The anatomy and palaeobiology of the early armoured dinosaur *Scutellosaurus lawleri* (Ornithischia: Thyreophora) from the Kayenta Formation (lower jurassic) of Arizona

Benjamin T. Breeden, Thomas J. Raven, Richard J. Butler, Timothy B. Rowe and Susannah C. R. Maidment

**Article citation details**
*R. Soc. open sci.* 8: 201676.
http://dx.doi.org/10.1098/rsos.201676

**Review timeline**
Original submission: 18 September 2020
1st revised submission: 9 March 2021
2nd revised submission: 8 June 2021
Final acceptance: 18 June 2021

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

Review History
RSOS-201676.R0 (Original submission)

Review form: Reviewer 1 (Marcos Becerra)

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 as is

Comments to the Author(s)
No comments are needed. The manuscript is well-written and I enjoyed reading it. It is informative and the bibliographic revision is comprehensive and exhaustive. The actualization of the description of Colbert was needed, and I’m happy for being selected to do it first hand.

Review form: Reviewer 2

Is the manuscript scientifically sound in its present form?
No

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?
Major revision is needed (please make suggestions in comments)

Comments to the Author(s)
This study provided a detailed description of the early armoured dinosaur Scutellosaurus lawleri from the Kayenta Formation of Arizona. This will help for improving the early evolution of ornithischians. Both the description and figures are good. But there are still some things that need to make it clear before publication. Here are my comments as follows:

1. I notice that the authors have already provided a detailed description of Scutellosaurus published in JVP recently, although the latter only contains specimens from TMM. This MS cited many times of that paper, and I think it is a little redundant. So I believe it is more appropriate that this paper is a complementary description for Scutellosaurus that no need to describe all the bones, but just contains new data and comparisons. This will make the paper more concise.

2. The authors mainly compared Scutellosaurus with basal thyreophorans. I hope the author adds more comparison with other ornithischians that have similar size or feature, such as Eocursor, Agilisaurus, Hexinlusaurus, Jeholosaurus, and also some primitive stegosaurs including Huayangosaurus. Isaberrysaura was original considered to a basal neornithischian, but re-put basal stegosaur in Han et al (2018). It should also be added for comparison. In addition, I notice that the dentary of Scutellosaurus is quite long and shallow dorsoventrally. The ratio of length to depth is also worth comparing with other ornithischians.
3. In the comparison, I notice many other specimens do not have references. Do you check this by yourself or from references? If you check by yourself, please mention that in the "material and method" part.

4. Page 48. The authors state that among ornithischians only Scutellosaurus have lamellar-zonal bone. This seems unlikely. In Padian (2004), we can see that Scutellosaurus still has abundant vascular canals in the inner region of a tibia (Padian 2004, Figure 3D), unlike the condition in modern crocodiles and lizards, but is similar to Jeholosaurus (Han et al 2020, bone histology of Jeholosaurus). Padian (2004) did mention that a radius shows lamellar-zonal pattern (Fig. 3A), but this is not the femur, tibia or humerus that we usually sampled. In fact, limb bones can show different bone patterns in different parts, the fibulae and ribs usually have less vascular canals that show parallel-fibered or lamellar bone.

5. As the author provided new features of Scutellosaurus, a new phylogenetic analysis is necessary. I find that the authors have provided phylogenetic analysis in another paper (JVP online), but they did not mention it here. Furthermore, I strongly suggest that they can do a new phylogenetic analysis of basal ornithischians based on newly published data, such as Boyd 2015 or Han et al 2018, and add some new related taxa. The matrix of Butler et al (2010) has already changed more or less.

I have more comments in a marked version of the pdf (see Appendix A). Thank you.

Review form: Reviewer 3

Is the manuscript scientifically sound in its present form?
Yes

Are the interpretations and conclusions justified by the results?
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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)
This is a well-written and highly detailed anatomical description of the key early dinosaur Scutellosaurus, and represents a very valuable addition to the literature that will no doubt be well-cited in the future. In its position at the base of the diverse and successful armoured dinosaur radiation, Scutellosaurus is a key taxon and the data contained in this manuscript will be invaluable for future research in taxonomy, cladistics, evolutionary dynamics and palaeobiology.

I have only a very few suggested changes for this manuscript prior to publication:
1. For several elements - the nasal, postorbital, squamosal and others, see annotated PDF - it is acknowledged in the text that better preserved and more complete elements exist for some specimens and indeed the text description is based on these best preserved examples. Yet they are not figured; instead, more poorly preserved specimens are figured. Why not figure the very best examples for each bone on which verbal descriptions are based?

2. I do not think Figure 17 is ever cited in the main text and it does not appear between references to Figures 16 and 18.

3. The authors make the very interesting observation on Page 50, Line 24 that different Early Jurassic localities featured different dinosaur faunas, in terms of composition of herbivores (sauropodomorphs, heterodontosaurids, thyreophorans). Any speculation on what was driving these variations?

4. Some minor errors in the references cited (see PDF), please check these carefully prior to submission.

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Lastly, there are some minor grammatical errors and a few places where the meaning of sentences could be clarified - I have made suggested changes in the attached annotated PDF (see Appendix B).

Overall, a major piece of work and again a very valuable addition to the literature, superb effort by the authors on this!

**Decision letter (RSOS-201676.R0)**

We hope you are keeping well at this difficult and unusual time. We continue to value your support of the journal in these challenging circumstances. If Royal Society Open Science can assist you at all, please don't hesitate to let us know at the email address below.

Dear Mr Breeden,

The Editors assigned to your paper RSOS-201676 "The anatomy and palaeobiology of the early armoured dinosaur *Scutellosaurus lawleri* from the Kayenta Formation (Lower Jurassic) of Arizona" have now received comments from reviewers and would like you to revise the paper in accordance with the reviewer comments and any comments from the Editors. Please note this decision does not guarantee eventual acceptance.

We invite you to respond to the comments supplied below and revise your manuscript. Below the referees' and Editors' comments (where applicable) we provide additional requirements. Final acceptance of your manuscript is dependent on these requirements being met. We provide guidance below to help you prepare your revision.

We do not generally allow multiple rounds of revision so we urge you to make every effort to fully address all of the comments at this stage. If deemed necessary by the Editors, your
The reviewers are happy to see this paper, and are generally enthusiastic about its publication. One raises what should be carefully considered so as to dispel any doubts about "shingling": it would be important to show how this paper differs from the JVP one, and to repeat only necessary details (although this is sometimes difficult). A new phylogeny is probably needed, but this should not be difficult. A wider inclusion of taxa is also recommended. The other reviewer asks why you are figuring sub-optimal specimens rather than better ones, and if this because the better specimens were already figured in the JVP paper please make that clear. Finally, some clarity about the histological features may be needed. It is common in virtually all non-avian dinosaurs that fibro-lamellar bone should be expressed at least in early growth and a transition made either to FL tissue that is less vascularized OR to lamellar-zonal bone before skeletal growth effectively ceases and the EFS is deposited. Smaller taxa tend to grow more slowly, but of course any given section represents its ontogenetic age, so perhaps you could clarify? I don’t mean at all to argue with your position, only to note that the outgroups to Dinosauria already grew very quickly and featured copious FL bone, yet they were not larger than Scutellosaurus. So the hypothesis that the larger, later Thyreophora evolved (not "developed," please) FL bone as a strategy for more rapid growth to larger size could be called into question. I will be interested in your perspective on this.

Also, I noted that on line 23 of your MS page 46, you have an extra "closure"

Overall, very well done and I look forward to your revisions. Because this is a large MS you may need more time to revise than our standard three weeks, and if so please just inform the office. Thanks for submitting this.
Reviewer comments to Author:
Reviewer: 1
Comments to the Author(s)

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one version identifying all the changes that have been made (for instance, in coloured highlight, in bold text, or tracked changes);
a 'clean' version of the new manuscript that incorporates the changes made, but does not highlight them. This version will be used for typesetting if your manuscript is accepted. Please ensure that any equations included in the paper are editable text and not embedded images.
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  2) A 'clean' version of the new manuscript that incorporates the changes made, but does not highlight them.
-- An individual file of each figure (EPS or print-quality PDF preferred [either format should be produced directly from original creation package], or original software format).
-- An editable file of each table (.doc, .docx, .xls, .xlsx, or .csv).
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Note: you may upload the figure, table, and caption files in a single Zip folder.
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-- If you are providing image files for potential cover images, please upload these at this step, and inform the editorial office you have done so. You must hold the copyright to any image provided.
-- A copy of your point-by-point response to referees and Editors. This will expedite the preparation of your proof.
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-- If you are requesting an article processing charge waiver, you must select the relevant waiver option (if requesting a discretionary waiver, the form should have been uploaded at Step 3 'File upload' above).

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At Step 7 'Review & submit', you must view the PDF proof of the manuscript before you will be able to submit the revision. Note: if any parts of the electronic submission form have not been completed, these will be noted by red message boxes.

Author's Response to Decision Letter for (RSOS-201676.R0)

See Appendix C.

RSOS-201676.R1 (Revision)

Review form: Reviewer 2

Is the manuscript scientifically sound in its present form?
No

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)
I still have some questions about the bone histology part. The original paper (Padian 2004) only mentioned the bone section of radius to be best characterized as lamellar-zonal. For the bone tissue of femur, he wrote: “Woven bone tissue of periosteal origin surrounds the numberous primary osteons, most of which are parallel and oriented longitudinally (P556), ----No LAGs are observed”. This is more like fibrolamellar bone. The original paper did mention that “the bone is parallel-fibered and not highly vascularized compared to the bones of most dinosaurs”. However, I am afraid this is also not an “autapomorphy” mentioned in their revised MS. For example, a noasaurids theropod Masiakasaurus also shows parallel-fibered bone type (see Lee and Connor, 2013, Bone histology confirms determinate growth and small body size in the noasaurid theropod Masiakasaurus knopleri). In sum, I agree that Scutellosaurus may have slower growth rates than most dinosaurs but we need be careful to say it to be autapomorph in dinosaurs.

Decision letter (RSOS-201676.R1)

We hope you are keeping well at this difficult and unusual time. We continue to value your support of the journal in these challenging circumstances. If Royal Society Open Science can assist you at all, please don’t hesitate to let us know at the email address below.

Dear Mr Breeden III

On behalf of the Editors, we are pleased to inform you that your Manuscript RSOS-201676.R1 “The anatomy and palaeobiology of the early armoured dinosaur <em>Scutellosaurus lawleri</em> from the Kayenta Formation (Lower Jurassic) of Arizona” has been accepted for publication in Royal Society Open Science subject to minor revision in accordance with the referees’ reports. Please find the referees’ comments along with any feedback from the Editors below my signature.

We invite you to respond to the comments and revise your manuscript. Below the referees’ and Editors’ comments (where applicable) we provide additional requirements. Final acceptance of your manuscript is dependent on these requirements being met. We provide guidance below to help you prepare your revision.

Please submit your revised manuscript and required files (see below) no later than 7 days from today’s (ie 01-Jun-2021) date. Note: the ScholarOne system will ‘lock’ if submission of the revision is attempted 7 or more days after the deadline. If you do not think you will be able to meet this deadline please contact the editorial office immediately.

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

Best regards,
Lianne Parkhouse
Dear Ben et al., thanks for your revisions on this. I tend to agree with the reviewer on the histology; we didn't sample a lot, but recall that small taxa grow more slowly than larger related taxa, and our specimen seemed quite typical of small ornithodirans, so I'm not sure this is a synapomorphy of anything, given the mixed tissue signal. Anyway, best wishes for revisions and I look forward to the finished product.

Reviewer comments to Author:

I still have some questions about the bone histology part. The original paper (Padian 2004) only mentioned the bone section of radius to be best characterized as lamellar-zonal. For the bone tissue of femur, he wrote: “Woven bone tissue of periosteal origin surrounds the numerous primary osteons, most of which are parallel and oriented longitudinally (P556), ---No LAGs are observed”. This is more like fibrolamellar bone. The original paper did mention that “the bone is parallel-fibered and not highly vascularized compared to the bones of most dinosaurs”. However, I am afraid this is also not an “autapomorphy” mentioned in their revised MS. For example, a noasaurids theropod Masiakasaurus also shows parallel-fibered bone type (see Lee and Connor, 2013, Bone histology confirms determinate growth and small body size in the noasaurid theropod Masiakasaurus knopfleri). In sum, I agree that Scutellosaurus may have slower growth rates than most dinosaurs but we need be careful to say it to be autapomorphic in dinosaurs.

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Please ensure that you include an acknowledgements' section before your reference list/bibliography. This should acknowledge anyone who assisted with your work, but does not qualify as an author per the guidelines at https://royalsociety.org/journals/ethics-policies/openness/.

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-- An editable file of each table (.doc, .docx, .xls, .xlsx, or .csv).
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Note: you may upload the figure, table, and caption files in a single Zip folder.
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please only include the 'For publication' link at this stage. You should remove the 'For review' link.
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See Appendix D.

Decision letter (RSOS-201676.R2)

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If you have not already done so, please remember to make any data sets or code libraries 'live' prior to publication, and update any links as needed when you receive a proof to check - for instance, from a private 'for review' URL to a publicly accessible 'for publication' URL. It is good practice to also add data sets, code and other digital materials to your reference list.

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On behalf of the Editors of Royal Society Open Science, thank you for your support of the journal and we look forward to your continued contributions to Royal Society Open Science.

Kind regards,
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on behalf of Prof Kevin Padian (Subject Editor)
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Appendix A

The anatomy and palaeobiology of the early armoured dinosaur *Scutellosaurus lawleri* from the Kayenta Formation (Lower Jurassic) of Arizona

| Journal:                     | Royal Society Open Science |
|------------------------------|---------------------------|
| Manuscript ID                | RSOS-201676               |
| Article Type:                | Research                  |
| Date Submitted by the Author:| 18-Sep-2020               |
| Complete List of Authors:    | Breeden III, Benjamin; The University of Utah, Geology & Geophysics; Natural History Museum of Utah; Raven, Thomas; Natural History Museum; Butler, Richard; University of Birmingham, School of Geography and Earth Sciences; Rowe, Timothy; The University of Texas at Austin, Jackson School of Geosciences; Maidment, Susannah; Natural History Museum |
| Subject:                     | Palaeontology < EARTH SCIENCES |
| Keywords:                    | Dinosauria, Ornithischia, Thyreophora, Kayenta Formation, Jurassic, *Scutellosaurus lawleri* |
| Subject Category:            | Organismal and Evolutionary Biology |

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CUST_STATE_CONFLICT :No data available.

Authors’ contributions

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

Statement (if applicable):
B.T.B., T.J.R., R.J.B., and S.C.R.M. conceived of the study and wrote the manuscript; T.B.R. revised the manuscript. All authors gave final approval for publication and agree to be held accountable for the work performed therein.
The anatomy and palaeobiology of the early armoured dinosaur *Scutellosaurus lawleri* (Ornithischia: Thyreophora) from the Kayenta Formation (Lower Jurassic) of Arizona

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Abstract

The armoured dinosaurs, Thyreophora, were a diverse clade of ornithischians known from the Early Jurassic to the end of the Cretaceous. During the Middle and Late Jurassic, the thyreophorans radiated to evolve large body size, quadrupedality, and complex chewing mechanisms, and members of the group are some of the most iconic dinosaurs, including the plated Stegosaurus and the club-tailed Ankylosaurus; however, the early stages of thyreophoran evolution are poorly understood due to a paucity of relatively complete remains from early-diverging thyreophoran taxa. *Scutellosaurus lawleri* is generally reconstructed as the earliest-diverging thyreophoran and is known from over 70 specimens from the Lower Jurassic Kayenta Formation of Arizona, USA. Whereas *Scutellosaurus lawleri* is pivotal to our understanding of character state changes at the base of Thyreophora that can shed light on the early evolution of the armoured dinosaurs, the taxon has received limited study. Herein, we provide a detailed account of the osteology of *Scutellosaurus lawleri*, figuring many elements for the first time.

*Scutellosaurus lawleri* was the only definitive bipedal thyreophoran. Histological studies indicate that it grew slowly throughout its life, possessing lamellar-zonal tissue that was a consequence neither of its small size nor phylogenetic position, but may instead be autapomorphic, and supporting other studies that suggest thyreophorans had lower basal metabolic rates than other ornithischian dinosaurs. Faunal diversity of the Kayenta Formation in comparison with other well-known Early Jurassic-aged dinosaur-bearing formations indicates that there was considerable spatial and/or environmental variation in Early Jurassic dinosaur faunas.
1. Introduction

Thyreophoran dinosaurs (the armoured dinosaurs - stegosaurs, ankylosaurs, and related forms) were important and diverse terrestrial herbivores from the Late Jurassic to the Late Cretaceous. They were characterised by the development of abundant cranial and postcranial osteoderms, expanded ribcages housing extensive guts, secondary quadrupedality, and medium–large body size. Thyreophorans split from their sister-clade, Neornithischia (including ornithopods, pachycephalosaurs, and ceratopsians) by the Early Jurassic and diverged into two major clades (Stegosauria and Ankylosauria, together forming the clade Eurypoda) by the Middle Jurassic [1,2,3,4,5,6]. However, the paucity of taxa known from these early phases of thyreophoran evolution (Late Triassic–Middle Jurassic) hampers attempts to understand thyreophoran systematics, palaeobiology and evolution.

Owen [7, 8] described the early thyreophoran Scelidosaurus harrisonii from the Early Jurassic (early Sinemurian–early Pliensbachian; [7]) of England. This taxon is represented by multiple well-preserved skeletons representing all parts of the skeleton; however, until recently very limited anatomical information had been published [10,11,12]. Other early thyreophorans are generally known from very limited material [13,14,15,16,17].

Colbert [18] described two specimens (MNA.V.175, MNA.V.1752) of a small armoured ornithischian from the Lower Jurassic Kayenta Formation of Arizona, USA (Fig. 1) as Scutellosaurus lawleri, emphasizing similarities to the early-branching ornithischian Lesothosaurus diagnosticus from the Early Jurassic of South Africa. Colbert [18] assigned Scutellosaurus lawleri to the family Fabrosauridae but suggested that Scutellosaurus lawleri could possibly be a “remote ancestor” of ankylosaurs and stegosaurs. Recent phylogenetic analyses and taxonomic reviews [1,2,3,4,5,19,20,21,22,23,24,25,26,27] have recovered Scutellosaurus lawleri as one of the earliest branching members of Thyreophora, and Fabrosauridae is now considered polyphyletic [1,3,5,20,25,28]. Detailed knowledge of the anatomy of Scutellosaurus lawleri is important for several reasons: 1) character polarisation during analyses of stegosaurian and ankylosaurian phylogeny and thyreophoran
functional evolution. This is especially important given there are several dozen specimens of
Scutellosaurus lawleri, including several relatively complete postcranial skeletons with associated cranial
material, making it one of the best-known early thyreophorans; 2) determination of the phylogenetic
position of Thyreophora within Ornithischia, and of the plesiomorphic character-states for Thyreophora in
broad-scale analyses of archosauromorph and dinosaurian evolution; and, 3) reconstruction of the character-
state changes that occurred at the Thyreophora–Neornithischia split, and during early thyreophoran
evolution.

Despite the obvious importance of Scutellosaurus lawleri, little further descriptive or systematic
work has been carried out since that of Colbert [18]. Rosenbaum & Padian [23] referred six specimens
from the collections of the University of California Museum of Paleontology (UCMP) to Scutellosaurus
lawleri but provided only very brief descriptions of most elements. Tykoski [29] figured one additional
specimen reposited at The University of Texas Vertebrate Paleontology Collections (TMM), and Breeden
& Rowe [30] described several additional specimens from TMM. Furthermore, there are inaccuracies in
the anatomical information provided by Colbert [18] and Rosenbaum & Padian [23], the only previous
diagnosis [18] did not attempt to distinguish autapomorphies and symplesiomorphies, and many
phylogenetically informative features have not been previously discussed. The primary aim of this paper
is to expand and emend previous anatomical descriptions, providing new data on non-eurypodan
thyreophoran morphology and new life reconstruction for Scutellosaurus lawleri.

1.1. Institutional abbreviations

AMNH, American Museum of Natural History, New York, NY, USA; CAMSM, Sedgwick Museum of
Earth Sciences, University of Cambridge, Cambridge, UK; CMN, Canadian Museum of Nature, Ottawa,
Ontario, Canada; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA;
MCZ VPRA, the designated prefix for fossil reptile and amphibian specimens at MCZ; MNA, Museum of
Northern Arizona, Flagstaff, AZ, USA; NHMUK, Natural History Museum (formerly NHM, BMNH),
London, UK; ROM, Royal Ontario Museum, Toronto, Canada; SAM-PK, Iziko South African Museum,
Cape Town, South Africa; SGWG, Greifswalder Geologische Sammlungen, Universität Greifswald (formerly Ernst-Moritz-Arndt-Universität Greifswald), Greifswald, Germany; TMM, The University of Texas Vertebrate Paleontology Collections (historically part of the Texas Memorial Museum, formerly referred to as Vertebrate Paleontology Laboratory), Austin, TX, USA; UCMP, University of California Museum of Paleontology, Berkeley, CA, USA; UCMP V, designated prefix for UCMP localities; UTCT, High-Resolution X-ray CT Facility at The University of Texas at Austin; ZDM, Zigong Dinosaur Museum, Zigong, Sichuan, People's Republic of China.

2. Geologic setting

The specimens of *Scutellosaurus lawleri* described below were all collected from the Lower Jurassic Kayenta Formation on lands of the Navajo Nation in northern Arizona. The Kayenta Formation is one of several formations comprising the Upper Triassic to Lower Jurassic Glen Canyon Group on the Colorado Plateau. Together they comprise a thick assemblage of terrestrial sediments that accumulated in a back-arc basin formed by subduction of the Pacific plate under the western margin of North America [31]. The Kayenta Formation lies unconformably atop the Dinosaur Canyon Member of the Moenave Formation, which is a mixture of aeolian and ephemeral fluvial deposits formed mostly by sheet-wash run-off. Without a sustained fluvial system, the Moenave Formation preserved very few vertebrate fossils [32, 33]. The Triassic-Jurassic boundary probably lies near the middle of the Moenave Formation [33,34,35]. The upper boundary of the Kayenta Formation interfingers with the upper Lower Jurassic aeolian Navajo Sandstone [36,37]. The Glen Canyon Group is made up almost entirely of fine, well-sorted sandstones, and it is widely understood to represent an immense, long-lived dune field or erg that accumulated from the latest Triassic until the end of the Early Jurassic. During this time, the region was characterized by an arid climate, with episodic wet intervals that deposited local fluvial and freshwater lacustrine sediments [33,36,37,38,39,40]. It was during one or more of these episodic wet intervals in which the specimens described below were buried [33].
The Kayenta Formation extends across the southern Colorado Plateau from eastern Arizona to western Utah. Geologists have divided it into a ‘typical’ or ‘sandy facies’ that forms the immense Vermillion Cliffs, which stretch east to west across the southern Plateau, and a ‘silty facies’ that is restricted to exposures in eastern Arizona [36,41,42,43]. The major exposures of the silty facies are along the eastern walls of the Little Colorado River Valley. Over some nearly a century of field research, fossils have been discovered throughout exposures of the Kayenta Formation. However, the most productive exposures by far are those of the silty facies, which represents a geographically and temporally localized fluvial interlude in what was otherwise a vast, prolonged aeolian landscape. The silty facies is a heterogeneous assemblage of coarse- to fine-grained clastic sediments that accumulated in channels of cross-bedded sands and lenses of overbank mud that represent a multi-channel fluvial system with low sinuosity and frequent flash flood stages that pulsed through sand dunes [36,39,40]. Also present are localized shallow freshwater lake and marsh deposits that produced lenses of freshwater limestone, and localized beds of blue mudstone that are rich in tetrapod fossils and that also contain ostracods [44] and carbonized sphenopsids [33]. Complex interfingering along their lengths of the Navajo Sandstone and the silty facies of the Kayenta Formation suggests that dominant southeasterly winds blew Navajo erg sands into the Kayenta stream systems [37]. Palaeocurrent analyses indicate that these streams generally flowed to the northwest and were deflated by the strong southeasterly winds. As a result, the fluvial system deposited sand along the dune fields, and continually recycled sediment from the Navajo to the Kayenta system and back again [31,33,37,45,46].

By far the greatest numbers and taxonomic diversity of Kayenta vertebrate fossils have been collected from exposures of the silty facies, including the *Scutellosaurus lawleri* material described below. Productive exposures of the silty facies are mostly confined to Moenkopi Wash, near Tuba City, and to a line of cliffs extending to the south that is made up of the Chinle, Moenave, Kayenta, and Navajo formations, in ascending order [18,29,33,47,48,49,50]. This escarpment bears various names, including
‘Adeii Eechii Cliffs’ [51,52], the ‘Tloi Eechii Cliffs’ [53], and the Echo Cliffs [43]. The sources of these names are unknown to us, nor do the local residents use or even recognize them.

To the south of Moenkopi Wash, the Adeii Eechii escarpment forms the western edge of the Moenkopi Plateau and the eastern flank of the Little Colorado River valley. Below the Adeii Eechii Cliffs is Ward Terrace, famous for its extensive badlands exposures of the Triassic Moenkopi and Chinle formations that are rich in vertebrate (mostly tetrapod) fossils [32]. From Moenkopi Wash southwards, exposures of the silty facies of the Kayenta Formation are steep and present little surface area for prospecting, although a few fossils have been recovered [54]. However, at the southern-most extent of the Adeii Eechii Cliffs, the underlying Dinosaur Canyon member of the Moenave Formation thickens to form 100-meter tall cliffs that broaden considerably to the west above Ward Terrace. Resting on this broad bench are expansive and heavily dissected badlands of the silty facies of the Kayenta Formation from which the _Scutellosaurus lawleri_ specimens described here were collected.

Most of the _Scutellosaurus lawleri_ specimens were collected from fluvial and blue mudstone layers that lie approximately 20–30 meters above the lower boundary of the Kayenta Formation. Among these is the type locality of _Sarahsaurus aurifontanalis_ [33,55]. During laboratory preparation of the _Sarahsaurus aurifontanalis_ type specimen from its encasing sandstone matrix, Adam Marsh extracted a large sample of detrital zircon crystals for dating. Preliminary laser ablation ICP-MS detrital zircon U-Pb results yielded a date of 183.7±2.7 Ma [34]. This date establishes this part of the Kayenta Formation (recorded in most field notes as the “middle third” of the Kayenta Formation) in the Pliensbachian and Toarcian stages of the Lower Jurassic. This is a considerably younger date than earlier U-Pb attempts based on smaller zircon samples that estimated a Triassic age for the Kayenta Formation [46]. The Early Jurassic U-Pb date is entirely consistent with Early Jurassic age estimates of the Kayenta Formation based on biostratigraphy [44,48,49,50,56,57,58].

3. History of discovery of the ornithischian dinosaurs of the Kayenta Formation
The first ornithischian dinosaur remains from the Kayenta Formation were discovered in 1971 by Mr. David Lawler, then a summer intern at the MNA. He collected a nearly complete skeleton of an armoured ornithischian dinosaur that would become the holotype specimen of *Scutellosaurus lawleri* (MNA.V.175) southeast of the topographic landmark Rock Head at MNA Locality 219. A second larger, but less complete, specimen of *Scutellosaurus lawleri* (MNA.V.1752) was discovered along Gold Spring Wash in 1977 by Mr. William Amaral as part of the Museum of Comparative Zoology (MCZ), Harvard University, in a joint expedition with MNA, under permits issued to MNA and funded by the National Science Foundation. This locality (MNA Locality 291, = MCZ Field Number 77 AR/4) is approximately 16 km to the northwest of the holotype locality (Fig. 1). These two specimens were described by the late Edwin H. Colbert, who had become a Research Associate of the MNA following his retirement from a long career as Curator of Fossil Reptiles at the American Museum of Natural History [18]. The holotype specimen comprises a nearly complete disarticulated postcranial skeleton with a few fragments of the skull preserved. Colbert [18] also referred to a femur from a much larger ornithischian than *Scutellosaurus lawleri* collected during this time; however, he did not cite a specimen number for the femur. We infer that this specimen is MNA.V.109, a large left femur referred to *Dilophosaurus wetherilli* by Gay [59].

Exploration of the silty facies continued during the late 1970s and early 1980s and resulted in the discovery of more ornithischian material by field parties from MNA, MCZ, and UCMP (Fig. 1). In 1981, William W. Amaral of the MCZ collected a partial skeleton of a juvenile heterodontosaurid (MCZ VPRA-9092) from a microvertebrate locality near Gold Spring [60], now known as the *Eocaecilia* Quarry [61]. This specimen has been mentioned by several authors [20,62,63] but still awaits a detailed description. In October 1981, James Clark of the UCMP discovered osteoderms of an animal larger than *Scutellosaurus lawleri*. Similar osteoderms were previously reported by Colbert ([18]; MNA.V.96, MNA.V.136) and attributed to aetosaurs and used in support of his argument of a Triassic age for the Kayenta Formation. However, Padian [58] noted similarity between these osteoderms and those of the...
Early Jurassic thyreophoran dinosaur *Scelidosaurus harrisonii* from the Charmouth Mudstone Formation of England and referred the osteoderms from the Kayenta Formation to that species. Norman *et al.* [24] suggested a more conservative assignment of “Thyreophora indet.” for these osteoderms, which has been adopted by some authors [64] while others have opted for a cautious assignment of “*Scelidosaurus sp.*” [29]. Regardless of their taxonomy, the presence of these osteoderms in the Kayenta Formation was used by Padian [58] to support the argument for an Early Jurassic age of the Kayenta Formation, an age assignment that is supported by the presence of both tritylodontids [65,66] and ostracods [44] with Early Jurassic affinities.

Field efforts by the UCMP during the early 1980s (Fig. 1) also led to the discovery of at least six new specimens of *Scutellosaurus lawleri*, which were later described by Rosenbaum & Padian [23]. The most complete of these specimens is UCMP 130580, an associated partial skeleton that preserves several cranial elements absent in the holotype.

The most recent fieldwork in the Kayenta Formation to yield new ornithischian specimens was conducted between 1997 and 2000 by The University of Texas (Fig. 1), whose vertebrate palaeontological collections were an administrative unit of the Texas Memorial Museum (TMM) at that time. This work yielded over 40 new specimens of *Scutellosaurus lawleri*, additional osteoderms from a larger unnamed thyreophoran like those reported by Padian [58], and other indeterminate ornithischian specimens [30,67]. The most significant of those specimens are TMM 43663-1 and TMM 43664-1, both of which are partial skeletons of *Scutellosaurus lawleri* that preserve portions of the skull and pelvis not known from any other specimen [30].

### 4. Systematic Palaeontology

Dinosauria [68]

Ornithischia [69]

Thyreophora [70] *sensu* [71]
Genus *Scutellosaurus* [18]

*Type Species*: *Scutellosaurus lawleri* Colbert, 1981 by monotypy.

*Scutellosaurus lawleri* [18]

*Etymology*: *Scutellosaurus*, from *scutellum* (Latin, a little shield) and *sauros* (Greek, lizard or reptile); *lawleri*, to honour David Lawler, who discovered and collected the holotype in 1971 [18].

*Holotype*: MNA.V.175, relatively complete postcranial skeleton, with some cranial fragments ([18]: figs 6–14, 16–24, 26–34; [22]: figs 20.1C–D, 20.3A, D; [24]: figs 15.1C–D, 15.5A, D). This specimen was first published using the retired catalogue number “MNA P1.175” [18].

*Holotype locality*: MNA Locality 219-1, Rock Head (“*Scutellosaurus lawleri* Locality”). Ward Terrace, Coconino County, Navajo Nation, Arizona, USA (Fig. 1).

*Paratype*: MNA.V.1752, an incomplete postcranial skeleton of an individual slightly larger than the holotype ([18]: figs. 15, 25, 31). This specimen was first published using the specimen number “MNA P1.1752” [18].

*Paratype locality*: MNA Locality 291-5, Gold Spring. Ward Terrace, Coconino County, Navajo Nation, Arizona, USA (Fig. 1).

*Referred specimens*: MNA.V.3133, MNA.V.3137, MNA.V.12395, UCMP 130580, UCMP 170829, UCMP 130581, UCMP 175166, UCMP 175167, UCMP 175168, MCZ VPRA-8792, MCZ VPRA-8793, MCZ VPRA-8794, MCZ VPRA-8795, MCZ VPRA-8796, MCZ VPRA-8797, MCZ VPRA-8798, MCZ VPRA-8799, MCZ VPRA-8800, MCZ VPRA-8801, MCZ VPRA-8802, MCZ VPRA-8803, MCZ VPRA-8804, MCZ VPRA-8805, MCZ VPRA-8806, MCZ VPRA-8808, MCZ VPRA-8810, MCZ VPRA-8820, TMM 43647-7, TMM 43647-8, TMM 43648-13, TMM 43656-2, TMM 43656-3, TMM 43656-5, TMM 43661-1, TMM 43663-1, TMM 43664-1, TMM 43664-2, TMM 43669-5, TMM 43669-6,
Stratigraphic Occurrence and Provenance: All known specimens of *Scutellosaurus lawleri* are derived from the ‘silty facies’ of the Kayenta Formation, Glen Canyon Group (Early Jurassic: Hettangian–Toarcian; [34]; [72]; Fig. 1) in Coconino County, Navajo Nation, Arizona, USA. Detailed locality information for all specimens described herein is on file at MCZ, MNA, TMM, and UCMP and is available from those institutions to qualified researchers upon request; however, general locality information for each individual specimen is provided within the specimen inventory (Supplementary Material).

Revised diagnosis. *Scutellosaurus lawleri* differs from all other ornithischians by the possession of the following autapomorphies: frontals are exceedingly narrow, maximum anteroposterior length more than 350% of minimum interorbital width; facets for atlantal neural arch extend onto lateral surface of odontoid process; cervical vertebrae with very prominent and rugose ventral keels; preacetabular process of ilium is narrow dorsoventrally relative to length, dorsal and ventral surfaces are drawn out medially into distinct flanges (modified from [1,30]).

Comments. *Scutellosaurus lawleri* is the most abundantly recognized dinosaurian taxon from the Kayenta Formation ([29]; pers. obs.); however, in some cases, specimens referred to *Scutellosaurus lawleri* are represented only by small assemblages of associated but disarticulated ornithischian bones and/or bone
fragments lacking diagnostic autapomorphies of Scutellosaurus lawleri [73,74]. These specimens nearly all preserve osteoderms superficially similar to those of MNA.V.175, and their size and shape are more consistent with the type and referred specimens of Scutellosaurus lawleri than to the two other unnamed ornithischian taxa that have been recognized from the Kayenta Formation, which at present include a larger thyreophoran (MNA.V.96, MNA.V.136, UCMP 130056: [58]; TMM 45608-1: [29]) and a heterodontosaurid (MCZ VPRA-9092: [60,63]).

Specimens of Scutellosaurus lawleri reposited at MNA were initially published by Colbert [18] using the catalogue number format “MNA P1.####” (e.g., “MNA P1.175”, “MNA P1.1752”); however, shortly after that publication in either 1982 or 1983, MNA changed their catalogue number format for vertebrate fossil specimens to “MNA V####” (e.g., “MNA V175,” “MNA V1752”). That change was not published at the time, and as a result, several subsequent publications cited the retired “MNA P1.####” catalogue numbers used by Colbert [18] for the type specimens of Scutellosaurus lawleri [1,16,17,23,28,29,75,76,77]. Additionally, the figure captions of Colbert [18] erroneously cited MNA.V.175 (=”MNA P1.175”) and MNA.V.1752 (=”MNA P1.1752”) as “MNA Pl. 175” and “MNA Pl. 1752,” respectively, and these erroneous specimen numbers have proliferated in the literature [78,79,80]. Several additional erroneous specimen numbers have been published for MNA.V.175 and MNA.V.1752, including “MNA 175” and “MNA 1752” [81,82]; “MNA PI.175” [83,84]; “MNA PI.175” and “MNA Pl.1752” [2,79,80,85,86,87,88]; and “MNA.Pl.1752” [89]. These variations are in part a result of the confusion of the numeral one (“1”) with the uppercase letter eye (the first letter in the word “India”) and the lowercase letter ‘l’ (the first letter in the word “lima”), both by researchers and internally by MNA cataloguers.

Subsequently, when MNA palaeontology collection records were first digitized in 2000, representatives of the database provider recommended that collections managers not use spaces in specimen numbers, and the catalogue number format “MNA.V.####” was adopted for vertebrate fossil specimens. For published specimen numbers to remain consistent with the MNA database, the catalogue...
number format of “MNA.V.####” is now preferred for all MNA vertebrate fossil specimens (J. Gillette, pers. comm.). This format is reflected herein and should be used henceforth when citing these specimens.

Six specimens were referred to *Scutellosaurus lawleri* by Rosenbaum & Padian [23] and are reposited at the University of California Museum of Paleontology (UCMP). These specimens were collected between 1981 and 1983 by field parties led by James M. Clark under permits issued to the MNA (J. Clark, pers. comm.). All six of these specimens were reported to have been collected from the same locality (UCMP V85010 – “Lower Blue”) by Rosenbaum & Padian [23]; however, only four of the six specimens (UCMP 130580; UCMP 175166; UCMP 175167; UCMP 175168) were actually collected from that locality. The other two specimens UCMP 170829 and UCMP 130581 were collected from the localities UCMP V85013 (“Gold Springs 1”) and UCMP V84235 (“Red Knob”), respectively. Additionally, UCMP 130580 was sometimes erroneously cited as “UCMP 130850” by Rosenbaum & Padian [23] in their report of these referred specimens.

All referred specimens of *Scutellosaurus lawleri* that are reposited at MCZ were collected during joint expeditions between MCZ and MNA in 1978 and 1982 under Navajo Nation Antiquities Permits issued to MNA. Interestingly, several MCZ specimens that were collected during the 1978 field season were referred in the field to “cf. *Kayentasaurus lawleri*,” which reflects Colbert’s tentative name for *Scutellosaurus lawleri* prior to its eventual description in 1981 (H.-D. Sues, pers. comm.).

5. Osteological Description

The following description is based upon the holotype specimen of *Scutellosaurus lawleri* (MNA.V.175) unless otherwise noted.

5.1. Skull

5.1.1 Premaxilla (Fig. 2)

The premaxilla (Fig. 2) comprises a horizontally aligned main body (beneath the external naris), which is
longer anteroposteriorly than wide mediolaterally. Posterodorsally directed maxillary (= “posterolateral process”) and nasal processes arise from this main body. The maxillary process is broken, and only the base is preserved on each side. The nasal process (Fig. 2A–C, np) projects from the anteromedial corner of the element at an angle of ~33˚ to the long axis of the main body, forming the anterior margin of the external naris. There is a sutural surface for the opposing element at the anterior end of the medial surface of each premaxilla (Fig. 2B). Together, the premaxillae form a long, narrow snout with a rounded anterior tip in dorsal view (Fig. 2C). As in other early ornithischians (e.g., Lesothosaurus diagnosticus: [28]) the first tooth of the premaxilla is inset a short distance from the anteriormost tip of the premaxilla; the anteriormost tip has a rugose, pitted texture, indicating the presence of a horny beak. There are six alveoli (Fig. 2D), indicating six premaxillary teeth, although the teeth themselves are missing and only the tips of a few replacement crowns are present. Six premaxillary teeth are also present in Lesothosaurus diagnosticus (NHMUK PV RUB17) and Laquintasaura venezuelae (MBLUZ P.5014). By contrast, some other early ornithischian dinosaurs have three (heterodontosaurids: [63]) or five (e.g., Agilisaurus louderbacki: [90]), the early thyreophorans Emausaurus ernsti (SGWG 85; [14]) and Scelidosaurus harrisonii (BRSMG Ce12785) also have five, and the early-diverging stegosaur Huayangosaurus taibaii (ZDM T7001; [91]) has seven.

The horizontal premaxillary palate is virtually absent between the two anteriormost teeth, but mediolaterally broadened posteriorly (Fig. 2D, pp), although the palate is comparatively narrow, and like that of other early ornithischians [28,63,76]. A deep and elongate anteriorly tapering groove (Fig. 2B, gr) is present on the medial surface of the premaxilla, which can be inferred to have accommodated a well-developed anterior process of the maxilla. A premaxillary foramen is present in the anteroventral corner of the narial fossa (MNA.V.175, 18: fig. 9A; Fig. 2A, fo), like the condition in other early ornithischians [28,63,76].

5.1.2. Maxilla (Fig. 3)
The left maxilla (Fig. 3A–B) of the holotype was misidentified by Colbert [18] as the right maxilla, and the two fragments that were identified as the left maxilla by Colbert [18] likely represent the right maxilla (Fig. 3C–F). In the left maxilla of MNA.V.175, there are seven teeth present, as well as three empty alveoli, and the tooth row is slightly inset from the lateral margin of the bone, similar to the condition in *Lesothosaurus diagnosticus* [28], *Laquintasaura venezuelae* (MBLUZ P.5016) and *Emausaurus ernsti* (SGWG 85). However, this buccal emargination is not as well developed as that in eurypodans [92, 93].

The tips of unerupted replacement teeth are also present medial and dorsal to the tooth row, lying within replacement tooth foramina (Fig. 3A, rtf). The maxillary teeth show an alternating eruption pattern in which every other tooth is more advanced in eruption than the intervening tooth. The tooth row is oriented in a straight line in ventral and medial views. The ascending process is mostly missing, with only the base being preserved.

Owing to incomplete preservation, it is not possible to determine whether a secondary maxillary palate is present. As in most ornithischians [94], a supra-alveolar lamina (Fig. 3B, sal) projects dorsally above the posterior end of the tooth row at the lateral margin of the bone, forming the ventral margin of the antorbital fenestra. Medial to this, a posteriorly opening groove is present on the dorsal surface of the bone, representing the groove for the neurovascular bundle. In *Scelidosaurus harrisonii* (NHMUK PV R1111) this neurovascular groove connects with the row of lateral neurovascular foramina positioned above the tooth row. If such lateral foramina were present in *Scutellosaurus*, as is the normal condition in ornithischians, they are obscured by the nasals.

### 5.1.3. Nasal (Fig. 3B)

Although portions of the nasals are preserved in MNA.V.175 (Fig. 3B, n), these are fractured and closely appressed to the left maxilla, so they yield limited anatomical information. A nearly complete nasal is preserved in TMM 43664-1 [30], from which the following comments are primarily derived. The nasal is mediolaterally arched with a concave ventral surface, as in *Scelidosaurus harrisonii* (NHMUK PV
A well-developed midline depression is absent, in contrast to many other early ornithischians (e.g., Agilisaurus louderbacki, ZDM 6011; Heterodontosaurus tucki, SAM-PK-K1332; Hexinlusaurus multidens, ZDM T6001), and the nasals articulate medially along a nearly straight contact. The dorsal surface of the nasal exhibits cortical remodelling in TMM 43664-1, as in Scelidosaurus harrisonii (NHMUK PV R1111) and stegosaurs (e.g., Stegosauria indet., CMNH 106; Miragaia longicollum, ML 433), and the ventral surface is relatively smooth. There are no anteroposteriorly-extending ridges on the dorsal surface of the nasal, unlike the condition in Paranthodon africanus (NHMUK PV OR47338; [4]) and Hesperosaurus mjosi (DMNH 29431; [95]).

5.1.4. Frontal (Fig. 4A–B)

Although a posterior portion of a left frontal is preserved in MNA.V.175 [30], more complete frontals are preserved in UCMP 130580 (Fig. 4A–B), TMM 43663-1, and TMM 43664-1 [30]. The frontals are much longer anteroposteriorly than wide mediolaterally, a feature we interpret to be an autapomorphy of Scutellosaurus. The frontals widen towards their posterior ends and are dorsoventrally thickened where they form a midline contact with one another. They are not extensively sculpted, but there is some weak sculpting of the dorsal surface immediately adjacent to the parietal contact and supratemporal fossa at the posterior end of the element. In Emausaurus ernsti (SGWG 85) the frontals are similarly unsculpted, except for a small region around the anterior orbital margin. The frontals are gently arched along their length. As in Lesothosaurus diagnosticus [28: fig. 12B], there is an elongate facet on the anterolateral surface of the frontal for a tapering posterior process of the prefrontal (Fig. 4A, a.pf). As noted by Maidment & Porro [96], there are a series of fine striations along the lateral margin of the frontal of UCMP 130580 (Fig. 4A, str), which were interpreted to represent an osteological correlate for soft tissue, and these striations are also present on the frontals of TMM 43663-1 and TMM 43664-1 [30] and on the frontals of Emausaurus ernsti (SGWG 85). The frontal formed part of the dorsal rim of the orbit (Fig. 4A–B, orb), as in most early ornithischians [28,63,76,90] but differing from the condition in Scelidosaurus harrisonii (NHMUK PV R1111), ankylosaurs [97], and stegosaurs [92], in which
supraorbital bones were incorporated into the skull roof and separated the frontals from the dorsal rim of the orbit. Medial to the orbital margin on the ventral surface of the frontal, there is an anteroposteriorly extending wide groove for the olfactory tract of the brain (Fig. 4B, olft). The posterior portion of the frontal possesses a prominent supratemporal fossa to accommodate the temporal musculature (Fig. 4A, stfo), as in saurischians [19] and some early ornithischians [28,76,98].

5.1.5. Parietal (Fig. 4A–B)

The parietal of *Scutellosaurus lawleri* is known only from a fragment in UCMP 130580 (Fig. 4A–B). Anteriorly, the parietal formed a nearly straight, interdigitating, transverse suture with the frontals. On each side of the parietal there is a sharp ridge (Fig. 4A, ri) that demarcates the supratemporal fossa and is continuous with the ridge defining the supratemporal fossa (Fig. 4A, stfo) on the frontal. These ridges on the parietal converge posteriorly, and together define a flat, triangular area on the dorsal surface of the bone.

5.1.6. Lacrimal

The lacrimal of *Scutellosaurus lawleri* is known only from TMM 43664-1, which preserves both right and left lacrimals [30]. The lacrimal comprises a subquadrangular main body with a curved and tapering posteroventral process, similar in morphology to that of *Lesothosaurus diagnosticus* [28] and *Emausaurus ernsti* (SGWG 85). The lateral surface of the body is cortically remodelled, in contrast to that of *Emausaurus ernsti* (SGWG 85), where it is smooth. The antorbital fossa extends onto the anteroventral portion of the main body of the lacrimal of *Scutellosaurus lawleri*, and the posteroventral process of the lacrimal forms the posterodorsal margin of the antorbital fenestra. It is unclear whether the lacrimal contacted the prefrontal.

5.1.7. Jugal (Fig. 4C–D)

A small portion of a left jugal is present in MNA.V.175, and a mostly complete right jugal is present in
UCMP 130580 (Fig. 4C–D), but the most complete jugals are known from TMM 43663-1 and TMM 43664-1 [30]. Sutural surfaces are here identified based upon comparison with the disarticulated holotype skull of *Scelidosaurus harrisonii* (NHMUK PV R1111). The lateral surface of the jugal ventral to the dorsal process and ventral to the ventral margin of the orbit is ornamented with several weak anterodorsal-to-posteroventrally extending, anastomosing ridges and shallow grooves (Fig. 4C, orn). This ornamentation is similar in position and form to that of *Emausaurus ernsti* (SGWG 85) and *Scelidosaurus harrisonii* [11], although it is less well developed than in the latter.

The anterior process of the jugal is mediolaterally expanded beneath the orbit (Fig. 4C). This mediolateral expansion does not occur along the entire anterior process but is confined to a short section immediately anterior to the dorsal process of the jugal. A medially and slightly ventrally facing facet for the ectopterygoid is present on the medial surface of this expansion (Fig. 4D, a.ect), like the condition in *Emausaurus ernsti* (SGWG 85) and *Scelidosaurus harrisonii* (NHMUK PV R1111). Two sutural surfaces are present on the jugal for the maxilla (Fig. 4C–D, a.max): an extensive ventrally and slightly medially facing surface, and a shorter and less well defined ventrally and laterally facing surface. The sutural surface for the lacrimal, positioned on the dorsal surface of the anterior end of the process in *Scelidosaurus harrisonii* (NHMUK PV R1111), may be represented in *Scutellosaurus lawleri* by a small dorsal notch in the extreme end of the anterior process of the jugal of TMM 43664-1. The dorsal process of the jugal is anteroposteriorly narrow and has an elongate narrow groove on the anterior portion of the lateral surface to articulate with the ventral process of the postorbital (Fig. 4C, a.po), as in *Emausaurus ernsti* (SGWG 85). The posterior process of the jugal has a V-shaped, anteriorly tapering depression on its medial surface, which articulates with the quadratojugal (Fig. 4D, a.qj); a facet with similar morphology is present in *Scelidosaurus* (BRSMG Ce12785).

### 5.1.8 Postorbital (Fig. 4E–F)

TMM 43663-1 and TMM 43664-1 possess the best preserved postorbitals [30], but a small portion of a
left postorbital is present in UCMP 130580 (Fig. 4E–F). The postorbital is a triradiate element with anteromedial, posterior, and ventral processes, which articulate with the frontal, squamosal, and jugal, respectively. The anterior margin of the postorbital between the anteromedial and ventral processes is rounded and forms the posterodorsal border of the orbit (Fig. 4E, orb). The anterior process is the shortest of the three processes and bifurcates anteriorly [30]. The posterior and ventral processes are both slender [30], similar to those of *Lesothosaurus diagnosticus* [28,99], heterodontosaurids [63,76], and *Emausaurus ernsti* (SGWG 85), but in contrast to that of *Scelidosaurus harrisonii* (NHMUK PV R1111) in which the main body of the postorbital and the posterior and ventral processes are more robust. The posterior and ventral processes taper towards their tips, as in other early thyreophorans (*Emausaurus ernsti*, SGWG 85; *Scelidosaurus harrisonii*, NHMUK PV R1111).

5.1.9 Quadratojugal

The quadratojugal is only known from TMM 43664-1 [30]. The quadratojugal is mediolaterally compressed and overlies the lateral ramus of the quadrate. There is a prominent foramen on the medial surface of the quadratojugal that does not extend through to the lateral surface [30]. *Scelidosaurus harrisonii* (NHMUK PV R1111) possesses a dorsal process of the quadratojugal, but this part of the bone is not preserved in TMM 43664-1 so its presence or absence in *Scutellosaurus lawleri* cannot be determined.

5.1.10 Squamosal

Although a possible portion of the squamosal in MNA.V.175 was noted by Colbert [18], we could not locate this; however, a complete squamosal is preserved in TMM 43663-1 [30]. This is a triradiate element comprising anterior, prequadratic, and postquadratic processes. The lateral surface of the squamosal is deeply excavated by a smooth concavity. The anterior process bifurcates into dorsal and ventral projections that flank the posterior process of the postorbital to form the upper temporal bar, and the prequadratic process is anteroposteriorly thin and poorly preserved. The postquadratic process is
anteroposteriorly broader than the prequadratic process and is the shortest of the three processes.

5.1.11 Quadrate (Fig 4G–K)

The quadrate is not known from the holotype or paratype specimens but is preserved in a number of other specimens (e.g., UCMP 130580 [Fig. 4J–K], UCMP 175166: [23]; TMM 43647-7, TMM 43687-121, TMM 43663-1, TMM 43664-1:[30]; MCZ VPRA-8795 [Fig. 4G–I]; MCZ VPRA-8797). The head is arched posteriorly relative to the shaft (Fig. 4H) and is not fused to the paroccipital process. It is moderately compressed in lateral view, like that of *Stegosaurus* (e.g., NHMUK PV R36730). The pterygoid wing (Fig. 4J–K, ptw) is best preserved in TMM 43664-1, and is subtriangular, dorsoventrally tall, tapers anteromedially, and bears a shallow fossa [30: fig. 10K–L], like that of *Stegosaurus* (NHMUK PV R36730). The lateral surface of the ventral end of the shaft bears an extensive articular surface for the quadratojugal (Fig. 4J, a.qj), which ventrally would have closely approached the quadrate condyles. As noted by Rosenbaum & Padian [23], the medial condyle is weakly enlarged relative to the lateral and resembles that of *Scelidosaurus harrisonii* (NHMUK PV R1111), and the lateral condyle tapers laterally where it curves anteriorly. A facet is present on the posteroventral surface of the condyles in UCMP 130580 (Fig. 4J, fc), but this is not present in any other specimen that preserves a quadrate (e.g., TMM 43663-1, TMM 43687-121). Such a facet does not appear to be present in *Scelidosaurus harrisonii* (NHMUK PV R1111) whereas the quadrate is not preserved in *Emausaurus ernsti* (SGWG 85).

5.1.12 Braincase (Fig. 5)

Only the basioccipital and the paroccipital process are known from the braincase of *Scutellosaurus lawleri*, and all examples of these elements are preserved disarticulated. None are well enough preserved to determine the exits of cranial nerves.

The basioccipital is preserved in MNA.V.175 (Fig. 5A–B), UCMP 130580 (Fig. 5C–D), and MCZ VPRA-8797 (Fig. 5E–H). A midline ridge is present on the ventral surface of the basioccipital
separating the basioccipital recesses (Fig. 5F, bor); a similar ridge is also present in *Lesothosaurus diagnosticus* [99], *Emausaurus ernsti* (SGWG 85) and *Scelidosaurus harrisonii* (NHMUK PV R1111). Anterior to the basioccipital recesses are rugose basal tubera (Fig. 5F–G, bt). The occipital condyle (Fig. 5F, H, occ) is convex and reniform in posterior view, with a concave dorsal surface demarcating the floor of the foramen magnum (Fig. 5H, fm). On the dorsal surface and lateral to the margin of the foramen magnum are roughened posterolaterally-oriented surfaces for articulation with the exoccipitals (Fig. 5E, H, a.ex). The endocranial floor (Fig. 5E, ef) on the dorsal surface of the basioccipital is generally smooth and concave except for a thin median ridge at the anterior end.

Paroccipital processes are preserved in TMM 43663-1 [30] and MCZ VPRA-8797 (Fig. 5I–J). The paraoccipital process flares laterally from the main body of the exoccipital-opisthotic. In posterior view, there are notches along the dorsal edge of the main body of the exoccipital-opisthotic presumably for articulation with the supraoccipital (Fig. 5I, a.so) and parietal (Fig. 5I, a.p). In anterior view, there is a rough subtriangular surface that is pierced by a small foramen, and there is a medial notch for articulation with the prootic (Fig. 5J, a.pr). Dorsal to this surface, there is a groove for articulation with the supraoccipital (Fig. 5J, a.so). The distal end of the paroccipital process is dorsoventrally expanded but is not pendant.

5.1.13 Dentary (Figs 6, 7A–C)

A nearly complete left (Fig. 6A–B) and partial right (Fig. 6C-D) dentary are preserved in the holotype, and several partial dentaries are preserved in other specimens (e.g., MCZ VPRA-8797: Fig. 7A–C). The dentary tooth row is slightly sinuous in dorsal view (Fig. 7C), but to a much lesser degree than that of derived nodosaurs (e.g., *Panoplosaurus mirus*, ROM 1215: [100]), and in lateral and medial views, the tooth row is sinuous with the anterior end downturned (Figs. 6–7), as in other thyreophorans (e.g., *Scelidosaurus harrisonii*, NHMUK PV R1111; *Emausaurus ernsti*, SSWG 85; [21]), but differing from early ornithischians [28,63,76]. There is a ridge on the dorsal half of the lateral surface that laterally...
defines a narrow buccal emargination posterior to the tenth tooth position (Figs. 6A, 7A, be). The ventral margin of the dentary is relatively straight, in contrast to the sinuous ventral margin in nodosaurs [26]. Colbert [18: 11] identified an unusual rugose depression on the ventral surface of the left dentary of MNA.V.175 as a possible pathologic feature (Fig. 6A); a similar depression is also present in an equivalent position of the right dentary, but is not present in the referred dentary of MCZ VPRA-8797 (Fig. 7A–C).

There is a broad, flat facet on the medial surface of the dentary for the symphysis (Fig. 6B, sym), although this is not ‘spout-shaped’ as in most other ornithischians [21,28], indicating that the articulation between the lower jaws would have been V-shaped in dorsal view. The tooth row appears to extend to the anterior end of the dentary, and there is no clear predentary facet on the dorsal surface. A small facet ventrally on the anterior dentary may be for a predentary, suggesting that if it existed at all, the predentary was very small. The dentary of *Emausaurus ernsti* (SGWG 85) is very similar, also possessing little evidence for a predentary. The maximum dorsoventral depth of the dentary ramus is at the posterior end and the depth of the dentary at the symphysis is shallower than half the maximum depth of the dentary in lateral view. The Meckelian groove on the medial surface (Figs. 6–7, Mg) does not extend anteriorly as far as the symphysial facet, in contrast to the condition in *Emausaurus ernsti* (SGWG 85). Small fragments of the splenial (Fig. 6B, spl) are present in the posterior end of the Meckelian groove of the left dentary of the holotype. Multiple nutrient foramina are present on the lateral surface of the anterior end of the left dentary (Figs. 6–7, for). Similar foramina are also present on the dentaries of *Emausaurus ernsti* (SGWG 85).

The size of the dentary tooth crowns increases posteriorly, and in MNA.V.175 the largest dorsoventral crown height is in the fourteenth tooth position. The tooth alveoli face dorsally, rather than dorsomedially as occurs in some eurypodans (e.g., *Stegosaurus stenops*, NHMUK PV R36730; *Edmontonia longiceps*, CMN 8531), and there is no lateral lamina present to obscure the tooth row in lateral view.
5.1.14 Surangular (Fig. 7D–E)

The surangular is known only from UCMP 130580 (Fig. 7D–E). It is a mediolaterally compressed element that is generally convex on its lateral surface, concave on its medial surface, and sigmoidal in lateral view. The surangular generally resembles that of *Lesothosaurus diagnosticus* (NHMUK PV RUB17), although it is broken anteriorly and dorsally, so the height of the coronoid process cannot be established with certainty. A prominent anteroposteriorly extending ridge is present on the lateral surface of the surangular (Fig. 7D, lr), anterodorsal to the jaw articulation, as in *Lesothosaurus diagnosticus* (Sereno, 1991: fig. 13F), *Scelidosaurus harrisonii* (NHMUK PV R1111) and *Emausaurus ernsti* (SGWG 85). This feature appears to have been lost in stegosaurs [101] and ankylosaurs [93]. The ridge is damaged posteriorly, and the presence or absence of a surangular foramen cannot be determined.

Posteriorly there is a well-developed, slightly upturned, retroarticular process (Fig. 7D–E, rp), the lateral surface of which is gently striated. Medially there is a well-developed internal adductor fossa (Fig. 7E, adf), and a medial flange that descends posteroventrally from the inferred position of the glenoid (Fig. 7E, mf).

5.1.15 Dentition (Fig. 8)

The dentition of the holotype was well described by Colbert [18] and that description is supplemented here. The premaxillae contain alveoli for six teeth, but all are empty and only one replacement tooth, the fifth most-posterior on the left premaxilla of MNA.V.175, is sufficiently erupted to decipher any morphology. It is triangular with a sharp, elongate apex, and fine denticles are present. There are no striations or ridges on the crown surface.

The maxillary teeth (Fig. 8A) are subtriangular, symmetrical and taller dorsoventrally than wide anteroposteriorly. They closely resemble those of *Lesothosaurus diagnosticus* [28] but are very distinct from the apicobasally expanded teeth of *Laquintasaura venezuelae* [102]. There is an labiolingual
swelling present at the base of the crown that sits above a constricted tooth root, similar to that in *Emausaurus ernsti* (SGWG 85) and *Scelidosaurus harrisonii* (NHMUK PV R1111), but not developed into a true cingulum like that of more derived thyreophorans [92, 93]. There is a broad central eminence which extends to the crown tip. There are eight marginal denticles present on each tooth, four either side of the central eminence. In contrast, the maxillary teeth of *Emausaurus ernsti* are asymmetrical with the crown tips offset slightly distally. There are four marginal denticles on the shorter distal side in *Emausaurus ernsti*, and six are present on the longer mesial side. In *Scelidosaurus harrisonii* (NHMUK PV R1111) the maxillary tooth crowns are also offset distally, and the marginal denticles are smaller and more numerous [103]. Striations confluent with the denticles in *Scutellosaurus lawleri* are not present on the surfaces of the maxillary crowns. Wear facets are not evident on the maxillary teeth, like *Emausaurus ernsti* (SGWG 85) but in contrast to *Scelidosaurus harrisonii* [103], although this could be due to poor preservation.

The dentary teeth (Fig. 8B) are similar in morphology to the maxillary teeth. There are six marginal denticles either side of a central apex, although these denticles appear to be larger than on the maxillary teeth, and there is a labiolingual swelling present that is not developed into a true cingulum.

### 5.2. Postcrania

#### 5.2.1. Cervical vertebrae (Figs 9, 10)

Colbert (18:15) suggested that there were nine cervical vertebrae in *Scutellosaurus lawleri*, accounting for the atlas and axis and inferring the absence of the fourth cervical vertebra; however, only six post-axial cervical centra are actually preserved. MCZ VPRA-8800 possesses six well-preserved postaxial cervical vertebrae and one postaxial cervical centrum, which is consistent with Colbert’s inference of nine total cervical vertebrae. This is typical of other small-bodied ornithischians (e.g., *Heterodontosaurus tucki*, [104]; *Agilisaurus louderbacki*, [90]) but differs from *Scelidosaurus harrisonii* (NHMUK PV R1111, CAMSM X.39256; [11]: fig. 10), which possesses eight cervical vertebrae.
Elements from the atlas-axis complex are sparsely preserved among specimens of *Scutellosaurus lawleri*. The intercentrum of the atlas is preserved in UCMP 130580 (Fig. 9A–B) a right atlas neural arch is preserved in MNA.V.175 (Fig. 9C), and an odontoid is preserved in UCMP 130580 (Fig. 9D–F). These elements of the atlas remain discrete and unfused in the specimens in which they are preserved. The neural arches are also unfused to the atlas intercentrum in *Emausaurus ernsti* (SGWG 85) and *Scelidosaurus harrisonii* (NHMUK PV R1111; CAMSM X.39256). In the latter the odontoid is fused to the axis centrum in larger individuals (NHMUK PV R1111), but not in smaller specimens (CAMSM X.39256). The intercentrum is reniform in anterior view with a concave dorsal margin and a convex ventral margin. It possesses an anteroventral depression for articulation with the basioccipital and a posterodorsal groove to receive the ventral lip of the odontoid. The lateral margins of the intercentrum are rounded as preserved and lack clearly defined facets for the neural arches or an atlantal rib. The neural arch has a short anterior process that includes the prezygapophysis (although this articular facet is not well preserved), whereas the postzygapophysis was presumably on the medial surface of the long posterior process of the neural arch but is not exposed. The odontoid process is wedge-shaped and is notable for the presence of prominent concave facets on its lateral surfaces (Fig. 9D, cf). This feature is not seen in other ornithischians for which there is comparable material, and thus is an autapomorphy of *Scutellosaurus lawleri*.

The axis is known from a posterior portion of a neural arch in UCMP 130580 (Fig. 9G–I) and a centrum in MCZ VPRA-8801 (Fig. 9J–L). The neural spine (Fig. 9G) is prominent and extends posterodorsally beyond the posterior margins of the postzygapophyses, broadening slightly posteriorly, as in *Scelidosaurus harrisonii* (NHMUK R1111; [11]: fig. 7). A midline ridge extends along the length of the dorsal surface of the neural spine. Only the right postzygapophysis (Fig. 9G, I, poz) is preserved, and it faces mostly ventrally and slightly laterally. The axis centrum of MCZ VPRA-8801 preserves portions of the base of the neural arch (Fig. 9, na) that show a circular neural canal (Fig. 9, nc), and the atlas intercentrum is not coossified to its anterior articular surface to form the odontoid. The axis centrum is
cylindrical and wider than tall. The anterior articular surface is a mediolaterally-wide oval bisected by a prominent dorsoventral ridge. There is a shallow facet on the dorsal half of the anterior articular surface for the odontoid (Fig. 9, odf) and a smaller but more prominent facet along the ventral edge for articulation with the atlas intercentrum (Fig. 9, axicf). The parapophyses are smooth and rounded (Fig. 9: para). The subcircular and concave posterior articular surface is mediolaterally narrower than the anterior surface.

Postaxial cervical centra are commonly preserved in specimens of *Scutellosaurus lawleri*, but complete cervical vertebrae preserving neural arches are rare. Posterior cervical centra are shorter anteroposteriorly than anterior centra. The sides of the centra are strongly constricted so that the lateral surfaces are concave dorsoventrally and anteroposteriorly. The ventral margin of the third cervical vertebra is concave upwards in lateral view. An extremely rugose and well-developed keel (Fig. 10, k) is present on the mid to posterior cervical vertebrae. This keel is swollen and tubercular towards its anterior end. Similar keels are present on the cervical and dorsal vertebrae of *Scelidosaurus harrisonii* (CAMSM X.39256, NHMUK PV R1111), as well as in other early ornithischians (e.g., *Hypsilophodon foxii*, [105]), although these are less prominent that those of *Scutellosaurus lawleri*; the possession of very prominent and rugose ventral keels is therefore considered an autapomorphy of *Scutellosaurus*.

One nearly complete cervical vertebra was described by Breeden & Rowe (in press: fig. 17C–G; TMM 45609-6), and the following description is based upon a single well-preserved posterior cervical vertebra (MCZ VPRA-8800; Fig. 10). The centrum of MCZ VPRA-8800 is weakly amphicoelous, and the anterior and posterior articular facets of the centra are nearly parallel to one another in lateral view. The parapophyseal facet (Fig. 10, para) is ovoid, with a substantial portion on the dorsolateral margin of the centrum and a small portion on the ventrolateral margin of the neural arch. The neural arch is taller than the centrum, and the neural spine (Fig. 10, ns) is incomplete. The anterior edge of the neural spine originates between the prezygapophyses (Fig. 10, prz). The prezygapophyses are anterodorsally directed and widely separated from one another with broad, subcircular articular facets that face dorsomedially,
like those in *Stegosaurus* (NHMUK PV R36730). Only the left transverse process is completely preserved (Fig. 10, tp), and it is ventrolaterally directed, contrary to the dorsolaterally directed transverse processes of the posterior cervical vertebrae of *Scelidosaurus harrisonii* [11:19]. The transverse process (Fig. 10, tp) narrows distally, terminating in a truncated convex diapophyseal facet. The postzygapophyses are posterolaterally directed with nearly horizontal articular facets. Both the pre- and postzygapophyses extend beyond the articular facets of the centra (Fig. 10C–D).

### 5.2.2. Dorsal vertebrae (Fig. 11)

Fifteen dorsal vertebrae, represented by 14 centra and one neural arch, are present in the holotype, along with one vertebra that is transitional in morphology between the dorsal and sacral vertebrae (a dorsosacral vertebra). Colbert [18] interpreted the series to represent a complete dorsal column. A count of 15 dorsal vertebrae is typical for small ornithischians [90,105], although only 12 are present in *Heterodontosaurus tucki* [104], and there are 16 in *Scelidosaurus harrisonii* (NHMUK PV R1111; CAMSM X39256). In the holotype, the centra and neural arches are disarticulated, and few of the neural arches are well preserved. The neurocentral sutures appear to have been unfused at time of death, and this is also seen in some other specimens of *Scutellosaurus lawleri*. There exist only a few complete presacral vertebrae with articulated neural arches and centra, although in most cases the neurocentral suture remains visible. Among these, MCZ VPRA-8801 preserves five nearly complete nonsequential dorsal vertebrae (Fig. 11A–E), and MCZ VPRA-8800 preserves a single complete dorsal vertebra (Fig. 11F–K).

The centra are anteroposteriorly longer than they are wide mediolaterally or tall dorsoventrally. There are no longitudinal keels on the ventral surfaces of the centra, and the lateral surfaces are gently concave anteroposteriorly, giving the centra a spool-shape in ventral view. The anterior and posterior articular facets of the centra are flat to slightly concave. Neural arches are dorsoventrally taller than the dorsoventral height of the centra. The neural canal is circular in cross-section. Parapophyses (Fig. 11; para) are subcircular in outline, concave, smooth, and are positioned on short stalks. The parapophyses lie
anteroventral to the transverse processes on anterior dorsal vertebrae but extending posteriorly down the
column the parapophyses are progressively more dorsally positioned such that the transverse processes of
posterior dorsal vertebrae lie almost directly posterior to the parapophyses. The dorsal surfaces of the
stalks of the parapophyses and the transverse processes are confluent on posterior dorsal vertebrae.

Transverse processes (Fig. 11; tp) are dorsoventrally compressed. They project laterally and slightly
dorsally in anterior dorsal vertebrae (Fig. 11A), but laterally in more posterior dorsal vertebrae, and they
become more dorsoventrally compressed extending down the column (Fig. 11E). The transverse
processes bear diapophyses (Fig. 11; dia) at their distal ends which are more dorsoventrally compressed
than the parapophyses and teardrop shaped with the apex pointing posteriorly in anterior dorsal vertebrae.
Extending posteriorly down the dorsal vertebral column, the diapophyseal facets become more strongly
dorsoventrally compressed. The facets themselves are concave and slightly smaller than the
parapophyses. Prezygapophyses (Fig. 11; prz) extend anteriorly, are separated from each other, and face
dorsally. Postzygapophyses (Fig. 11; poz) are either sub-equal in size to the prezygapophyses (in the
MCZ specimens; Fig. 11) or are smaller (in the holotype) and were separated by a deep midline fossa.

Both pre- and postzygapophyses overhang the articular facets of the centrum. Neural spines (Fig. 11, ns)
are subrectangular in lateral view. They are dorsoventrally tall and anteroposteriorly narrow in anterior
dorsal vertebrae, and become shorter, anteroposteriorly wider, and posteriorly positioned on the neural
arch in posterior dorsal vertebrae. In the posterior dorsal vertebrae, they are longer anteroposteriorly than
they are tall dorsoventrally in lateral view. In Scelidosaurus harrisonii (CAMSM X.39256), neural spines
are dorsoventrally taller than they are long anteroposteriorly.

5.2.3. Sacral vertebrae (Fig. 12)

Colbert [18] identified five sacral vertebrae present in the holotype of Scutellosaurus lawleri; they are not
fused to one another and only the centra are preserved. The centrum identified as S1 by Colbert [18]
appears to be transitional in morphology between the dorsal vertebrae and sacral vertebrae (Fig. 12A); it
is longer anteroposteriorly than it is wide mediolaterally, as in the dorsal vertebrae but in contrast to the
other sacral vertebrae, and does not appear to have well-developed sacral rib facets on the lateral surfaces of the centrum. We therefore identify this vertebra as a dorsosacral. The lateral surfaces of the centrum are flat anteroposteriorly, and gently convex dorsoventrally. The articular facets are sub-quadrate and flat. The sacral vertebrae identified as 2–4 by Colbert ([18]; Fig. 12B–D) are wider mediolaterally than they are dorsoventrally tall or long anteroposteriorly. Their articular facets are reniform in anterior and posterior views. The anterior articular facet of the sacral identified as S2 by Colbert ([18]; Fig. 12B) is flat; the articular facets on the other sacral vertebrae are gently concave (e.g., Fig. 12D). The anterior and posterior articular facets are subequal in size in the vertebrae identified by Colbert [18] as S2–3; in S4 the anterior articular facet is larger than the posterior one. Large sacral rib facets occupy the anterolateral surfaces of the centra; it appears that each sacral rib articulated with just one vertebra. Ventrally, the sacral centra lack longitudinal grooves or keels. Unfortunately, the vertebra identified as S5 by Colbert [18] is obscured under other bone fragments and its morphology is unclear. TMM 43664-1 preserves one dorsosacral and four articulated sacral centra, but no other specimen of Scutellosaurus lawleri preserves a complete sacrum. The sacrum of Scutellosaurus lawleri therefore possessed one dorsosacral vertebra and at least four sacral vertebrae. Five sacral vertebrae are present in early-diverging ornithischians such as Lesothosaurus diagnosticus [27] and Agilisaurus louderbacki [90], whereas there are six in Heterodontosaurus tucki [104]. In contrast, there are four sacral vertebrae in Scelidosaurus harrisonii (NHMUK PV R1111).

5.2.4. Caudal vertebrae (Fig. 13)

Fifty-eight caudal vertebrae are preserved in the holotype, and this likely represents nearly the whole tail. Caudal vertebrae are commonly preserved among specimens of Scutellosaurus lawleri, although anterior caudal vertebrae with complete neural arches (e.g., MCZ VPRA-8801: Fig. 13L–P) are rare. The neural arches are fused to the centra from caudal seven posteriorly in MNA.V.175, and the vertebrae decrease in size posteriorly. The anterior caudal centra are either equidimensional or slightly longer anteroposteriorly than they are wide mediolaterally or tall dorsoventrally (Figs 13A–C, 13L–P). There are facets for
articulation with the haemal arches along the ventral edges of the articular surfaces of the centra, and
these are especially well developed on the posterior articular surfaces. Caudal ribs (Fig. 13, cr) project
laterally and are mediolaterally compressed, and these disappear after the twenty-first caudal vertebra,
marking the transition between anterior and posterior caudal vertebrae. The remnants of caudal ribs
disappear between caudal vertebrae 22 and 23 in *Scelidosaurus harrisonii* ([11: fig. 47]; NHMUK
R1111). The neural spines (Fig. 13, ns) in the anterior caudal vertebrae of the holotype are generally
incomplete, but they are angled strongly posteriorly, and appear to lack the bulbous swelling that is
present in more derived thyreophorans (e.g., *Scelidosaurus harrisonii*, NHMUK PV R1111; *Dacentrurus
armatus*, NHMUK PV OR46013; *Stegosaurus stenops*, YPM 1856; *Hesperosaurus mjosi*, DMNH 29431;
*Ankylosaurus*, AMNH 5895; *Sauroptela*, AMNH 3032; *Edmontonia longiceps*, CMN 8531; *Polacanthus*,
NHMUK PV R175). The complete neural arch of MCZ VPRA-8801 is taller than the centrum and
includes a tall neural spine is dorsally directed. The prezygapophyses (Fig. 13, prz) extend anterodorsally
beyond the anterior articular facet of the centrum, whereas the postzygapophyses (Fig. 13, poz) are
shorter and do not extend beyond the posterior articular facet.

In posterior caudal vertebrae (Fig. 13D–K), the centra are more elongate and are much longer
anteroposteriorly than they are wide mediolaterally. After the twenty-eighth caudal, chevron facets
disappear. Both pre- and postzygapophyses are poorly preserved in the posterior caudal vertebrae but they
do not extend substantially beyond the articular facets of the centra.

5.2.5. Pectoral girdle (Fig. 14)

The pectoral girdle is described with the blade of the scapula in a horizontal orientation. The scapula and
coracoid are unfused in all known specimens of *Scutellosaurus lawleri*, as in *Lesothosaurus diagnosticus*
(NHMUK PV RUB17; [27]) and other early-diverging thyreophorans (e.g., *Scelidosaurus harrisonii*,
NHMUK PV R1111). The scapulae are nearly complete in the holotype, although the posteriormost
portions of the blades are missing. The scapulae of TMM 43663-1 and TMM 43664-1 are more
completely preserved; however, in both specimens, the scapulae are mediolaterally compressed taphonomically [30]. The scapula is dorsoventrally expanded at both its anterior and posterior ends with concave dorsal and ventral margins, giving it an asymmetrical hourglass shape in lateral view. The blade of the scapula (Fig. 14, bl) curves medially, such that the medial surface of the scapular blade is concave along the anteroposterior axis, and the blade flares posteriorly in lateral view. The blade is mediolaterally compressed relative to the proximal plate (Fig. 14, pp). The proximal plate is small relative to derived thyreophorans such as *Stegosaurus stenops* (NHMUK PV R36730), and it has a smaller area than the coracoid. The proximal plate is triangular in lateral view, with the anterior margin forming the articular surface for the coracoid, the acromial process (Fig. 14, ap) extending at \(~25^\circ\) from the scapular blade, and a mediolaterally broad ventral process present at the posteroventral margin of the glenoid. The scapula is significantly shorter than the humerus. In MNA.V.175, in which the scapula is incompletely preserved, the scapula length is 63% of the humerus length, and in TMM 43663-1, in which the humerus is incompletely preserved, the scapula length is 70% of the humerus length [30]. This contrasts with some other early ornithischians: for example, the equivalent ratio is 122% in *Lesothosaurus diagnosticus* (NHMUK PV RUB17; [27]), 115% in *Scelidosaurus harrisonii* (CAMSM X.39256) and 106% in *Heterodontosaurus tucki* (SAM-PK-K1332; [104]). However, the humerus is also longer than the scapula in *Agilisaurus louderbacki* (85%; [90]) and *Hexinlusaurus consors* (78%; [106]).

The holotype preserves both coracoids, which are missing only portions of their dorsal margins. The coracoids are D-shaped elements with a rounded anteroventral surface, a raised posterovertral glenoid surface (Fig. 14, gl), and no distinct corners. The dorsoventral height is subequal to the anteroposterior length. A coracoid foramen (Fig. 14, cf) is present on the lateral surface near the posterior articular surface for the scapula. There is no anteroventral (sternal) process present and the preserved portion of the ventral margin is rounded in lateral view. The contribution of the coracoid to the glenoid is subequal to that of the scapula (Fig. 14).
5.2.6. Humerus (Fig. 15)

The holotype preserves a complete right humerus (Fig. 15) and a nearly complete left humerus. The humerus is straight along most of its length in anterior view, but there is a prominent medial projection proximally, the medial tuberosity (Fig. 15, mt). This projection is less pronounced than in *Eocursor parvus* [62], but more pronounced than other early ornithischians such as *Heterodontosaurus tucki* (SAM-PK-K1332) and *Lesothosaurus diagnosticus* (NHMUK PV RUB17). The proximal articular surface of the humerus is anteroposteriorly compressed and weakly sigmoidal in proximal view (Fig. 15C). The proximal articular surface is thickest medially and tapers laterally. The humeral head is not well developed in comparison to *Scelidosaurus harrisonii* (NHMUK PV R1111), but better developed than in *Lesothosaurus diagnosticus* (NHMUK PV RUB17). The deltopectoral crest (Fig. 15, dpc) projects anterolaterally, with an apex occurring at just under 30% of the total shaft length, and distally merges into the shaft just proximal to the midlength of the bone. The deltopectoral crest is a relatively slender protuberance that is triangular in lateral view (Fig. 15C) with a prominent tubercle present at its apex for the attachment of the *m. pectoralis* [80]. In *Scelidosaurus harrisoni* the deltopectoral crest is considerably larger and projects more strongly anteriorly (CAMSM X.39256; [11]). There is no distinct notch between the humeral head and the deltopectoral crest or between the humeral head and the medial tuberosity in anterior view. The anterior surface of the proximal end of the humerus is relatively flat between the deltopectoral crest and the medial projection compared to the humerus of *Lesothosaurus diagnosticus* (NHMUK PV RUB17), in which there is a deep anterior depression [27: fig. 7A]. The shaft of the humerus is ovoid in cross-section, with the long axis oriented mediolaterally. The proximal end of the humerus is sub-equal in transverse width to the distal end. The distal articular surface is figure of eight-shaped in distal view, forming a trochlear surface comprising a subovoid lateral (ulnar) condyle (Fig. 15, lc) and a subquadrangular medial (radial) condyle (Fig. 15, mc). The medial condyle is slightly wider mediolaterally than the lateral condyle. The anterolateral corner of the lateral condyle forms a point in distal view. The distal end is expanded mediolaterally to approximately twice the width of the midshaft.
5.2.7. Radius (Fig. 16A–D)

Although the holotype preserves fragments of the radius, complete radii are preserved in UCMP 130580, of which the left is better preserved (Fig. 16A–D). The proximal articular surface of the radius is anteroposteriorly compressed with a flat to concave posterior surface for articulation with the ulna and a convex anterior surface. The shaft is generally straight with a convex anterior margin and is subtriangular in cross-section. There is a well-defined facet on the posterior surface of the distal end of the radius for articulation with the distal end of the ulna. The distal articular surface is convex and is subcircular in distal view. The radius is approximately 60% of the length of the humerus, which is much lower than the 83% estimated by Colbert [18] based on his reconstruction of the radius of MNA.V.175.

5.2.8. Ulna (Fig. 16E–H)

As with the radius, UCMP 130580 includes better-preserved ulnae than the holotype; however, no complete ulna is known (Fig. 16E–H). The ulna is expanded at both the proximal and distal ends in anterior view. The proximal articular surface of the ulna is anteroposteriorly compressed and subtriangular in proximal view. The olecranon process (Fig. 16, ole) is weakly developed, and there is a very weakly-developed anterior process. There is a weakly defined articular facet for the radius on the anterior surface of the proximal end of the ulna. The posterior surface of the proximal end of the ulna is generally smooth. The midshaft of the ulna is subovoid in cross-section. The distal end of the ulna is anteroposteriorly compressed and smaller than the proximal end. The anterior surface of the distal end of the ulna is concave to form a facet for the distal end of the radius. The posterior surface of the distal end of the ulna is convex. The distal articular surface is reniform in distal view, with a rounded medial margin and a pointed lateral margin.

5.2.9. Manus

The holotype preserves two metacarpals, which were interpreted by Colbert [18: fig. 20B] as left metacarpals II and III; however, we cannot confidently confirm these positions. One metacarpal is
missing its distal end. The other metacarpal is missing only a small midshaft portion, and its proximal end remains closely appressed to several other bone fragments such that most of it is obscured from view. The proximal ends of both metacarpals of the holotype have approximately the same dorsoventral width. One metacarpal is present in UCMP 130580, which was identified by Rosenbaum & Padian [23] as either metacarpal III or IV. The proximal ends of all preserved metacarpals are dorsoventrally expanded relative to their midshafts, as in other early ornithischian dinosaurs (e.g., *Lesothosaurus diagnosticus*, NHMUK PV RUB17; *Scelidosaurus harrisonii*, BRSMG LEGL 0005). The proximal articular surfaces are smooth and flat to gently convex. The dorsal surfaces of the proximal ends of the metacarpals are convex and rounded, whereas the ventral surfaces are nearly flat. All metacarpals have midshafts that are ovoid in cross-section. The distal ends of the metacarpals are dorsoventrally and mediolaterally expanded relative to their shafts and bear a weakly-developed flexor pit on their ventral surfaces and well-developed ligament pits on their medial and lateral surfaces. However, they lack well-developed extensor pits on their dorsal surfaces.

Several manual phalanges are also present in the holotype, which were tentatively assigned to digits II and IV in the reconstruction of the manus by Colbert [18: fig. 20]; however, none of these phalanges were preserved in articulation and their positional identities are uncertain. Non-ungual manual phalanges are dorsoventrally and mediolaterally expanded at both their proximal and distal ends. The proximal articular surfaces are convex with flat ventral margins and round dorsal margins. The distal ends bear prominent flexor and extensor pits on their ventral and dorsal surfaces and well-developed ligament pits on their medial and lateral surfaces. The distal articular surfaces are rounded and spool-shaped.

Colbert [18] emphasized the relatively large size of the manus of *Scutellosaurus lawleri*, which he suggested may be indicative of on facultative bipedalism; however, this claim relies heavily on both his composite reconstruction of the manus based on limited material (18: fig. 20B) and his estimated lengths of the radius and ulna (18: fig. 20A). As such, the relative size of the manus in *Scutellosaurus lawleri* remains uncertain.
5.2.10. Ilium (Fig. 18)

The right ilium of MNA.V.175 (Fig. 18B) is incomplete and was erroneously identified as the left ilium by Colbert [18]. It is fractured and poorly preserved, however, and little information is available on the morphology of the pubic and ischiadic peduncles, postacetabular process, and brevis shelf. Previous reconstructions of these areas are therefore largely speculative (e.g., 18: fig. 23). The left ilium (Fig. 18A) is preserved together with the left femur and is less complete than the right; it has a triangular outline owing to the loss of the posteromedial and anteromedial parts of the bone. Partial ilia are known from several specimens, including fragments in MNA.V.175, MCZ VPRA-8792, and UCMP 170829, and portions of both ilia are present in UCMP 130580. A nearly complete right ilium is preserved in TMM 43664-1 [30]; however, this ilium is mediolaterally compressed by taphonomy.

A deep medioventral flange of the ilium (Fig. 18, mf) partially closes the acetabulum medially, as in many other early-diverging ornithischians (*Lesothosaurus diagnosticus*, [28]; *Laquintasaura venezuelae*, MBLUZ P1443) including the early-diverging thyreophoran (*Scelidosaurus harrisonii*, NHMUK PV R1111). A broad lateral expansion (Fig. 18, le) is present above the acetabulum [18]. This lateral expansion of the dorsal surface of the acetabulum is generally referred to as a ‘supraacetabular flange’ in early dinosaurs and ornithischians. However, the term ‘supraacetabular flange’ has also been used to refer to a lateral expansion of the dorsal margin of the ilium above the ischiadic peduncle seen in derived eurypodans, whereas a similar feature in ceratopsians and hadrosaurs has been termed an ‘antitrochanter’ [2]. As the term ‘supraacetabular flange’ is used by different authors to refer to non-homologous features within Thyreophora, we avoid using it here to refer to the lateral expansion above the acetabulum of *Scutellosaurus lawleri*. The lateral expansion bounding the acetabulum dorsally is continuous with the lateral edge of the pubic peduncle (Fig. 18, ppd).

The pubic peduncle is mediolaterally broad and thickest anteriorly, such that the articular surface is subtriangular. In lateral view, the anterodorsal edge of the pubic peduncle is very gently convex, and
the ventral articular surface is more strongly convex and rounded. The distal end of the pubic peduncle is swollen and rough, and the articular surface is rugose. The ischial peduncle (Fig. 18, ispd) is poorly defined relative to some other early ornithischians (e.g., *Eocursor parvus*, SAM-PK-K8025; [62: fig. 13A]) but similar to *Scelidosaurus harrisonii* (NHMUK PV R1111; [11: fig. 68A]). It is a broad swollen surface at the posterior end of the medioventral flange of the acetabulum. The ischial peduncle is anteroposteriorly expanded relative to its mediolateral width.

Rosenbaum & Padian [23] figured, but did not describe in detail, the unusual preacetabular process (Fig. 18, pre) of the ilium of UCMP 130580. The preacetabular process is elongate and dorsoventrally compressed (Fig. 18E–F). Dorsal and ventral margins of the preacetabular process are drawn out medially into narrow flanges that give it a C-shape in cross-section. Anteriorly the dorsal (Fig. 18, dfpre) and ventral (Fig. 18, vfpre) flanges converge upon one another, eventually fusing to form an expanded and dorsolaterally to ventromedially flattened tip (Fig. 18, ftp). The dorsolateral surface of this expanded tip bears anteroposteriorly-extending striations, indicating muscle attachment for the *m. iliotibialis* (Maidment & Barrett 2011). The preacetabular process of the ilium of TMM 43664-1 similarly possesses dorsal and ventral medial flanges, but these converge upon each other anteriorly and fuse to form a more strictly dorsoventrally flattened tip to the preacetabular process, and the process is overall straighter than the bowed process of the ilium of UCMP 130580 [30].

The dorsal margin of the main body of the ilium above the acetabulum is mediolaterally expanded into a narrow shelf (Fig. 18, sh) that bears prominent vertical striations on its medial surface; however, it is not drawn out medially into a distinct flange, as on the preacetabular process. Mediolateral expansion above the acetabulum in *Scutellosaurus lawleri* exceeds that seen in *Lesothosaurus diagnosticus* (NHMUK PV RU B17) and *Laquintasaura venezuelae* (MBLUZ P1443), but it is less developed than in other thyreophorans (e.g., *Scelidosaurus harrisonii*, NHMUK PV R1111; stegosaurs, [2]; ankylosaurs, [93]). The dorsal margin of the ilium above the postacetabular process is not expanded mediolaterally. The postacetabular process of the ilium is relatively short and blunt, with a shallow,
ventrally-facing brevis fossa. One sacral rib impression can be identified (contra [18]) on the partial right ilium of MNA.V.175. This impression is positioned at the base of the preacetabular process and the pubic peduncle; an equivalent rib scar has been identified as the attachment site for the rib of the first true sacral vertebra in *Lesothosaurus diagnosticus* (Sereno, 1991: fig. 9C; [25]).

**5.2.11. Ischium (Fig. 19)**

The holotype preserves the right and left ischia, although both elements are fragmentary. The right ischium, of which the proximal (18: fig. 22A; misidentified as the left ischium) and distal (18: fig. 22C) ends are preserved, is attached to the pelvic block that also contains the right ilium, right pubis and the proximal end of the right femur, and it is found on the underside of the ilium. The left ischium, which was not figured by Colbert [18] and of which only the distal end is preserved, is found as part of an associated block together with the complete left femur, the left ilium and the left pubis. MCZ VPRA-8801 preserves a nearly complete right ischium (Fig. 19A–C), which is the best-preserved ischium known for *Scutellosaurus lawleri*. UCMP 130580 preserves a nearly complete right ischium (Fig. 19D–F; misidentified as the left ischium by Rosenbaum & Padian [23: fig. 3]) and a midshaft portion of the left ischium (Fig. 19G–H).

At the proximal end of the ischium, the pubic (Fig. 19, ppd) and iliac (Fig. 19, ilp) peduncles are connected by a mediolaterally compressed and anteriorly concave acetabular region (Fig. 19, ace). The iliac peduncle of the right ischium of MNA.V.175 and UCMP 130580 partially occludes the acetabulum with an anteriorly-extending flange; however, this condition is absent in the right ischium of MCZ VPRA-8801. The ischial shaft is twisted along its length so that the distal end is rotated medially and the distal ischial shaft is mediolaterally expanded; this would have formed an elongate ischial symphysis with the opposing ischium, as in other early-diverging ornithischians [25], but in contrast to *Scelidosaurus harrisonii* (NHMUK PV R1111) in which the ischial symphysis was restricted to the distal end of the bone and strong torsion of the shaft is absent. There is a ridge along the dorsal portion of the lateral
surface of the shaft (Fig. 19, lr). Much of the narrow symphyseal margin of the ischial shaft is incomplete
in the preserved specimens, giving the impression of a discrete, tab-like obturator process [23: fig. 2B],
and a tab-like obturator process has previously been reconstructed for *Scutellosaurus lawleri* [18: fig. 23];
however, this is likely an artefact of poor preservation. The right ischium of MCZ VPRA-8801 clearly
lacks a prominent obturator process, and the obturator process is not observed on the ischia of other
thyreophorans (e.g., *Scelidosaurus harrisonii*, NHMUK PV R1111; stegosaurs, [92]; ankylosaurs, [93]).
A weak groove is present on the dorsal margin of the ischial shaft, and distally passes onto the medial side
of the shaft. An identical groove was described for *Lesothosaurus diagnosticus* [28,80,107,111],
*Agilisaurus louderbacki* [90], and ornithischian outgroups [108], and probably represents the origin of the
*m. adductor femoris* 2 [80].

5.2.12. Pubis

The anterior end of the left pubis is present in the holotype (Fig. 20A, pub; 18: fig. 22B) along with part
of the pubic shaft and is preserved underneath the left ilium. We were not able to locate the distal end,
despite it being described as present by Colbert [18]. The right pubis, of which only the distal end is
preserved (18: fig. 22C), is preserved underneath the right pelvic block and next to the distal end of the
right ischium. Despite it being described as present by Colbert [18], the anterior end of the right pubis
could not be located. No other specimens preserve a pubis.

There is no evidence to support reconstructions of an elongate prepubis (18: fig. 23); the
mediolaterally compressed prepubis was probably short as in *Eocursor parvus* [62], *Lesothosaurus
diagnosticus* [27,28], *Laquintasaura venezuelae* (MBLUZ P.5008) and *Scelidosaurus harrisonii*
(NHMUK PV R1111). The pubic shaft is long, thin, and rod-like, with a smaller diameter than the shaft
of the ischium, and there does not appear to be a distal expansion, like the condition in *Lesothosaurus
diagnosticus* (NHMUK PV RUB17; [27]). At the anterior end there is a large obturator foramen which is
not closed posteriorly; this is similar to the condition in *Scelidosaurus harrisonii* (NHMUK PV R1111),
but contrasts with the condition in some specimens of *Lesothosaurus diagnosticus* (e.g., NHMUK PV RUB17; [27]) and *Laquintasaura venezuelae* (MBLUZ P.5008), in which the obturator foramen is fully enclosed. There is a large facet on the dorsal surface for the acetabulum [18] and at the posterior end of the obturator foramen there is a smaller facet for articulation with the ischium.

### 5.2.13. Femur (Fig. 20)

Femora are commonly preserved among specimens of *Scutellosaurus lawleri*, and both left (Fig. 20A–C) and right femora are nearly complete in the holotype. As noted by Colbert [18], the femur of *Scutellosaurus lawleri* is morphologically like the femora of other early ornithischians such as *Lesothosaurus diagnosticus* [27,28,107], *Laquintasaura venezuelae* (MBLUZ P.5003), and *Scelidosaurus harrisonii* (NHMUK PV R1111). The length of the complete left femur of MNA.V.175 given by Colbert [18] is inaccurate; the correct length is 83.5 mm, and the femur is substantially shorter than the tibia (87% of tibial length), as in other small-bodied early ornithischians (*contra* [18]), but it is longer than the humerus (121% of humeral length).

The femur is straight in anterior or posterior view but bowed slightly anteriorly in lateral or medial view. The broadest anteroposterior width of the proximal femoral surface occurs centrally, as in dinosauriforms and early saurischian dinosaurs [108: fig. 4C], and in other early ornithischians (*Lesothosaurus diagnosticus*, [28]; *Scelidosaurus harrisonii*, NHMUK PV R1111; *Laquintasaura venezuelae*, MBLUZ P.5003), rather than laterally as in most other ornithischians. A weak groove extends from the anteromedial corner posterolaterally across the proximal surface of the femur, dividing the surface into anterolateral and posteromedial areas. A similar groove is present in most other early dinosaurs [108, 109]. This groove is continuous with a distinct depression on the posterolateral corner of the proximal surface (the ‘articularis antitrochanterica’), considered to represent the articulation surface for the mediolaterally thickened dorsal margin of the acetabulum of the ilium by Langer [108]. The
Articularis antitrochanterica is bounded medially by a weak medial tuber (see discussion in [98]). A broad and well-developed ligament sulcus is present medial to the tuberosity.

Many studies have identified the greater trochanter as limited to the posterolateral margin of the proximal femur [18,28]; by contrast, Langer [108] proposed that in early dinosaurs the groove on the proximal surface separates the greater trochanter from the medially-facing femoral head. As a result, the greater trochanter occupies the whole of the lateral and anterolateral surface, although there is not a distinct constriction between the greater trochanter and the femoral head. A low proximodistally-extending ridge, the dorsolateral trochanter, is present on the lateral surface of the greater trochanter, as in *Scelidosaurus harrisonii* (NHMUK PV R6704) and early saurischian dinosaurs [108,110]. In some other early ornithischians (e.g., *Lesothosaurus diagnosticus*, [28,80]; *Laquintasaura venezuelae*, MBLUZ P.5003) the dorsolateral trochanter is extended anteriorly as a distinct flange, and this probably represents the initial stage in the development of the neornithischian femur in which the greater trochanter is anteroposteriorly expanded, limited to the lateral margin of the femur, and separated from the femoral head by a distinct constriction.

A distinct cleft separates the dorsolateral trochanter from the large, finger-like anterior trochanter. As in early ornithischians (*Lesothosaurus diagnosticus*, [28]; *Scelidosaurus harrisonii*, NHMUK PV R1111) the anterior trochanter is anteroposteriorly broad and positioned rather distally on the shaft relative to the proximal surface of the femoral head.

The attachment of the pendent fourth trochanter (Fig. 20A; ft) is positioned entirely on the proximal half of the femur (contra [22]) and projects ventromedially. A small nutritive foramen is present proximolateral to the base of the trochanter. Distally, a muscle-scar is present on the anterolateral surface of the distal femur, probably for the *m. femorotibialis lateralis* [80]. The angle between the long axis of the femoral head and the long axis of the femoral shaft is roughly 90°. In distal view, the distal end is U-shaped (Fig. 20D), with roughly equal-sized condyles and a large intercondylar fossa, and the fibular
epicondyle is not medially inset, unlike the condition in *Laquintasaura venezuelae* (Barrett et al., 2014), a taxon recovered as sister taxon to *Scutellosaurus lawleri* in some recent phylogenetic analyses [27,111].

### 5.2.14. Tibia (Fig. 21)

Both tibiae are well preserved in the holotype, and the right tibia (Fig. 21) is nearly complete. The tibiae are plesiomorphically longer than the femora, contrary to the condition in *Scelidosaurus harrisonii* (NHMUK PV R1111, [11]) and eurypodans [1,112], but similar to the condition in other early ornithischians (e.g., *Heterodontosaurus tucki*, [104]; *Agilisaurus louderbacki*, [90]; *Lesothosaurus diagnosticus*, [27]). The proximal end of the tibia is expanded anteroposteriorly such that the anteroposterior length is greater than the transverse width; at the distal end, the opposite is true. The proximal articular surface of the tibia comprises a well-developed cnemial crest (Fig. 21, cnc) and two prominent posteriorly-directed condyles. The cnemial crest projects anterolaterally, and the two posterior condyles include the posterolaterally-directed fibular condyle (Fig. 21, fibc) and the larger medial condyle (Fig. 21, mc). The fibular condyle lies slightly distal to the cnemial crest and the medial condyle. The distal end of the tibia is triangular in cross-section, with a posteriorly-directed apex. The anterior surface of the lateral malleolus (Fig. 21, lm) is flat for articulation with the fibula, and is slightly offset anteriorly from the medial malleolus (Fig. 21, mm), from which it is separated by a ridge. It also extends further ventrally than the medial malleolus but not to the degree seen in *Scelidosaurus harrisonii* (NHMUK PV R1111).

### 5.2.15. Fibula (Fig. 22)

The holotype preserves a nearly complete but badly fragmented left fibula and the proximal and distal ends of the right fibula (Fig. 1). The fibula is an elongate, thin element, with an anteroposteriorly and mediolaterally expanded proximal end, although this expansion is not as well developed as that of *Lesothosaurus diagnosticus* (NHMUK PV RUB17; [27]). The proximal end of the fibula is concave medially where it articulates with the tibia (Fig. 22, a.tib) and convex laterally. The proximal articular
surface is smooth, convex, and reniform in proximal view. The shaft does not appear to be bowed anteriorly as it is in *Eocursor parvus* [62], *Lesothosaurus diagnosticus* (NHMUK PV RUB17; [27]) or *Hypsilophodon foxii* [105], although the element is so fragmentary that this could be an artifact of its reconstruction. The distal end of the fibula is both anteroposteriorly and mediolaterally expanded but less so than the proximal end. The anterolateral surface of the distal end is concave and smooth, and there is a flat posterior surface for articulation with the tibia (Fig. 22, a.tib). The distal articular surface is rough and subquadrangular in distal view.

5.2.16. Tarsus (Fig. 23A–I)

Both the holotype and paratype include complete and well-preserved astragali. The astragalus (Fig. A–F) is subquadrangular in proximal or distal view with a transverse long axis. The proximal surface of the astragalus is smooth and subdivided into two bowl-like concave surfaces for the distal malleoli of the tibia. The medial surface is larger than the lateral surface and would have received the medial malleolus of the tibia (Fig. 23, a.mm), whereas the distolaterally-sloping lateral surface received the medial portion of the lateral malleolus of the tibia (Fig. 23, a.lm). Novas [98: fig. 5D] figured the astragalus of *Scutellosaurus lawleri* in proximal view and misidentified the lateral concave surface as the fibular facet; a well-defined fibular facet is absent from the astragalus of all known ornithischians [21]. The anterior surface of the astragalus is concave in proximal view, with a distinct notch separating the strongly projecting anteromedial corner from the ascending process. In anterior view the ascending process (Fig. 23, ap) is low and broad, with the apex positioned laterally; a small fossa (Fig. 23, fo) is present on its anterior surface. The lateral surface of the astragalus is concave for articulation with the calcaneum (Fig. 23, cal). The distal surface of the astragalus is mediolaterally concave and anteroposteriorly convex, forming a trochlear surface.

The calcaneum is partially coossified to the astragalus in MNA.V.1752 (Fig. 23E–F), and isolated calcanea are present in several other specimens that represent smaller individuals than MNA.V.1752 (e.g.,

https://mc.manuscriptcentral.com/rsos
MNA.V.175, MNA.V.3133, MCZ VPRA-8796). In lateral view, the calcaneum has a rounded distal margin with one small concave depression (the fibular facet) on the anterior part of the proximal surface to receive the fibula and a second, larger concave depression more posteriorly on the proximal surface to receive the lateral portion of the lateral malleolus of the distal tibia. This larger concave proximal surface is continuous with the concave proximal surfaces of the astragalus, together forming a mediolaterally wide trough-like surface to receive the tibia. The fibular facet is a bowl-shaped concavity that is nearly continuous with the fossa on the anterior portion of the ascending process of the astragalus. The lateral surface of the calcaneum has a pitted, rugose texture.

Colbert [18:31] tentatively noted a “flattened, somewhat quadrangular element with rounded corners” that might represent a distal tarsal bone in MNA.V.175, but this was not figured. We have identified a right distal tarsal 3 that fits the description of the element noted by Colbert, which we interpret to be the same element (Fig. 23G). Distal tarsal 3 is proximodistally thin and wider anteroposteriorly than mediolaterally. The proximal articular surface is slightly concave but nearly flat, whereas the distal articular surface has two shallow concave depressions for articulation with metatarsal III. Distal tarsal 3 is thickest along its lateral margin, which is slightly rough in texture. The shape of distal tarsal 3 in *Scutellosaurus lawleri* is generally consistent with that of *Scelidosaurus harrisonii* figured by Norman [11: fig. 87; NHMUK R1111].

A right distal tarsal 4 is preserved in UCMP 130850 (Fig. 23H–I), although this was identified as a distal tarsal 2 by Rosenbaum and Padian [23: fig. 5N]. The proximal surface of the right distal tarsal 4 is concave, with a convex anterior surface and a concave posterior surface which is wider mediolaterally than the anterior surface. The medial surface is rugose where it contacted distal tarsal 3, and two small facets are present on the anterior and anterolateral surfaces. A concavity is present on the proximal surface of metatarsal IV for articulation with distal tarsal 4; the fact that this concavity does not extend onto the proximal surface of metatarsal III suggests that distal tarsal 4 only distally articulated with
metatarsal IV. Distal tarsals are unknown in eurypodan thyreophorans [92,93].

5.2.17. Pes (Fig 23J–M)

Metatarsals and phalanges are widely preserved among specimens of *Scutellosaurus lawleri*; however, no single specimen preserves a complete pes. There are four metatarsals present in the holotype material. Metatarsals II and IV are missing only their distal ends, whereas metatarsal I only has the distal end preserved, and only the proximal end of metatarsal III is preserved. A partial ungual phalanx of digit I is present, as are phalanges II and III of digit II, phalanges I and IV of digit III, and phalanges I, IV and V of digit IV. No pes material is present in the paratype material, but UCMP 130580 preserves right metatarsals I-IV, of which only III and IV are mostly complete (Fig. 23J–M; mostly identified as left metatarsals by Rosenbaum & Padian [23]); however, these represent the best-preserved associated metatarsus. Rosenbaum & Padian [23] identified the proximal end of a metatarsal as that of the left metatarsal I. However, this identification seems unlikely as the proximal end of this bone is strongly expanded anteroposteriorly; it is possible that this bone is right metatarsal II, but if so, it has undergone post-mortem deformation.

Right metatarsal I has a strongly mediolaterally compressed and splint-like proximal end. The shaft is flattened laterally and would have been closely appressed to metatarsal II along its length. All these features resemble metatarsal I of other early ornithischians, including *Agilisaurus* [90] and *Lesothosaurus diagnosticus* [27,107].

5.2.18. Osteoderms

Osteoderms are widely preserved among nearly all specimens of *Scutellosaurus lawleri*. The morphology of the osteoderms of *Scutellosaurus lawleri* was described in detail by Colbert [18] and their histology was studied by Main *et al.* [113]. The holotype of *Scutellosaurus lawleri* contains at least 304 osteoderms, and there are 17 osteoderms in the paratype, although they were found disarticulated in both specimens.
Colbert [18] recognized six osteoderm morphotypes but conceding that several of the categories graded into one another other and that the distinctions were subjective. Breeden & Rowe [30] proposed four revised osteoderm morphotypes, including symmetrical broad, subovoid, flat osteoderms with longitudinal keels that were aligned along the antero-posterior bony axis (Morphotype A; Fig. 24A–F); symmetrical osteoderms that possess two long sides sloping up to a ridge of varying height and that are deeply concave ventrally, and the basal plate of each osteoderm maintains a fairly uniform thickness (Morphotype B; Fig. G–J); symmetrical flat osteoderms that are wider than long, with two longitudinal ridges flanking the midline (Morphotype C; Figs. 24K–L, 25); and anteroposteriorly long, transversely narrow osteoderms with hollow bases that are approximately as long as the caudal centra (Morphotype D; Figs. 13G–J, 24M–P). For a more detailed discussion of these morphotypes and how they compare to other thyreophoran dinosaurs, see Breeden & Rowe [30].

Main et al. [113] analyzed the histology of osteoderms from several thyreophoran taxa, including *Scutellosaurus lawleri* (UCMP 130580), and concluded that thyreophoran osteoderms are homologous. The histology of the osteoderms of *Scutellosaurus lawleri* suggests that the earliest thyreophoran osteoderms developed from compact dermal bone that was ontogenetically replaced internally.

6. Discussion

6.1. Ontogeny and growth

Histological thin sections were taken from one radius, one tibia, and an osteoderm of UCMP 130580 (an individual somewhat smaller than MNA.V.175) and from one radius and one femur of UCMP 170829 (an individual about 20% larger than UCMP 130580) in order to study the ontogeny of *Scutellosaurus lawleri* by Padian et al. ([114]; also [113]). At least three lines of arrested growth in the right tibia and seven lines of arrested growth in the radius of UCMP 130580 were observed by Padian et al. (2004), who noted that growth appeared to be ceasing in both bones, which may indicate that UCMP 130580 was nearly fully grown. A slightly larger individual displayed calcified cartilage on the epiphysal surface of the radius,
indicating that the animal also was adult [114]. Indeed, closure of the neurocentral suture in cervical and dorsal vertebrae is only present in a few of the over 70 known specimens of *Scutellosaurus lawleri*.

Conversely, Tykoski [29] suggested that MNA.V.175 and other specimens of *Scutellosaurus lawleri* were probably juveniles, presumably because of the lack of fusion of the neural arches to the centra of the presacral series of vertebrae. However, although the anterior to posterior sequence of neurocentral suture closure during ontogeny noted in crocodylians by Brochu [115] is sometimes invoked to interpret the ontogeny of dinosaurs [16,17,18], its utility as a proxy for skeletal maturity in dinosaurs was called into question by Irmis [119]. Irmis concluded that whereas phytosaurs share the crocodylian state of neurocentral suture closure and that this was plesiomorphic for Pseudosuchia, some dinosaurian taxa (e.g., Ceratopsia, *Camarasaurus*, and crown-group Aves) definitely lack closure the crocodylian pattern of closure and that it was unwise to apply the crocodylian pattern to other archosaurian taxa *a priori*. The neurocentral sutures remain at least partially open in all but the posterior caudal vertebrae in the type and referred specimens of *Scutellosaurus lawleri*, and the lack of neurocentral suture closure is common among early ornithischians (e.g., *Lesothosaurus diagnosticus*, NHMUK RUB17; *Stormbergia dangershoeki*, SAM-PK-K1105), which the relationship between neural arch closure, size, and ontogeny was requires further examination.

Histological examination of the limb elements of *Scutellosaurus lawleri* by Padian *et al.* (2004) revealed very poorly vascularized lamellar-zonal bone throughout the cortex of all specimens examined. Dinosaurs typically possess more highly vascularized fibrolamellar bone [114,120], which led Padian *et al.* [114] to conclude that *Scutellosaurus lawleri* grew slowly throughout its life as a function of its small body size. The histology of the small early-branching ornithischian *Lesothosaurus diagnosticus* has subsequently been examined [121], and it possesses fibrolamellar bone at early growth stages, indicating a more typical dinosaurian pattern of rapid early growth, followed by a decline in growth rate through ontogeny [114,122,123]. *Lesothosaurus diagnosticus* is variably reconstructed phylogenetically as a non-genasaurian ornithischian [1], an early-diverging thyreophoran [3], or an early-diverging neornithischian.
[75], but wherever it fits, it is clear that it is a very early-branching member of the ornithischian lineage which, like *Scutellosaurus lawleri*, had a small adult body size [28]. The presence of fibrolamellar bone in *Lesothosaurus diagnosticus*, therefore, suggests that lamellar-zonal bone in *Scutellosaurus lawleri* is not necessarily a consequence of either small body size or its phylogenetic position close to the base of Ornithischia.

The histology of the limb elements of both stegosaurs [122,123] and ankylosaurs [120] has been investigated. Adults of both clades possess poorly vascularized fibrolamellar bone, which becomes avascular and lamellar-zonal in the final stages of growth [120,122,123]. In ankylosaurs, very strong secondary remodelling is observed [120]. The bone tissues of these derived thyreophorans are less well-vascularized than those of other dinosaurs [120,123] and indicate slower growth rates and perhaps lower metabolic rates [123] than in other dinosaurian clades. It seems most likely, therefore, that slow growth rates are a derived characteristic of Thyreophora (also noted by [123]), and the possession of lamellar-zonal bone throughout the cortex may be autapomorphic for *Scutellosaurus lawleri* among ornithischians. Larger-bodied thyreophorans, the ankylosaurs and stegosaurs, may have developed fibrolamellar bone because of higher growth rates needed to attain large size.

### 6.2. Body proportions and locomotion

Maidment & Barrett [112] included *Scutellosaurus lawleri* in a study of osteological correlates for quadrupedal stance in ornithischian dinosaurs. Of the five anatomical features identified in that study as robust indicators of quadrupedality, *Scutellosaurus lawleri* could only be scored for three, all of which indicate that it was an obligate biped. This conflicts with the interpretation of Colbert [18] of *Scutellosaurus lawleri* as a facultative quadruped based on its limb proportions relative to the obligate biped *Lesothosaurus diagnosticus*. In contrast, Maidment & Barrett [112] interpreted the early thyreophoran *Scelidosaurus harrisonii* as predominantly quadrupedal while retaining some vestiges of its bipedal ancestry, and all eurypodan thyreophorans as obligate quadrupeds. Colbert [18] suggested that the
early ancestors of the armoured stegosaurs and ankylosaurs may have been facultative quadrupeds in order to support the additional weight of their bony armour. Maidment et al. [86] tested the hypothesis that the additional mass of osteoderms forced the centre of mass to move anteriorly in early thyreophorans, driving the evolution of quadrupedality, and they used Scutellosaurus lawleri as a model early thyreophoran. The centre of mass in Scutellosaurus lawleri was computed without armour, with the armour of Stegosaurus, and with the armour of Euoplocephalus. The addition of Stegosaurus and Euoplocephalus armour on Scutellosaurus lawleri resulted in small movements of the centre of mass posteriorly, and it was not possible to force the centre of mass anteriorly with the addition of armour. Among non-eurypodan thyreophorans, Scelidosaurus harrisonii was definitely quadrupedal [124], but the postcrania of the only specimen of Emausaurus ernsti is too incomplete to infer a mode of locomotion. However, it therefore seems most likely that Scutellosaurus lawleri was the only bipedal member of Thyreophora (Fig. 26), and that more derived members of the clade acquired quadrupedality for reasons other than the acquisition of hypertrophied dermal armour.

6.3. Phylogenetic position and character evolution

Scutellosaurus lawleri was originally described as a member of Fabrosauridae by Colbert [18], although it was suggested it could be ancestral to ankylosaurs and stegosaurs. Fabrosauridae is now considered polyphyletic [1,3,5,20,25,28], and Scutellosaurus lawleri is generally considered an early-diverging member of Thyreophora [1,2,3,4,5,19,20,21,22,23,24,25,26,27]. This phylogenetic position is backed up by numerous aspects of morphology and subsequently numerous phylogenetic characters. In the ornithischian phylogeny of Butler et al. [1], Scutellosaurus lawleri is scored as containing four of the six thyreophoran synapomorphies, including characters 46 (state 1; the absence of a forked posterior ramus of the jugal), 101 (state 0, an absent or weak coronoid process), 106 (state 1, the presence of a strong, anteroposteriorly extended ridge on the lateral surface of the surangular) and 112 (state 0, the presence of six premaxillary teeth). Additionally, Scutellosaurus lawleri is also scored as possessing the
synapomorphy of the clade Thyreophora excluding Lesothosaurus diagnosticus, character 89 (state 1, the presence of cortical remodelling on the surface of the skull bones). Similarly, in the ornithischian phylogeny of Boyd [3], Scutellosaurus lawleri is scored as possessing the five thyreophoran synapomorphies identified in the analysis, including characters 52 (state 0, the presence of horizontally oriented distal condyles of the quadrates), 86 (state 1, the presence of a strong, anteroposteriorly extended ridge on the lateral surface of the surangular), 112 (state 0, the presence of six premaxillary teeth), 122 (state 0, a concave lingual surface of the maxillary teeth) and 131 (state 0, maxillary teeth positioned near the lateral margin). Scutellosaurus lawleri is, therefore, unequivocally a thyreophoran. Within Thyreophora, Scutellosaurus lawleri is also excluded from Thyreophoroidea (Eurypoda + Scelidosaurus harrisonii) by lacking numerous morphological features. In the ornithischian phylogeny of Butler et al. [1], Scutellosaurus lawleri contains none of the 16 synapomorphies of Thyreophoroidea identified, and in the ornithischian phylogeny of Boyd [3], Scutellosaurus lawleri contains none of the two synapomorphies of Thyreophoroidea identified. Therefore, there is strong evidence for a phylogenetic placement of Scutellosaurus lawleri within Thyreophora but outside of Thyreophoroidea, alongside the fragmentary taxon Emausaurus ernsti.

6.4. Ornithischian dinosaur diversity in the Kayenta Formation

To date, three ornithischian taxa have been identified from the Kayenta Formation: Scutellosaurus lawleri, an unnamed larger thyreophoran taxon known from rare osteoderms and postcraniaal elements [18,58], and an undescribed heterodontosaurid known from a single partial skeleton [20,63,75]. Of these taxa, Scutellosaurus lawleri is overwhelmingly the most abundant, with ~80 specimens known. Indeed, Scutellosaurus lawleri is the most common tetrapod recovered from the Kayenta Formation and is much more common than remains of theropod [125,126] and sauropodomorph [33] dinosaurs. This represents an unusual situation for Early Jurassic dinosaur faunal assemblages: in the well-sampled upper Elliot Formation of South Africa ornithischian remains are relatively abundant but considerably less common than those of sauropodomorphs [127], whereas ornithischian fossils are exceptionally scarce in the Lufeng
Formation of China in comparison to sauropodomorphs [16,17,128]. Other Lower Jurassic formations
that have yielded ornithischian dinosaur material are generally not sufficiently well sampled to assess
relative abundances of ornithischians versus other dinosaurs [10,11,12,14,102,124]. Unambiguous
members of Thyreophora from the Early Jurassic have only been identified from the northern palaeo-
hemisphere to date, from the USA (Scutellosaurus lawleri) and Europe (Scelidosaurus harrisonii,
Emausaurus ernsti), as well as probably from China (‘Bienosaurus lufengensis’, ‘Tatisaurus oehleri’).
The possible thyreophoran affinities of Lesothosaurus diagnosticus (southern Africa) and Laquintasaura
venezuelae (Venezuela) remain unclear. By contrast, the only Early Jurassic heterodontosaurid known to
date from the northern palaeo-hemisphere is the single undescribed Kayenta specimen, whereas
heterodontosaurids are moderately abundant (c. 20 known specimens) in the upper Elliot Formation of
southern Africa [63,76,129]. These patterns suggest that there was considerable spatial and/or
environmental variation in Early Jurassic ornithischian faunas globally.

Acknowledgements: First and foremost, we acknowledge the people of the Navajo Nation for facilitating
continued palaeontological research on their land. The specimens described herein were collected by the
Museum of Northern Arizona, University of California Museum of Paleontology, and Museum of
Comparative Zoology between the years of 1971 and 1983 during fieldwork on the lands of the Navajo
Nation under permits issued to MNA. We thank Akhtar Zaman, Bradley Nesemeier, and Richard Carlton
of the Navajo Nation Minerals Department for their assistance and support of this research. Any persons
wishing to conduct geologic investigations on the Navajo Nation must first apply for and receive a permit
from the Navajo Nation Minerals Department, P.O. Box 1910, Window Rock, Arizona 86515 and phone
number (928) 871-6588.

Thanks to David Gillette and Janet Gillette (MNA); Mark Goodwin and Patricia Holroyd
(UCMP); Christina Byrd, Jessica Cundiff, and Stephanie Pierce (MCZ); and Matthew Brown and
Christopher Sagebiel (TMM) for provided access to specimens, locality data, and historical archives and correspondence in their respective museum collections. We acknowledge and thank William Amaral, James Clark, Emily CoBabe, William Downs, Farish Jenkins, David Lawler, Charles R. Schaff, B. Schubert, Kathleen Smith, and Hans-Dieter Sues for discovering the specimens described herein. We also acknowledge and thank William Downs, Ann Johnson, Randy Johnson, David Lawler, Nova Young, and any other preparators whose hard work went undocumented for the preparation of the specimens described herein. We thank Matthew Baron, Christopher Bell, Matthew Brown, Christopher Griffin, Randall Irmis, Joshua Lively, Adam Marsh, Keegan Melstrom, Sterling Nesbitt, David Norman, Kevin Padian, and Zackery Wistort for helpful discussions and advice.

BTB was funded for this work by the Ernest L. and Judith W. Lundelius Endowment in Vertebrate Paleontology and the Jackson School of Geosciences at The University of Texas at Austin and the Doris O. and Samuel P. Welles Research Fund at the University of California Museum of Paleontology; TJR was funded by a University of Brighton Science Scholarship; RJB was funded by a NERC PhD studentship during the early stages of this work; TBR was funded by National Science Foundation grants EAR 1258878 and IIS-9874781; and SCRM was funded by a University of Cambridge Domestic Research Studentship during the early stages of this work.
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Figure 1. (A) Geologic map of the Adeii Eechii Cliffs on Ward Terrace in northern Arizona. General geographic regions in which specimens of *Scutellosaurus lawleri* have been collected from the Kayenta Formation are highlighted. Modified from Clark & Fastovsky (1986) and Breeden & Rowe (in press). (B) Idealized outcrop lithostratigraphy and chronostratigraphy of Ward Terrace. Lithostratigraphy after Harshbarger et al. (1959) and chronostratigraphy after Marsh et al. (2014), Suarez et al. (2017), and Marsh (2018). (C) Key to the field seasons that have yielded specimens of *Scutellosaurus lawleri* by the institution in which specimens are reposited and the year in which they were collected. Abbreviations: Jk, Kayenta Formation; Jn, Navajo Sandstone; TrJm, Moenave Formation.
Figure 2. *Scutellosaurus lawleri*, holotype (MNA.V.175) left premaxilla in lateral (A) and medial (B) views, and left and right premaxillae in articulation in dorsal (C) and ventral (D) views. Abbreviations: alv1–alv6, alveoli; en, external naris; fo, foramen; gr, groove on medial surface of premaxilla for anterior process of maxilla; mp, maxillary process; np, nasal process; pp, premaxillary palate; rpt, replacement tooth; sym, flattened symphysial surface.
Figure 3. *Scutellosaurus lawleri*, holotype (MNA.V.175) maxillae. Partial left maxilla in medial (A) and dorsolateral (B) views. Fragments of right maxilla in medial (C, E) and lateral (D, F) views. Abbreviations: aof, ventral border of the antorbital fossa; apm, base of the ascending process of the maxilla; gr, groove on dorsal surface of posterior end of bone, medial to the supra-alveolar lamina; n, nasals appressed to lateral surface of left maxilla; rtf, replacement tooth foramina; sal, supra-alveolar lamina.
Figure 4. Scutellosaurus lawleri, referred cranial bones. Frontals and parietal of UCMP 130580 in dorsal (A) and ventral (B) views. Right jugal of UCMP 130580 in lateral (C) and medial (D) views. Left postorbital of UCMP 130580 in lateral (E) and medial (F) views. Left quadrate of UCMP 130580 in posterior (J) and anterior (K) views. Right quadrate of MCZ VPRA-8795 in posterior (G), medial (H), and anterior (I) views. Abbreviations: a.ect, articular surface for the ectopterygoid; a.max, articular surface for the maxilla; a.pf, articular surface for the prefrontal; a.po, articular surface for the postorbital; a.qj, articular surface for the quadratojugal; fc, facet; olft, olfactory tract; orb, orbit; orn, ornamentation (cortical remodelling); ptw, pterygoid wing; ri, ridge; stfo, supratemporal fossa; str, striations.
Figure 6. *Scutellosaurus lawleri*, holotype (MNA.V.175) dentaries. Left dentary in lateral (A) and medial (B) views. Right dentary in lateral (C) and medial (D) views. Abbreviations: be, buccal emargination; for, foramen; Mg, Meckelian groove; rep, replacement tooth; rug, rugose surface; spl, splenial; sym, symphysial surface for the opposing dentary; 1, first tooth position; 15, fifteenth tooth position.
Figure 5. *Scutellosaurus lawleri*, braincase elements. Basioccipitals of the holotype (MNA.V.175; A–B), UCMP 130580 (C–D), and MCZ VPRA-8797 (E–F) in dorsal (A, C, E), ventral (B, D, F), anterior (G), and posterior (H) views. Paraoccipital process of MCZ VPRA-8797 in posterior (I) and anterior (J) views. Abbreviations: a.ex, articular surface for the exoccipital; a.p, articular surface for the parietal; a.pr, articular surface for the prootic; a.so, articular surface for the supraoccipital; bt, basal tubera; ef, endocranial floor; fm, foramen magnum; occ, occipital condyle.
Figure 7. *Scutellosaurus lawleri*, referred mandibular bones. Left dentary of MCZ VPRA-8797 in lateral (A), medial (B), and dorsal (C) views. Right surangular of UCMP 130580 in lateral (D) and medial (E) views. Abbreviations: adf, adductor fossa; be, buccal emargination; for, foramen; lr, lateral ridge; mf, medial flange; Mg, Meckelian groove; rp, retroarticular process; sym, symphysis with antimere; 1, first tooth position; 10, tenth tooth position.
Figure 8. *Scutellosaurus lawleri*, holotype (MNA.V.175) maxillary (A) and dentary (B) teeth, both in lingual view.
Figure 9. *Scutellosaurus lawleri*, atlas and axis. Referred (UCMP 130580) atlas intercentrum in anterior (A) and posterior (B) views. Holotype (MNA V.175) right atlas neural arch in lateral view (C). Odontoid of UCMP 130580 in left lateral (D), ventral (E), and dorsal (F) views. Referred (UCMP 130580) axis neural arch in right lateral (G), dorsal (H), and ventral (I) views. Referred (MCZ VPRA-8801) axis centrum in anterior (J), posterior (K) and ventral (L) views. Abbreviations: cf, concave facet on lateral surface of odontoid, probably for atlas neural arch; aticf, articular facet for the atlas intercentrum on the atlas neural arch; axicf, articular facet for the atlas intercentrum on the axis; na, neural arch; nc, neural canal; odf, facet for odontoid; para, parapophysis; poz, postzygapophysis; prz, prezygapophysis.
Figure 10. *Scutellosaurus lawleri*, referred (MCZ VPRA-8800) cervical vertebra in anterior (A), posterior (B), right lateral (C), left lateral (D), ventral (E), and dorsal (F) views. Abbreviations: k, keel; ns, neural spine; para, parapophysis; poz, postzygapophysis; prz, prezygapophysis; tp, transverse process.
Figure 11. *Scutellosaurus lawleri*, referred dorsal vertebrae. A–E, series of dorsal vertebrae of MCZ VPRA-8800 in lateral view. F–K, dorsal vertebra of MCZ VPRA-8801 in left lateral (F), right lateral (G), dorsal (H), anterior (I), posterior (J), and ventral (K) views. Abbreviations: l.poz, left postzygapophysis; l.prz, left prezygapophysis; ncs, neurocentral suture; ns, neural spine; para, parapophysis; poz, postzygapophysis; prz, prezygapophysis; r.poz, right postzygapophysis; tp, transverse process.
Figure 12. *Scutellosaurus lawleri*, holotype (MNA.V.175) sacral vertebrae. Transitional dorsosacral (labelled S1) exposed on a block in ventral view (A); true sacral 1 (labelled S2) in dorsal (B) and ventral (C) views. True sacral 3 (labelled S4) exposed on a block in ventral view (D). Abbreviations: ost, osteoderm; scf, sacral rib facet. Scale bar relates only to B and C; a scale bar is not given for A and D because the specimens are preserved in blocks of other material and thus the photos are somewhat oblique.
Figure 13. *Scutellosaurus lawleri*, caudal vertebrae. A–K, representative caudal vertebrae of the holotype (MNA.V.175): anterior caudals (labelled caudals 1 and 2) exposed ventrally in a block (A); anterior caudal (labelled caudal 10) in left lateral (B) and dorsal (C) views; posterior caudal (labelled caudal 19) in dorsal (D), ventral (E), and left lateral (F) views; posterior caudal (labelled caudal 30) in left (G) and right (H) lateral views; caudal 43 in left (I) and right (J) lateral views; posterior caudal (labelled caudal 50) in left (K) lateral view. Caudals 30 and 43 (G–J) have osteoderms associated with their neural spines, presumably in close to life position. L–P, referred anterior caudal vertebra of MCZ VPRA-8801 in anterior (L), posterior (M), left lateral (N), right lateral (O), and dorsal (P) views. Abbreviations: cr, caudal rib; ns, neural spine; ost, osteoderm; poz, postzygapophysis; prz, prezygapophysis.
Figure 14. Scutellosaurus lawleri, holotype (MNA.V.175) scapulae and coracoids. Re-articulated right scapula and coracoid in oblique ventrolateral view (A). B–C, right scapula in proximal (B) and lateral (C) views. Right coracoid in lateral (D) view. E and H, left coracoid in lateral (E) and medial (H) views. F–G, left scapula in lateral (F) and medial (G) views. Abbreviations: a.co, articulation with the coracoid; ap, acromion process; bl, blade; cf, coracoid foramen; cor, coracoid; gl, glenoid; pp, proximal plate.
Figure 15. *Scutellosaurus lawleri*, holotype (MNA.V.175) right humerus in anterior (A), posterior (B), lateral (C), proximal (D), and distal (E) views. Abbreviations: dpc, deltopectoral crest; hd, head; lc, lateral condyle; mc, medial condyle; mt, medial tuberosity.
Figure 16. *Scutellosaurus lawleri*, referred (UCMP 130580) radius and ulnae. A–D, left radius in posterior (A), lateral (B), anterior (C), and medial (D) views. E–F, left ulna in posterior (E) and anterior (F) views. G–H, right ulna in posterior (G) and anterior (H) views. Abbreviations: ole, olecranon process.
Figure 17. *Scutellosaurus lawleri*, preservation of the holotype (MNA.V.175) right hindlimb. Photograph of painted cast of field jacket (A) and interpretive line drawing of cast of field jacket (B).
Figure 18. *Scutellosaurus lawleri*, ilia. A–B, holotype (MNA.V.175) left (A) and right (B) ilia in medial view. C–D, referred (MCZ VPRA-8792) right ilium in lateral (C) and medial (D) views. E–F, referred (UCMP 130580) left ilium, preacetabular process in lateral (E) and medial (F) views. Abbreviations: dfpre, dorsal flange of the preacetabular process; ftp, flattened tip; ispd, ischial peduncle; le, lateral expansion above the acetabulum; mf, medioventral flange; ppd, pubic peduncle; pre, preacetabular process; sh, shelf; vfpre, ventral flange of the preacetabular process.
Figure 19. Scutellosaurus lawleri, referred ischia. A–C, right ischium of MCZ VPRA-8801 in lateral (A), medial (B), and proximal (C) views. D–G, right ischium of UCMP 130580 in lateral (D), medial (E), and proximal (F) views. G–H, shaft of left ischium in lateral (G) and medial (H) views. Abbreviations: ace, acetabulum; gr, groove; ilp, iliac peduncle; lr, lateral ridge; ppd, pubic peduncle.
Figure 20. Scutelloaurus lawleri, femora. A–D, holotype (MNA.V.175) left femur in posterior (A), anterior (B), proximal (C), and distal (D) views. E–G, referred (UCMP 130580) left femur, proximal portion in posterior (E), lateral (F), and anterior (G) views. Abbreviations: aat, articularis antitrochanterica; at, anterior trochanter; dlt, dorsolateral trochanter; ft, fourth trochanter; icf, posterior intercondylar fossa; lsu, ligament groove on the proximal end of the femur; nt, notch separating anterior and dorsolateral trochanters; pub, pubis.
Figure 21. *Scutellosaurus lawleri*, holotype (MNA.V.175) right tibia in anterior (A), lateral (B), posterior (C), medial (D), proximal (E), and distal (F) views. Abbreviations: cnc, cnemial crest; fibc, fibular condyle; lm, lateral malleolus; mc, medial condyle; mm, medial malleolus.
Figure 22. *Scutellosaurus lawleri*, holotype (MNA.V.175) fibulae. A–C, left fibula in lateral (A), proximal (B), and distal (C) views; D–G, right fibula, proximal end in lateral (D) and medial (F) views, distal end in anterior (E) and posterior (G) views. Abbreviations: a.cal, articular surface for the calcaneum; a.tib, articular surface for the tibia; pin, metal pin.
Figure 23. *Scutellosaurus lawleri*, tarsus and pes. A–C, holotype (MNA.V.175) left astragalus in proximal (A), anterior (B), and distal (C) views. D, holotype (MNA.V.175) left astragalus in articulation with distal end of left tibia in anterior view; E–F, paratype (MNA.V.1752) right astragalus and calcaneum in proximal (E) and distal (F) views; G, holotype (MNA.V.175) right distal tarsal 3 in proximal view; H–I, referred (UCMP 130580) right distal tarsal 4 in proximal (H) and distal (I) views; J–M, referred (UCMP 130580) right metatarsus in anterior view, right metatarsal IV (J), right metatarsal III (K), proximal end of possible metatarsal II (L), distal end of metatarsal I (M). Abbreviations: a.lm, articular surface for the lateral malleolus of the tibia; a.mm, articular surface for the medial malleolus of the tibia; ap, ascending process; cal, calcaneum; fo, fossa on anterior surface of the ascending process.
Figure 24. *Scutellosaurus lawleri*, holotype (MNA.V.175) osteoderms. A–F, flat-based osteoderms (Morphotype A) in dorsal (A, C, E) and ventral (B, D, F) views. G–J, concave-based osteoderms (Morphotype B) in dorsal (G, H) and ventral (I, J) views. K–L, two-keeled osteoderm (Morphotype C) in dorsal (K) and ventral (L) views. M–P, hollow-based osteoderms (Morphotype D) in lateral (M, O) and ventral (N, P) views.
Figure 25. *Scutellosaurus lawleri*, referred two-keeled osteoderms (Morphotype C) in dorsal view. A, TMM 43664-1. B, MCZ VPRA-8792. C, MCZ VPRA-8799.
Figure 26. Life reconstruction of the thyreophoran ornithischian dinosaur *Scutellosaurus lawleri* from the Lower Jurassic Kayenta Formation rendered as an obligate biped with a speculative osteoderm arrangement. Artwork used with permission by Gabriel Ugueto, who retains the copyright (gabrielugueto.com).
Appendix B

The anatomy and palaeobiology of the early armoured dinosaur *Scutellosaurus lawleri* from the Kayenta Formation (Lower Jurassic) of Arizona

| Journal:       | Royal Society Open Science |
|----------------|----------------------------|
| Manuscript ID  | RSOS-201676                |
| Article Type:  | Research                   |
| Date Submitted by the Author: | 18-Sep-2020 |
| Complete List of Authors: Breeden III, Benjamin; The University of Utah, Geology & Geophysics; Natural History Museum of Utah Raven, Thomas; Natural History Museum Butler, Richard; University of Birmingham, School of Geography and Earth Sciences Rowe, Timothy; The University of Texas at Austin, Jackson School of Geosciences Maidment, Susannah; Natural History Museum |
| Subject:       | Palaeontology < EARTH SCIENCES |
| Keywords:      | Dinosauria, Ornithischia, Thyreophora, Kayenta Formation, Jurassic, *<i>Scutellosaurus lawleri</i>* |
| Subject Category: | Organismal and Evolutionary Biology |

https://mc.manuscriptcentral.com/rsos
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Ethics

Does your article include research that required ethical approval or permits?:
Yes

Statement (if applicable):
We describe fossil specimens collected from the lands of the Navajo Nation, which require the written permission from the Navajo Nation Minerals Department prior to publication. We sent a draft of our manuscript to the Navajo Nation Minerals Department for approval to publish on 14 August 2020, and we received approval in writing dated 17 August 2020.

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):
Detailed data regarding referred specimens are available as electronic supplementary material.

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):
B.T.B., T.J.R., R.J.B., and S.C.R.M. conceived of the study and wrote the manuscript; T.B.R. revised the manuscript. All authors gave final approval for publication and agree to be held accountable for the work performed therein.
The anatomy and palaeobiology of the early armoured dinosaur *Scutellosaurus lawleri* (Ornithischia: Thyreophora) from the Kayenta Formation (Lower Jurassic) of Arizona

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Abstract

The armoured dinosaurs, Thyreophora, were a diverse clade of ornithischians known from the Early Jurassic to the end of the Cretaceous. During the Middle and Late Jurassic, the thyreophorans radiated to evolve large body size, quadrupedality, and complex chewing mechanisms, and members of the group are some of the most iconic dinosaurs, including the plated Stegosaurus and the club-tailed Ankylosaurus; however, the early stages of thyreophoran evolution are poorly understood due to a paucity of relatively complete remains from early-diverging thyreophoran taxa. Scutellosaurus lawleri is generally reconstructed as the earliest-diverging thyreophoran and is known from over 70 specimens from the Lower Jurassic Kayenta Formation of Arizona, USA. Whereas Scutellosaurus lawleri is pivotal to our understanding of character state changes at the base of Thyreophora that can shed light on the early evolution of the armoured dinosaurs, the taxon has received limited study. Herein, we provide a detailed account of the osteology of Scutellosaurus lawleri, figuring many elements for the first time. Scutellosaurus lawleri was the only definitive bipedal thyreophoran. Histological studies indicate that it grew slowly throughout its life, possessing lamellar-zonal tissue that was a consequence neither of its small size nor phylogenetic position, but may instead be autapomorphic, and supporting other studies that suggest thyreophorans had lower basal metabolic rates than other ornithischian dinosaurs. Faunal diversity of the Kayenta Formation in comparison with other well-known Early Jurassic-aged dinosaur-bearing formations indicates that there was considerable spatial and/or environmental variation in Early Jurassic dinosaur faunas.
1. Introduction

Thyreophoran dinosaurs (the armoured dinosaurs - stegosaurs, ankylosaurs, and related forms) were important and diverse terrestrial herbivores from the Late Jurassic to the Late Cretaceous. They were characterised by the development of abundant cranial and postcranial osteoderms, expanded ribcages housing extensive guts, secondary quadrupedality, and medium–large body size. Thyreophorans split from their sister-clade, Neornithischia (including ornithopods, pachycephalosaurs, and ceratopsians) by the Early Jurassic and diverged into two major clades (Stegosauria and Ankylosauria, together forming the clade Eurypoda) by the Middle Jurassic [1,2,3,4,5,6]. However, the paucity of taxa known from these early phases of thyreophoran evolution (Late Triassic–Middle Jurassic) hampers attempts to understand thyreophoran systematics, palaeobiology and evolution.

Owen [7, 8] described the early thyreophoran Scelidosaurus harrisonii from the Early Jurassic (early Sinemurian–early Pliensbachian; [7]) of England. This taxon is represented by multiple well-preserved skeletons representing all parts of the skeleton; however, until recently very limited anatomical information had been published [10,11,12]. Other early thyreophorans are generally known from very limited material [13,14,15,16,17].

Colbert [18] described two specimens (MNA.V.175, MNA.V.1752) of a small armoured ornithischian from the Lower Jurassic Kayenta Formation of Arizona, USA (Fig. 1) as Scutellosaurus lawleri, emphasizing similarities to the early-branching ornithischian Lesothosaurus diagnosticus from the Early Jurassic of South Africa. Colbert [18] assigned Scutellosaurus lawleri to the family Fabrosauridae but suggested that Scutellosaurus lawleri could possibly be a “remote ancestor” of ankylosaurs and stegosaurs. Recent phylogenetic analyses and taxonomic reviews [1,2,3,4,5,19,20,21,22,23,24,25,26,27] have recovered Scutellosaurus lawleri as one of the earliest branching members of Thyreophora, and Fabrosauridae is now considered polyphyletic [1,3,5,20,25,28]. Detailed knowledge of the anatomy of Scutellosaurus lawleri is important for several reasons: 1) character polarisation during analyses of stegosaurian and ankylosaurian phylogeny and thyreophoran
functional evolution. This is especially important given there are several dozen specimens of
Scutellosaurus lawleri, including several relatively complete postcranial skeletons with associated cranial
material, making it one of the best-known early thyreophorans; 2) determination of the phylogenetic
position of Thyreophora within Ornithischia, and of the plesiomorphic character-states for Thyreophora in
broad-scale analyses of archosaurian and dinosaurian evolution; and, 3) reconstruction of the character-
state changes that occurred at the Thyreophora–Neornithischia split, and during early thyreophoran
evolution.

Despite the obvious importance of Scutellosaurus lawleri, little further descriptive or systematic
work has been carried out since that of Colbert [18]. Rosenbaum & Padian [23] referred six specimens
from the collections of the University of California Museum of Paleontology (UCMP) to Scutellosaurus
lawleri but provided only very brief descriptions of most elements. Tykoski [29] figured one additional
specimen reposited at The University of Texas Vertebrate Paleontology Collections (TMM), and Breeden
& Rowe [30] described several additional specimens from TMM. Furthermore, there are inaccuracies in
the anatomical information provided by Colbert [18] and Rosenbaum & Padian [23], the only previous
diagnosis [18] did not attempt to distinguish autapomorphies and symplesiomorphies, and many
phylogenetically informative features have not been previously discussed. The primary aim of this paper
is to expand and emend previous anatomical descriptions, providing new data on non-eurypodan
thyreophoran morphology and new life reconstruction for Scutellosaurus lawleri.

1.1. Institutional abbreviations

AMNH, American Museum of Natural History, New York, NY, USA; CAMSM, Sedgwick Museum of
Earth Sciences, University of Cambridge, Cambridge, UK; CMN, Canadian Museum of Nature, Ottawa,
Ontario, Canada; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA;
MCZ VPRA, the designated prefix for fossil reptile and amphibian specimens at MCZ; MNA, Museum of
Northern Arizona, Flagstaff, AZ, USA; NHMUK, Natural History Museum (formerly NHM, BMNH),
London, UK; ROM, Royal Ontario Museum, Toronto, Canada; SAM-PK, Iziko South African Museum,
Cape Town, South Africa; SGWG, Greifswaler Geologische Sammlungen, Universität Greifswald (formerly Ernst-Moritz-Arndt-Universität Greifswald), Greifswald, Germany; TMM, The University of Texas Vertebrate Paleontology Collections (historically part of the Texas Memorial Museum, formerly referred to as Vertebrate Paleontology Laboratory), Austin, TX, USA; UCMP, University of California Museum of Paleontology, Berkeley, CA, USA; UCMP V, designated prefix for UCMP localities; UTCT, High-Resolution X-ray CT Facility at The University of Texas at Austin; ZDM, Zigong Dinosaur Museum, Zigong, Sichuan, People's Republic of China.

2. Geologic setting

The specimens of *Scutellosaurus lawleri* described below were all collected from the Lower Jurassic Kayenta Formation on lands of the Navajo Nation in northern Arizona. The Kayenta Formation is one of several formations comprising the Upper Triassic to Lower Jurassic Glen Canyon Group on the Colorado Plateau. Together they comprise a thick assemblage of terrestrial sediments that accumulated in a back-arc basin formed by subduction of the Pacific plate under the western margin of North America [31]. The Kayenta Formation lies unconformably atop the Dinosaur Canyon Member of the Moenave Formation, which is a mixture of aeolian and ephemeral fluvial deposits formed mostly by sheet-wash run-off. Without a sustained fluvial system, the Moenave Formation preserved very few vertebrate fossils [32, 33]. The Triassic-Jurassic boundary probably lies near the middle of the Moenave Formation [33,34,35]. The upper boundary of the Kayenta Formation interfingers with the upper Lower Jurassic aeolian Navajo Sandstone [36,37]. The Glen Canyon Group is made up almost entirely of fine, well-sorted sandstones, and it is widely understood to represent an immense, long-lived dune field or erg that accumulated from the latest Triassic until the end of the Early Jurassic. During this time, the region was characterized by an arid climate, with episodic wet intervals that deposited local fluvial and freshwater lacustrine sediments [33,36,37,38,39,40]. It was during one or more of these episodic wet intervals in which the specimens described below were buried [33].
The Kayenta Formation extends across the southern Colorado Plateau from eastern Arizona to western Utah. Geologists have divided it into a ‘typical’ or ‘sandy facies’ that forms the immense Vermillion Cliffs, which stretch east to west across the southern Plateau, and a ‘silty facies’ that is restricted to exposures in eastern Arizona [36,41,42,43]. The major exposures of the silty facies are along the eastern walls of the Little Colorado River Valley. Over some nearly a century of field research, fossils have been discovered throughout exposures of the Kayenta Formation. However, the most productive exposures by far are those of the silty facies, which represents a geographically and temporally localized fluvial interlude in what was otherwise a vast, prolonged aeolian landscape. The silty facies is a heterogeneous assemblage of coarse- to fine-grained clastic sediments that accumulated in channels of cross-bedded sands and lenses of overbank mud that represent a multi-channel fluvial system with low sinuosity and frequent flash flood stages that pulsed through sand dunes [36,39,40]. Also present are localized shallow freshwater lake and marsh deposits that produced lenses of freshwater limestone, and localized beds of blue mudstone that are rich in tetrapod fossils and that also contain ostracods [44] and carbonized sphenopsids [33]. Complex interfingering along their lengths of the Navajo Sandstone and the silty facies of the Kayenta Formation suggests that dominant southeasterly winds blew Navajo erg sands into the Kayenta stream systems [37]. Palaeocurrent analyses indicate that these streams generally flowed to the northwest and were deflated by the strong southeasterly winds. As a result, the fluvial system deposited sand along the dune fields, and continually recycled sediment from the Navajo to the Kayenta system and back again [31,33,37,45,46].

By far the greatest numbers and taxonomic diversity of Kayenta vertebrate fossils have been collected from exposures of the silty facies, including the *Scutellosaurus lawleri* material described below. Productive exposures of the silty facies are mostly confined to Moenkopi Wash, near Tuba City, and to a line of cliffs extending to the south that is made up of the Chinle, Moenave, Kayenta, and Navajo formations, in ascending order [18,29,33,47,48,49,50]. This escarpment bears various names, including
‘Adeii Eechii Cliffs’ [51,52], the ‘Tloi Eechii Cliffs’ [53], and the Echo Cliffs [43]. The sources of these names are unknown to us, nor do the local residents use or even recognize them.

To the south of Moenkopi Wash, the Adeii Eechii escarpment forms the western edge of the Moenkopi Plateau and the eastern flank of the Little Colorado River valley. Below the Adeii Eechii Cliffs is Ward Terrace, famous for its extensive badlands exposures of the Triassic Moenkopi and Chinle formations that are rich in vertebrate (mostly tetrapod) fossils [32]. From Moenkopi Wash southwards, exposures of the silty facies of the Kayenta Formation are steep and present little surface area for prospecting, although a few fossils have been recovered [54]. However, at the southern-most extent of the Adeii Eechii Cliffs, the underlying Dinosaur Canyon member of the Moenave Formation thickens to form 100-meter tall cliffs that broaden considerably to the west above Ward Terrace. Resting on this broad bench are expansive and heavily dissected badlands of the silty facies of the Kayenta Formation from which the Scutellosaurus lawleri specimens described here were collected.

Most of the Scutellosaurus lawleri specimens were collected from fluvial and blue mudstone layers that lie approximately 20–30 meters above the lower boundary of the Kayenta Formation. Among these is the type locality of Sarahsaurus aurifontanalis [33,55]. During laboratory preparation of the Sarahsaurus aurifontanalis type specimen from its encasing sandstone matrix, Adam Marsh extracted a large sample of detrital zircon crystals for dating. Preliminary laser ablation ICP-MS detrital zircon U-Pb results yielded a date of 183.7±2.7 Ma [34]. This date establishes this part of the Kayenta Formation (recorded in most field notes as the “middle third” of the Kayenta Formation) in the Pliensbachian and Toarcian stages of the Lower Jurassic. This is a considerably younger date than earlier U-Pb attempts based on smaller zircon samples that estimated a Triassic age for the Kayenta Formation [46]. The Early Jurassic U-Pb date is entirely consistent with Early Jurassic age estimates of the Kayenta Formation based on biostratigraphy [44,48,49,50,56,57,58].

3. History of discovery of the ornithischian dinosaurs of the Kayenta Formation
The first ornithischian dinosaur remains from the Kayenta Formation were discovered in 1971 by Mr. David Lawler, then a summer intern at the MNA. He collected a nearly complete skeleton of an armoured ornithischian dinosaur that would become the holotype specimen of *Scutellosaurus lawleri* (MNA.V.175) southeast of the topographic landmark Rock Head at MNA Locality 219. A second larger, but less complete, specimen of *Scutellosaurus lawleri* (MNA.V.1752) was discovered along Gold Spring Wash in 1977 by Mr. William Amaral as part of the Museum of Comparative Zoology (MCZ), Harvard University, in a joint expedition with MNA, under permits issued to MNA and funded by the National Science Foundation. This locality (MNA Locality 291, = MCZ Field Number 77 AR/4) is approximately 16 km to the northwest of the holotype locality (Fig. 1). These two specimens were described by the late Edwin H. Colbert, who had become a Research Associate of the MNA following his retirement from a long career as Curator of Fossil Reptiles at the American Museum of Natural History [18]. The holotype specimen comprises a nearly complete disarticulated postcranial skeleton with a few fragments of the skull preserved. Colbert [18] also referred to a femur from a much larger ornithischian than *Scutellosaurus lawleri* collected during this time; however, he did not cite a specimen number for the femur. We infer that this specimen is MNA.V.109, a large left femur referred to *Dilophosaurus wetherilli* by Gay [59].

Exploration of the silty facies continued during the late 1970s and early 1980s and resulted in the discovery of more ornithischian material by field parties from MNA, MCZ, and UCMP (Fig. 1). In 1981, William W. Amaral of the MCZ collected a partial skeleton of a juvenile heterodontosaurid (MCZ VPRA-9092) from a microvertebrate locality near Gold Spring [60], now known as the *Eocaecilia* Quarry [61]. This specimen has been mentioned by several authors [20,62,63] but still awaits a detailed description. In October 1981, James Clark of the UCMP discovered osteoderms of an animal larger than *Scutellosaurus lawleri*. Similar osteoderms were previously reported by Colbert ([18]; MNA.V.96, MNA.V.136) and attributed to aetosaurs and used in support of his argument of a Triassic age for the Kayenta Formation. However, Padian [58] noted similarity between these osteoderms and those of the
Early Jurassic thyreophoran dinosaur *Scelidosaurus harrisonii* from the Charmouth Mudstone Formation of England and referred the osteoderms from the Kayenta Formation to that species. Norman *et al.* [24] suggested a more conservative assignment of “Thyreophora indet.” for these osteoderms, which has been adopted by some authors [64] while others have opted for a cautious assignment of “*Scelidosaurus sp.*” [29]. Regardless of their taxonomy, the presence of these osteoderms in the Kayenta Formation was used by Padian [58] to support the argument for an Early Jurassic age of the Kayenta Formation, an age assignment that is supported by the presence of both tritylodontids [65,66] and ostracods [44] with Early Jurassic affinities.

Field efforts by the UCMP during the early 1980s (Fig. 1) also led to the discovery of at least six new specimens of *Scutellosaurus lawleri*, which were later described by Rosenbaum & Padian [23]. The most complete of these specimens is UCMP 130580, an associated partial skeleton that preserves several cranial elements absent in the holotype.

The most recent fieldwork in the Kayenta Formation to yield new ornithischian specimens was conducted between 1997 and 2000 by The University of Texas (Fig. 1), whose vertebrate palaeontological collections were an administrative unit of the Texas Memorial Museum (TMM) at that time. This work yielded over 40 new specimens of *Scutellosaurus lawleri*, additional osteoderms from a larger unnamed thyreophoran like those reported by Padian [58], and other indeterminate ornithischian specimens [30,67]. The most significant of those specimens are TMM 43663-1 and TMM 43664-1, both of which are partial skeletons of *Scutellosaurus lawleri* that preserve portions of the skull and pelvis not known from any other specimen [30].

### 4. Systematic Palaeontology

Dinosauria [68]

Ornithischia [69]

Thyreophora [70] *sensu* [71]
Genus *Scutellosaurus* [18]

*Type Species: Scutellosaurus lawleri* Colbert, 1981 by monotypy.

*Scutellosaurus lawleri* [18]

*Etymology:* *Scutellosaurus*, from *scutellum* (Latin, a little shield) and *sauros* (Greek, lizard or reptile); *lawleri*, to honour David Lawler, who discovered and collected the holotype in 1971 [18].

*Holotype:* MNA.V.175, relatively complete postcranial skeleton, with some cranial fragments ([18]: figs 6–14, 16–24, 26–34; [22]: figs 20.1C–D, 20.3A, D; [24]: figs 15.1C–D, 15.5A, D). This specimen was first published using the retired catalogue number “MNA P1.175” [18].

*Holotype locality:* MNA Locality 219-1, Rock Head (“*Scutellosaurus lawleri* Locality”). Ward Terrace, Coconino County, Navajo Nation, Arizona, USA (Fig. 1).

*Paratype:* MNA.V.1752, an incomplete postcranial skeleton of an individual slightly larger than the holotype ([18]: figs. 15, 25, 31). This specimen was first published using the specimen number “MNA P1.1752” [18].

*Paratype locality:* MNA Locality 291-5, Gold Spring. Ward Terrace, Coconino County, Navajo Nation, Arizona, USA (Fig. 1).

*Referred specimens:* MNA.V.3133, MNA.V.3137, MNA.V.12395, UCMP 130580, UCMP 170829, UCMP 130581, UCMP 175166, UCMP 175167, UCMP 175168, MCZ VPRA-8792, MCZ VPRA-8793, MCZ VPRA-8794, MCZ VPRA-8795, MCZ VPRA-8796, MCZ VPRA-8797, MCZ VPRA-8798, MCZ VPRA-8799, MCZ VPRA-8800, MCZ VPRA-8801, MCZ VPRA-8802, MCZ VPRA-8803, MCZ VPRA-8804, MCZ VPRA-8805, MCZ VPRA-8806, MCZ VPRA-8808, MCZ VPRA-8810, MCZ VPRA-8820, TMM 43647-7, TMM 43647-8, TMM 43648-13, TMM 43656-2, TMM 43656-3, TMM 43656-5, TMM 43661-1, TMM 43663-1, TMM 43664-1, TMM 43664-2, TMM 43669-5, TMM 43669-6,
TMM 43690-6, TMM 43691-18, TMM 43691-20, TMM 45608-3, TMM 45609-4, TMM 45609-5, TMM 45609-6, TMM 47001-1. See Supplementary Material for detailed inventory of each MNA, UCMP, and MCZ specimen listed and discussed herein. For a detailed inventory of TMM specimens, see Breeden and Rowe [30].

**Stratigraphic Occurrence and Provenance:** All known specimens of *Scutellosaurus lawleri* are derived from the ‘silty facies’ of the Kayenta Formation, Glen Canyon Group (Early Jurassic: Hettangian–Toarcian; [34]; [72]; Fig. 1) in Coconino County, Navajo Nation, Arizona, USA. Detailed locality information for all specimens described herein is on file at MCZ, MNA, TMM, and UCMP and is available from those institutions to qualified researchers upon request; however, general locality information for each individual specimen is provided within the specimen inventory (Supplementary Material).

**Revised diagnosis.** *Scutellosaurus lawleri* differs from all other ornithischians by the possession of the following autapomorphies: frontals are exceedingly narrow, maximum anteroposterior length more than 350% of minimum interorbital width; facets for atlantal neural arch extend onto lateral surface of odontoid process; cervical vertebrae with very prominent and rugose ventral keels; preacetabular process of ilium is narrow dorsoventrally relative to length, dorsal and ventral surfaces are drawn out medially into distinct flanges (modified from [1,30]).

**Comments.** *Scutellosaurus lawleri* is the most abundantly recognized dinosaurian taxon from the Kayenta Formation ([29]; pers. obs.); however, in some cases, specimens referred to *Scutellosaurus lawleri* are represented only by small assemblages of associated but disarticulated ornithischian bones and/or bone
fragments lacking diagnostic autapomorphies of *Scutellosaurus lawleri* [73,74]. These specimens nearly all preserve osteoderms superficially similar to those of MNA.V.175, and their size and shape are more consistent with the type and referred specimens of *Scutellosaurus lawleri* than to the two other unnamed ornithischian taxa that have been recognized from the Kayenta Formation, which at present include a larger thyreophoran (MNA.V.96, MNA.V.136, UCMP 130056: [58]; TMM 45608-1: [29]) and a heterodontosaurid (CZ VPRA-9092: [60,63]).

Specimens of *Scutellosaurus lawleri* reposited at MNA were initially published by Colbert [18] using the catalogue number format “MNA P1.####” (e.g., “MNA P1.175”, “MNA P1.1752”); however, shortly after that publication in either 1982 or 1983, MNA changed their catalogue number format for vertebrate fossil specimens to “MNA V####” (e.g., “MNA V175,” “MNA V1752”). That change was not published at the time, and as a result, several subsequent publications cited the retired “MNA P1.####” catalogue numbers used by Colbert [18] for the type specimens of *Scutellosaurus lawleri* [1,16,17,23,28,29,75,76,77]. Additionally, the figure captions of Colbert [18] erroneously cited MNA.V.175 (“MNA P1.175”) and MNA.V.1752 (“MNA P1.1752”) as “MNA Pl. 175” and “MNA Pl. 1752,” respectively, and these erroneous specimen numbers have proliferated in the literature [78,79,80]. Several additional erroneous specimen numbers have been published for MNA.V.175 and MNA.V.1752, including “MNA 175” and “MNA 1752” [81,82]; “MNA Pl.175” [83,84]; “MNA Pl.175” and “MNA Pl.1752” [2,79,80,85,86,87,88]; and “MNA Pl.1752” [89]. These variations are in part a result of the confusion of the numeral *one* (“1”) with the uppercase letter *eye* (the first letter in the word “India”) and the lowercase letter *l’* (the first letter in the word “lima”), both by researchers and internally by MNA cataloguers.

Subsequently, when MNA palaeontology collection records were first digitized in 2000, representatives of the database provider recommended that collections managers not use spaces in specimen numbers, and the catalogue number format “MNA.V.####” was adopted for vertebrate fossil specimens. For published specimen numbers to remain consistent with the MNA database, the catalogue
number format of “MNA.V.####” is now preferred for all MNA vertebrate fossil specimens (J. Gillette, pers. comm.). This format is reflected herein and should be used henceforth when citing these specimens.

Six specimens were referred to *Scutellosaurus lawleri* by Rosenbaum & Padian [23] and are reposited at the University of California Museum of Paleontology (UCMP). These specimens were collected between 1981 and 1983 by field parties led by James M. Clark under permits issued to the MNA (J. Clark, pers. comm.). All six of these specimens were reported to have been collected from the same locality (UCMP V85010 – “Lower Blue”) by Rosenbaum & Padian [23]; however, only four of the six specimens (UCMP 130580; UCMP 175166; UCMP 175167; UCMP 175168) were actually collected from that locality. The other two specimens UCMP 170829 and UCMP 130581 were collected from the localities UCMP V85013 (“Gold Springs 1”) and UCMP V84235 (“Red Knob”), respectively. Additionally, UCMP 130580 was sometimes erroneously cited as “UCMP 130850” by Rosenbaum & Padian [23] in their report of these referred specimens.

All referred specimens of *Scutellosaurus lawleri* that are reposited at MCZ were collected during joint expeditions between MCZ and MNA in 1978 and 1982 under Navajo Nation Antiquities Permits issued to MNA. Interestingly, several MCZ specimens that were collected during the 1978 field season were referred in the field to “cf. *Kayentasaurus lawleri,*” which reflects Colbert’s tentative name for *Scutellosaurus lawleri* prior to its eventual description in 1981 (H.-D. Sues, pers. comm.).

5. Osteological Description

The following description is based upon the holotype specimen of *Scutellosaurus lawleri* (MNA.V.175) unless otherwise noted.

5.1. Skull

5.1.1 Premaxilla (Fig. 2)

The premaxilla (Fig. 2) comprises a horizontally aligned main body (beneath the external naris), which is
longer anteroposteriorly than wide mediolaterally. Posterodorsally directed maxillary (= “posterolateral process”) and nasal processes arise from this main body. The maxillary process is broken, and only the base is preserved on each side. The nasal process (Fig. 2A–C, np) projects from the anteromedial corner of the element at an angle of ~33˚ to the long axis of the main body, forming the anterior margin of the external naris. There is a sutural surface for the opposing element at the anterior end of the medial surface of each premaxilla (Fig. 2B). Together, the premaxillae form a long, narrow snout with a rounded anterior tip in dorsal view (Fig. 2C). As in other early ornithischians (e.g., Lesothosaurus diagnosticus: [28]) the first tooth of the premaxilla is inset a short distance from the anteriormost tip of the premaxilla; the anteriormost tip has a rugose, pitted texture, indicating the presence of a horny beak. There are six alveoli (Fig. 2D), indicating six premaxillary teeth, although the teeth themselves are missing and only the tips of a few replacement crowns are present. Six premaxillary teeth are also present in Lesothosaurus diagnosticus (NHMUK PV RUB17) and Laquintasaura venezuelae (MBLUZ P.5014). By contrast, some other early ornithischian dinosaurs have three (heterodontosaurids: [63]) or five (e.g., Agilisaurus louderbacki: [90]), the early thyreophorans Emausaurus ernsti (SGWG 85; [14]) and Scelidosaurus harrisonii (BRSMG Ce12785) also have five, and the early-diverging stegosaur Huayangosaurus taibaii (ZDM T7001; [91]) has seven.

The horizontal premaxillary palate is virtually absent between the two anteriormost teeth, but mediolaterally broadened posteriorly (Fig. 2D, pp), although the palate is comparatively narrow, and like that of other early ornithischians [28,63,76]. A deep and elongate anteriorly tapering groove (Fig. 2B, gr) is present on the medial surface of the premaxilla, which can be inferred to have accommodated a well-developed anterior process of the maxilla. A premaxillary foramen is present in the anteroventral corner of the narial fossa (MNA.V.175, 18: fig. 9A; Fig. 2A, fo), like the condition in other early ornithischians [28,63,76].

5.1.2. Maxilla (Fig. 3)
The left maxilla (Fig. 3A–B) of the holotype was misidentified by Colbert [18] as the right maxilla, and the two fragments that were identified as the left maxilla by Colbert [18] likely represent the right maxilla (Fig. 3C–F). In the left maxilla of MNA.V.175, there are seven teeth present, as well as three empty alveoli, and the tooth row is slightly inset from the lateral margin of the bone, similar to the condition in *Lesothosaurus diagnosticus* [28], *Laquintasaura venezuelae* (MBLUZ P.5016) and *Emausaurus ernsti* (SGWG 85). However, this buccal emargination is not as well developed as that in eurypodans [92, 93]. The tips of unerupted replacement teeth are also present medial and dorsal to the tooth row, lying within replacement tooth foramina (Fig. 3A, rtf). The maxillary teeth show an alternating eruption pattern in which every other tooth is more advanced in eruption than the intervening tooth. The tooth row is oriented in a straight line in ventral and medial views. The ascending process is mostly missing, with only the base being preserved.

Owing to incomplete preservation, it is not possible to determine whether a secondary maxillary palate is present. As in most ornithischians [94], a supra-alveolar lamina (Fig. 3B, sal) projects dorsally above the posterior end of the tooth row at the lateral margin of the bone, forming the ventral margin of the antorbital fenestra. Medial to this, a posteriorly opening groove is present on the dorsal surface of the bone, representing the groove for the neurovascular bundle. In *Scelidosaurus harrisonii* (NHMUK PV R1111) this neurovascular groove connects with the row of lateral neurovascular foramina positioned above the tooth row. If such lateral foramina were present in *Scutellosaurus*, as is the normal condition in ornithischians, they are obscured by the nasals.

### 5.1.3. Nasal (Fig. 3B)

Although portions of the nasals are preserved in MNA.V.175 (Fig. 3B, n), these are fractured and closely appressed to the left maxilla, so they yield limited anatomical information. A nearly complete nasal is preserved in TMM 43664-1 [30], from which the following comments are primarily derived. The nasal is mediolaterally arched with a concave ventral surface, as in *Scelidosaurus harrisonii* (NHMUK PV
A well-developed midline depression is absent, in contrast to many other early ornithischians (e.g., *Agilisaurus louderbacki*, ZDM 6011; *Heterodontosaurus tucki*, SAM-PK-K1332; *Hexinlusaurus multidens*, ZDM T6001), and the nasals articulate medially along a nearly straight contact. The dorsal surface of the nasal exhibits cortical remodelling in TMM 43664-1, as in *Scelidosaurus harrisonii* (NHMUK PV R1111) and stegosaurs (e.g., Stegosauria indet., CMNH 106; *Miragaia longicollum*, ML 433), and the ventral surface is relatively smooth. There are no anteroposteriorly-extending ridges on the dorsal surface of the nasal, unlike the condition in *Paranthodon africanus* (NHMUK PV OR47338; [4]) and *Hesperosaurus mjosi* (DMNH 29431; [95]).

### 5.1.4. Frontal (Fig. 4A–B)

Although a posterior portion of a left frontal is preserved in MNA.V.175 [30], more complete frontals are preserved in UCMP 130580 (Fig. 4A–B), TMM 43663-1, and TMM 43664-1 [30]. The frontals are much longer anteroposteriorly than wide mediolaterally, a feature we interpret to be an autapomorphy of *Scutellosaurus*. The frontals widen towards their posterior ends and are dorsoventrally thickened where they form a midline contact with one another. They are not extensively sculpted, but there is some weak sculpting of the dorsal surface immediately adjacent to the parietal contact and supratemporal fossa at the posterior end of the element. In *Emausaurus ernsti* (SGWG 85) the frontals are similarly unsculpted, except for a small region around the anterior orbital margin. The frontals are gently arched along their length. As in *Lesothosaurus diagnosticus* [28: fig. 12B], there is an elongate facet on the anterolateral surface of the frontal for a tapering posterior process of the prefrontal (Fig. 4A, a.pf). As noted by Maidment & Porro [96], there are a series of fine striations along the lateral margin of the frontal of UCMP 130580 (Fig. 4A, str), which were interpreted to represent an osteological correlate for soft tissue, and these striations are also present on the frontals of TMM 43663-1 and TMM 43664-1 [30] and on the frontals of *Emausaurus ernsti* (SGWG 85). The frontal formed part of the dorsal rim of the orbit (Fig. 4A–B, orb), as in most early ornithischians [28,63,76,90] but differing from the condition in *Scelidosaurus harrisonii* (NHMUK PV R1111), ankylosaurs [97], and stegosaurs [92], in which
supraorbital bones were incorporated into the skull roof and separated the frontals from the dorsal rim of the orbit. Medial to the orbital margin on the ventral surface of the frontal, there is an anteroposteriorly extending wide groove for the olfactory tract of the brain (Fig. 4B, olft). The posterior portion of the frontal possesses a prominent supratemporal fossa to accommodate the temporal musculature (Fig. 4A, stfo), as in saurischians [19] and some early ornithischians [28,76,98].

5.1.5. Parietal (Fig. 4A–B)

The parietal of *Scutellosaurus lawleri* is known only from a fragment in UCMP 130580 (Fig. 4A–B). Anteriorly, the parietal formed a nearly straight, interdigitating, transverse suture with the frontals. On each side of the parietal there is a sharp ridge (Fig. 4A, ri) that demarcates the supratemporal fossa and is continuous with the ridge defining the supratemporal fossa (Fig. 4A, stfo) on the frontal. These ridges on the parietal converge posteriorly, and together define a flat, triangular area on the dorsal surface of the bone.

5.1.6. Lacrimal

The lacrimal of *Scutellosaurus lawleri* is known only from TMM 43664-1, which preserves both right and left lacrimals [30]. The lacrimal comprises a subquadranular main body with a curved and tapering posteroventral process, similar in morphology to that of *Lesothosaurus diagnosticus* [28] and *Emausaurus ernsti* (SGWG 85). The lateral surface of the body is cortically remodelled, in contrast to that of *Emausaurus ernsti* (SGWG 85), where it is smooth. The antorbital fossa extends onto the anteroventral portion of the main body of the lacrimal of *Scutellosaurus lawleri*, and the posteroventral process of the lacrimal forms the posterodorsal margin of the antorbital fenestra. It is unclear whether the lacrimal contacted the prefrontal.

5.1.7. Jugal (Fig. 4C–D)

A small portion of a left jugal is present in MNA.V.175, and a mostly complete right jugal is present in...
UCMP 130580 (Fig. 4C–D), but the most complete jugals are known from TMM 43663-1 and TMM 43664-1 [30]. Sutural surfaces are here identified based upon comparison with the disarticulated holotype skull of *Scelidosaurus harrisonii* (NHMUK PV R1111). The lateral surface of the jugal ventral to the dorsal process and ventral to the ventral margin of the orbit is ornamented with several weak anterodorsal-to-posteroventrally extending, anastomosing ridges and shallow grooves (Fig. 4C, orn). This ornamentation is similar in position and form to that of *Emausaurus ernsti* (SGWG 85) and *Scelidosaurus harrisonii* [11], although it is less well developed than in the latter.

The anterior process of the jugal is mediolaterally expanded beneath the orbit (Fig. 4C). This mediolateral expansion does not occur along the entire anterior process but is confined to a short section immediately anterior to the dorsal process of the jugal. A medially and slightly ventrally facing facet for the ectopterygoid is present on the medial surface of this expansion (Fig. 4D, a.ect), like the condition in *Emausaurus ernsti* (SGWG 85) and *Scelidosaurus harrisonii* (NHMUK PV R1111). Two sutural surfaces are present on the jugal for the maxilla (Fig. 4C–D, a.max): an extensive ventrally and slightly medially facing surface, and a shorter and less well defined ventrally and laterally facing surface. The sutural surface for the lacrimal, positioned on the dorsal surface of the anterior end of the process in *Scelidosaurus harrisonii* (NHMUK PV R1111), may be represented in *Scutellosaurus lawleri* by a small dorsal notch in the extreme end of the anterior process of the jugal of TMM 43664-1. The dorsal process of the jugal is anteroposteriorly narrow and has an elongate narrow groove on the anterior portion of the lateral surface to articulate with the ventral process of the postorbital (Fig. 4C, a.po), as in *Emausaurus ernsti* (SGWG 85). The posterior process of the jugal has a V-shaped, anteriorly tapering depression on its medial surface, which articulates with the quadratojugal (Fig. 4D, a.qj); a facet with similar morphology is present in *Scelidosaurus* (BRSMG Ce12785).

5.1.8 Postorbital (Fig. 4E–F)

TMM 43663-1 and TMM 43664-1 possess the best preserved postorbitals [30], but a small portion of a
left postorbital is present in UCMP 130580 (Fig. 4E–F). The postorbital is a triradiate element with anteromedial, posterior, and ventral processes, which articulate with the frontal, squamosal, and jugal, respectively. The anterior margin of the postorbital between the anteromedial and ventral processes is rounded and forms the posterodorsal border of the orbit (Fig. 4E, orb). The anterior process is the shortest of the three processes and bifurcates anteriorly [30]. The posterior and ventral processes are both slender [30], similar to those of *Lesothosaurus diagnosticus* [28,99], heterodontosaurids [63,76], and *Emausaurus ernsti* (SGWG 85), but in contrast to that of *Scelidosaurus harrisonii* (NHMUK PV R1111) in which the main body of the postorbital and the posterior and ventral processes are more robust. The posterior and ventral processes taper towards their tips, as in other early thyreophorans (*Emausaurus ernsti*, SGWG 85; *Scelidosaurus harrisonii*, NHMUK PV R1111).

5.1.9 Quadratojugal

The quadratojugal is only known from TMM 43664-1 [30]. The quadratojugal is mediolaterally compressed and overlies the lateral ramus of the quadrate. There is a prominent foramen on the medial surface of the quadratojugal that does not extend through to the lateral surface [30]. *Scelidosaurus harrisonii* (NHMUK PV R1111) possesses a dorsal process of the quadratojugal, but this part of the bone is not preserved in TMM 43664-1 so its presence or absence in *Scutellosaurus lawleri* cannot be determined.

5.1.10 Squamosal

Although a possible portion of the squamosal in MNA.V.175 was noted by Colbert [18], we could not locate this; however, a complete squamosal is preserved in TMM 43663-1 [30]. This is a triradiate element comprising anterior, prequadratic, and postquadratic processes. The lateral surface of the squamosal is deeply excavated by a smooth concavity. The anterior process bifurcates into dorsal and ventral projections that flank the posterior process of the postorbital to form the upper temporal bar, and the prequadratic process is anteroposteriorty thin and poorly preserved. The postquadratic process is
anteroposteriorly broader than the prequadratic process and is the shortest of the three processes.

5.1.11 Quadrate (Fig 4G–K)

The quadrate is not known from the holotype or paratype specimens but is preserved in a number of other specimens (e.g., UCMP 130580 [Fig. 4J–K], UCMP 175166: [23]; TMM 43647-7, TMM 43687-121, TMM 43663-1, TMM 43664-1:[30]; MCZ VPRA-8795 [Fig. 4G–I]; MCZ VPRA-8797). The head is arched posteriorly relative to the shaft (Fig. 4H) and is not fused to the paroccipital process. It is moderately compressed in lateral view, like that of *Stegosaurus* (e.g., NHMUK PV R36730). The pterygoid wing (Fig. 4J–K, ptw) is best preserved in TMM 43664-1, and is subtriangular, dorsoventrally tall, tapers anteromedially, and bears a shallow fossa [30: fig. 10K–L], like that of *Stegosaurus* (NHMUK PV R36730). The lateral surface of the ventral end of the shaft bears an extensive articular surface for the quadratojugal (Fig. 4J, a.qj), which ventrally would have closely approached the quadrate condyles. As noted by Rosenbaum & Padian [23], the medial condyle is weakly enlarged relative to the lateral and resembles that of *Scelidosaurus harrisonii* (NHMUK PV R1111), and the lateral condyle tapers laterally where it curves anteriorly. A facet is present on the posteroverentral surface of the condyles in UCMP 130580 (Fig. 4J, fc), but this is not present in any other specimen that preserves a quadrate (e.g., TMM 43663-1, TMM 43687-121). Such a facet does not appear to be present in *Scelidosaurus harrisonii* (NHMUK PV R1111) whereas the quadrate is not preserved in *Emausaurus ernsti* (SGWG 85).

5.1.12 Braincase (Fig. 5)

Only the basioccipital and the paroccipital process are known from the braincase of *Scutellosaurus lawleri*, and all examples of these elements are preserved disarticulated. None are well enough preserved to determine the exits of cranial nerves.

The basioccipital is preserved in MNA.V.175 (Fig. 5A–B), UCMP 130580 (Fig. 5C–D), and MCZ VPRA-8797 (Fig. 5E–H). A midline ridge is present on the ventral surface of the basioccipital
separating the basioccipital recesses (Fig. 5F, bor); a similar ridge is also present in *Lesothosaurus diagnosticus* [99], *Emausaurus ernsti* (SGWG 85) and *Scelidosaurus harrisonii* (NHMUK PV R1111). Anterior to the basioccipital recesses are rugose basal tubera (Fig. 5F–G, bt). The occipital condyle (Fig. 5F, H, occ) is convex and reniform in posterior view, with a concave dorsal surface demarcating the floor of the foramen magnum (Fig. 5H, fm). On the dorsal surface and lateral to the margin of the foramen magnum are roughened posterolaterally-oriented surfaces for articulation with the exoccipitals (Fig. 5E, H, a.ex). The endocranial floor (Fig. 5E, ef) on the dorsal surface of the basioccipital is generally smooth and concave except for a thin median ridge at the anterior end.

Paroccipital processes are preserved in TMM 43663-1 [30] and MCZ VPRA-8797 (Fig. 5I–J). The paroccipital process flares laterally from the main body of the exoccipital-opisthotic. In posterior view, there are notches along the dorsal edge of the main body of the exoccipital-opisthotic presumably for articulation with the supraoccipital (Fig. 5I, a.so) and parietal (Fig. 5I, a.p). In anterior view, there is a rough subtriangular surface that is pierced by a small foramen, and there is a medial notch for articulation with the prootic (Fig. 5J, a.pr). Dorsal to this surface, there is a groove for articulation with the supraoccipital (Fig. 5J, a.so). The distal end of the paroccipital process is dorsoventrally expanded but is not pendant.

5.1.13 Dentary (Figs 6, 7A–C)

A nearly complete left (Fig. 6A–B) and partial right (Fig. 6C-D) dentary are preserved in the holotype, and several partial dentaries are preserved in other specimens (e.g., MCZ VPRA-8797: Fig. 7A–C). The dentary tooth row is slightly sinuous in dorsal view (Fig. 7C), but to a much lesser degree than that of derived nodosaurs (e.g., *Panoplosaurus mirus*, ROM 1215: [100]), and in lateral and medial views; the tooth row is sinuous with the anterior end downturned (Figs. 6–7), as in other thyreophorans (e.g., *Scelidosaurus harrisonii*, NHMUK PV R1111; *Emausaurus ernsti*, SGWG 85; [21]), but differing from early ornithischians [28,63,76]. There is a ridge on the dorsal half of the lateral surface that laterally
defines a narrow buccal emargination posterior to the tenth tooth position (Figs. 6A, 7A, be). The ventral margin of the dentary is relatively straight, in contrast to the sinuous ventral margin in nodosaurs [26]. Colbert [18: 11] identified an unusual rugose depression on the ventral surface of the left dentary of MNA.V.175 as a possible pathologic feature (Fig. 6A); a similar depression is also present in an equivalent position of the right dentary, but is not present in the referred dentary of MCZ VPRA-8797 (Fig. 7A–C).

There is a broad, flat facet on the medial surface of the dentary for the symphysis (Fig. 6B, sym), although this is not ‘spout-shaped’ as in most other ornithischians [21,28], indicating that the articulation between the lower jaws would have been V-shaped in dorsal view. The tooth row appears to extend to the anterior end of the dentary, and there is no clear predentary facet on the dorsal surface. A small facet ventrally on the anterior dentary may be for a predentary, suggesting that if it existed at all, the predentary was very small. The dentary of *Emausaurus ernsti* (SGWG 85) is very similar, also possessing little evidence for a predentary. The maximum dorsoventral depth of the dentary ramus is at the posterior end and the depth of the dentary at the symphysis is shallower than half the maximum depth of the dentary in lateral view. The Meckelian groove on the medial surface (Figs. 6–7, Mg) does not extend anteriorly as far as the symphysial facet, in contrast to the condition in *Emausaurus ernsti* (SGWG 85). Small fragments of the splenial (Fig. 6B, spl) are present in the posterior end of the Meckelian groove of the left dentary of the holotype. Multiple nutrient foramina are present on the lateral surface of the anterior end of the left dentary (Figs. 6–7, for). Similar foramina are also present on the dentaries of *Emausaurus ernsti* (SGWG 85).

The size of the dentary tooth crowns increases posteriorly, and in MNA.V.175 the largest dorsoventral crown height is in the fourteenth tooth position. The tooth alveoli face dorsally, rather than dorsomedially as occurs in some eurypodans (e.g., *Stegosaurus stenops*, NHMUK PV R36730; *Edmontonia longiceps*, CMN 8531), and there is no lateral lamina present to obscure the tooth row in lateral view.
5.1.14 Surangular (Fig. 7D–E)

The surangular is known only from UCMP 130580 (Fig. 7D–E). It is a mediolaterally compressed element that is generally convex on its lateral surface, concave on its medial surface, and sigmoidal in lateral view. The surangular generally resembles that of *Lesothosaurus diagnosticus* (NHMUK PV RUB17), although it is broken anteriorly and dorsally, so the height of the coronoid process cannot be established with certainty. A prominent anteroposteriorly extending ridge is present on the lateral surface of the surangular (Fig. 7D, lr), anterodorsal to the jaw articulation, as in *Lesothosaurus diagnosticus* (Sereno, 1991: fig. 13F), *Scelidosaurus harrisonii* (NHMUK PV R1111) and *Emausaurus ernsti* (SGWG 85). This feature appears to have been lost in stegosaurs [101] and ankylosaurs [93]. The ridge is damaged posteriorly, and the presence or absence of a surangular foramen cannot be determined.

Posteriorly there is a well-developed, slightly upturned, retroarticular process (Fig. 7D–E, rp), the lateral surface of which is gently striated. Medially there is a well-developed internal adductor fossa (Fig. 7E, adf), and a medial flange that descends posteroventrally from the inferred position of the glenoid (Fig. 7E, mf).

5.1.15 Dentition (Fig. 8)

The dentition of the holotype was well described by Colbert [18] and that description is supplemented here. The premaxillae contain alveoli for six teeth, but all are empty and only one replacement tooth, the fifth most-posterior on the left premaxilla of MNA.V.175, is sufficiently erupted to decipher any morphology. It is triangular with a sharp, elongate apex, and fine denticles are present. There are no striations or ridges on the crown surface.

The maxillary teeth (Fig. 8A) are subtriangular, symmetrical and taller dorsoventrally than wide anteroposteriorly. They closely resemble those of *Lesothosaurus diagnosticus* [28] but are very distinct from the apicobasally expanded teeth of *Laquintasaura venezuelae* [102]. There is an labiolingual
swelling present at the base of the crown that sits above a constricted tooth root, similar to that in *Emausaurus ernsti* (SGWG 85) and *Scelidosaurus harrisonii* (NHMUK PV R1111), but not developed into a true cingulum like that of more derived thyreophorans [92, 93]. There is a broad central eminence which extends to the crown tip. There are eight marginal denticles present on each tooth, four either side of the central eminence. In contrast, the maxillary teeth of *Emausaurus ernsti* are asymmetrical with the crown tips offset slightly distally. There are four marginal denticles on the shorter distal side in *Emausaurus ernsti*, and six are present on the longer mesial side. In *Scelidosaurus harrisonii* (NHMUK PV R1111) the maxillary tooth crowns are also offset distally, and the marginal denticles are smaller and more numerous [103]. Striations confluent with the denticles in *Scutellosaurus lawleri* are not present on the surfaces of the maxillary crowns. Wear facets are not evident on the maxillary teeth, like *Emausaurus ernsti* (SGWG 85) but in contrast to *Scelidosaurus harrisonii* [103], although this could be due to poor preservation.

The dentary teeth (Fig. 8B) are similar in morphology to the maxillary teeth. There are six marginal denticles either side of a central apex, although these denticles appear to be larger than on the maxillary teeth, and there is a labiolingual swelling present that is not developed into a true cingulum.

5.2. Postcrania

5.2.1. Cervical vertebrae (Figs 9, 10)

Colbert (18:15) suggested that there were nine cervical vertebrae in *Scutellosaurus lawleri*, accounting for the atlas and axis and inferring the absence of the fourth cervical vertebra; however, only six post-axial cervical centra are actually preserved. MCZ VPRA-8800 possesses six well-preserved postaxial cervical vertebrae and one postaxial cervical centrum, which is consistent with Colbert’s inference of nine total cervical vertebrae. This is typical of other small-bodied ornithischians (e.g., *Heterodontosaurus tucki*, [104]; *Agilisaurus louderbacki*, [90]) but differs from *Scelidosaurus harrisonii* (NHMUK PV R1111, CAMSM X.39256; [11]: fig. 10), which possesses eight cervical vertebrae.
Elements from the atlas-axis complex are sparsely preserved among specimens of *Scutellosaurus lawleri*. The intercentrum of the atlas is preserved in UCMP 130580 (Fig. 9A–B), a right atlas neural arch is preserved in MNA.V.175 (Fig. 9C), and an odontoid is preserved in UCMP 130580 (Fig. 9D–F). These elements of the atlas remain discrete and unfused in the specimens in which they are preserved. The neural arches are also unfused to the atlas intercentrum in *Emausaurus ernsti* (SGWG 85) and *Scelidosaurus harrisonii* (NHMUK PV R1111; CAMSM X.39256). In the latter the odontoid is fused to the axis centrum in larger individuals (NHMUK PV R1111), but not in smaller specimens (CAMSM X.39256). The intercentrum is reniform in anterior view with a concave dorsal margin and a convex ventral margin. It possesses an anterodorsal depression for articulation with the basioccipital and a posterodorsal groove to receive the ventral lip of the odontoid. The lateral margins of the intercentrum are rounded as preserved and lack clearly defined facets for the neural arches or an atlantal rib. The neural arch has a short anterior process that includes the prezygapophysis (although this articular facet is not well preserved), whereas the postzygapophysis was presumably on the medial surface of the long posterior process of the neural arch but is not exposed. The odontoid process is wedge-shaped and is notable for the presence of prominent concave facets on its lateral surfaces (Fig. 9D, cf). This feature is not seen in other ornithischians for which there is comparable material, and thus is an autapomorphy of *Scutellosaurus lawleri*.

The axis is known from a posterior portion of a neural arch in UCMP 130580 (Fig. 9G–I) and a centrum in MCZ VPRA-8801 (Fig. 9J–L). The neural spine (Fig. 9G) is prominent and extends posterodorsally beyond the posterior margins of the postzygapophyses, broadening slightly posteriorly, as in *Scelidosaurus harrisonii* (NHMUK R1111; [11]: fig. 7). A midline ridge extends along the length of the dorsal surface of the neural spine. Only the right postzygapophysis (Fig. 9G, I, poz) is preserved, and it faces mostly ventrally and slightly laterally. The axis centrum of MCZ VPRA-8801 preserves portions of the base of the neural arch (Fig. 9, na) that show a circular neural canal (Fig. 9, nc), and the atlas intercentrum is not coossified to its anterior articular surface to form the odontoid. The axis centrum is
cylindrical and wider than tall. The anterior articular surface is a mediolaterally-wide oval bisected by a
prominent dorsoventral ridge. There is a shallow facet on the dorsal half of the anterior articular surface
for the odontoid (Fig. 9, odf) and a smaller but more prominent facet along the ventral edge for
articulation with the atlas intercentrum (Fig. 9, axicf). The parapophyses are smooth and rounded (Fig. 9:
para). The subcircular and concave posterior articular surface is mediolaterally narrower than the anterior
surface.

Postaxial cervical centra are commonly preserved in specimens of *Scutellosaurus lawleri*, but
complete cervical vertebrae preserving neural arches are rare. Posterior cervical centra are shorter
anteroposteriorly than anterior centra. The sides of the centra are strongly constricted so that the lateral
surfaces are concave dorsoventrally and anteroposteriorly. The ventral margin of the third cervical
vertebra is concave upwards in lateral view. An extremely rugose and well-developed keel (Fig. 10, k) is
present on the mid to posterior cervical vertebrae. This keel is swollen and tubercular towards its anterior
end. Similar keels are present on the cervical and dorsal vertebrae of *Scelidosaurus harrisonii* (CAMSM
X.39256, NHMUK PV R1111), as well as in other early ornithischians (e.g., *Hypsilophodon foxii*, [105]),
although these are less prominent that those of *Scutellosaurus lawleri*; the possession of very prominent
and rugose ventral keels is therefore considered an autapomorphy of *Scutellosaurus*.

One nearly complete cervical vertebra was described by Breeden & Rowe (in press: fig. 17C–G;
TMM 45609-6), and the following description is based upon a single well-preserved posterior cervical
vertebra (MCZ VPRA-8800; Fig. 10). The centrum of MCZ VPRA-8800 is weakly amphicoelous, and
the anterior and posterior articular facets of the centra are nearly parallel to one another in lateral view.
The parapophyseal facet (Fig. 10, para) is ovoid, with a substantial portion on the dorsolateral margin of
the centrum and a small portion on the ventrolateral margin of the neural arch. The neural arch is taller
than the centrum, and the neural spine (Fig. 10, ns) is incomplete. The anterior edge of the neural spine
originates between the prezygapophyses (Fig. 10, prz). The prezygapophyses are anterodorsally directed
and widely separated from one another with broad, subcircular articular facets that face dorsomedially,
like those in *Stegosaurus* (NHMUK PV R36730). Only the left transverse process is completely preserved (Fig. 10, tp), and it is ventrolaterally directed, contrary to the dorsolaterally directed transverse processes of the posterior cervical vertebrae of *Scelidosaurus harrisonii* [11:19]. The transverse process (Fig. 10, tp) narrows distally, terminating in a truncated convex diapophyseal facet. The postzygapophyses are posterolaterally directed with nearly horizontal articular facets. Both the pre- and postzygapophyses extend beyond the articular facets of the centra (Fig. 10C–D).

### 5.2.2. Dorsal vertebrae (Fig. 11)

Fifteen dorsal vertebrae, represented by 14 centra and one neural arch, are present in the holotype, along with one vertebra that is transitional in morphology between the dorsal and sacral vertebrae (a dorsosacral vertebra). Colbert [18] interpreted the series to represent a complete dorsal column. A count of 15 dorsal vertebrae is typical for small ornithischians [90,105], although only 12 are present in *Heterodontosaurus tucki* [104], and there are 16 in *Scelidosaurus harrisonii* (NHMUK PV R1111; CAMSM X39256). In the holotype, the centra and neural arches are disarticulated, and few of the neural arches are well preserved. The neurocentral sutures appear to have been unfused at time of death, and this is also seen in some other specimens of *Scutellosaurus lawleri*. There exist only a few complete presacral vertebrae with articulated neural arches and centra, although in most cases the neurocentral suture remains visible. Among these, MCZ VPRA-8801 preserves five nearly complete nonsequential dorsal vertebrae (Fig. 11A–E), and MCZ VPRA-8800 preserves a single complete dorsal vertebra (Fig. 11F–K).

The centra are anteroposteriorly longer than they are wide mediolaterally or tall dorsoventrally. There are no longitudinal keels on the ventral surfaces of the centra, and the lateral surfaces are gently concave anteroposteriorly, giving the centra a spool-shape in ventral view. The anterior and posterior articular facets of the centra are flat to slightly concave. Neural arches are dorsoventrally taller than the dorsoventral height of the centra. The neural canal is circular in cross-section. Parapophyses (Fig. 11; para) are subcircular in outline, concave, smooth, and are positioned on short stalks. The parapophyses lie
anteroventral to the transverse processes on anterior dorsal vertebrae but extending posteriorly down the
column the parapophyses are progressively more dorsally positioned such that the transverse processes of
posterior dorsal vertebrae lie almost directly posterior to the parapophyses. The dorsal surfaces of the
stalks of the parapophyses and the transverse processes are confluent on posterior dorsal vertebrae.

Transverse processes (Fig. 11; tp) are dorsoventrally compressed. They project laterally and slightly
dorsally in anterior dorsal vertebrae (Fig. 11A), but laterally in more posterior dorsal vertebrae, and they
become more dorsoventrally compressed extending down the column (Fig. 11E). The transverse
processes bear diapophyses (Fig. 11; dia) at their distal ends which are more dorsoventrally compressed
than the parapophyses and teardrop shaped with the apex pointing posteriorly in anterior dorsal vertebrae.
Extending posteriorly down the dorsal vertebral column, the diapophyseal facets become more strongly
dorsoventrally compressed. The facets themselves are concave and slightly smaller than the
parapophyses. Prezygapophyses (Fig. 11; prz) extend anteriorly, are separated from each other, and face
dorsally. Postzygapophyses (Fig. 11; poz) are either sub-equal in size to the prezygapophyses (in the
MCZ specimens; Fig. 11) or are smaller (in the holotype) and were separated by a deep midline fossa.

Both pre- and postzygapophyses overhang the articular facets of the centrum. Neural spines (Fig. 11, ns)
are subrectangular in lateral view. They are dorsoventrally tall and anteroposteriorly narrow in anterior
dorsal vertebrae, and become shorter, anteroposteriorly wider, and posteriorly positioned on the neural
arch in posterior dorsal vertebrae. In the posterior dorsal vertebrae, they are longer anteroposteriorly than
they are tall dorsoventrally in lateral view. In Scelidosaurus harrisonii (CAMSM X.39256), neural spines
are dorsoventrally taller than they are long anteroposteriorly.

5.2.3. Sacral vertebrae (Fig. 12)

Colbert [18] identified five sacral vertebrae present in the holotype of Scutellosaurus lawleri; they are not
fused to one another and only the centra are preserved. The centrum identified as S1 by Colbert [18]
appears to be transitional in morphology between the dorsal vertebrae and sacral vertebrae (Fig. 12A); it
is longer anteroposteriorly than it is wide mediolaterally, as in the dorsal vertebrae but in contrast to the
other sacral vertebrae, and does not appear to have well-developed sacral rib facets on the lateral surfaces of the centrum. We therefore identify this vertebra as a dorsosacral. The lateral surfaces of the centrum are flat anteroposteriorly, and gently convex dorsoventrally. The articular facets are sub-quadrate and flat. The sacral vertebrae identified as 2–4 by Colbert ([18]; Fig. 12B–D) are wider mediolaterally than they are dorsoventrally tall or long anteroposteriorly. Their articular facets are reniform in anterior and posterior views. The anterior articular facet of the sacral identified as S2 by Colbert ([18]; Fig. 12B) is flat; the articular facets on the other sacral vertebrae are gently concave (e.g., Fig. 12D). The anterior and posterior articular facets are subequal in size in the vertebrae identified by Colbert [18] as S2–3; in S4 the anterior articular facet is larger than the posterior one. Large sacral rib facets occupy the anterolateral surfaces of the centra; it appears that each sacral rib articulated with just one vertebra. Ventrally, the sacral centra lack longitudinal grooves or keels. Unfortunately, the vertebra identified as S5 by Colbert [18] is obscured under other bone fragments and its morphology is unclear. TMM 43664-1 preserves one dorsosacral and four articulated sacral centra, but no other specimen of Scutellosaurus lawleri preserves a complete sacrum. The sacrum of Scutellosaurus lawleri therefore possessed one dorsosacral vertebra and at least four sacral vertebrae. Five sacral vertebrae are present in early-diverging ornithischians such as Lesothosaurus diagnosticus [27] and Agilisaurus louderbacki [90], whereas there are six in Heterodontosaurus tucki [104]. In contrast, there are four sacral vertebrae in Scelidosaurus harrisonii (NHMUK PV R1111).

5.2.4. Caudal vertebrae (Fig. 13)

Fifty-eight caudal vertebrae are preserved in the holotype, and this likely represents nearly the whole tail. Caudal vertebrae are commonly preserved among specimens of Scutellosaurus lawleri, although anterior caudal vertebrae with complete neural arches (e.g., MCZ VPRA-8801: Fig. 13L–P) are rare. The neural arches are fused to the centra from caudal seven posteriorly in MNA.V.175, and the vertebrae decrease in size posteriorly. The anterior caudal centra are either equidimensional or slightly longer anteroposteriorly than they are wide mediolaterally or tall dorsoventrally (Figs 13A–C, 13L–P). There are facets for
articulation with the haemal arches along the ventral edges of the articular surfaces of the centra, and these are especially well developed on the posterior articular surfaces. Caudal ribs (Fig. 13, cr) project laterally and are mediolaterally compressed, and these disappear after the twenty-first caudal vertebra, marking the transition between anterior and posterior caudal vertebrae. The remnants of caudal ribs disappear between caudal vertebrae 22 and 23 in *Scelidosaurus harrisonii* ([11: fig. 47]; NHMUK R1111). The neural spines (Fig. 13, ns) in the anterior caudal vertebrae of the holotype are generally incomplete, but they are angled strongly posteriorly, and appear to lack the bulbous swelling that is present in more derived thyreophorans (e.g., *Scelidosaurus harrisonii*, NHMUK PV R1111; *Dacentrurus armatus*, NHMUK PV OR46013; *Stegosaurus stenops*, YPM 1856; *Hesperosaurus mjosi*, DMNH 29431; *Ankylosaurus*, AMNH 5895; *Sauroptela*, AMNH 3032; *Edmontonia longiceps*, CMN 8531; *Polacanthus*, NHMUK PV R175). The complete neural arch of MCZ VPRA-8801 is taller than the centrum and includes a tall neural spine is dorsally directed. The prezygapophyses (Fig. 13, prz) extend anterodorsally beyond the anterior articular facet of the centrum, whereas the postzygapophyses (Fig. 13, poz) are shorter and do not extend beyond the posterior articular facet.

In posterior caudal vertebrae (Fig. 13D–K), the centra are more elongate and are much longer anteroposteriorly than they are wide mediolaterally. After the twenty-eighth caudal, chevron facets disappear. Both pre- and postzygapophyses are poorly preserved in the posterior caudal vertebrae but they do not extend substantially beyond the articular facets of the centra.

5.2.5. Pectoral girdle (Fig. 14)

The pectoral girdle is described with the blade of the scapula in a horizontal orientation. The scapula and coracoid are unfused in all known specimens of *Scutellosaurus lawleri*, as in *Lesothosaurus diagnosticus* (NHMUK PV RUB17; [27]) and other early-diverging thyreophorans (e.g., *Scelidosaurus harrisonii*, NHMUK PV R1111). The scapulae are nearly complete in the holotype, although the posteriormost portions of the blades are missing. The scapulae of TMM 43663-1 and TMM 43664-1 are more
completely preserved; however, in both specimens, the scapulae are mediolaterally compressed taphonomically [30]. The scapula is dorsoventrally expanded at both its anterior and posterior ends with concave dorsal and ventral margins, giving it an asymmetrical hourglass shape in lateral view. The blade of the scapula (Fig. 14, bl) curves medially, such that the medial surface of the scapular blade is concave along the anteroposterior axis, and the blade flares posteriorly in lateral view. The blade is mediolaterally compressed relative to the proximal plate (Fig. 14, pp). The proximal plate is small relative to derived thyreophorans such as *Stegosaurus stenops* (NHMUK PV R36730), and it has a smaller area than the coracoid. The proximal plate is triangular in lateral view, with the anterior margin forming the articular surface for the coracoid, the acromial process (Fig. 14, ap) extending at ~25° from the scapular blade, and a mediolaterally broad ventral process present at the posteroventral margin of the glenoid. The scapula is significantly shorter than the humerus. In MNA.V.175, in which the scapula is incompletely preserved, the scapula length is 63% of the humerus length, and in TMM 43663-1, in which the humerus is incompletely preserved, the scapula length is 70% of the humerus length [30]. This contrasts with some other early ornithischians: for example, the equivalent ratio is 122% in *Lesothosaurus diagnosticus* (NHMUK PV RUB17; [27]), 115% in *Scelidosaurus harrisonii* (CAMSM X.39256) and 106% in *Heterodontosaurus tucki* (SAM-PK-K1332; [104]). However, the humerus is also longer than the scapula in *Agilisaurus louderbacki* (85%; [90]) and *Hexinlusaurus consors* (78%; [106]).

The holotype preserves both coracoids, which are missing only portions of their dorsal margins. The coracoids are D-shaped elements with a rounded anteroventral surface, a raised posteroventral glenoid surface (Fig. 14, gl), and no distinct corners. The dorsoventral height is subequal to the anteroposterior length. A coracoid foramen (Fig. 14, cf) is present on the lateral surface near the posterior articular surface for the scapula. There is no anteroventral (sternal) process present and the preserved portion of the ventral margin is rounded in lateral view. The contribution of the coracoid to the glenoid is subequal to that of the scapula (Fig. 14).
5.2.6. Humerus (Fig. 15)

The holotype preserves a complete right humerus (Fig. 15) and a nearly complete left humerus. The humerus is straight along most of its length in anterior view, but there is a prominent medial projection proximally, the medial tuberosity (Fig. 15, mt). This projection is less pronounced than in *Eocursor parvus* [62], but more pronounced than other early ornithischians such as *Heterodontosaurus tucki* (SAM-PK-K1332) and *Lesothosaurus diagnosticus* (NHMUK PV RUB17). The proximal articular surface of the humerus is anteroposteriorly compressed and weakly sigmoidal in proximal view (Fig. 15C). The proximal articular surface is thickest medially and tapers laterally. The humeral head is not well developed in comparison to *Scelidosaurus harrisonii* (NHMUK PV R1111), but better developed than in *Lesothosaurus diagnosticus* (NHMUK PV RUB17). The deltopectoral crest (Fig. 15, dpc) projects anterolaterally, with an apex occurring at just under 30% of the total shaft length, and distally merges into the shaft just proximal to the midlength of the bone. The deltopectoral crest is a relatively slender protuberance that is triangular in lateral view (Fig. 15C) with a prominent tubercle present at its apex for the attachment of the *m. pectoralis* [80]. In *Scelidosaurus harrisonii* the deltopectoral crest is considerably larger and projects more strongly anteriorly (CAMSM X.39256; [11]). There is no distinct notch between the humeral head and the deltopectoral crest or between the humeral head and the medial tuberosity in anterior view. The anterior surface of the proximal end of the humerus is relatively flat between the deltopectoral crest and the medial projection compared to the humerus of *Lesothosaurus diagnosticus* (NHMUK PV RUB17), in which there is a deep anterior depression [27: fig. 7A]. The shaft of the humerus is ovoid in cross-section, with the long axis oriented mediolaterally. The proximal end of the humerus is sub-equal in transverse width to the distal end. The distal articular surface is figure of eight-shaped in distal view, forming a trochlear surface comprising a subovoid lateral (ulnar) condyle (Fig. 15, lc) and a subquadrangular medial (radial) condyle (Fig. 15, mc). The medial condyle is slightly wider mediolaterally than the lateral condyle. The anterolateral corner of the lateral condyle forms a point in distal view. The distal end is expanded mediolaterally to approximately twice the width of the midshaft.
5.2.7. Radius (Fig. 16A–D)

Although the holotype preserves fragments of the radius, complete radii are preserved in UCMP 130580, of which the left is better preserved (Fig. 16A–D). The proximal articular surface of the radius is anteroposteriorly compressed with a flat to concave posterior surface for articulation with the ulna and a convex anterior surface. The shaft is generally straight with a convex anterior margin and is subtriangular in cross-section. There is a well-defined facet on the posterior surface of the distal end of the radius for articulation with the distal end of the ulna. The distal articular surface is convex and is subcircular in distal view. The radius is approximately 60% of the length of the humerus, which is much lower than the 83% estimated by Colbert [18] based on his reconstruction of the radius of MNA.V.175.

5.2.8. Ulna (Fig. 16E–H)

As with the radius, UCMP 130580 includes better-preserved ulnae than the holotype; however, no complete ulna is known (Fig. 16E–H). The ulna is expanded at both the proximal and distal ends in anterior view. The proximal articular surface of the ulna is anteroposteriorly compressed and subtriangular in proximal view. The olecranon process (Fig. 16, ole) is weakly developed, and there is a very weakly-developed anterior process. There is a weakly defined articular facet for the radius on the anterior surface of the proximal end of the ulna. The posterior surface of the proximal end of the ulna is generally smooth. The midshaft of the ulna is subovoid in cross-section. The distal end of the ulna is anteroposteriorly compressed and smaller than the proximal end. The anterior surface of the distal end of the ulna is concave to form a facet for the distal end of the radius. The posterior surface of the distal end of the ulna is convex. The distal articular surface is reniform in distal view, with a rounded medial margin and a pointed lateral margin.

5.2.9. Manus

The holotype preserves two metacarpals, which were interpreted by Colbert [18: fig. 20B] as left metacarpals II and III; however, we cannot confidently confirm these positions. One metacarpal is
missing its distal end. The other metacarpal is missing only a small midshaft portion, and its proximal end remains closely appressed to several other bone fragments such that most of it is obscured from view. The proximal ends of both metacarpals of the holotype have approximately the same dorsoventral width. One metacarpal is present in UCMP 130580, which was identified by Rosenbaum & Padian [23] as either metacarpal III or IV. The proximal ends of all preserved metacarpals are dorsoventrally expanded relative to their midshafts, as in other early ornithischian dinosaurs (e.g., *Lesothosaurus diagnosticus*, NHMUK PV RUB17; *Scelidosaurus harrisonii*, BRSMG LEGL 0005). The proximal articular surfaces are smooth and flat to gently convex. The dorsal surfaces of the proximal ends of the metacarpals are convex and rounded, whereas the ventral surfaces are nearly flat. All metacarpals have midshafts that are ovoid in cross-section. The distal ends of the metacarpals are dorsoventrally and mediolaterally expanded relative to their shafts and bear a weakly-developed flexor pit on their ventral surfaces and well-developed ligament pits on their medial and lateral surfaces. However, they lack well-developed extensor pits on their dorsal surfaces.

Several manual phalanges are also present in the holotype, which were tentatively assigned to digits II and IV in the reconstruction of the manus by Colbert [18: fig. 20]; however, none of these phalanges were preserved in articulation and their positional identities are uncertain. Non-ungual manual phalanges are dorsoventrally and mediolaterally expanded at both their proximal and distal ends. The proximal articular surfaces are convex with flat ventral margins and round dorsal margins. The distal ends bear prominent flexor and extensor pits on their ventral and dorsal surfaces and well-developed ligament pits on their medial and lateral surfaces. The distal articular surfaces are rounded and spool-shaped.

Colbert [18] emphasized the relatively large size of the manus of *Scutellosaurus lawleri*, which he suggested may be indicative of facultative bipedalism; however, this claim relies heavily on both his composite reconstruction of the manus based on limited material (18: fig. 20B) and his estimated lengths of the radius and ulna (18: fig. 20A). As such, the relative size of the manus in *Scutellosaurus lawleri* remains uncertain.
5.2.10. Ilium (Fig. 18)

The right ilium of MNA.V.175 (Fig. 18B) is incomplete and was erroneously identified as the left ilium by Colbert [18]. It is fractured and poorly preserved, however, and little information is available on the morphology of the pubic and ischiadic peduncles, postacetabular process, and brevis shelf. Previous reconstructions of these areas are therefore largely speculative (e.g., 18: fig. 23). The left ilium (Fig. 18A) is preserved together with the left femur and is less complete than the right; it has a triangular outline owing to the loss of the posteromedial and anteromedial parts of the bone. Partial ilia are known from several specimens, including fragments in MNA.V.1752, MCZ VPRA-8792, and UCMP 170829, and portions of both ilia are present in UCMP 130580. A nearly complete right ilium is preserved in TMM 43664-1 [30]; however, this ilium is mediolaterally compressed by taphonomy.

A deep medioventral flange of the ilium (Fig. 18, mf) partially closes the acetabulum medially, as in many other early-diverging ornithischians (Lesothosaurus diagnosticus, [28]; Laquintasaura venezuelae, MBLUZ P1443) including the early-diverging thyreophoran (Scelidosaurus harrisonii, NHMUK PV R1111). A broad lateral expansion (Fig. 18, le) is present above the acetabulum [18]. This lateral expansion of the dorsal surface of the acetabulum is generally referred to as a ‘supraacetabular flange’ in early dinosaurs and ornithischians. However, the term ‘supraacetabular flange’ has also been used to refer to a lateral expansion of the dorsal margin of the ilium above the ischiadic peduncle seen in derived eurypodans, whereas a similar feature in ceratopsians and hadrosaurs has been termed an ‘antitrochanter’ [2]. As the term ‘supraacetabular flange’ is used by different authors to refer to non-homologous features within Thyreophora, we avoid using it here to refer to the lateral expansion above the acetabulum of Scutellosaurus lawleri. The lateral expansion bounding the acetabulum dorsally is continuous with the lateral edge of the pubic peduncle (Fig. 18, ppd).

The pubic peduncle is mediolaterally broad and thickest anteriorly, such that the articular surface is subtriangular. In lateral view, the anterodorsal edge of the pubic peduncle is very gently convex, and
the ventral articular surface is more strongly convex and rounded. The distal end of the pubic peduncle is swollen and rough, and the articular surface is rugose. The ischial peduncle (Fig. 18, ispd) is poorly defined relative to some other early ornithischians (e.g., *Eocursor parvus*, SAM-PK-K8025; [62: fig. 13A]) but similar to *Scelidosaurus harrisonii* (NHMUK PV R1111; [11: fig. 68A]). It is a broad swollen surface at the posterior end of the medioventral flange of the acetabulum. The ischial peduncle is anteroposteriorly expanded relative to its mediolateral width.

Rosenbaum & Padian [23] figured, but did not describe in detail, the unusual preacetabular process (Fig. 18, pre) of the ilium of UCMP 130580. The preacetabular process is elongate and dorsoventrally compressed (Fig. 18E–F). Dorsal and ventral margins of the preacetabular process are drawn out medially into narrow flanges that give it a C-shape in cross-section. Anteriorly the dorsal (Fig. 18, dfpre) and ventral (Fig. 18, vfpre) flanges converge upon one another, eventually fusing to form an expanded and dorsolaterally to ventromedially flattened tip (Fig. 18, ftp). The dorsolateral surface of this expanded tip bears anteroposteriorly-extending striations, indicating muscle attachment for the *m. iliotibialis* (Maidment & Barrett 2011). The preacetabular process of the ilium of TMM 43664-1 similarly possesses dorsal and ventral medial flanges, but these converge upon each other anteriorly and fuse to form a more strictly dorsoventrally flattened tip to the preacetabular process, and the process is overall straighter than the bowed process of the ilium of UCMP 130580 [30].

The dorsal margin of the main body of the ilium above the acetabulum is mediolaterally expanded into a narrow shelf (Fig. 18, sh) that bears prominent vertical striations on its medial surface; however, it is not drawn out medially into a distinct flange, as on the preacetabular process. Mediolateral expansion above the acetabulum in *Scutellosaurus lawleri* exceeds that seen in *Lesothosaurus diagnosticus* (NHMUK PV RU B17) and *Laquintasaura venezuelae* (MBLUZ P1443), but it is less developed than in other thyreophorans (e.g., *Scelidosaurus harrisonii*, NHMUK PV R1111; stegosaurs, [2]; ankylosaurs, [93]). The dorsal margin of the ilium above the postacetabular process is not expanded mediolaterally. The postacetabular process of the ilium is relatively short and blunt, with a shallow,
ventrally-facing brevis fossa. One sacral rib impression can be identified (contra [18]) on the partial right ilium of MNA.V.175. This impression is positioned at the base of the preacetabular process and the pubic peduncle; an equivalent rib scar has been identified as the attachment site for the rib of the first true sacral vertebra in Lesothosaurus diagnosticus (Sereno, 1991: fig. 9C; [25]).

5.2.11. Ischium (Fig. 19)

The holotype preserves the right and left ischia, although both elements are fragmentary. The right ischium, of which the proximal (18: fig. 22A; misidentified as the left ischium) and distal (18: fig. 22C) ends are preserved, is attached to the pelvic block that also contains the right ilium, right pubis and the proximal end of the right femur, and it is found on the underside of the ilium. The left ischium, which was not figured by Colbert [18] and of which only the distal end is preserved, is found as part of an associated block together with the complete left femur, the left ilium and the left pubis. MCZ VPRA-8801 preserves a nearly complete right ischium (Fig. 19A–C), which is the best-preserved ischium known for Scutellosaurus lawleri. UCMP 130580 preserves a nearly complete right ischium (Fig. 19D–F; misidentified as the left ischium by Rosenbaum & Padian [23: fig. 3]) and a midshaft portion of the left ischium (Fig. 19G–H).

At the proximal end of the ischium, the pubic (Fig. 19, ppd) and iliac (Fig. 19, ilp) peduncles are connected by a mediolaterally compressed and anteriorly concave acetabular region (Fig. 19, ace). The iliac peduncle of the right ischium of MNA.V.175 and UCMP 130580 partially occludes the acetabulum with an anteriorly-extending flange; however, this condition is absent in the right ischium of MCZ VPRA-8801. The ischial shaft is twisted along its length so that the distal end is rotated medially and the distal ischial shaft is mediolaterally expanded; this would have formed an elongate ischial symphysis with the opposing ischium, as in other early-diverging ornithischians [25], but in contrast to Scelidosaurus harrisonii (NHMUK PV R1111) in which the ischial symphysis was restricted to the distal end of the bone and strong torsion of the shaft is absent. There is a ridge along the dorsal portion of the lateral
surface of the shaft (Fig. 19, lr). Much of the narrow symphyseal margin of the ischial shaft is incomplete in the preserved specimens, giving the impression of a discrete, tab-like obturator process [23: fig. 2B], and a tab-like obturator process has previously been reconstructed for Scutellosaurus lawleri [18: fig. 23]; however, this is likely an artefact of poor preservation. The right ischium of MCZ VPRA-8801 clearly lacks a prominent obturator process, and the obturator process is not observed on the ischia of other thyreophorans (e.g., Scelidosaurus harrisonii, NHMUK PV R1111; stegosaurs, [92]; ankylosaurs, [93]).

A weak groove is present on the dorsal margin of the ischial shaft, and distally passes onto the medial side of the shaft. An identical groove was described for Lesothosaurus diagnosticus [28,80,107,111], Agilisaurus louderbacki [90], and ornithischian outgroups [108], and probably represents the origin of the m. adductor femoris 2 [80].

5.2.12. Pubis

The anterior end of the left pubis is present in the holotype (Fig. 20A, pub; 18: fig. 22B) along with part of the pubic shaft and is preserved underneath the left ilium. We were not able to locate the distal end, despite it being described as present by Colbert [18]. The right pubis, of which only the distal end is preserved (18: fig. 22C), is preserved underneath the right pelvic block and next to the distal end of the right ischium. Despite it being described as present by Colbert [18], the anterior end of the right pubis could not be located. No other specimens preserve a pubis.

There is no evidence to support reconstructions of an elongate prepubis (18: fig. 23); the mediolaterally compressed prepubis was probably short as in Eocursor parvus [62], Lesothosaurus diagnosticus [27,28], Laquintasaura venezuelae (MBLUZ P.5008) and Scelidosaurus harrisonii (NHMUK PV R1111). The pubic shaft is long, thin, and rod-like, with a smaller diameter than the shaft of the ischium, and there does not appear to be a distal expansion, like the condition in Lesothosaurus diagnosticus (NHMUK PV RUB17; [27]). At the anterior end there is a large obturator foramen which is not closed posteriorly; this is similar to the condition in Scelidosaurus harrisonii (NHMUK PV R1111),
but contrasts with the condition in some specimens of *Lesothosaurus diagnosticus* (e.g., NHMUK PV RUB17; [27]) and *Laquintasaura venezuelae* (MBLUZ P.5008), in which the obturator foramen is fully enclosed. There is a large facet on the dorsal surface for the acetabulum [18] and at the posterior end of the obturator foramen there is a smaller facet for articulation with the ischium.

5.2.13. Femur (Fig. 20)

Femora are commonly preserved among specimens of *Scutellosaurus lawleri*, and both left (Fig. 20A–C) and right femora are nearly complete in the holotype. As noted by Colbert [18], the femur of *Scutellosaurus lawleri* is morphologically like the femora of other early ornithischians such as *Lesothosaurus diagnosticus* [27,28,107], *Laquintasaura venezuelae* (MBLUZ P.5003), and *Scelidosaurus harrisonii* (NHMUK PV R1111). The length of the complete left femur of MNA.V.175 given by Colbert [18] is inaccurate; the correct length is 83.5 mm, and the femur is substantially shorter than the tibia (87% of tibial length), as in other small-bodied early ornithischians (*contra* [18]), but it is longer than the humerus (121% of humeral length).

The femur is straight in anterior or posterior view but bowed slightly anteriorly in lateral or medial view. The broadest anteroposterior width of the proximal femoral surface occurs centrally, as in dinosauriforms and early saurischian dinosaurs [108: fig. 4C], and in other early ornithischians (*Lesothosaurus diagnosticus*, [28]; *Scelidosaurus harrisonii*, NHMUK PV R1111; *Laquintasaura venezuelae*, MBLUZ P.5003), rather than laterally as in most other ornithischians. A weak groove extends from the anteromedial corner posterolaterally across the proximal surface of the femur, dividing the surface into anterolateral and posteromedial areas. A similar groove is present in most other early dinosaurs [108, 109]. This groove is continuous with a distinct depression on the posterolateral corner of the proximal surface (the ‘articularis antitrochanterica’), considered to represent the articulation surface for the mediolaterally thickened dorsal margin of the acetabulum of the ilium by Langer [108]. The
articulans antitrochanterica is bounded medially by a weak medial tuber (see discussion in [98]). A broad and well-developed ligament sulcus is present medial to the tuberosity.

Many studies have identified the greater trochanter as limited to the posterolateral margin of the proximal femur [18,28]; by contrast, Langer [108] proposed that in early dinosaurs the groove on the proximal surface separates the greater trochanter from the medially-facing femoral head. As a result, the greater trochanter occupies the whole of the lateral and anterolateral surface, although there is not a distinct constriction between the greater trochanter and the femoral head. A low proximodistally-extending ridge, the dorsolateral trochanter, is present on the lateral surface of the greater trochanter, as in *Scelidosaurus harrisonii* (NHMUK PV R6704) and early saurischian dinosaurs [108,110]. In some other early ornithischians (e.g., *Lesothosaurus diagnosticus*, [28,80]; *Laquintasaura venezuelae*, MBLUZ P.5003) the dorsolateral trochanter is extended anteriorly as a distinct flange, and this probably represents the initial stage in the development of the neornithischian femur in which the greater trochanter is anteroposteriorly expanded, limited to the lateral margin of the femur, and separated from the femoral head by a distinct constriction.

A distinct cleft separates the dorsolateral trochanter from the large, finger-like anterior trochanter. As in early ornithischians (*Lesothosaurus diagnosticus*, [28]; *Scelidosaurus harrisonii*, NHMUK PV R1111) the anterior trochanter is anteroposteriorly broad and positioned rather distally on the shaft relative to the proximal surface of the femoral head.

The attachment of the pendent fourth trochanter (Fig. 20A; ft) is positioned entirely on the proximal half of the femur (contra [22]) and projects ventromedially. A small nutritive foramen is present proximolateral to the base of the trochanter. Distally, a muscle-scar is present on the anterolateral surface of the distal femur, probably for the *m. femorotibialis lateralis* [80]. The angle between the long axis of the femoral head and the long axis of the femoral shaft is roughly 90°. In distal view, the distal end is U-shaped (Fig. 20D), with roughly equal-sized condyles and a large intercondylar fossa, and the fibular
epicondyle is not medially inset, unlike the condition in *Laquintasaura venezuelae* (Barrett et al., 2014), a taxon recovered as sister taxon to *Scutellosaurus lawleri* in some recent phylogenetic analyses [27,111].

### 5.2.14. Tibia (Fig. 21)

Both tibiae are well preserved in the holotype, and the right tibia (Fig. 21) is nearly complete. The tibiae are plesiomorphically longer than the femora, contrary to the condition in *Scelidosaurus harrisonii* (NHMUK PV R1111, [11]) and eurypodans [1,112], but similar to the condition in other early ornithischians (e.g., *Heterodontosaurus tucki*, [104]; *Agilisaurus louderbacki*, [90]; *Lesothosaurus diagnosticus*, [27]). The proximal end of the tibia is expanded anteroposteriorly such that its anteroposterior length is greater than the transverse width; at the distal end, the opposite is true. The proximal articular surface of the tibia comprises a well-developed cnemial crest (Fig. 21, cnc) and two prominent posteriorly-directed condyles. The cnemial crest projects anterolaterally, and the two posterior condyles include the posterolaterally-directed fibular condyle (Fig. 21, fibc) and the larger medial condyle (Fig. 21, mc). The fibular condyle lies slightly distal to the cnemial crest and the medial condyle. The distal end of the tibia is triangular in cross-section, with a posteriorly-directed apex. The anterior surface of the lateral malleolus (Fig. 21, lm) is flat for articulation with the fibula, and is slightly offset anteriorly from the medial malleolus (Fig. 21, mm), from which it is separated by a ridge. It also extends further ventrally than the medial malleolus but not to the degree seen in *Scelidosaurus harrisonii* (NHMUK PV R1111).

### 5.2.15. Fibula (Fig. 22)

The holotype preserves a nearly complete but badly fragmented left fibula and the proximal and distal ends of the right fibula (Fig. 1). The fibula is an elongate, thin element, with an anteroposteriorly and mediolaterally expanded proximal end, although this expansion is not as well developed as that of *Lesothosaurus diagnosticus* (NHMUK PV RUB17; [27]). The proximal end of the fibula is concave medially where it articulates with the tibia (Fig. 22, a.tib) and convex laterally. The proximal articular
surface is smooth, convex, and reniform in proximal view. The shaft does not appear to be bowed
anteriorly as it is in *Eocursor parvus* [62], *Lesothosaurus diagnosticus* (NHMUK PV RUB17; [27]) or
*Hypsilophodon foxii* [105], although the element is so fragmentary that this could be an artifact of its
reconstruction. The distal end of the fibula is both anteroposteriorly and mediolaterally expanded but less
so than the proximal end. The anterolateral surface of the distal end is concave and smooth, and there is a
flat posterior surface for articulation with the tibia (Fig. 22, a.tib). The distal articular surface is rough and
subquadrangular in distal view.

5.2.16. Tarsus (Fig. 23A–I)

Both the holotype and paratype include complete and well-preserved astragali. The astragalus (Fig. A–F)
is subquadrangular in proximal or distal view with a transverse long axis. The proximal surface of the
astragalus is smooth and subdivided into two bowl-like concave surfaces for the distal malleoli of the
tibia. The medial surface is larger than the lateral surface and would have received the medial malleolus
of the tibia (Fig. 23, a.mm), whereas the distolaterally-sloping lateral surface received the medial portion
of the lateral malleolus of the tibia (Fig. 23, a.lm). Novas [98: fig. 5D] figured the astragalus of
*Scutellosaurus lawleri* in proximal view and misidentified the lateral concave surface as the fibular facet;
a well-defined fibular facet is absent from the astragalus of all known ornithischians [21]. The anterior
surface of the astragalus is concave in proximal view, with a distinct notch separating the strongly
projecting anteromedial corner from the ascending process. In anterior view the ascending process (Fig.
23, ap) is low and broad, with the apex positioned laterally; a small fossa (Fig. 23, fo) is present on its
anterior surface. The lateral surface of the astragalus is concave for articulation with the calcaneum (Fig.
23, cal). The distal surface of the astragalus is mediolaterally concave and anteroposteriorly convex,
forming a trochlear surface.

The calcaneum is partially coossified to the astragalus in MNA.V.1752 (Fig. 23E–F), and isolated
calcanea are present in several other specimens that represent smaller individuals than MNA.V.1752 (e.g.,
MNA.V.175, MNA.V.3133, MCZ VPRA-8796). In lateral view, the calcaneum has a rounded distal margin with one small concave depression (the fibular facet) on the anterior part of the proximal surface to receive the fibula and a second, larger concave depression more posteriorly on the proximal surface to receive the lateral portion of the lateral malleolus of the distal tibia. This larger concave proximal surface is continuous with the concave proximal surfaces of the astragalus, together forming a mediolaterally wide trough-like surface to receive the tibia. The fibular facet is a bowl-shaped concavity that is nearly continuous with the fossa on the anterior portion of the ascending process of the astragalus. The lateral surface of the calcaneum has a pitted, rugose texture.

Colbert [18:31] tentatively noted a “flattened, somewhat quadrangular element with rounded corners” that might represent a distal tarsal bone in MNA.V.175, but this was not figured. We have identified a right distal tarsal 3 that fits the description of the element noted by Colbert, which we interpret to be the same element (Fig. 23G). Distal tarsal 3 is proximodistally thin and wider anteroposteriorly than mediolaterally. The proximal articular surface is slightly concave but nearly flat, whereas the distal articular surface has two shallow concave depressions for articulation with metatarsal III. Distal tarsal 3 is thickest along its lateral margin, which is slightly rough in texture. The shape of distal tarsal 3 in *Scutellosaurus lawleri* is generally consistent with that of *Scelidosaurus harrisonii* figured by Norman [11: fig. 87; NHMUK R1111].

A right distal tarsal 4 is preserved in UCMP 130850 (Fig. 23H–I), although this was identified as a distal tarsal 2 by Rosenbaum and Padian [23: fig. 5N]. The proximal surface of the right distal tarsal 4 is concave, with a convex anterior surface and a concave posterior surface which is wider mediolaterally than the anterior surface. The medial surface is rugose where it contacted distal tarsal 3, and two small facets are present on the anterior and anterolateral surfaces. A concavity is present on the proximal surface of metatarsal IV for articulation with distal tarsal 4; the fact that this concavity does not extend onto the proximal surface of metatarsal III suggests that distal tarsal 4 only distally articulated with
metatarsal IV. Distal tarsals are unknown in eurypodan thyreophorans [92,93].

5.2.17. Pes (Fig 23J–M)

Metatarsals and phalanges are widely preserved among specimens of Scutellosaurus lawleri; however, no single specimen preserves a complete pes. There are four metatarsals present in the holotype material. Metatarsals II and IV are missing only their distal ends, whereas metatarsal I only has the distal end preserved, and only the proximal end of metatarsal III is preserved. A partial ungual phalanx of digit I is present, as are phalanges II and III of digit II, phalanges I and IV of digit III, and phalanges I, IV and V of digit IV. No pes material is present in the paratype material, but UCMP 130580 preserves right metatarsals I-IV, of which only III and IV are mostly complete (Fig. 23J–M; mostly identified as left metatarsals by Rosenbaum & Padian [23]); however, these represent the best-preserved associated metatarsus. Rosenbaum & Padian [23] identified the proximal end of a metatarsal as that of the left metatarsal I. However, this identification seems unlikely as the proximal end of this bone is strongly expanded anteroposteriorly; it is possible that this bone is right metatarsal II, but if so, it has undergone post-mortem deformation.

Right metatarsal I has a strongly mediolaterally compressed and splint-like proximal end. The shaft is flattened laterally and would have been closely appressed to metatarsal II along its length. All these features resemble metatarsal I of other early ornithischians, including Agilisaurus [90] and Lesothosaurus diagnosticus [27,107].

5.2.18. Osteoderms

Osteoderms are widely preserved among nearly all specimens of Scutellosaurus lawleri. The morphology of the osteoderms of Scutellosaurus lawleri was described in detail by Colbert [18] and their histology was studied by Main et al. [113]. The holotype of Scutellosaurus lawleri contains at least 304 osteoderms, and there are 17 osteoderms in the paratype, although they were found disarticulated in both specimens.
Colbert [18] recognized six osteoderm morphotypes but conceding that several of the categories graded into one another other and that the distinctions were subjective. Breeden & Rowe [30] proposed four revised osteoderm morphotypes, including symmetrical broad, subovoid, flat osteoderms with longitudinal keels that were aligned along the antero-posterior bony axis (Morphotype A; Fig. 24A–F); symmetrical osteoderms that possess two long sides sloping up to a ridge of varying height and that are deeply concave ventrally, and the basal plate of each osteoderm maintains a fairly uniform thickness (Morphotype B; Fig. G–J); symmetrical flat osteoderms that are wider than long, with two longitudinal ridges flanking the midline (Morphotype C; Figs. 24K–L, 25); and anteroposteriorly long, transversely narrow osteoderms with hollow bases that are approximately as long as the caudal centra (Morphotype D; Figs. 13G–J, 24M–P). For a more detailed discussion of these morphotypes and how they compare to other thyreophoran dinosaurs, see Breeden & Rowe [30].

Main et al. [113] analyzed the histology of osteoderms from several thyreophoran taxa, including *Scutellosaurus lawleri* (UCMP 130580), and concluded that thyreophoran osteoderms are homologous. The histology of the osteoderms of *Scutellosaurus lawleri* suggests that the earliest thyreophoran osteoderms developed from compact dermal bone that was ontogenetically replaced internally.

### 6. Discussion

#### 6.1. Ontogeny and growth

Histological thin sections were taken from one radius, one tibia, and an osteoderm of UCMP 130580 (an individual somewhat smaller than MNA.V.175) and from one radius and one femur of UCMP 170829 (an individual about 20% larger than UCMP 130580) in order to study the ontogeny of *Scutellosaurus lawleri* by Padian et al. ([114]; also [113]). At least three lines of arrested growth in the right tibia and seven lines of arrested growth in the radius of UCMP 130580 were observed by Padian et al. (2004), who noted that growth appeared to be ceasing in both bones, which may indicate that UCMP 130580 was nearly fully grown. A slightly larger individual displayed calcified cartilage on the epiphyseal surface of the radius,
indicating that the animal also was adult [114]. Indeed, closure of the neurocentral suture in cervical and dorsal vertebrae is only present in a few of the over 70 known specimens of Scutellosaurus lawleri. Conversely, Tykoski [29] suggested that MNA.V.175 and other specimens of Scutellosaurus lawleri were probably juveniles, presumably because of the lack of fusion of the neural arches to the centra of the presacral series of vertebrae. However, although the anterior to posterior sequence of neurocentral suture closure during ontogeny noted in crocodylians by Brochu [115] is sometimes invoked to interpret the ontogeny of dinosaurs [16,17,18], its utility as a proxy for skeletal maturity in dinosaurs was called into question by Irmis [119]. Irmis concluded that whereas phytosaurs share the crocodylian state of neurocentral suture closure and that this was plesiomorphic for Pseudosuchia, some dinosaurian taxa (e.g., Ceratopsia, Camarasaurus, and crown-group Aves) definitely lack closure the crocodylian pattern of closure and that it was unwise to apply the crocodylian pattern to other archosaurian taxa a priori. The neurocentral sutures remain at least partially open in all but the posterior caudal vertebrae in the type and referred specimens of Scutellosaurus lawleri, and the lack of neurocentral suture closure is common among early ornithischians (e.g., Lesothosaurus diagnosticus, NHMUK RUB17; Stormbergia dangershoeki, SAM-PK-K1105), which the relationship between neural arch closure, size, and ontogeny was requires further examination.

Histological examination of the limb elements of Scutellosaurus lawleri by Padian et al. (2004) revealed very poorly vascularized lamellar-zonal bone throughout the cortex of all specimens examined. Dinosaurs typically possess more highly vascularized fibrolamellar bone [114,120], which led Padian et al. [114] to conclude that Scutellosaurus lawleri grew slowly throughout its life as a function of its small body size. The histology of the small early-branching ornithischian Lesothosaurus diagnosticus has subsequently been examined [121], and it possesses fibrolamellar bone at early growth stages, indicating a more typical dinosaurian pattern of rapid early growth, followed by a decline in growth rate through ontogeny [114,122,123]. Lesothosaurus diagnosticus is variably reconstructed phylogenetically as a non-genasaurian ornithischian [1], an early-diverging thyreophoran [3], or an early-diverging neornithischian
but wherever it fits, it is clear that it is a very early-branching member of the ornithischian lineage which, like *Scutellosaurus lawleri*, had a small adult body size [28]. The presence of fibrolamellar bone in *Lesothosaurus diagnosticus*, therefore, suggests that lamellar-zonal bone in *Scutellosaurus lawleri* is not necessarily a consequence of either small body size or its phylogenetic position close to the base of Ornithischia.

The histology of the limb elements of both stegosaurs [122,123] and ankylosaurs [120] has been investigated. Adults of both clades possess poorly vascularized fibrolamellar bone, which becomes avascular and lamellar-zonal in the final stages of growth [120,122,123]. In ankylosaurs, very strong secondary remodelling is observed [120]. The bone tissues of these derived thyreophorans are less well-vascularized than those of other dinosaurs [120,123] and indicate slower growth rates and perhaps lower metabolic rates [123] than in other dinosaurian clades. It seems most likely, therefore, that slow growth rates are a derived characteristic of Thyreophora (also noted by [123]), and the possession of lamellar-zonal bone throughout the cortex may be autapomorphic for *Scutellosaurus lawleri* among ornithischians. Larger-bodied thyreophorans, the ankylosaurs and stegosaurs, may have developed fibrolamellar bone because of higher growth rates needed to attain large size.

### 6.2. Body proportions and locomotion

Maidment & Barrett [112] included *Scutellosaurus lawleri* in a study of osteological correlates for quadrupedal stance in ornithischian dinosaurs. Of the five anatomical features identified in that study as robust indicators of quadrupedality, *Scutellosaurus lawleri* could only be scored for three, all of which indicate that it was an obligate biped. This conflicts with the interpretation of Colbert [18] of *Scutellosaurus lawleri* as a facultative quadruped based on its limb proportions relative to the obligate biped *Lesothosaurus diagnosticus*. In contrast, Maidment & Barrett [112] interpreted the early thyreophoran *Scelidosaurus harrisonii* as predominantly quadrupedal while retaining some vestiges of its bipedal ancestry, and all eurypodan thyreophorans as obligate quadrupeds. Colbert [18] suggested that the
early ancestors of the armoured stegosaurs and ankylosaurs may have been facultative quadrupeds in order to support the additional weight of their bony armour. Maidment et al. [86] tested the hypothesis that the additional mass of osteoderms forced the centre of mass to move anteriorly in early thyreophorans, driving the evolution of quadrupedality, and they used Scutellosaurus lawleri as a model early thyreophoran. The centre of mass in Scutellosaurus lawleri was computed without armour, with the armour of Stegosaurus, and with the armour of Euoplocephalus. The addition of Stegosaurus and Euoplocephalus armour on Scutellosaurus lawleri resulted in small movements of the centre of mass posteriorly, and it was not possible to force the centre of mass anteriorly with the addition of armour. Among non-eurypodan thyreophorans, Scelidosaurus harrisonii was definitely quadrupedal [124], but the postcranial skeleton of the only specimen of Emausaurus ernsti is too incomplete to infer a mode of locomotion. However, it therefore seems most likely that Scutellosaurus lawleri was the only bipedal member of Thyreophora (Fig. 26), and that more derived members of the clade acquired quadrupedality for reasons other than the acquisition of hypertrophied dermal armour.

6.3. Phylogenetic position and character evolution

Scutellosaurus lawleri was originally described as a member of Fabrosauridae by Colbert [18], although it was suggested it could be ancestral to ankylosaurs and stegosaurs. Fabrosauridae is now considered polyphyletic [1,3,5,20,25,28], and Scutellosaurus lawleri is generally considered an early-diverging member of Thyreophora [1,2,3,4,5,19,20,21,22,23,24,25,26,27]. This phylogenetic position is backed up by numerous aspects of morphology and subsequently numerous phylogenetic characters. In the ornithischian phylogeny of Butler et al. [1], Scutellosaurus lawleri is scored as containing four of the six thyreophoran synapomorphies, including characters 46 (state 1: the absence of a forked posterior ramus of the jugal), 101 (state 0, an absent or weak coronoid process), 106 (state 1, the presence of a strong, anteroposteriorly extended ridge on the lateral surface of the surangular) and 112 (state 0, the presence of six premaxillary teeth). Additionally, Scutellosaurus lawleri is also scored as possessing the
synapomorphy of the clade Thyreophora excluding *Lesothosaurus diagnosticus*, character 89 (state 1, the presence of cortical remodelling on the surface of the skull bones). Similarly, in the ornithischian phylogeny of Boyd [3], *Scutellosaurus lawleri* is scored as possessing the five thyreophoran synapomorphies identified in the analysis, including characters 52 (state 0, the presence of horizontally oriented distal condyles of the quadrates), 86 (state 1, the presence of a strong, anteroposteriorly extended ridge on the lateral surface of the surangular), 112 (state 0, the presence of six premaxillary teeth), 122 (state 0, a concave lingual surface of the maxillary teeth) and 131 (state 0, maxillary teeth positioned near the lateral margin). *Scutellosaurus lawleri* is, therefore, unequivocally a thyreophoran. Within Thyreophora, *Scutellosaurus lawleri* is also excluded from Thyreophoroidea (Eurypoda + *Scelidosaurus harrisonii*) by lacking numerous morphological features. In the ornithischian phylogeny of Butler *et al.* [1], *Scutellosaurus lawleri* contains none of the 16 synapomorphies of Thyreophoroidea identified, and in the ornithischian phylogeny of Boyd [3], *Scutellosaurus lawleri* contains none of the two synapomorphies of Thyreophoroidea identified. Therefore, there is strong evidence for a phylogenetic placement of *Scutellosaurus lawleri* within Thyreophora but outside of Thyreophoroidea, alongside the fragmentary taxon *Emausaurus ernsti*.

### 6.4. Ornithischian dinosaur diversity in the Kayenta Formation

To date, three ornithischian taxa have been identified from the Kayenta Formation: *Scutellosaurus lawleri*, an unnamed larger thyreophoran taxon known from rare osteoderms and postcranial elements [18,58], and an undescribed heterodontosaurid known from a single partial skeleton [20,63,75]. Of these taxa, *Scutellosaurus lawleri* is overwhelmingly the most abundant, with ~80 specimens known. Indeed, *Scutellosaurus lawleri* is the most common tetrapod recovered from the Kayenta Formation and is much more common than remains of theropod [125,126] and sauropodomorph [33] dinosaurs. This represents an unusual situation for Early Jurassic dinosaur faunal assemblages: in the well-sampled upper Elliot Formation of South Africa ornithischian remains are relatively abundant but considerably less common than those of sauropodomorphs [127], whereas ornithischian fossils are exceptionally scarce in the Lufeng
Formation of China in comparison to sauropodomorphs [16,17,128]. Other Lower Jurassic formations that have yielded ornithischian dinosaur material are generally not sufficiently well sampled to assess relative abundances of ornithischians versus other dinosaurs [10,11,12,14,102,124]. Unambiguous members of Thyreophora from the Early Jurassic have only been identified from the northern palaeo-hemisphere to date, from the USA (Scutellosaurus lawleri) and Europe (Scelidosaurus harrisonii, Emausaurus ernsti), as well as probably from China (‘Bienosaurus lufengensis’, ‘Tatisaurus oehleri’).

The possible thyreophoran affinities of Lesothosaurus diagnosticus (southern Africa) and Laquintasaura venezuelae (Venezuela) remain unclear. By contrast, the only Early Jurassic heterodontosaurid known to date from the northern palaeo-hemisphere is the single undescribed Kayenta specimen, whereas heterodontosaurids are moderately abundant (c. 20 known specimens) in the upper Elliot Formation of southern Africa [63,76,129]. These patterns suggest that there was considerable spatial and/or environmental variation in Early Jurassic ornithischian faunas globally.

Acknowledgements: First and foremost, we acknowledge the people of the Navajo Nation for facilitating continued palaeontological research on their land. The specimens described herein were collected by the Museum of Northern Arizona, University of California Museum of Paleontology, and Museum of Comparative Zoology between the years of 1971 and 1983 during fieldwork on the lands of the Navajo Nation under permits issued to MNA. We thank Akhtar Zaman, Bradley Nesemeier, and Richard Carlton of the Navajo Nation Minerals Department for their assistance and support of this research. Any persons wishing to conduct geologic investigations on the Navajo Nation must first apply for and receive a permit from the Navajo Nation Minerals Department, P.O. Box 1910, Window Rock, Arizona 86515 and phone number (928) 871-6588.

Thanks to David Gillette and Janet Gillette (MNA); Mark Goodwin and Patricia Holroyd (UCMP); Christina Byrd, Jessica Cundiff, and Stephanie Pierce (MCZ); and Matthew Brown and
Christopher Sagebiel (TMM) for provided access to specimens, locality data, and historical archives and correspondence in their respective museum collections. We acknowledge and thank William Amaral, James Clark, Emily CoBabe, William Downs, Farish Jenkins, David Lawler, Charles R. Schaff, B. Schubert, Kathleen Smith, and Hans-Dieter Sues for discovering the specimens described herein. We also acknowledge and thank William Downs, Ann Johnson, Randy Johnson, David Lawler, Nova Young, and any other preparators whose hard work went undocumented for the preparation of the specimens described herein. We thank Matthew Baron, Christopher Bell, Matthew Brown, Christopher Griffin, Randall Irmis, Joshua Lively, Adam Marsh, Keegan Melstrom, Sterling Nesbitt, David Norman, Kevin Padian, and Zackery Wistort for helpful discussions and advice.

BTB was funded for this work by the Ernest L. and Judith W. Lundelius Endowment in Vertebrate Paleontology and the Jackson School of Geosciences at The University of Texas at Austin and the Doris O. and Samuel P. Welles Research Fund at the University of California Museum of Paleontology; TJR was funded by a University of Brighton Science Scholarship; RJB was funded by a NERC PhD studentship during the early stages of this work; TBR was funded by National Science Foundation grants EAR 1258878 and IIS-9874781; and SCRM was funded by a University of Cambridge Domestic Research Studentship during the early stages of this work.
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Figure 1. (A) Geologic map of the Adeii Eechii Cliffs on Ward Terrace in northern Arizona. General geographic regions in which specimens of *Scutellosaurus lawleri* have been collected from the Kayenta Formation are highlighted. Modified from Clark & Fastovsky (1986) and Breeden & Rowe (in press). (B) Idealized outcrop lithostratigraphy and chronostratigraphy of Ward Terrace. Lithostratigraphy after Harshbarger et al. (1959) and chronostratigraphy after Marsh et al. (2014), Suarez et al. (2017), and Marsh (2018). (C) Key to the field seasons that have yielded specimens of *Scutellosaurus lawleri* by the institution in which specimens are reposited and the year in which they were collected. Abbreviations: Jk, Kayenta Formation; Jn, Navajo Sandstone; TrJm, Moenave Formation.
Figure 2. *Scutellosaurus lawleri*, holotype (MNA.V.175) left premaxilla in lateral (A) and medial (B) views, and left and right premaxillae in articulation in dorsal (C) and ventral (D) views. Abbreviations: alv1–alv6, alveoli; en, external naris; fo, foramen; gr, groove on medial surface of premaxilla for anterior process of maxilla; mp, maxillary process; np, nasal process; pp, premaxillary palate; rpt, replacement tooth; sym, flattened symphysial surface.
Figure 3. *Scutellosaurus lawleri*, holotype (MNA.V.175) maxillae. Partial left maxilla in medial (A) and dorsolateral (B) views. Fragments of right maxilla in medial (C, E) and lateral (D, F) views. Abbreviations: aof, ventral border of the antorbital fossa; apm, base of the ascending process of the maxilla; gr, groove on dorsal surface of posterior end of bone, medial to the supra-alveolar lamina; n, nasals appressed to lateral surface of left maxilla; rtf, replacement tooth foramina; sal, supra-alveolar lamina.
Figure 4. Scutellosaurus lawleri, referred cranial bones. Frontals and parietal of UCMP 130580 in dorsal (A) and ventral (B) views. Right jugal of UCMP 130580 in lateral (C) and medial (D) views. Left postorbital of UCMP 130580 in lateral (E) and medial (F) views. Left quadrate of UCMP 130580 in posterior (J) and anterior (K) views. Right quadrate of MCZ VPRA-8795 in posterior (G), medial (H), and anterior (I) views. Abbreviations: a.ect, articular surface for the ectopterygoid; a.max, articular surface for the maxilla; a.pf, articular surface for the prefrontal; a.po, articular surface for the postorbital; a.qj, articular surface for the quadratojugal; fc, facet; olft, olfactory tract; orb, orbit; orn, ornamentation (cortical remodelling); ptw, pterygoid wing; ri, ridge; stfo, supratemporal fossa; str, striations.
Figure 6. *Scutellosaurus lawleri*, holotype (MNA.V.175) dentaries. Left dentary in lateral (A) and medial (B) views. Right dentary in lateral (C) and medial (D) views. Abbreviations: be, buccal emargination; for, foramen; Mg, Meckelian groove; rep, replacement tooth; rug, rugose surface; spl, splenial; sym, symphysial surface for the opposing dentary; 1, first tooth position; 15, fifteenth tooth position.
Figure 5. *Scutellosaurus lawleri*, braincase elements. Basioccipitals of the holotype (MNA.V.175; A–B), UCMP 130580 (C–D), and MCZ VPRA-8797 (E–F) in dorsal (A, C, E), ventral (B, D, F), anterior (G), and posterior (H) views. Paraoccipital process of MCZ VPRA-8797 in posterior (I) and anterior (J) views. Abbreviations: a.ex, articular surface for the exoccipital; a.p, articular surface for the parietal; a.pr, articular surface for the prootic; a.so, articular surface for the supraoccipital; bt, basal tubera; ef, endocranial floor; fm, foramen magnum; occ, occipital condyle.
Figure 7. *Scutellosaurus lawleri*, referred mandibular bones. Left dentary of MCZ VPRA-8797 in lateral (A), medial (B), and dorsal (C) views. Right surangular of UCMP 130580 in lateral (D) and medial (E) views. Abbreviations: adf, adductor fossa; be, buccal emargination; for, foramen; lr, lateral ridge; mf, medial flange; Mg, Meckelian groove; rp, retroarticular process; sym, symphysis with antimere; 1, first tooth position; 10, tenth tooth position.
Figure 8. *Scutellosaurus lawleri*, holotype (MNA.V.175) maxillary (A) and dentary (B) teeth, both in lingual view.
Figure 9. *Scutellosaurus lawleri*, atlas and axis. Referred (UCMP 130580) atlas intercentrum in anterior (A) and posterior (B) views. Holotype (MNA V.175) right atlas neural arch in lateral view (C). Odontoid of UCMP 130580 in left lateral (D), ventral (E), and dorsal (F) views. Referred (UCMP 130580) axis neural arch in right lateral (G), dorsal (H), and ventral (I) views. Referred (MCZ VPRA-8801) axis centrum in anterior (J), posterior (K) and ventral (L) views. Abbreviations: cf, concave facet on lateral surface of odontoid, probably for atlas neural arch; aticf, articular facet for the atlas intercentrum on the atlas neural arch; axicf, articular facet for the atlas intercentrum on the axis; na, neural arch; nc, neural canal; odf, facet for odontoid; para, parapophysis; poz, postzygapophysis; prz, prezygapophysis.
Figure 10. *Scutellosaurus lawleri*, referred (MCZ VPRA-8800) cervical vertebra in anterior (A), posterior (B), right lateral (C), left lateral (D), ventral (E), and dorsal (F) views. Abbreviations: k, keel; ns, neural spine; para, parapophysis; poz, postzygapophysis; prz, prezygapophysis; tp, transverse process.
Figure 11. *Scutellosaurus lawleri*, referred dorsal vertebrae. A–E, series of dorsal vertebrae of MCZ VPRA-8800 in lateral view. F–K, dorsal vertebra of MCZ VPRA-8801 in left lateral (F), right lateral (G), dorsal (H), anterior (I), posterior (J), and ventral (K) views. Abbreviations: l.poz, left postzygapophysis; l.prz, left prezygapophysis; ncs, neurocentral suture; ns, neural spine; para, parapophysis; poz, postzygapophysis; prz, prezygapophysis; r.poz, right postzygapophysis; tp, transverse process.
Figure 12. *Scutellosaurus lawleri*, holotype (MNA.V.175) sacral vertebrae. Transitional dorsosacral (labelled S1) exposed on a block in ventral view (A); true sacral 1 (labelled S2) in dorsal (B) and ventral (C) views. True sacral 3 (labelled S4) exposed on a block in ventral view (D). Abbreviations: ost, osteoderm; scf, sacral rib facet. Scale bar relates only to B and C; a scale bar is not given for A and D because the specimens are preserved in blocks of other material and thus the photos are somewhat oblique.
Figure 13. *Scutellosaurus lawleri*, caudal vertebrae. A–K, representative caudal vertebrae of the holotype (MNA.V.175): anterior caudals (labelled caudals 1 and 2) exposed ventrally in a block (A); anterior caudal (labelled caudal 10) in left lateral (B) and dorsal (C) views; posterior caudal (labelled caudal 19) in dorsal (D), ventral (E), and left lateral (F) views; posterior caudal (labelled caudal 30) in left (G) and right (H) lateral views; caudal 43 in left (I) and right (J) lateral views; posterior caudal (labelled caudal 50) in left (K) lateral view. Caudals 30 and 43 (G–J) have osteoderms associated with their neural spines, presumably in close to life position. L–P, referred anterior caudal vertebra of MCZ VPRA-8801 in anterior (L), posterior (M), left lateral (N), right lateral (O), and dorsal (P) views. Abbreviations: cr, caudal rib; ns, neural spine; ost, osteoderm; poz, postzygapophysis; prz, prezygapophysis.
Figure 14. *Scutellosaurus lawleri*, holotype (MNA.V.175) scapulae and coracoids. Re-articulated right scapula and coracoid in oblique ventrolateral view (A). B–C, right scapula in proximal (B) and lateral (C) views. Right coracoid in lateral (D) view. E and H, left coracoid in lateral (E) and medial (H) views. F–G, left scapula in lateral (F) and medial (G) views. Abbreviations: a.co, articulation with the coracoid; ap, acromion process; bl, blade; cf, coracoid foramen; cor, coracoid; gl, glenoid; pp, proximal plate.
Figure 15. *Scutellosaurus lawleri*, holotype (MNA.V.175) right humerus in anterior (A), posterior (B), lateral (C), proximal (D), and distal (E) views. Abbreviations: dpc, deltopectoral crest; hd, head; lc, lateral condyle; mc, medial condyle; mt, medial tuberosity.
Figure 16. *Scutellosaurus lawleri*, referred (UCMP 130580) radius and ulnae. A–D, left radius in posterior (A), lateral (B), anterior (C), and medial (D) views. E–F, left ulna in posterior (E) and anterior (F) views. G–H, right ulna in posterior (G) and anterior (H) views. Abbreviations: ole, olecranon process.
Figure 17. *Scutellosaurus lawleri*, preservation of the holotype (MNA.V.175) right hindlimb. Photograph of painted cast of field jacket (A) and interpretive line drawing of cast of field jacket (B).
Figure 18. *Scutellosaurus lawleri*, ilia. A–B, holotype (MNA.V.175) left (A) and right (B) ilia in medial view. C–D, referred (MCZ VPRA-8792) right ilium in lateral (C) and medial (D) views. E–F, referred (UCMP 130580) left ilium, preacetabular process in lateral (E) and medial (F) views. Abbreviations: dfpre, dorsal flange of the preacetabular process; ftp, flattened tip; ispd, ischial peduncle; le, lateral expansion above the acetabulum; mf, medioventral flange; ppd, pubic peduncle; pre, preacetabular process; sh, shelf; vfpre, ventral flange of the preacetabular process.
Figure 19. *Scutellosaurus lawleri*, referred ischia. A–C, right ischium of MCZ VPRA-8801 in lateral (A), medial (B), and proximal (C) views. D–G, right ischium of UCMP 130580 in lateral (D), medial (E), and proximal (F) views. G–H, shaft of left ischium in lateral (G) and medial (H) views. Abbreviations: ace, acetabulum; gr, groove; ilp, iliac peduncle; lr, lateral ridge; ppd, pubic peduncle.
Figure 20. *Scutellosaurus lawleri*, femora. A–D, holotype (MNA.V.175) left femur in posterior (A), anterior (B), proximal (C), and distal (D) views. E–G, referred (UCMP 130580) left femur, proximal portion in posterior (E), lateral (F), and anterior (G) views. Abbreviations: aat, articularis antitrochanterica; at, anterior trochanter; dlt, dorsolateral trochanter; ft, fourth trochanter; icf, posterior intercondylar fossa; lsu, ligament groove on the proximal end of the femur; nt, notch separating anterior and dorsolateral trochanters; pub, pubis.
Figure 21. Scutellosaurus lawleri, holotype (MNA.V.175) right tibia in anterior (A), lateral (B), posterior (C), medial (D), proximal (E), and distal (F) views. Abbreviations: cnc, cnemial crest; fibc, fibular condyle; lm, lateral malleolus; mc, medial condyle; mm, medial malleolus.
Figure 22. *Scutellosaurus lawleri*, holotype (MNA.V.175) fibulae. A–C, left fibula in lateral (A), proximal (B), and distal (C) views; D–G, right fibula, proximal end in lateral (D) and medial (F) views, distal end in anterior (E) and posterior (G) views. Abbreviations: a.cal, articular surface for the calcaneum; a.tib, articular surface for the tibia; pin, metal pin.
Figure 23. *Scutellosaurus lawleri*, tarsus and pes. A–C, holotype (MNA.V.175) left astragalus in proximal (A), anterior (B), and distal (C) views. D, holotype (MNA.V.175) left astragalus in articulation with distal end of left tibia in anterior view; E–F, paratype (MNA.V.1752) right astragalus and calcaneum in proximal (E) and distal (F) views; G, holotype (MNA.V.175) right distal tarsal 3 in proximal view; H–I, referred (UCMP 130580) right distal tarsal 4 in proximal (H) and distal (I) views; J–M, referred (UCMP 130580) right metatarsus in anterior view, right metatarsal IV (J), right metatarsal III (K), proximal end of possible metatarsal II (L), distal end of metatarsal I (M). Abbreviations: a.lm, articular surface for the lateral malleolus of the tibia; a.mm, articular surface for the medial malleolus of the tibia; ap, ascending process; cal, calcaneum; fo, fossa on anterior surface of the ascending process.
Figure 24. *Scutellosaurus lawleri*, holotype (MNA.V.175) osteoderms. A–F, flat-based osteoderms (Morphotype A) in dorsal (A, C, E) and ventral (B, D, F) views. G–J, concave-based osteoderms (Morphotype B) in dorsal (G, H) and ventral (I, J) views. K–L, two-keeled osteoderm (Morphotype C) in dorsal (K) and ventral (L) views. M–P, hollow-based osteoderms (Morphotype D) in lateral (M, O) and ventral (N, P) views.
Figure 25. *Scutellosaurus lawleri*, referred two-keeled osteoderms (Morphotype C) in dorsal view. A, TMM 43664-1. B, MCZ VPRA-8792. C, MCZ VPRA-8799.
Figure 26. Life reconstruction of the thyreophoran ornithischian dinosaur *Scutellosaurus lawleri* from the Lower Jurassic Kayenta Formation rendered as an obligate biped with a speculative osteoderm arrangement. Artwork used with permission by Gabriel Ugueto, who retains the copyright (gabrielugueto.com).
Responses to Reviewer Comments

Subject Editor comments to Author:

The reviewers are happy to see this paper, and are generally enthusiastic about its publication. One raises what should be carefully considered so as to dispel any doubts about "shingling": it would be important to show how this paper differs from the JVP one, and to repeat only necessary details (although this is sometimes difficult). A new phylogeny is probably needed, but this should not be difficult. A wider inclusion of taxa is also recommended. The other reviewer asks why you are figuring sub-optimal specimens rather than better ones, and if this because the better specimens were already figured in the JVP paper please make that clear.

Redundancies with Breeden & Rowe (2020) have been removed, and we have clarified in the manuscript that the specimens from TMM described in that paper are not re-described here. See comments below in response to Reviewer 2 regarding the exclusion of a phylogeny.

Finally, some clarity about the histological features may be needed. It is common in virtually all non-avian dinosaurs that fibro-lamellar bone should be expressed at least in early growth and a transition made either to FL tissue that is less vascularized OR to lamellar-zonal bone before skeletal growth effectively ceases and the EFS is deposited. Smaller taxa tend to grow more slowly, but of course any given section represents its ontogenetic age, so perhaps you could clarify? I don't mean at all to argue with your position, only to note that the outgroups to Dinosauria already grew very quickly and featured copious FL bone, yet they were not larger than Scutellosaurus. So the hypothesis that the larger, later Thyreophora evolved (not "developed," please) FL bone as a strategy for more rapid growth to larger size could be called into question. I will be interested in your perspective on this.

Padian et al. (2004) noted that in contrast to most dinosaurs, *Scutellosaurus* possesses lamellar-zonal bone throughout the cortex of the bones they examined. We might expect lamellar-zonal bone to be deposited during final stages of growth (during deposition of the EFS), but dinosaurs and their outgroups generally possess faster-growing, better vascularized fibrolamellar bone in earlier-deposited parts of the cortex. The point we are making here is that *Scutellosaurus* does not possess this earlier signature of rapid growth, unlike many dinosaurs. Padian et al. (2004) concluded that *Scutellosaurus* had slow growth throughout its life as a consequence of its small body size, but subsequent work on taxa including the small-bodied basal ornithischian *Lesothosaurus* has indicated that *Lesothosaurus* had typically dinosaurian fibrolamellar bone during early growth. This suggests that *Scutellosaurus* is unique in having slow growth throughout its life, and indeed this slow growth may be a synapomorphy of Thyreophora, because other studies we quote in this section of our paper have also suggested that stegosaurs and ankylosaurs have histological signatures indicative of slow growth relative to other dinosaurs. What we are trying to say here is that the basal condition for Thyreophora was slow growth (lamellar-zonal bone), but as thyreophorans got bigger, they grew faster than their smaller, earlier-diverging relatives. They still grew slower than other dinosaurs (they have more poorly vascularized bone), but relative to basal thyreophorans, they grew faster because they were bigger. We’ve attempted to nuance the text to explain this better. If the subject editor feels
we have either mischaracterized previous studies or haven’t done a sufficient job of expressing what we mean here, we are happy to make further changes if advised.

Also, I noted that on line 23 of your MS page 46, you have an extra "closure"

Corrected.

Reviewer: 2

This study provided a detailed description of the early armoured dinosaur Scutellosaurus lawleri from the Kayenta Formation of Arizona. This will help for improving the early evolution of ornithischians. Both the description and figures are good. But there are still some things that need to make it clear before publication. Here are my comments as follows:

1. I notice that the authors have already provided a detailed description of Scutellosaurus published in JVP recently, although the latter only contains specimens from TMM. This MS cited many times of that paper, and I think it is a little redundant. So I believe it is more appropriate that this paper is a complementary description for Scutellosaurus that no need to describe all the bones, but just contains new data and comparisons. This will make the paper more concise.

Redundancies with Breeden & Rowe (2020) have been removed.

2. The authors mainly compared Scutellosaurus with basal thyreophorans. I hope the author adds more comparison with other ornithischians that have similar size or feature, such as Eocursor, Agilisaurus, Hexinlusaurus, Jeholosaurus, and also some primitive stegosaurs including Huayangosaurus. Isaberrysaura was original considered to a basal neornithischian, but re-put basal stegosaur in Han etal (2018). It should also be added for comparison. In addition, I notice that the dentary of Scutellosaurus is quite long and shallow dorsoventrally. The ratio of length to depth is also worth comparing with other ornithischians.

We have added comparisons to Jeholosaurus, Huayangosaurus, and Isaberrysaura. Comparisons to Eocursor, Agilisaurus, and Hexinlusaurus were already present in the manuscript, but we have added additional references where suggested in Reviewer 2’s marked PDF.

3. In the comparison, I notice many other specimens do not have references. Do you check this by yourself or from references? If you check by yourself, please mention that in the "material and method" part.

We have added a paragraph clarifying which comparative taxa were examined firsthand and which were referenced from the literature.

4. Page 48. The authors state that among ornithischians only Scutellosaurus have lamellar-zonal bone. This seems unlikely. In Padian (2004), we can see that Scutellosaurus still has abundant vascular canals in the inner region of a tibia (Padian 2004, Figure 3D), unlike the condition in
modern crocodiles and lizards, but is similar to Jeholosaurus (Han et al. 2020, bone histology of Jeholosaurus). Padian (2004) did mention that a radius shows lamellar-zonal pattern (Fig. 3A), but this is not the femur, tibia or humerus that we usually sampled. In fact, limb bones can show different bone patterns in different parts, the fibulae and ribs usually have less vascular canals that show parallel-fibered or lamellar bone.

This comment of the reviewer is difficult to reconcile with the information provided in the respective papers. Padian et al. (2004: 559), on the histology of three limb bones of *Scutellosaurus*, stated:

“In summary, there is very little if any typical fibro-lamellar bone in most of these elements; instead, the bone is parallel-fibered and not highly vascularized compared to the bones of most dinosaurs… Its “lamellar-zonal” structure is similar to that of crocodylians.”

They also noted that bone of the basal ornithopod *Orodromeus* is “more highly vascularized than *Scutellosaurus*…”.

Han et al. (2020), on the histology of the tibia and fibula of the basal ornithopod *Jeholosaurus*, stated that bone tissue in all growth stages they investigated was fibro-lamellar (Table 3, p. 6), and that the bone tissue throughout was highly vascularized.

Han et al. (2020) did not refer to the paper of Padian et al. (2004) or contrast the condition seen in *Jeholosaurus* with that in *Scutellosaurus*. Padian et al. (2004) showed an image of the tibia of *Scutellosaurus*, which can be compared directly with the tibia of *Jeholosaurus*. The difference in presentation of these images makes comparison a bit difficult, but it does appear that the *Jeholosaurus* tibia is more highly vascularized than that of *Scutellosaurus*, which accords with Padian et al’s findings that *Orodromeus* is also more highly vascularized than *Scutellosaurus*.

It would certainly be interesting to update the study of Padian et al. (2004) in the light of new specimens of *Scutellosaurus* and the vast number of histological studies that have been carried out on basal ornithopods and other small dinosaurs in the 17 years since the former was published. However, that is vastly beyond the scope of the present work. Given the information that is available in the literature, we stand by our original hypothesis that the evidence currently suggests that *Scutellosaurus* had slower growth rates than other dinosaurs. This isn’t particularly controversial as slow growth rates have been hypothesized for other thyreophorans. We have attempted to nuance the text to express these things better.

5. As the author provided new features of Scuttelosaurus, a new phylogenetic analysis is necessary. I find that the authors have provided phylogenetic analysis in another paper (JVP online), but they did not mention it here. Furthermore, I strongly suggest that they can do a new phylogenetic analysis of basal ornithischians based on newly published data, such as Boyd 2015 or Han et al 2018, and add some new related taxa. The matrix of Butler et al (2010) has already changed more or less.
We argue that a phylogeny is beyond the scope of this paper and is not necessary because the phylogenetic position of Scutellosaurus as a thyreophoran is not controversial. In every matrix to which it has been added since the earliest phylogenetic analyses of ornithischian dinosaurs (e.g., Sereno, 1986), it has been recovered as an early-diverging thyreophoran. This includes analyses designed to focus on basal ornithischian relationships (e.g., Butler et al., 2008 and all matrices derived from that), basal dinosaur relationships (e.g., Baron et al., 2017), basal ornithopod relationships (e.g., Boyd et al., 2015; Han et al., 2018), ankylosaurs (e.g., Thompson et al., 2012), and stegosaurs (e.g., Maidment et al., 2008 and matrices derived from that). These analyses have used a variety of different character sets but result in the same phylogenetic position for Scutellosaurus as a non-eurypodan thyreophoran. Further, new observations on the anatomy of Scutellosaurus resulting from the work submitted here have already been incorporated into phylogenies by authors of this manuscript (e.g., Butler et al. 2008; Maidment et al. 2008; Raven & Maidment, 2017; Breeden & Rowe, 2020), some of which have then been incorporated into later ornithischian analyses. Lastly, the ornithischian data matrices Reviewer 2 suggests using to test the phylogenetic position of Scutellosaurus are not appropriate because they are not explicitly designed to test thyreophoran relationships, and its placement within Ornithischia as a thyreophoran is not in question. The most appropriate dataset would be a total-group thyreophoran dataset, which one of the authors (Tom Raven) currently has in preparation. That is a substantial piece of work on its own that will be published as a separate paper.

I have more comments in a marked version of the pdf. Please also see that. Thank you.

We have addressed the notes and comments in the marked PDF, perhaps the most significant of which is the addition of a figure showing the holotype manus (Figure 17 of the revised manuscript).

Reviewer: 3
Comments to the Author(s)

This is a well-written and highly detailed anatomical description of the key early dinosaur Scutellosaurus, and represents a very valuable addition to the literature that will no doubt be well-cited in the future. In its position at the base of the diverse and successful armoured dinosaur radiation, Scutellosaurus is a key taxon and the data contained in this manuscript will be invaluable for future research in taxonomy, cladistics, evolutionary dynamics and palaeobiology.

I have only a very few suggested changes for this manuscript prior to publication:

1. For several elements - the nasal, postorbital, squamosal and others, see annotated PDF - it is acknowledged in the text that better preserved and more complete elements exist for some specimens and indeed the text description is based on these best preserved examples. Yet they are not figured; instead, more poorly preserved specimens are figured. Why not figure the very best examples for each bone on which verbal descriptions are based?

As noted in our response to Review 2, redundancies with Breeden & Rowe (2020) have been removed, and we have also more explicitly stated that skeletal elements only present in specimens from TMM are fully described in that paper and are therefore not re-described here.
2. I do not think Figure 17 is ever cited in the main text and it does not appear between references to Figures 16 and 18.

We have added citations to Figure 17 (which is now Figure 18 with the addition of a new figure of the manus).

3. The authors make the very interesting observation on Page 50, Line 24 that different Early Jurassic localities featured different dinosaur faunas, in terms of composition of herbivores (sauropodomorphs, heterodontosaurids, thyreophorans). Any speculation on what was driving these variations?

We agree that this question is interesting, but it is beyond the scope of this study and warrants further study on its own. We refrain from speculating further here without additional data.

4. Some minor errors in the references cited (see PDF), please check these carefully prior to submission.

Corrected.

5. Also a few, very minor errors with figure captions, particularly abbreviations. Again, please check carefully. Depending on the final size of the figure, you may want to consider increasing the size of labels on the figures (abbreviations) as they are currently very small and can be difficult to discern. It would be very useful for Figure 8 to indicate which directions are anterior and posterior.

We have addressed the errors in figure captions and revised Figure 8 to include arrows; however, we have opted against increasing the font size of the labels.

Lastly, there are some minor grammatical errors and a few places where the meaning of sentences could be clarified - I have made suggested changes in the attached annotated PDF.

Corrected.
Responses to Editor and Reviewer Comments

Subject Editor comments to Author:

Dear Ben et al., thanks for your revisions on this. I tend to agree with the reviewer on the histology; we didn't sample a lot, but recall that small taxa grow more slowly than larger related taxa, and our specimen seemed quite typical of small ornithodirans, so I'm not sure this is a synapomorphy of anything, given the mixed tissue signal. Anyway, best wishes for revisions and I look forward to the finished product.

Reviewer comments to Author:

Reviewer: 2
Comments to the Author(s)

I still have some questions about the bone histology part. The original paper (Padian 2004) only mentioned the bone section of radius to be best characterized as lamellar-zonal. For the bone tissue of femur, he wrote:“Woven bone tissue of periosteal origin surrounds the numerous primary osteons, most of which are parallel and oriented longitudinally (P556). ----No LAGs are observed”. This is more like fibrolamellar bone. The original paper did mention that “the bone is parallel-fibered and not highly vascularized compared to the bones of most dinosaurs”. However, I am afraid this is also not an “autapomorphy” mentioned in their revised MS. For example, a noasaurids theropod *Masiakasaurus* also shows parallel-fibered bone type (see Lee and Connor, 2013, Bone histology confirms determinate growth and small body size in the noasaurid theropod *Masiakasaurus knopfleri*). In sum, I agree that *Scutellosaurus* may have slower growth rates than most dinosaurs but we need be careful to say it to be autapomorphic in dinosaurs.

Although we maintain that the apparent slow growth of *Scutellosaurus* seems unique among its close relatives, we have removed language referring to this phenomenon as apomorphic per the feedback from the Subject Editor and Reviewer 2.