Rolando et al., 2019) Chilantaisaurus does not exhibit synapomorphies of Megaraptoridae. The same comments apply for the poorly known Siats, the morphology of which is sharply different from that of megaraptorans. Regarding Thai coelurosaurians Phuwiianvenator and Vayuraptor, they show some similarities with megaraptorans, although they can be also interpreted because these two Thai theropods and megaraptorans are basal coelurosaurians. In sum, let me repeat: best source for megaraptorid anatomy comes from Australia and Argentina.

SYSTEMATIC PALEONTOLOGY

PAGE 6 - TETANURAE - Increasing morphological evidence bolsters Megaraptora as basal Coelurosauria (see Novas et al., 2013, 2016; Porfiri et al., 2014, 2018; Aranciaga Rolando et al., 2019; Apesteguía et al., 2016). By citing Tetanurae alone, this Systematic Paleontology section oversees such information.

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It is appropriate the use of any well-known theropod (let say: Allosaurus, Tyrannosaurus, Deinonychus, Neovenator) to identify isolated bone materials. However, the old (2009) idea that the allosauroid Neovenator is closely related with coelurosaurian megaraptorans has been demonstrated wrong in several recent contributions (see Novas et al. 2013; Porfiri et al., 2014; Aranciaga Rolando et al., 2019).

Authors are sure of the megaraptoran affiliation of the available bones. Then, it seems enough compare with "other megaraptorans". Citing of Neovenator here is not required (even theropods other than megaraptorans).

The bone illustrated on figure 5 of present ms, seems fairly symmetrical in distal view, being similar to mtt III as well as to some non-ungual pedal phalanges. On the contrary, metatarsal IV in theropods is beveled in distal view. Please, have a look at Calvo et al., 2004 paper (your reference number 35), figure 10 A,C, illustrating the mtt IV of Megaraptor namunhuaiquii. Also, consider the possibility that this bone corresponds to a pedal phalanx.

Are you meaning that the specimen here described resembles more Megaraptor sp from Patagonia, rather than to Australovenator? Please, clarify. However, and based on the figures here afforded, distal end of mtt II of Australovenator matches well with that of Megaraptor sp. from Patagonia, both being different from the new Megaraptoridae from Winton in the ventral projection of both inner and outer condyles. Then, let me ask whether shape “distinctions” of the later one are due to erosion, rather than true anatomical features.

Please, replace “Golfo do” for "Golfo de ".

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Is this taxonomically correct? Or it may be "Megaraptoridae indet."?

Please, remove this phrase. It is not the software what allows recognizing distinctions.

I completely agree with this cautious and reasonable expression. Authors must apply this view in the rest of the text.

I completely agree with authors in this regard, even recognizing a single megaraptorid species for the Winton Formation.

Please, detail reference source for such "previous claims"
Review form: Reviewer 2 (Mauro Aranciaga Rolando)

Is the manuscript scientifically sound in its present form?
Yes

Are the interpretations and conclusions justified by the results?
Yes

Is the language acceptable?
Yes

Do you have any ethical concerns with this paper?
No

Have you any concerns about statistical analyses in this paper?
No

Recommendation?
Accept with minor revision (please list in comments)

Comments to the Author(s)
Dear authors and editor of the Royal Society Open Science:

The contribution is well-writen, interesting and useful. I have attached a PDF file (Appendix A) with some minor comments. I am very happy to say that this paper is able to be published in the Royal Society Open Science.

Yours sincerely,

Alexis Mauro Aranciaga Rolando

Decision letter (RSOS-191462.R0)

22-Nov-2019

Dear Dr White,

On behalf of the Editors, I am pleased to inform you that your Manuscript RSOS-191462 entitled "New theropod remains and implications for megaraptorid diversity in the Winton Formation (lower Upper Cretaceous), Queensland, Australia" has been accepted for publication in Royal Society Open Science subject to minor revision in accordance with the referee suggestions. Please find the referees' comments at the end of this email.

The reviewers and handling editors have recommended publication, but also suggest some minor revisions to your manuscript. Therefore, I invite you to respond to the comments and revise your manuscript. The suggested minor corrections are important and will improve your manuscript, but will not take you long to perform. If there are any changes that you do not wish to make, please explain clearly your reasons.
• Ethics statement
If your study uses humans or animals please include details of the ethical approval received, including the name of the committee that granted approval. For human studies please also detail whether informed consent was obtained. For field studies on animals please include details of all permissions, licences and/or approvals granted to carry out the fieldwork.

• Data accessibility
It is a condition of publication that all supporting data are made available either as supplementary information or preferably in a suitable permanent repository. The data accessibility section should state where the article's supporting data can be accessed. This section should also include details, where possible of where to access other relevant research materials such as statistical tools, protocols, software etc can be accessed. If the data has been deposited in an external repository this section should list the database, accession number and link to the DOI for all data from the article that has been made publicly available. Data sets that have been deposited in an external repository and have a DOI should also be appropriately cited in the manuscript and included in the reference list.

If you wish to submit your supporting data or code to Dryad (http://datadryad.org/), or modify your current submission to dryad, please use the following link:
http://datadryad.org/submit?journalID=RSOS&manu=RSOS-191462

• Competing interests
Please declare any financial or non-financial competing interests, or state that you have no competing interests.

• Authors’ contributions
All submissions, other than those with a single author, must include an Authors’ Contributions section which individually lists the specific contribution of each author. The list of Authors should meet all of the following criteria; 1) substantial contributions to conception and design, or acquisition of data, or analysis and interpretation of data; 2) drafting the article or revising it critically for important intellectual content; and 3) final approval of the version to be published.

All contributors who do not meet all of these criteria should be included in the acknowledgements.

We suggest the following format:
AB carried out the molecular lab work, participated in data analysis, carried out sequence alignments, participated in the design of the study and drafted the manuscript; CD carried out the statistical analyses; EF collected field data; GH conceived of the study, designed the study, coordinated the study and helped draft the manuscript. All authors gave final approval for publication.

• Acknowledgements
Please acknowledge anyone who contributed to the study but did not meet the authorship criteria.

• Funding statement
Please list the source of funding for each author.

Please ensure you have prepared your revision in accordance with the guidance at https://royalsociety.org/journals/authors/author-guidelines/ -- please note that we cannot publish your manuscript without the end statements. We have included a screenshot example of
the end statements for reference. If you feel that a given heading is not relevant to your paper, please nevertheless include the heading and explicitly state that it is not relevant to your work.

Because the schedule for publication is very tight, it is a condition of publication that you submit the revised version of your manuscript before 01-Dec-2019. Please note that the revision deadline will expire at 00.00am on this date. If you do not think you will be able to meet this date please let me know immediately.

To revise your manuscript, log into https://mc.manuscriptcentral.com/rsos and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions". Under "Actions," click on "Create a Revision." You will be unable to make your revisions on the originally submitted version of the manuscript. Instead, revise your manuscript and upload a new version through your Author Centre.

When submitting your revised manuscript, you will be able to respond to the comments made by the referees and upload a file "Response to Referees" in "Section 6 - File Upload". You can use this to document any changes you make to the original manuscript. In order to expedite the processing of the revised manuscript, please be as specific as possible in your response to the referees. We strongly recommend uploading two versions of your revised manuscript:

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2) A 'clean' version of the new manuscript that incorporates the changes made, but does not highlight them.

When uploading your revised files please make sure that you have:

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3) Included a 100 word media summary of your paper when requested at submission. Please ensure you have entered correct contact details (email, institution and telephone) in your user account;
4) Included the raw data to support the claims made in your paper. You can either include your data as electronic supplementary material or upload to a repository and include the relevant doi within your manuscript. Make sure it is clear in your data accessibility statement how the data can be accessed;
5) All supplementary materials accompanying an accepted article will be treated as in their final form. Note that the Royal Society will neither edit nor typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details where possible (authors, article title, journal name).

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Once again, thank you for submitting your manuscript to Royal Society Open Science and I look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Kind regards,

Lianne Parkhouse
Editorial Coordinator
Royal Society Open Science
openscience@royalsociety.org

on behalf of Dr Julia Brenda Desojo (Associate Editor) and Jon Blundy (Subject Editor)
openscience@royalsociety.org

Reviewer comments to Author:

Reviewer: 1
Comments to the Author(s)

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SYSTEMATIC PALEONTOLOGY

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I completely agree with authors in this regard, even recognizing a single megaraptorid species for the Winton Formation.

Please, detail reference source for such "previous claims"

Reviewer: 2
Comments to the Author(s)

Dear authors and editor of the Royal Society Open Science:

The contribution is well-written, interesting and useful. I have attached a PDF file with some minor comments. I am very happy to say that this paper is able to be published in the Royal Society Open Science.

Yours sincerely,
Alexis Mauro Aranciaga Rolando

Author's Response to Decision Letter for (RSOS-191462.R0)

See Appendix B.

Decision letter (RSOS-191462.R1)

28-Nov-2019

Dear Dr White,

It is a pleasure to accept your manuscript entitled "New theropod remains and implications for"
megaraptorid diversity in the Winton Formation (lower Upper Cretaceous), Queensland, Australia" in its current form for publication in Royal Society Open Science. The comments of the reviewer(s) who reviewed your manuscript are included at the foot of this letter.

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Thank you for your fine contribution. On behalf of the Editors of Royal Society Open Science, we look forward to your continued contributions to the Journal.

Kind regards,
Andrew Dunn
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on behalf of Dr Julia Brenda Desojo (Associate Editor) and Jon Blundy (Subject Editor)
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## Appendix A

**New theropod remains and implications for megaraptorid diversity in the Winton Formation (lower Upper Cretaceous), Queensland, Australia**

| Journal: | *Royal Society Open Science* |
|----------|----------------------------|
| Manuscript ID | RSOS-191462 |
| Article Type: | Research |
| Date Submitted by the Author: | 30-Aug-2019 |
| Complete List of Authors: | White, Matt; University of New England, Environmental and Rural Science; Australian Age of Dinosaurs Museum of Natural History, Palaeontology  
Bell, Phil; University of New England, Environmental and Rural Science; 4 Pipestone Creek Dinosaur Initiative  
Poropat, Stephen; Swinburne University of Technology Faculty of Science Engineering and Technology; Australian Age of Dinosaurs Natural History Museum,  
Cook, Alex; Australian Age of Dinosaur Museum of Natural History  
Pentland, Adele; Swinburne University of Technology Faculty of Science Engineering and Technology; Australian Age of Dinosaurs Museum of Natural History, Palaeontology  
Rigby, Samantha; Swinburne University of Technology Faculty of Science Engineering and Technology; Australian Age of Dinosaurs Museum of Natural History  
Sloan, Trish; Australian Age of Dinosaurs Museum of Natural History, Palaeontology  
Elliott, David; Australian Age of Dinosaurs Museum of Natural History, Palaeontology |
| Subject: | evolution < BIOLOGY, palaeontology < BIOLOGY |
| Keywords: | megaraptorids, Australovenator wintonensis, Winton Formation, theropod, dinosaur |
| Subject Category: | Earth science |
Author-supplied statements

Relevant information will appear here if provided.

Ethics

Does your article include research that required ethical approval or permits?:
This article does not present research with ethical considerations

Statement (if applicable):
CUST_IF_YES_ETHICS :No data available.

Data

It is a condition of publication that data, code and materials supporting your paper are made publicly available. Does your paper present new data?:
Yes

Statement (if applicable):
The 3D data that support the findings of this study are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.4q5j211

Reviewer URL: https://datadryad.org/review?doi=doi:10.5061/dryad.4q5j211

Conflict of interest

I/We declare we have no competing interests

Statement (if applicable):
CUST_STATE_CONFLICT :No data available.

Authors’ contributions

This paper has multiple authors and our individual contributions were as below

Statement (if applicable):
MAW, PRB designed the project. MAW, PRB, SFP described the specimens. MAW assembled the figures. MAW, PRB, SFP, AHP, SLR, AGC contributed to writing of the paper. MAW, TS, DAE oversaw the collection, preparation and curation of the fossils. MAW, PRB, SFP, AHP, SLR, AGC, TS, DAE approve of the version to be published. MAW, PRB, SFP, AHP, SLR, AGC, TS, DAE agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.
New theropod remains and implications for megaraptorid diversity in the Winton Formation (lower Upper Cretaceous), Queensland, Australia

Matt A. White1,2; Phil R. Bell1; Stephen F. Poropat2,3; Adele H. Pentland2,3; Samantha L. Rigby2,3; Alex G. Cook2; Trish Sloan2; David A. Elliott2

1School of Environmental & Rural Science, University of New England, Armidale, New South Wales 2351, Australia
2Australian Age of Dinosaurs Natural History Museum, The Jump-Up, Winton, Queensland 4735, Australia
3Faculty of Science, Engineering and Technology, Swinburne University of Technology, John St, Hawthorn, Victoria 3122, Australia

Keywords: Megaraptorids, Australovenator, Megaraptora, Winton Formation, dinosaurs, theropods

1. Summary

The holotype specimen of the megaraptorid Australovenator wintonensis, from the Upper Cretaceous Winton Formation (Rolling Downs Group, Eromanga Basin) of central Queensland, is the most complete non-avian theropod found in Australia to date. In fact, the holotype of A. wintonensis and isolated megaraptorid teeth (possibly referable to Australovenator) constitute the only theropod body fossils reported from the Winton Formation. Herein, we describe a new fragmentary megaraptorid specimen from the Winton Formation, found near the type locality of A. wintonensis. The new specimen comprises parts of two vertebrae, two metatarsals, a pedal phalanx and multiple unidentifiable bone fragments. Although the new megaraptorid specimen is poorly preserved, it includes the only megaraptorid vertebrae known from Queensland. The presence of pleurocoels and highly pneumatic caudal centra with camerate and camellate internal structures, permit the assignment of these remains to Megaraptora gen. et sp. indet. A morphological comparison revealed that the distal end of metatarsal II and the partial pedal phalanx II-1 of the new specimen are morphologically divergent from Australovenator. This might indicate the presence of a second megaraptorid taxon in the Winton Formation, or possibly intraspecific variation.

*Author for correspondence (Matt A White: fossilised@hotmail.com; mwhite62@une.edu.au)
†Present address: Environmental and Rural Science, University of New England, Armidale NSW, 2351, Australia
2. Introduction

Theropod discoveries in Australia are extremely rare and often constitute fragmentary and/or isolated bones. Consequently, their precise phylogenetic affinities have often proven difficult to determine with any certainty [1]. Although at least six Australian non-avian theropod taxa have been named, most of these are represented by only a single element and are regarded—although not always universally—as nomina dubia. These are: Rapator ornitholestoides, known only from a metacarpal I [2-4]; Walgettosuchus woodwardi, represented by a partial caudal vertebra [2, 3]; Kakuru kujani, restricted to an incomplete tibia [3, 5-7]; Timimus hermani, known only from a femur [3, 8-12]; and Ozraptor subotaii, a distal tibia [3, 6, 13-20]. The only exception is Australovenator wintonensis, represented by a partial skeleton [4, 21-26], which was initially classified as an indeterminate allosauroid but has since been universally allied with Megaraptor and its kin [27, 28]. The completeness of the Australovenator type specimen has been fundamental to our current understanding of megaraptorid anatomy and phylogenetic hypotheses, and provided robust comparative data that have permitted the assignment of numerous isolated theropod specimens from the mid-Cretaceous of New South Wales [29, 30] and Victoria [1, 9] to Megaraptora (or its subclade Megaraptoridae), and validated an earlier report of a Megaraptor-like theropod from Victoria, based on an ulna [31]. The spatiotemporal range of Megaraptora (and Megaraptoridae) is becoming ever better understood as a result of numerous discoveries made within the last two decades. The South American record is the most extensive, diverse and abundant, with six taxa named to date: Aoniraptor libertatem [32], Orkoraptor burkei [33]; Megaraptor namunhuaiquii [34-36]; Murusraptor barrosoensis [37-39]; Aerosteon riocoloradensis [40]; and Tratayenia rosalesi [41]. Numerous fragmentary specimens have also been reported from South America (see [1] supplementary table 7], which include the oldest (Albian [42]) and the youngest (Santonian [41, 43, 44]) occurrences of the clade—unless Orkoraptor is truly Coniacian–Campanian in age [45], contra previous assessments [10, 46, 47] and more in line with its original reported age [33].
The Asian record of megaraptorans is steadily improving, with occurrences in Japan (*Fukuiraptor kitadaniensis* [48, 49]), China (*Chilantaisaurus tashukouensis* [50, 51]) and Thailand (*Phuwiangvenator yaemniyomi* and possibly *Vayuraptor nongbualamphuensis* [52]) (Samathi, Chanthasit & Sander 2019). No megaraptorans are known from Antarctica, Europe or Africa (unless Bahariasauridae is a subclade of Megaraptora [32]) and only one taxon (*Siats meekerorum* [53]) is known from North America. These discoveries — and those made in Australia — have provided a much-improved understanding of megaraptoran skeletal anatomy, thereby facilitating the identification of isolated megaraptorid material. Herein, we describe the fragmentary remains of only the second megaraptorid specimen (excluding shed teeth) from the lower Upper Cretaceous Winton Formation near Winton, central Queensland, Australia. Morphological comparisons aided by three dimensional software imaging were conducted in order to constrain its phylogenetic position, the implications of which are discussed herein.

3. Institutional Abbreviations

Australian Age of Dinosaurs Museum of Natural History, Winton, Queensland, Australia (AAOD);
Australian Age of Dinosaurs Fossil (AODF); Australian Age of Dinosaurs Locality (AODL);
Museums Victoria (formerly National Museum of Victoria), Melbourne, Victoria, Australia (NMV).
4. Geological Setting

The Winton Formation is the uppermost unit of the Eromanga Basin, a large continental basin that covers much of western Queensland [54]. The Winton Formation is transitional from the underlying marginal marine Mackunda Formation, with thin lenses of coastal and estuarine deposits persisting in the lower part of the formation [54] and dominated by sand- and mud-dominated facies representative of fluvial conditions in the upper (Cenomanian–lower Turonian) part of the formation [55,56]. The ‘Marilyn’ Site (AODL 261; nicknamed for its proximity to Mount Munro) was discovered and excavated on Elderslie Station in 2018, roughly 500 m west from the *Australovenator* type locality [21]. Rocks in this area are interpreted to come from the uppermost part of the Winton Formation close to the Cenomanian-Turonian boundary [56]. Surface exposures of the local geology are lacking in this area: The majority of specimens collected from this locality were exposed at or close to the surface within the montmorillonite-rich vertisol layer (colloquially termed “black soil”) that blankets the Winton Formation across much of the Winton Shire. Each bone fragment exposed on the surface was flagged prior to collection so that the aereal extent of the specimens could be determined: The main concentration of bone occupied an area no more than 15 square metres.

Vertebrate remains in this area are naturally exhumed from deeper (i.e. bedrock) layers by convective processes caused by the wetting/drying and the resulting swelling/contraction of the clay-rich soils. Deeper excavations at AODL 261 failed to recover additional remains; the layer presumed to be the source of the dinosaur remains was a ~5–10 cm thick layer of very fine sandy-clay with sporatic reworked plant fossils that were not formally identified. Below the plant-bearing layer was a barren, bluish-grey clay (> 1m thick) entirely devoid of fossils (figure 1). Such clays, including those thought to have been the source of the current specimens, have been interpreted to represent low energy fluvial deposits [4, 21, 23-25, 57-60].
5. Materials and Methods

The *Australovenator wintonensis* holotype specimens were computed tomography (CT) scanned at Queensland X-ray (Mackay Mater Hospital, Mackay, Queensland) using a Philips Brilliance CT 64-slice machine capable of producing 0.9 mm slices. Mimics version 10.01 (Materialise HQ, Leuven, Belgium) was used to create the 3D surface meshes of the specimens. The meshes were exported as Binary *.stl files into Rhinoceros 5.0 (64-bit; Robert McNeal & Associates, Seattle, WA, USA), which was used to convert the files from *.stl to *.obj file format so they could be imported into Zbrush 4R7 P3 (Pixologic). The fragmentary megaraptorid specimens described herein were scanned using an Artec Space Spider 3D surface scanner.

The resulting 3D scans were exported as *.obj files so that they could be imported into Zbrush 4R7 P3 (Pixologic). Zbrush was used to digitally align and scale these specimens with the corresponding elements in *Australovenator* to confirm initial visual identification.

6. Systematic Palaeontology

**Theropoda** Marsh, 1881 [61]

**Tetanurae** Gauthier, 1986 [62]

Megaraptora Benson, Carrano & Brusatte, 2010 [27]

Megaraptora gen. et sp. indet.

6.1 Material

Two incomplete caudal centra (AODF967-968) (figures 2–3), proximal end of metatarsal II (AODF977) (figure 4), distal end of metatarsal II (AODF 978) (figure 5) distal end of metatarsal IV (AODF979) (figure 6), distal end of left pedal phalanx II-1 (AODF972) (figure 7), and numerous unidentified fragments.
6.2 Locality

The ‘Marilyn’ Site (AODL 261), Elderslie Station, ~60 km NW of Winton, Queensland, Australia.

6.3 Horizon and Age

Uppermost Winton Formation, Rolling Downs Group, Eromanga Basin. Cenomanian–lowermost Turonian [55, 56].

7. Results

Specimen descriptions

Vertebrae (AODF 967–968)

The likely positions of AODF 967 and AOD 968 within the vertebral series were estimated by comparisons with other megaraptorids [33, 36, 37, 40, 41, 63] and augmented by Neovenator salerii [64], which is considered by some authors as the sister taxon (or one of the successive outgroups) to Megaraptora [27]. Although incomplete, AODF 968 would likely have been longer than it is wide or tall (based in part on the presumed mid-centrum position of the pleurocoel; see below) with a nearly flat (anterior) endplate and no indication of paraphophyses. This combination of features is typical of caudal centra but unlike the anteroposteriorly short dorsal vertebrae and opisthocoleous cervical vertebrae of Neovenator and megaraptorans [27, 36, 37, 40]. The absence of chevron facets in AODF 968 further identifies it as the anterior part of the centrum. Overall, AODF 968 resembles the caudal vertebrae of the mid caudal region of in Aerosteon riocoloradensis (see figure 9B in Sereno [40]) and Neovenator (see Plates 18 in Brusatte [63]). AODF 967 is less complete than AOF 968 and lacks the ventral edge of the centrum. Its proportions are therefore equivocal although its larger overall size suggests a more anterior position in the column than AODF 968 (Table 1). The shallowly concave endplate and absence of paraphophyses or sacral rib attachment scars eliminate a position in the cervical, anteriormost dorsal or sacral series.
Its relatively small size in comparison to the metapodials (Table 1) suggest that it does not pertain to one of the dorsal vertebrae, which are typically much larger and have a stronger hour-glass shape than the caudal vertebrae (e.g. [36, 41, 63]). A caudal position more anterior than AODF 968 is therefore tenable. For descriptive purposes, AODF 967 is considered the anterior part of the centrum, although we concede that these attributions (i.e. the anterior part of a caudal centrum) are equivocal. AODF 967 constitutes the anterior portion of a vertebral centrum and lacking the ventral margin (figure 2). In posterior and ventral views, the broken surfaces reveal the camerate and camellate internal structures (figure 2A,B,K,L). The anterior articular surface (figure 2C,D) is shallowly concave and, when complete, would have been subcircular. Dorsally, the left and right neurocentral sutures are open (unfused), and their long axes extend anteromedially–posterolaterally (figure 2I,J). The mediolaterally-concave neural canal is widest anteriorly, becoming narrower more posteriorly. Posterior to the articular endplate, the centrum is mediolaterally constricted, which, when complete, would depict an hour-glass shape in ventral view. The right lateral wall (which is more complete than the left side; figure 2E,F) preserves a small fossa approximately mid-height on the centrum, which appears to represent the posterior margin of a plurocoel. The ventral, right lateral and anterior surfaces are incomplete and poorly preserved, obscuring further morphological details of the centrum. AODF 968 comprises the anterior half of a caudal centrum (figure 3). The broken posterior surface reveals camerate and camellate internal structures (figure 3A,B). The anterior articular surface is elliptical (dorsoventrally taller than wide) and shallowly concave (figure 3C,D). The centrum is mediolaterally constricted posterior to the articular endplate whereas the ventral edge (in lateral aspect) is nearly perpendicular to the endplate suggesting that the centrum was notably dorsoventrally constricted. In right lateral view there is a semicircular fossa situated close to the broken posterior edge at roughly two-thirds the height of the centrum and perforated by a pleurocoeloous foramen (figure 3E,F). Directly posteromedial to this depression is a camerate internal structure resembling a pleurocoel. In dorsal view (figure 3I,J), the neural canal is mediolaterally concave and posteriorly tapering, bounded on either side by an anterolaterally–posteromedially oriented neurocentral suture.
The open sutural surfaces preserve numerous mediolaterally oriented grooves and ridges that would have reinforced the union with the pedicels of the corresponding neural arch. In ventral view (figure 3K,L), the centrum is transversely convex with no indication of a ventral groove or keel.

**Proximal end of left metatarsal II (AODF 977)**

The proximal end of a partial left metatarsal II is preserved. The proximal articular surface is somewhat pear shaped (narrowest posteriorly) and nearly flat (figure 4A,B). The proximal part of the metatarsal tapers immediately distal to the proximal articular surface, forming a shaft that is circular in cross section (figure 4C,D), which is similar to the circular shaft in the metatarsal II of *Australovenator* [24] (see figure 7 in White [24]). In medial (figure 4E,F) and lateral (figure 4G,H) views, the posterior margin is extended posteriorly relative to the preserved shaft. The medial margin is incomplete, exposing trabecular bone. The lateral margin is more complete, laterally convex and distomedially inclined, providing an articular surface for metatarsal III.

**Distal end of right metatarsal IV (AODF 979)**

This specimen is interpreted as the distal end of a right metatarsal IV (AODF 979) based on comparisons with *Neovenator* (see Plate 43 in Brusatte [63]). In distal view (figure 5A,B), the lateral malleolus is inclined (~70°) dorsomedially, whereas the medial malleolus is nearly vertical (~5°). The borders of the medial and lateral collateral ligament pits are heavily eroded; nevertheless, the pits are distinguishable. The lateral malleolus is larger than the medial one and the two are separated by a sulcus (flexor groove), which extends from the posterior (plantar) surface where it is deepest, to the anterior (dorsal) surface where it is comparatively shallow (figure 5A-D). This groove does not extend onto the short section of the preserved shaft nor is there any indication of an extensor pit proximal to the articular surface. The left metatarsal IV is present in the holotype of *Australovenator* (AODF 604) but its distal end is not preserved (see Figures 9 & 10 in White [24], preventing any comparisons between the two.
Distal end of right metatarsal II (AODF 978)

Based on comparisons with *Australovenator* (see figure 7 in White [24]) and *Neovenator* (see Plate 42 in Brusatte [63]), AODF 978 is interpreted as the incomplete distal end of a right metatarsal II. The distal articular surface is nearly hemispherical but separated posteriorly (ventrally) into subequal medial and lateral malleoli by a broad, flexor groove. This groove is shallow, but likely misrepresented due to breakage and weathering of both medial and lateral malleolus. In anterior (dorsal) view (figure 6A,F), the distal condyle terminates proximally in a lip that borders a prominent extensor pit. In ventral (plantar) view, the medial malleolus extends further proximally than the lateral one. The medial malleolus is incomplete posteriorly and probably would have been somewhat longer still in life (based on comparisons with *Australovenator* (see figure 7 in White [24]). A shallow collateral ligament pit is present on the medial surface (figure 6C,H), whereas the lateral pit is deep but missing part of the ventral rim (figure 6D,I). Digitally superimposing AODF 978 with the distal end of metatarsal II of *Australovenator*, helps to visualise a number of non-trivial differences (figure 6). The distal end of AODF 978 is more hemispherical in dorsal aspect than the strongly asymmetrical metatarsal II of *Australovenator* (figure 6P,Q). More specifically, the medial malleolus of *Australovenator* is proximally positioned relative to the medial malleolus, mediolaterally compressed and bladelike (figure 6T). In contrast, the medial malleolus of AODF 978 falls along the same transverse plane as the lateral malleolus (in posterior aspect; figure 6G) and, despite being incomplete, is relatively robust. In posterior view, the sulcus separating the malleoli is shallower in AODF 978 than in *Australovenator* (figure 6Q), although this may be exaggerated by breakage/weathering in the former. Additionally, AODF 978 is distinctly larger than *Australovenator* (Table 1). Intriguingly, the distal end of metatarsal II (AODF 978) closely resembles the same element (UNPSJB-Pv944) that was tentatively assigned to *Megaraptor* sp. [65] (figure 7) from the roughly coeval Bajo Barreal Formation (Chubut Group, Golfo do San Jorge Basin) of Chubut Province, Argentina.
In particular, both specimens share a distal articular surface that somewhat hemispherical with medial and lateral malleoli that fall along the same transverse plane (or nearly so in the case of UNPSJB-Pv944) in ventral aspect. In distal view, the flexor groove separating the medial and lateral malleoli is relatively shallow (although possibly an artefact, accentuated in AODF 978 by breakage) compared to *Australovenator*. The weathering suffered by AODF 978 precludes any useful comparisons of the medial or lateral surfaces. Unfortunately, a transparent overlay could not be replicated for the UNPSJB-PV 944 specimen as a 3D surface mesh has not yet been developed for the specimen.

**Distal end of left pedal phalanx II-1 (AODF 972)**

The sole pedal phalanx (AODF 972) recovered from AODL 261 is interpreted as left II-1, based on comparisons with *Australovenator* [24]; however, due to the specimen’s incompleteness this identification is tentative. The specimen consists of the distal articular end and a short section of the shaft, which is subcircular in cross section and hollow. The distal articular surface is ginglymous, dorsoventrally and, to a lesser extent, mediolaterally expanded relative to the shaft (figure 8E,J). Although broken, the medial condyle is dorsoventrally shorter than the lateral one but roughly equal in mediolateral width (Table 1). The collateral ligament pits, while present, are infilled with ironstone (figure 8C,D,H,I). This element does not differ notably from that of *Australovenator* (figure 8P–T). Minor areas of morphological discrepancy can be attributed to breakage and/or the adherent ironstone matrix (figure 8A–E).

**8. Discussion**

Fragmentary theropod remains recovered from the ‘Marilyn’ Site (AODL 261) constitute only the second theropod specimen (excluding shed teeth) from the Winton Formation. The close proximity and size congruence of the specimens recovered from AODL 261 suggests that they pertain to a single individual.
Unfortunately, our failure to locate further theropod remains in the suspected source layer precludes identification of the taphonomic processes to which these bones were subjected prior to their exposure: the effects of all such processes have been overprinted by much more recent weathering. Identifiable elements are limited in number—two fragmentary vertebrae, three partial metatarsals and the distal end of a pedal phalanx—and all were significantly weathered. The poor preservation and lack of diagnostic features amongst the described specimens prevented a meaningful phylogenetic analysis from being undertaken. Nevertheless, some characters typical of megaraptorids — including camerate and camellate vertebral centra [30, 36] and the presence of pleurocoels [39] — are both evident in AODF 967 and AODF 968. The identification of the AODL 261 material as megaraptorid lies principally on the presence of pleurocoels on the two incomplete caudal centra (although we concede that the caudal position of one of these [AOD 968] is equivocal). Pleurocoels are uncommon in the caudal vertebrae of theropods [33]. Although few megaraptorid caudal vertebrae are known, pleurocoels are present in Aerosteon [40], Megaraptor [36], and Orkoraptor [33] but absent in Aoniraptor [32] and possibly the Brazilian megaraptorid SMNS 58023 [42]. Caudal pleurocoels are absent in the immediate outgroups to Megaraptoridae (e.g., Fukuiraptor [49], unknown in Chilantaisaurus) as well as Neovenator [63] but are present in the megalosaurid Torvosaurus [Britt 1991] [66], the carcharodontosaurid Carcharodontosaurus [67] and oviraptorosaurs, none of which have been unambiguously identified from Australia [3][9]. The distal end of metatarsal II (AODF 978) also bears some resemblance to that of a specimen assigned to Megaraptor sp. (UNPSJB-PV 944 [65]) and to a lesser extent Australovenator [24]. It alone is not diagnostic enough to identify as a megaraptorid; however, alongside the pleurocoelus caudal vertebrae, its dimensions suggest the individual to which they pertained was slightly larger than the Australovenator wintonensis type individual (AODF 604), and that it was possibly similar in size to the largest megaraptorids known from Victoria (NMV P186153) [1, 68] and New South Wales [29]. Our preliminary results indicate that these remains belong to a second megaraptorid taxon from the Winton Formation based primarily on the distal end of metatarsal II; however, more complete and better-preserved material is required to establish this claim.
The occurrence of sympatric megaraptorans within a single formation is potentially predicated by the discovery of Phuwiangvenator and Vayuraptor from the Sao Khua Formation in Thailand [52].

9. Conclusion

This paper describes the fragmentary remains of only the second non-avian theropod skeleton recovered from the Winton Formation in Central Queensland, Australia. The remains, presumed to have come from a single individual are assigned to Megaraptoridae gen. et sp. indet. based on the presence of camerate and camellate internal structures and the presence of pleurocoels in caudal vertebrae. Given the size of the distal ends of metatarsal II (AODF 972) and IV (AODF 979), this individual would have been larger than the holotype of Australovenator (AODF604). Additionally, morphological discrepancies between Australovenator and the new specimens highlighted with the use of three dimensional software, may be representative of either ontogenetic/intraspecific variation or indicative of the presence of a second megaraptorid from the Winton Formation. If correct, the latter interpretation adds further support to previous claims that megaraptorids were the dominant large predator in many Australian mid-Cretaceous terrestrial ecosystems.

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Ethical Statement
N/A

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Data Accessibility
The 3D data that support the findings of this study are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.4q5j211

Competing Interests
We have no competing interests.
Authors’ Contributions

MAW, PRB designed the project. MAW, PRB, SFP described the specimens. MAW collected synchrotron data. MAW assembled the figures. MAW, PRB, SFP, AHP, SLR, AGC contributed to writing of the paper. MAW, TS, DAE oversaw the collection, preparation and curation of the fossils. MAW, PRB, SFP, AHP, SLR, AGC, TS, DAE approve of the version to be published. MAW, PRB, SFP, AHP, SLR, AGC, TS, DAE agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

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Table 1. Selected postcranial measurements of megaraptorid remains from AODL261 compared to Australovenator.
Specimens with broken or worn edges (representing incomplete measurements) are marked with an asterisk (*).  

| Specimens          | AODF967 (Fig 2) | AODF968 (Fig 3) | AODF977 (Fig 4) | AODF979 (Fig 5) | AODF978 (Fig 6) | Austrolovenat or holotype AODF604 (Fig 6) Metatarsal II | Metatarsal II | AODF9172 (Fig 7) MT II-1 | Austrolovenat or holotype AODF604 (Fig 7) MT II-1 |
|---------------------|----------------|----------------|----------------|----------------|----------------|---------------------------------------------------------|--------------|--------------------------|--------------------------|
| Centrum width at narrowest point | 30* | 23 | | | | | | | |
| Centrum height (to neurocentral suture) | 45* | 41 | | | | | | | |
| Centrum width (anterior end) | 46 | 36 | | | | | | | |
| Proximal width | | 45* | | | | | | | |
| Proximal height | | | 67* | | | | | | |
| Distal malleolus height (medial, lateral) | | | 41*, 42* | 44*, 45* | 42, 40 | 30*, 35* | 37, 33 | | |
| Distal width (measured ventrally) | | | 57* | 50* | 46 | - | 43 | | |

**Figures**

For final submissions, figures should be uploaded as separate files.

Figure and table captions
Figure 1. Locality and geological setting of AODL 261 (the ‘Marilyn’ Site). (A) Location of Elderslie Station (star) within the context of the Eromanga Basin (green), Central West Queensland, Australia. (B) Aerial photograph of AODL 261. (C) Schematic interpretation of the sub-surface stratigraphy of AODL 261. Here, fossils are naturally brought to the surface from deeper fossiliferous horizons by the expansion-contraction of the clay-rich soils.

Figure 2. Megaraptorid ?caudal centrum (AODF 967) in (A,B) anterior, (C,D) posterior (E,F) right lateral, (G,H) left lateral (I,J) dorsal, (K,L) ventral views. Abbreviations: car, camerate internat structure; cam, camellate internal structure; nc, neural canal; p, pleurocoel.
Figure 3. Megaraptorid caudal vertebra (AODF 968) in (A,B) posterior, (C,D) anterior, (E,F) right lateral, (G,H) left lateral, (I, J) dorsal, and (K,L) ventral views. Abbreviations: car, camerate internal structure; cam, camellate internal structure; nc, neural canal; p, pleurocoel.
**Figure 4.** Megaraptorid proximal left metatarsal II (AODF 977) in (A,B) proximal, (C,D) distal, (E,F) medial (G,H) lateral views.

**Figure 5.** Megaraptorid distal right metatarsal IV (AODF 979) In (A,B) distal, (C,D) anterior, (E,F) posterior, (G,H) lateral, and (I,J) medial views. Missing parts are reconstructed with a dashed line.
Figure 6. Megaraptorid distal right metatarsal II (AODF 978) compared with the right metatarsal II of *Australovenator wintonensis* (AODF 604). Photographs (A–E) and digital renders (F–J) of megaraptorid right metatarsal II (AODF 978) in (A,F) anterior, (B,G) posterior, (C,H) medial, (D,I) lateral and (E,J) distal views. Digital renders (K–O) of *Australovenator wintonensis* right metatarsal II (AODF 604) in (K) anterior, (L) posterior, (M) medial, (N) lateral and (O) distal views. Digital comparison (P–T) of right second metatarsals of AODF 978 (solid tan) with AODF 604 (*Australovenator*; transparent grey) corrected for scale and orientation in (P) anterior, (Q) posterior, (R) medial, (S) lateral and (T) distal views.
Figure 7. Megaraptorid distal right metatarsal II (AODF 978) compared with distal right metatarsal II of *Megaraptor* sp. (UNPSJB-PV 944). Photographs (A–E) of megaraptorid right metatarsal II (AODF 978) in (A) anterior, (B) posterior, (C) medial, (D) lateral and (E) distal views. Photographs (F–J) of *Megaraptor* sp. right metatarsal II (UNPSJB-PV 944) in (F) anterior, (G) posterior, (H) medial, (I) lateral and (J) distal views.
Figure 8. Megaraptorid distal left pedal phalanx II-1 (AODF 972) compared with left pedal phalanx II-1 of *Australovenator wintonensis* (AODF 604). Photographs (A–E) and digital renders (F–J) of megaraptorid left pedal phalanx II-1 (AODF 972) in (A,F) anterior, (B,G) posterior, (C,H) medial, (D,I) lateral and (E,J) distal views. Digital renders (K–O) of *Australovenator wintonensis* left pedal phalanx II-1 (AODF 604) in (K) anterior, (L) posterior, (M) medial, (N) lateral and (O) distal views. Digital comparison (P–T) of left pedal phalanges II-1 of AODF 978 (solid tan) with AODF 604 (*Australovenator*; transparent grey) in (P) anterior, (Q) posterior, (R) medial, (S) lateral and (T) distal views.
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Dear Lianne Parkhouse,

Please find my response to the reviewers’ comments below,

Response to Reviewers:

Reviewer 1: Changes have been made with tracked changes and disagreements have been noted below.

“PAGE 9 – Lines 31 and 32. The bone illustrated on figure 5 of present ms, seems fairly symmetrical in distal view, being similar to mtt III as well as to some non-ungual pedal phalanges. On the contrary, metatarsal IV in theropods is beveled in distal view. Please, have a look at Calvo et al., 2004 paper (your reference number 35), figure 10 A,C, illustrating the mtt IV of Megaraptor namunhuaiquii. Also, consider the possibility that this bone corresponds to a pedal phalanx”

I am familiar with the Calvo et al. 2004 publication however the diagrams provided in this manuscript are extremely poor. The specimen we describe and figure is definitely not symmetrical. The eroded sections as depicted in our figure demonstrate its asymmetrical morphology. Therefore, we have disregarded this recommendation.

PAGE 10. Lines 51-54. Are you meaning that the specimen here described resembles more Megaraptor sp from Patagonia, rather than to Australovenator? Please, clarify. However, and based on the figures here afforded, distal end of mtt II of Australovenator matches well with that of Megaraptor sp. from Patagonia, both being different from the new Megaraptoridae from Winton in the ventral projection of both inner and outer condyles. Then, let me ask whether shape “distinctions” of the later one are due to erosion, rather than true anatomical features.

The first part of this is addressed “….Formation (Chubut Group, Golfo do San Jorge Basin) of Chubut Province, Argentina rather than Australovenator.”

However the second portion was already stated “The weathering suffered by AODF 978 precludes any useful comparisons of the medial or lateral surfaces”.

Reviewer 2:

I have made the recommended changes to the manuscript.

Regards
Dr Matt A White