**Pendraig milnerae**, a new small-sized coelophysoid theropod from the Late Triassic of Wales

Stephan N. F. Spiekman, Martin D. Ezcurra, Richard J. Butler, Nicholas C. Fraser and Susannah C. R. Maidment

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Original submission: 7 June 2021
Revised submission: 25 August 2021
Final acceptance: 7 September 2021

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

**Review History**

RSOS-210915.R0 (Original submission)

Review form: Reviewer 1 (Christopher Griffin)

Is the manuscript scientifically sound in its present form?
Yes

Are the interpretations and conclusions justified by the results?
No

Is the language acceptable?
Yes

Do you have any ethical concerns with this paper?
No

Have you any concerns about statistical analyses in this paper?
No
Recommendation?
Major revision is needed (please make suggestions in comments)

Comments to the Author(s)
This manuscript presents a thorough comparative description of a new theropod dinosaur and places it into a phylogenetic hypothesis using a relevant and recent character matrix. The small size of the holotype individual is striking, so the authors also conduct an ancestral state reconstruction for body size among early theropod dinosaurs and also attempt to take the individual’s ontogenetic status into account to be sure that the small size does not simply stem from the individual’s immaturity.

The manuscript is well-written and thorough, the comparative descriptions sound, the figures are clear and informative, and the analyses all appear to be properly conducted (but see below for problems with the R code). In my opinion the manuscript is largely sound and can be accepted for publication with moderate revision. I have attached a PDF (see Appendix A) with my minor edits and comments.

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maximum body size and would not have gotten much larger. Instead, I think that there is not enough evidence to say one way or another.

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and I think the authors can incorporate the concerns from my comment #3 without including
histology. I know that it is not always possible or desirable to destructively sample a holotype.
However, I do think that it would make the paper stronger, more convincing, and more citable,
and therefore I recommend the authors add this to their study if it is possible.

The authors are free to contact me with any questions, requests for clarification, or concerns.

Chris Griffin
chris.griffin@yale.edu

See attached file (Appendix B) for the modified figures referenced above, showing suggested
locations for histological sampling.

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

Comments to the Author(s)
I congratulate the authors on what is a well-researched and well-written manuscript. The
description is a good length and provides sufficient comparisons, the assessment and subsequent
discussion of skeletal maturity in the new taxon is welcome and justified, and the figures
appropriately provide the reader with visual representations of important anatomical
characteristics. I conducted the phylogenetic analysis in TNT and have no concerns about that
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some comments on interpretation). I have attached my grammar and syntax edits/comments in a
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changes below. Thank you for the opportunity to review this work; it’s an important new taxon
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eventually help stabilize this part of the tree.
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Page 19, line 46: The holotype of kayentakatae is MNA V2623, is that what you mean here and a few other places?

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The fossil record is actually pretty bad and the fact that we can use it to say anything at all is always so incredible to me.

Again, this is overall a very well-written and important contribution and I congratulate the authors on a good piece of work. Please consider my thoughts and let me know if you have any questions or want any clarifications.

Adam Marsh

Decision letter (RSOS-210915.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 Dr Spiekman

The Editors assigned to your paper RSOS-210915 "Pendraig orynys, a new small-sized coelophysoid theropod from the Late Triassic of Wales" 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 manuscript will be sent back to one or more of the original reviewers for assessment. If the original reviewers are not available, we may invite new reviewers.

Please submit your revised manuscript and required files (see below) no later than 21 days from today’s (ie 16-Jul-2021) date. Note: the ScholarOne system will ‘lock’ if submission of the revision is attempted 21 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.

Kind regards,
Royal Society Open Science Editorial Office
Royal Society Open Science
Associate Editor Comments to Author (Dr Jennifer Botha):
Associate Editor: 1
Comments to the Author:
This is a good paper, well worth publishing. However, there are some corrections necessary before the paper can be accepted for publication. Two important points worth noting specifically:
(1) one of the reviewers tested the code and was unable to replicate the results - the code needs to be checked for errors and (2) the interpretation that this individual is a small taxon as opposed to being a juvenile requires further evidence, and reviewer one makes a good case for thin sectioning part of the femur to check for the presence of an EFS. Otherwise there is simply not enough evidence for small size. I encourage the authors to look seriously into this suggestion.

Reviewer comments to Author:
Reviewer: 1
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===PREPARING YOUR MANUSCRIPT===

Your revised paper should include the changes requested by the referees and Editors of your manuscript. You should provide two versions of this manuscript and both versions must be provided in an editable format:

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.

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/.

While not essential, it will speed up the preparation of your manuscript proof if accepted if you format your references/bibliography in Vancouver style (please see https://royalsociety.org/journals/authors/author-guidelines/#formatting). You should include DOIs for as many of the references as possible.

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See Appendix D.

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# Appendix A

## ROYAL SOCIETY OPEN SCIENCE

**Pendraig orynys, a new small-sized coelophysoid theropod from the Late Triassic of Wales**

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Ethics

Does your article include research that required ethical approval or permits?:
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Statement (if applicable):
CUST_IF_YES_ETHICS :No data available.

Data

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

Statement (if applicable):
All data are provided for initial review as supplementary material.

Zip folders are provided for the R code and associated data files for both the regression and ancestral state reconstruction analyses. The initial code for the ancestral state reconstruction is provided for the analysis figured in Figure 8. Th parameters can easily be changed manually by reviewers familiar with R to perform the analyses under the various settings provided in the Supplements. Different MPTs and the femoral lengths used for the conservative analyses are provided in the zip folder and minimum branch length can easily be adjusted from 1.0 to 0.5 and 0.1 in the code.

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):
SNFS, MDE, RJB, and SCRM designed the study. SNFS and MDE contributed to data collection. SNFS, MDE, and RJB analysed the data. SNFS made the figures and wrote the majority of the manuscript. All authors contributed to the writing and reviewing of the manuscript.
Pendraig orynys, a new small-sized coelophysoid theropod from the Late Triassic of Wales

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Abstract.

We describe a new genus and species of small-bodied coelophysoid theropod dinosaur, Pendraig orynys gen. et sp. nov, from the Late Triassic fissure fill deposits of Pant-y-ffynnon in southern Wales. The species is represented by the holotype, consisting of an articulated pelvic girdle, sacrum and posterior dorsal vertebrae, and an associated left femur, and by two referred specimens, comprising an isolated dorsal vertebra and a partial left ischium. Our phylogenetic analysis recovers Pendraig orynys as a non-coelophysid coelophysoid theropod, representing the first named unambiguous theropod from the Triassic of the United Kingdom. Recently it has been suggested that the faunas of Pant-y-ffynnon and other nearby Late Triassic to Early Jurassic fissure fill localities might have been subjected to insular dwarfism. To test this hypothesis for Pendraig orynys, we performed an ancestral state reconstruction analysis of body size in early neotheropods. Although our results indicate that a reduced body size is autapomorphic for Pendraig orynys, some other coelophysoid taxa show a similar size reduction, and there is therefore ambiguous evidence to indicate that this species was subjected to dwarfism. Our analyses further indicate that, in contrast to averostran-line neotheropods, which increased in body size during the Triassic, coelophysoids underwent a body size decrease early in their evolution.

Introduction.

The Late Triassic and Early Jurassic fissure fill deposits of southwestern England and southern Wales were formed as Mississippian Carboniferous Limestone exposed at the land surface that underwent karstic weathering processes and faulting [1, 2]. Previously, the putative Triassic age of the sediments was largely assessed as such on their basic lack of mammal remains and their occurrence
in generally wider, distinctly solution-etched karstic features; they were considered to be representative of an upland environment (e.g., [2]). Other fissures containing generally less diverse vertebrate assemblages, but including extensive mammalian remains, and occurring in more restricted slot-like openings in the limestone were regarded as representative of island communities – most specifically Early Jurassic as corroborated by palynomorphs [3, 4]. Since then, many new discoveries have been made and evidence has been presented to suggest that at least some of the putative Triassic fissure fills were subject to the influences of marine transgressions and they are now considered to have been distributed among various nearshore islands [5-9]. Dating the fissure fills has continued to prove difficult due to their depositional setting, but some recent revisions, including faunal comparisons and palynological analyses, now argue that they are between early Rhaetian and early Sinemurian in age [1, 6, 10]. Yet doubt still remains and others [11, 12] continue to contend that some of the assemblages date back to the Norian and were filled at a time when the area was probably more akin to a broad sabkha-type environment.

Due to their unique preservational setting, a rich assemblage of mostly small-bodied vertebrates has been recovered from the fissure fills, which has provided important insights into the early evolution of major tetrapod groups such as mammaliaforms, rhynchocephalians, crocodylomorphs, and dinosaurs, as well as enigmatic diapsid groups such as kuehneosaurids (e.g., [13-18]). It has been suggested that taxa known from the fissure fills are smaller than their close relatives [19-21]. Although this has not been tested quantitatively, it has tentatively been attributed to insular dwarfism, which is a manifestation of the biogeographical concept known as the ‘Island Rule’ [22, 23]. However, most of the specimens are preserved as isolated fragments, meaning that the taxonomic status and phylogenetic position of much of the material has remained controversial.

Among the fissure fills faunas, archosaurs are represented by aetosaurs, phytosaurs, an enigmatic pseudosuchian, crocodylomorphs, sauropodomorph dinosaurs, and theropod dinosaurs, many of which have not been formally described (e.g., [1, 6, 24]). *Thecodontosaurus antiquus* and *Pantydraco caducus*, two sauropodomorph dinosaurs, represent the best studied archosaurs from the fissure fills. *Thecodontosaurus antiquus* was the fourth British dinosaur to be described [25, 26] and is represented by mostly isolated remains from Durdham Down Quarry in Bristol and Tytherington Quarry (Rhaetian) [20, 27]. *Pantydraco caducus* is known from the putatively coeval Pant-y-ffynnon Quarry and is represented by a partial articulated skeleton including most of the skull, as well as a few partial skeletons and isolated elements [28, 29]. The material of *Pantydraco caducus* is considerably smaller than that described for *Thecodontosaurus antiquus*, and it was originally described and identified as *Thecodontosaurus* sp. [30]. The Pant-y-ffynnon specimens were subsequently referred to *Thecodontosaurus caducus* [29] and later *Pantydraco caducus* [31] and
considered to differ from *Thecodontosaurus antiquus* in the morphology of the cervical vertebrae, ilium, and humerus. Although *Pantydraco caducus* has been described in detail [28, 29], its taxonomic status is contentious, since the observed morphological differences with *Thecodontosaurus antiquus* are minor and could be attributable to taphonomic deformation or ontogenetic variation, and *Pantydraco caducus* might represent an early ontogenetic stage of *Thecodontosaurus antiquus* [20].

Crocodylomorphs are currently represented by a single taxon, *Terrestrisuchus gracilis*, a gracile non-crocodyliform crocodylomorph known from several partially articulated and many disarticulated specimens from Pant-y-ffynnon Quarry [18]. However, extensive crocodylomorph material is also known from Cromhall Quarry and might represent two separate species, both different from *Terrestrisuchus gracilis* [32], but this material has not yet been studied in detail. Cromhall Quarry has also yielded isolated material, comprising an ilium, maxilla, humerus, two astragali, and a tooth that were interpreted to represent a single dinosauriform taxon, ‘*Agnosphytis cromhallensis*’ [32]. The ‘*Agnosphytis cromhallensis*’ specimens were inferred to represent a single taxon because of the absence of additional archosaurian material among the Cromhall Quarry specimens, except for confidently identified crocodylomorph and ‘rauisuchian’ remains. However, the astragalus possessed several dinosaurian traits, the holotype specimen, an ilium, appeared similar to sauropodomorphs, and the maxilla had features present in non-dinosaurian dinosauriforms; consequently, it was suggested that ‘*Agnosphytis cromhallensis*’ might represent a chimera and a *nomen dubium* [33-37]. The original hypodigm of ‘*Agnosphytis cromhallensis*’ was recovered as a silesaurid in the analysis of Baron et al. [33] and in subsequent revisions of this analysis in a large polytomy at the base of Saurischia [38] or as the sister taxon to Herrerasauridae and Dinosauria [39]. Recently, an enigmatic pseudosuchian archosaur of equivocal phylogenetic affinity, *Aenigmaspinia pantyffynnonensis*, has been described from Pant-y-ffynnon based on two complementary blocks comprising semi-articulated vertebrae, ribs, osteoderms, a scapula, and a number of fragments including skull bones, in addition to several fragmentary remains [24]. Additional fragmentary archosaur remains have also been identified from various fissure cuts from Cromhall Quarry [40] and a phytosaur tooth and a possible humerus from Durdham Down Quarry assigned to ‘*Paleosaurus platyodon*’, which is now considered to represent a *nomen dubium* [27].

Finally, a theropod has been reported from Pant-y-ffynnon Quarry. It was originally described in the unpublished PhD thesis of Warrener [41] and interpreted as a coelurosaur. In it, an articulated pelvic girdle, associated with the two posteriormost dorsal vertebrae and four sacral vertebrae, a largely complete femur, an isolated dorsal vertebra, and a partial ischium were referred to the unnamed theropod. Additionally, it was suggested that three phalanges, including one ungual, and a
metapodial that were associated with the other remains could possibly be referred to the same
taxon. Subsequently, the Pant-y-ffynnon theropod was briefly described and interpretative drawings
of the pelvic girdle and femur were presented by Rauhut and Hungerbühler [42]. Therein, the
material was assigned to Syntarsus sp. and considered to be closely related to the coelophysoid
theropods ‘Syntarsus’ rhodesiensis (now Megapnosaurus rhodesiensis) and Procompsognathus
triassicus. The Pant-y-ffynnon theropod was also mentioned by Galton and Kermack [28] and therein
referred to as Coelophysis without providing further justification for this assignment. Recently it was
reported that the material could not be located within the NHMUK collections [43]. However, the
articulated partial pelvic girdle and vertebrae, as well as the femur and complete isolated dorsal
vertebra referred to the theropod by Warrener [41] have now been relocated. Here, we provide the
first detailed comparative description of this new taxon. We incorporate it in a phylogenetic analysis
and compare its relative body size to other early theropod dinosaurs to examine whether the small
size of the taxon might be a consequence of island dwarfism, as has been suggested for other
elements of the fissure fills faunas [19-21].

**Systematic Palaeontology.**

Archosauria Cope, 1869-1870 [44] [Gauthier & Padian, 2020] [45]

Dinosauria Owen, 1842 [46] [Langer, Novas, Bittencourt, Ezcurra & Gauthier, 2020] [47]

Theropoda Marsh, 1881 [48] [Naish, Cau, Holtz, Fabbri & Gauthier, 2020] [49]

Neotheropoda Bakker, 1986 [50], sensu Sereno, 1998 [51]

Coelophysoidea Nopcsa, 1928 [52], sensu Sereno, 1998 [51]

*Pendraig orynys* gen. et sp. nov.

Etymology. *Pendraig* from the Welsh *Pen* (‘head’, ‘chief’ or ‘top’) and *Draig* (‘dragon’), literally
meaning ‘chief dragon’ but used in a figurative sense in Medieval Welsh to mean ‘chief warrior’. The
anglicised form, Pendragon, was the epithet of Uther, father of King Arthur in medieval legend.

*Orynys*, from the Welsh ‘o’r ynys’, meaning ‘of the island’.

Diagnosis. *Pendraig orynys* is a small-sized non-averostran theropod (estimated femoral length:
10.21 cm; lower 95% CI: 8.60 cm; upper 95% CI: 12.08 cm; see below) that differs from other
dinosaurs in the following unique combination of character states present in the holotype
(autapomorphies indicated with an asterisk): posteriormost dorsal vertebrae with a strongly
elongated centrum (c. length c. 2.6 times its anterior height), ilium with a distinctly anteroventrally
slanting dorsal margin of the preacetabular process, and posterodorsal margin of the postacetabular
process curving abruptly posteroventrally and, as a result, the posteroventral end of the process is
formed by an acute angle of approximately 65 degrees in lateral view*; pubis with pubic fenestra;
ischium with well-developed obturator plate but without posteroventral projection forming a deep
U-shaped or V-shaped notch with the shaft; and femur with fourth trochanter posteriorly developed
to a height similar to the mid-depth of the shaft at that level. In addition, the referred middle-
posterior dorsal vertebra differs from other early neotheropods in the absence of an accessory
hyosphene-hypantrum articulation, and the presence of an anteriorly expanded neural spine*.

Holotype. NHMUK PV R 37591: An articulated vertebral series and pelvic girdle comprising the two
posteriormost dorsal vertebrae missing most of the neural spines, three sacral vertebrae and a small
fragment of the centrum of the fourth sacral, a complete left ilium, a largely complete left pubis
missing the distal end, a left ischium missing most of the distal portion, a largely complete right
pubis missing the distal end, and a right ischium missing most of the dorsal and distal portions (field
number P77/1) (Figs. 1 and 2). Additionally, a left femur was found disarticulated from the left
hemipelvis in the same block (field number P76/1). It has been completely freed from the matrix and
is confidently referred to the same individual as the vertebral column and pelvis (Fig. 3).

Referred material. NHMUK PV R 37596 (field number P83/1): A complete middle to posterior dorsal
vertebra completely freed from matrix (Fig. 4). NHMUK PV R 37597 (field number P65/66b): the
proximal end of a left ischium preserving the articular facet with the left ilium (Fig. 5). A counterslab
to this specimen, listed as field number P65/66a and comprising the base of the distal portion and
part of the proximal expansion of the ischium, was described and figured in the unpublished PhD
thesis of Warrener (1983). However, there is no record of this specimen in the collections at NHMUK
and is therefore not considered here.

Locality and horizon. Fissure fills of Pant-y-ffynnon Quarry, southern Wales; earliest occurrence
possibly late Norian, latest occurrence possibly late Rhaetian; 214.7 to 201.3 million years ago [1].

Remarks. Additional material from Pant-y-ffynnon, comprising two isolated non-ungual phalanges
(field numbers P65/30 and P65/49), an isolated metapodial (field number P65/23), and an isolated
ungual (field number P65/45), were considered to possibly be conspecific with *Pendraig orynys* by
Warrener [41] and interpretative drawings of these elements were provided therein. These
elements cannot be confidently attributed to any other known taxa known from Pant-y-ffynnon and
were likely recovered from the same block as the partial left ischium of *Pendraig orynys* (field
number P65/66b) as indicated by the shared number 65 in their field number. The location of these
elements is currently unknown and there is no record of them in the NHMUK collections. Since these
elements do not exhibit diagnostic theropod features, there is currently insufficient support for an unequivocal attribution of this material to *Pendraig orynys*.

Ontogenetic assessment. The limited material currently referable to *Pendraig orynys* limits interpretations of intraspecific variation related to ontogeny, and therefore a comprehensive assessment of maturity cannot be provided. However, we approximate the ontogenetic stage of the holotype NHMUK PV R 37591 by scoring it for the maturity assessment matrix that has been formulated for early theropods (*Coelophysis bauri* and *Megapnosaurus rhodesiensis*) and a non-dinosaurian dinosauriform (*Asilisaurus kongwe*) [53-55]. Based on the results of our phylogenetic analysis (see below), these taxa provide a narrow phylogenetic bracket, and the characters are therefore likely suitable for approximating the maturity of *Pendraig orynys* (see also [56]). However, it is important consider that it cannot be confidently ascertained whether all characters that were scored are truly ontogenetically dependent for this specific taxon. Out of 32 characters of the maturity assessment matrix, 16 could be scored for NHMUK PV R 37591. Eight characters were scored as mature (1) and another eight were scored as immature (0). None of the characters considered highly informative of maturity (see figure 22a in [53]) are scored as 1, nor are any of the characters considered highly informative of immaturity scored as 0. Of the sequence order of mature state attainment (between 1 and 29) [53, 56], NHMUK PV R 37591 has a relative minimum maturity of 5 based on the presence of a mound-like dorsolateral trochanter on the femur (16-1), the presence of the *linea intermuscularis caudalis* on the femur (18-1), and the presence of an obturator ridge on the femur (20-1), and a maximum maturity of 19 based on the co-ossification of less than four sacral vertebrae (2-0), the absence of co-ossification between the ilium and pubis (8-0), the absence of an ‘anterolateral scar’ on the femur (19-0), and the presence of a gracile and thin fourth trochanter of the femur (23-0). The relative maximum maturity indicates that the holotype of *Pendraig orynys* was likely not fully skeletally mature, but the relatively large number of characters scored as 1 indicates that it likely also did not represent an early ontogenetic stage. For example, the holotype of *Pendraig orynys* is interpreted as more skeletally mature than the type specimens of *Liliensternus liliensterni* and as mature as or potentially more mature than the holotype of *Gojirasaurus quayi* [56], which are considerably larger than the new taxon.

**Morphological description and comparisons.**

Here we describe in detail the holotype and referred specimens of *Pendraig orynys* and compare it exhaustively with other non-averostran neotheropods and the early theropod *Eodromaeus murphi*, which has been found as the sister taxon to Neotheropoda in recent analyses (e.g., [57, 58]).

Axial skeleton.
Four largely complete vertebrae are preserved in the holotype specimen NHMUK PV R 37591 (Fig. 2A). Additionally, a partial vertebra is preserved at the anterior end of the preserved vertebral column and a tiny fragment of a sacral vertebra is preserved at the posterior end of the column. The anterior two vertebrae are identified as dorsal vertebrae and the other four as sacral vertebrae based on the presence of articulations with the ilia, as is explained in more detail below. The isolated dorsal vertebra NHMUK PV R 37596 (Fig. 4) was not associated with NHMUK PV R 37591 and thus cannot unequivocally be referred to the same individual. However, as is explained below, NHMUK PV R 37596 can be relatively confidently referred to *Pendraig orynys* based on a strong morphological overlap with NHMUK PV R 37591 and because both specimens were recovered from the same locality.

Dorsal vertebrae.

The most anterior vertebra of the articulated vertebral series preserved in NHMUK PV R 37591 comprises a partial centrum and neural arch, which preserves the left diapophysis (Figs. 1B and 2A, C). The neural spine and anterior portion of the vertebra are completely missing. The right side of the specimen is damaged and partly missing. The centrum is only exposed on its broken right lateral side. There is no visible suture between the centrum and neural arch. On the left side the diapophysis is complete and has an anteroposteriorly elongate, oval articular facet (Fig. 1A). The process reaches less far laterally than the diapophysis of the succeeding vertebra (Fig. 2A). In dorsal view, the diapophysis is sub-trapezoidal, with the posterior margin of the diapophysis being slightly concave and the anterior margin being anteriorly curved at its base. This almost certainly represents the paradiapophyseal lamina (*sensu* [59]) that connected the diapophysis to the parapophysis — which is not preserved—, as occurs in the middle-posterior dorsal vertebrae of other early neotheropods (e.g., *Megapnosaurus rhodesiensis* [60]; *Liliensternus liliensterni*: HMN MB.R.2175; *Dilophosaurus wetherilli* [61]). The left postzygapophysis is poorly preserved and its morphology cannot therefore be inferred, but it is still in articulation with the corresponding prezygapophysis of the succeeding dorsal vertebra.

The last dorsal vertebra of NHMUK PV R 37591 comprises a complete centrum and a neural arch missing the neural spine, right diapophysis, and right postzygapophysis (Figs. 1B and 2A). Its centrum is 14.7 mm long, being 2.63 times the height of its anterior surface (Table 1). This ratio matches that of at least some specimens of *Coelophysis bauri* (e.g., [62]: ratio = 1.98–2.87, D11–D13 of AMNH 7228 based on the posterior height of the centrum) and is slightly proportionally longer than those of the posterior dorsal vertebrae of *Eodromaeus murphi* (PVSJ 562: ratio = 2.0–2.18), *Panguraptor lufengensis* ([63], fig. 1: ratio = c. 2.0–2.11 in the last two dorsal vertebrae), and *Megapnosaurus*
rhodesiensis ([60]: ratio = 2.10, D13 of NHMB QG 1). By contrast, these vertebrae are considerably proportionally shorter in Liliensternus liliasterni (HMN MB.R.2175 2.22–2.24: ratio = 1.58–1.67, posterior dorsal vertebrae), Lucianovenator bonoi (PVSJ 906: ratio = 1.63, last dorsal vertebra), Lophostropheus airelensis ([64]: ratio = 1.32, last dorsal vertebra), Dracoraptor hanigani (NMW 2015.5G.1–2015.5G.11: ratio = 1.63–1.75, middle–posterior dorsal vertebrae), Cryolophosaurus elliotti (FMNH PR1821: ratio 1.07, posterior dorsal vertebra), Dilophosaurus wetherilli ([61]: ratio = 1.16–1.52, D10, D11 and D13 of UCMP 37302; ratio = 1.19 D14 of UCMP 77270), and Sarcosaurus woodi ([57]: ratio = c. 1.9, middle–posterior dorsal vertebra of WARMS G678). The ventral surface of the centrum is anteroposteriorly concave and lacks a ventral keel (Fig. 1B). The centrum is amphiplatyan with very slightly concave anterior and posterior articular surfaces. As in the preceding vertebra, no visible suture is present between the centrum and neural arch. The lateral surface of the centrum bears an anteroposteriorly elongate but shallow fossa just ventral to the articulation with the neural arch, which is a common condition in the middle–posterior dorsal vertebrae of early neotheropods (e.g., Liliensternus liliasterni: HMN MB.R.2175; Procompsognathus triassicus: SMNS 12591; Lucianovenator bonoi: PVSJ 906; Lophostropheus airelensis [64]; Sarcosaurus woodi [57]). The last dorsal vertebra possessed only a single articular facet for the rib on each side, located at the end of a transversely wide, wing-like transverse process (Fig. 2A). In dorsal view, its posterior margin is concave and its anterior margin appears to be somewhat sinusoidal. There is no distinct fossa on the dorsal surface of the base of the transverse process. The articular surfaces of the prezygapophyses face dorsomedially. The articular surface of the left postzygapophysis is poorly preserved. No hyposphene articular surface is preserved, but this region is poorly preserved. The prezygapophyses diverge from each other in dorsal view and their tips are well separated from the median line, contrasting with the sub-parallel prezygapophyses of Sarcosaurus woodi [57].

The isolated dorsal vertebra NHMUK PV 37596 is virtually complete, undistorted, and freed from matrix (Fig. 4). The centrum is 14.6 mm long and 2.59 times longer than the height of its anterior articular surface (Table 1). The elongation of this centrum matches or closely resembles that of the middle dorsal vertebrae of the coelophysids Coelophysis bauri (e.g., NMV P231382: c. 2.6, middle dorsal vertebra), Megapnosaurus rhodesiensis ([60]: 2.33–2.64, D6 and D7 of NHMB QG 1), and Procompsognathus triassicus (SMNS 12591: 2.70–2.91, D7 and D8), whereas in other early neotheropods the middle-posterior dorsal vertebrae are proportionally shorter (e.g., Liliensternus liliasterni, Gojirasaurus quayi; Dilophosaurus wetherilli, Dracoraptor hanigani, Cryolophosaurus elliotti; Sarcosaurus woodi) [57, 61, 65–67]. The ventral surface of NHMUK PV 37596 is concave in lateral view and there is no ventral keel. A single nutrient foramen can be observed close to the anterior end of the centrum on its right ventrolateral side. The anterior and posterior articular
surfaces of the centrum are both very slightly concave and transversely broader than tall, resembling the condition in *Gojirasaurus quayi* [65]. By contrast, the centrum is taller than broad in the posterior dorsal vertebrae of *Megapnosaurus rhodesiensis* ([60]: table 6), *Sarcosaurus woodi* (only the anterior surface is preserved) [57], *Cryolophosaurus elliotti* [67], and *Dilophosaurus wetherilli* [61], approximately as broad as tall in *Liliensternus liliensterni* (HMN MB.R.2175), and both conditions occur in *Eodromaeus murphi* (PVSJ 562). The lateral surfaces of the centrum bear a shallow fossa directly ventral to the connection to the neural arch, as occurs in NHMUK PV R 37591 and other early neotheropods (see above). The neurocentral suture is closed along most of its extension, being only visible on the most posterior region of the neural arch peduncle on both sides of the bone.

The diapophysis is placed on a wide sub-trapezoidal or wing-like transverse process (Fig. 4D). In dorsal view, the posterior margin of this process is mainly laterally oriented and slightly concave, whereas the anterior margin is anteromedially to posterolaterally oriented and somewhat sinusoidal. The anteroposteriory long base of the transverse process and strong posterolateral slating of its anterior margin resemble the condition in the middle dorsal vertebrae of *Eodromaeus murphi* (PVSJ 562) and the coelophysids *Coelophysis bauri* (AMNH 7224), *Megapnosaurus rhodesiensis* [60], and *Procompsognathus triassicus* (SMNS 12591). The parapophysis is placed on a strongly developed, narrow and rod-like stalk, but it is considerably less extended laterally than the diapophysis, resembling the condition in the middle-posterior dorsal vertebrae of at least some other early neotheropods (e.g., *Liliensternus liliensterni*: HMN MB.R.2175; *Megapnosaurus rhodesiensis* [60]). Both processes are positioned fully on the neural arch and are connected through a thin paradiapophyseal lamina (*sensu* [59]). The diapophysis is located slightly dorsal to the parapophysis (Fig. 4A-B). The articular facet of the diapophysis is oval and anteroposteriory elongated, whereas the facet of the parapophysis is subcircular. The parapophyseal centrodiaophyseal fossa ventral to the diapophysis is shallow, whereas the parapophyseal centroprezygapophyseal and postzygapophyseal centrodiaophyseal fossae are very deep and framed by pronounced and thin laminae (*sensu* [68]). The laminae framing the parapophyseal prezygapophyseal fossa are the prezygaparapophyseal lamina dorsally and the anterior centroparapophyseal lamina ventrally, whereas the postzygapophyseal centrodiaophyseal fossa is framed by the postzygodiapophyseal lamina dorsally and the posterior centrodiaophyseal lamina ventrally (*sensu* [59]). This pattern of laminae and fossae matches that of a posterior dorsal vertebra of *Liliensternus liliensterni* (HMN MB.R.2175 2.22). There are no pneumatic foramina within the fossae. The transition between the transverse process of the diapophysis and the neural spine forms an angle of approximately 90 degrees, and there is no fossa present in this region. The
postzygapophyses are closely placed together and their articulation facets face ventrolaterally. A hyposphene is absent between the postzygapophyses and therefore there is no accessory intervertebral articulation (Fig. 4F), contrasting with its presence in the middle-posterior dorsal vertebrae of *Eodromaeus murphi* (PVSJ 562), *Megapnosaurus rhodesiensis* [60], *Gojirasaurus quayi* [65], *Cryolophosaurus ellioti* [67], *Sarcosaurus woodi* [57], and *Dilophosaurus wetherilli* [61]. The articulation facets of the prezygapophyses face dorsomedially (Fig. 4E). Both the spinoprezygapophyseal and spinopostzygapophyseal fossae are very narrow slit-like openings between the pre- and postzygapophyses, respectively [68], and they do not extend onto the surface of the neural spine. The spinopostzygapophyseal fossa is considerably larger than the spinoprezygapophyseal one.

The neural spine is proportionally low, being 0.4 times taller than anteroposteriorly long at its base, resembling the condition in the middle and posterior — but not the posteriormost — dorsal vertebrae of *Coelophysis bauri* (AMNH 7224) and *Megapnosaurus rhodesiensis* [60]. By contrast, *Eodromaeus murphi* and other early neotheropods (e.g., *Dilophosaurus wetherilli* [61]; *Gojirasaurus quayi* [65]; *Panguraptor lufengensis* [63]) have proportionally taller middle-posterior dorsal neural spines (ratio >0.5). The anterior margin of the neural spine is located at the level of the parapophysis (Fig. 4A-B). It curves from its base into an anterodorsal direction and subsequently becomes posterodorsally oriented distally. The posterior margin of the neural spine is notched proximally as a result of strongly anterior bowing in lateral view. Distally, the posterior margin is posterodorsally directed and convex. The posterior end of the neural spine is slightly further extended posteriorly than the postzygapophyses. The presence of middle-posterior dorsal vertebrae with a curved posterior margin of the neural spine that overhangs the postzygapophysis also occurs in *Coelophysis bauri* (NMV P231382), *Procompsognathus triassicus* (SMNS 12591), and *Dilophosaurus wetherilli* [61]. In some other early theropods the neural spine also extends posteriorly close to or beyond the level of the postzygapophysis, but the posterior margin of the spine is straight (e.g., *Eodromaeus murphi*: PVSJ 562; *Gojirasaurus quayi* [65]). The distal margin of the neural spine is not transversely expanded (Fig. 4E-F). Most of the distal margin is straight and slightly anteroventrally directed in lateral view. Posteriorly, the distal margin is convex, sloping down towards the posterior margin. The neural spine is 14.3 mm long and 5.0 mm tall (Table 1). Its left lateral surface is largely missing (Fig. 4B).

Compared to NHMUK PV R 37596, only few morphological features of the posterior dorsal vertebrae can be deduced from the articulated vertebral series of NHMUK PV R 37591. Nevertheless, the overall size, as well as the relative proportions of the vertebral centrum of NHMUK PV 37596 correspond with that of the posteriormost dorsal vertebra of NHMUK PV R 37591 (e.g., centrum...
length versus anterior height ratio). Both vertebrae also lack a ventral keel and possess a similar curvature of the ventral margin of the centrum and are amphiplatyan. Furthermore, the diapophysis of NHMUK PV R 37596 has a similar wing shape and concave posterior margin as the penultimate and last dorsal vertebrae of NHMUK PV R 37591. Based on the position of the parapophysis, which is completely located on the neural arch (Fig. 4A-B), NHMUK PV 37596 can be interpreted as a middle to posterior dorsal vertebra [60, 61, 69].

Sacral vertebrae.

The first sacral vertebra of NHMUK PV R 37591 is disarticulated from the rest of the vertebral column and has shifted approximately 90 degrees so that its posterior articular facet faces in a right lateral direction relative to the rest of the vertebral column (Fig. 1B). Therefore, the first sacral centrum was not fused to adjacent vertebrae. However, based on its position in the vertebral column and the width of its complete, wing-like right transverse process-rib, it most likely would have attached to the preacetabular process of the ilium (Fig. 2A). This element is therefore interpreted as a dorsosacral vertebra, and functionally, as the first vertebra of the sacrum. The left transverse process-rib is incomplete distally. The neural spine is broken, and its height can therefore not be assessed. However, the base of the spine is preserved, revealing that the spine arose along the entire length of the neural arch. The neural arch is fused to the centrum along its entire anteroposterior length. Its lateral surfaces are lateromedially very thin and markedly laterally convex on both sides, extending considerably further laterally at their mid-height than the centrum. The neural arch encloses a very large neural canal that is virtually circular in cross-section (Fig. 1B). The centrum is small relative to the size of the vertebra and considerably lateromedially wider than dorsoventrally tall. It has a concave posterior articular surface. The transition between the neural arch and centrum is demarcated by a clear anteroposteriorly directed groove in lateral view (Fig. 2D). The length of the vertebra cannot be measured because the anterior end is covered in matrix. The right prezygapophysis is visible and has a similar morphology to that of the preceding vertebra and that of NHMUK PV 37596.

The centra of the subsequent two vertebrae of NHMUK PV R 37591 are fused, but their margins can be deduced from slight dorsoventral expansions that demarcate the articulations (Fig. 2B). It is unclear whether the zygapophyses are also fused between the two vertebrae since they are insufficiently preserved. The second sacral centrum is longer (13.3 mm) than the centrum of the third sacral (11.1 mm; Table 1), a condition that also occurs in Lucianovenator bonoi (PVSJ 906). Both vertebrae preserve the centrum and the left side of the neural arches. The position of the second sacral vertebra matches that of the first primordial sacral of archosauriforms with two sacral
vertebrae. The third sacral probably represents an “inserted” sacral (sensu [70]) because its rib articulates with the ilium anteriorly to the level of the base of the ischiadic peduncle, where the second primordial sacral vertebra articulates in earlier archosauriforms [70]. Only the left prezygapophysis of the second sacral vertebra is partially preserved, and its articular surface faces dorsomedially. The left ribs of both vertebrae are fused to the left ilium, as occurs in skeletally mature individuals of other early neotheropods [71, 72]. The right side of the neural arch and the neural spine are completely missing. The vertebral centra are dorsoventrally shorter than in the preceding vertebrae; the anterior articular surface of the centrum of the second sacral is 5.2 mm tall, whereas that of the posteriormost dorsal vertebra is 6.4 mm (Table 1), and the dorsal surfaces of the centra are gently concave (Fig. 2D). The ventral margins of the centra are slightly anteroposteriorly concave, but considerably less so than the posteriormost dorsal vertebra (Fig. 1B).

The transverse processes of both vertebrae are fused to their corresponding ribs and are somewhat dorsolaterally extended, in the third sacral vertebra more so than in the second (Fig. 2A). The fused transverse process and rib of the second sacral vertebra taper slightly distally and have a concave posterior margin and a straight anterior margin. The anteroposterior width of the fused process and rib at their distal end is 3.7 mm. Matrix supports the transverse process of the second sacral vertebra ventrally, and it is therefore not possible to discern its thickness, nor the presence of a ventral lamina. The combined transverse process and rib of the third sacral vertebra is anteroposteriorly 5.7 mm wide at its distal end and therefore wider than that of the second sacral (Table 1). It broadens distally and has a concave posterior margin and a slightly convex anterior margin. This transverse process has mostly been freed from the surrounding matrix and is dorsoventrally thin. A very thin, ventrally directed lamina is projected from the anterior margin of the transverse process (Fig. 2D), giving the entire process an L-shape in lateral view. The ventral extent of this lamina cannot be discerned because its ventral section is surrounded by matrix. The attachment sites on the medial surface of the ilium for the second and third sacral ribs are positioned on an anteroposteriorly directed rim that extends further posterior to these attachment sites (Fig. 1B). This rim terminates posteriorly at a dorsoventrally oriented thickening of the medial surface of the ilium. This thickening connects the rim with the ridge that forms the dorsomedial margin of the brevis fossa. This thickening represents an attachment site scar for the fourth sacral rib.

A small fragment of the centrum of the fourth sacral vertebra is preserved and fused to the centrum of the third sacral of NHMUK PV R 37591. The second, third and fourth sacral centra form a straight structure in lateral view, resembling Lucianovenator bonoi (PVSJ 899), Coelophysis bauri (CMNH 10971), and Megapnosaurus rhodesiensis [60], but contrasting with the dorsally arched sacrum of
‘Syntarsus’ kayentakatae (TMM 43688-1). There are no visible additional attachment site scars preserved on the medial surface of the ilium. Nevertheless, the presence of another posterior sacral vertebra cannot be ruled out. Therefore, *Pendraig orynys* possessed at least four sacral vertebrae.

Appendicular skeleton.

The pelvic girdle of NHMUK PV R 37591 comprises a complete left hemipelvis excluding the distal ends of the left pubis and ischium, as well as a largely complete right pubis and ischium (Fig. 1). In addition, a partial left ischium, NHMUK PV R 37597 (Fig. 5), comprising the iliac peduncle and part of the ischial plate, can be confidently assigned to *Pendraig orynys* based on the presence and shape of the antitrochanter and the concavity on the acetabular rim, which are in correspondence with the morphology of the left ischium of NHMUK PV R 37591. NHMUK PV R 37597 is slightly larger than the holotype. Finally, a largely complete left femur (Fig. 3) is referred to the same individual as the articulated pelvic girdle and vertebral series and together comprise the holotype (NHMUK PV R 37591) of *Pendraig orynys* (see Systematic Palaeontology section). Measurements of the appendicular skeleton of NHMUK PV R 37591 are provided in Table 2.

Ilium.

The left ilium of NHMUK PV R 37591 is completely preserved, with exception of some damage on the posterior end of the postacetabular process, and in articulation with the left pubis and ischium, and with the second and third sacral ribs (Figs. 1 and 2). The dorsal margin of the iliac blade is straight to slightly convex on its middle and posterior portions, which comprises the section dorsal to the supraacetabular crest and the elongate postacetabular process (Fig. 1A). Anteriorly, the dorsal margin of the preacetabular process is more distinctly convex and forms a relatively abrupt anteroventral transition to the anterior margin of the preacetabular process, resembling the condition in *Sarcosaurus woodi* [57]. By contrast, the dorsal margin of the preacetabular process is straight or only slightly convex in other non-averostran neotheropods (e.g., *Coelophysis bauri*: USNM 529376; *Liliensternus liliesterni*: HMN MB.R.2175; *Lucianovenator bonoi*: PVSJ 906; *Coelophysis* sp.: UCMP 129618; *Notatesseraeraptor frickensis* [73]; *Megapnosaurus rhodesiensis*: NHMB QG 1; *Dilophosaurus wetherilli* [61]). The dorsal margin of the iliac blade of *Pendraig orynys* possesses a somewhat thickened, mostly flat surface that faces slightly laterally. This flat surface extends along most of the bone, with exception of the anteriormost region of the preacetabular process and starts to taper anteriorly at the mid-length of this process. On the posterior region of the iliac blade, this flat surface extends ventrally as a raised region to occupy the entire dorsoventral height of the lateral surface of the posterior end of the postacetabular process. It has been inferred that the anterior rim of this raised surface probably delimited the attachment site of the *M. iliofemoralis* [72,
This same condition occurs in *Coelophysis bauri* (USNM 529376), *Lucianovenator bonoi* (PVSJ 899, 906), *Coelophysis* sp. (UCMP 129618), ‘*Syntarsus’ kayentakatae* [75], and *Megapnosaurus rhodesiensis* (NHMB QG 1), but not in other early neotheropods [72]. The anterior margin of the preacetabular process is continuously rounded and extends considerably further anterior than the pubic peduncle of the ilium, as occurs in other neotheropods [76]. The preacetabular process is transversely very thin (i.e., laminar) and slightly medially curved in dorsal view. The ventral margin of the preacetabular process is slightly convex and oriented somewhat anteroventrally to posterodorsally. However, the overall orientation of the preacetabular process is anteriorly facing and a broad gap separates it from the pubic peduncle. This morphology corresponds to that of most theropods, but contrasts with the anteroventrally directed processes of *Sarcosaurus woodi* and some ceratosaurs (e.g., *Ceratosaurus nasicornis*, *Eoabelisaurus mefi*) [57]. At its posterodorsal end, the postacetabular process curves abruptly posterovertrally and the posterovertral end of the process is formed by an acute angle of approximately 65 degrees in lateral view. By contrast, the posterovertral corner of the postacetabular process is approximately right-angled or slightly acute in other non-averostran neotheropods (e.g., *Coelophysis bauri*: USNM 529376; *Liliensternus liliensterni*: HMN MB.R.2175; *Lucianovenator bonoi*: PVSJ 906; *Coelophysis* sp.: UCMP 129618; ‘*Syntarsus’ kayentakatae*: Tykoski 2005; *Megapnosaurus rhodesiensis*: NHMB QG 1; *Dilophosaurus wetherilli*: Marsh & Rowe 2020; *Sarcosaurus woodi*: NHMUK PV R4840). A notch on the posterior end of the postacetabular process, as has been described for various coelophysoid taxa (e.g., *Coelophysis bauri*, *Coelophysis* sp., *Megapnosaurus rhodesiensis*, ‘*Syntarsus’ kayentakatae’ [72]), is absent. In dorsal view the ilium is oriented approximately straight antero posteriorly (Fig. 2A) and the postacetabular process expands gradually laterally towards its posterior end, resembling the condition in *Liliensternus liliensterni* (HMN MB.R.2175), *Lucianovenator bonoi* (PVSJ 906), and *Dilophosaurus wetherilli* (UCMP 37302). By contrast, the the postacetabular process is distinctly more laterally expanded, extending beyond the level of the outer rim of the supra-acetabular crest in dorsal view, in *Coelophysis bauri* (USNM 529376), *Coelophysis* sp. (UCMP 129618), and *Megapnosaurus rhodesiensis* [60].

The lateral surface of the iliac blade is concave along its entire anteroposterior length. A shallow, not well-rimmed fossa is present immediately dorsal to the supra-acetabular crest and this region lacks the vertical ridge present in *Lophostropheus airelensis* [64, 77]. The ventral margin of the postacetabular process is formed by a distinct and sharp brevis shelf (Fig. 1A). The concave portion of the postacetabular process positioned medioventrally to this shelf is the brevis fossa [74]. This fossa is inferred to have formed the attachment site for the *M. caudofemoralis brevis* and is mediodorsally framed by a distinct ridge (Fig. 1B). The brevis fossa is only visible in lateral view in its anterior
portion. The remainder of the fossa faces ventrally or medioventrally and is obscured by the brevis shelf in lateral view, a condition typical of neotheropods [70].

The acetabulum is fully perforated and mostly formed by the ilium (Fig. 1A). On the posterior surface of the acetabulum a well-posteriorly delimited, crescent-shaped rugosity is present, which represents the antitrochanter. The dorsal portion of the antitrochanter is positioned on the ilium, whereas most of its surface is present on the ischial portion of the acetabular margin. The development of this antitrochanter closely resembles those observed in *Megapnosaurus rhodesiensis* (NHMB QG 1), *Coelophysis bauri* (USNM 529376), *Coelophysis* sp. (UCMP 129618), ‘Syntarsus’ *kayentakatae* [72], and *Lucianovenator bonoi* (PVSJ 906). Dorsally, the acetabulum is framed by a pronounced supra-acetabular crest, which projects laterally and slightly ventrally (Figs. 1A and 2C). The rim of the crest extends close to the connection with the pubis anteriorly and to the origin of the brevis shelf posteriorly. However, the supra-acetabular crest and the brevis shelf do not form the continuous, well-laterally developed ridge present in *Megapnosaurus rhodesiensis* (NHMB QG 1), *Coelophysis bauri* (USNM 529376), *Lophostropheus airelensis* [77], *Procompsognathus triassicus* (SMNS 12591), ‘Syntarsus’ *kayentakatae* [72], and *Lucianovenator bonoi* (PVSJ 906). The condition of *Pendraig orynys* resembles that of *Liliensternus liliensterni* (HMN MB.R.2175), *Coelophysis* sp. (UCMP 129618), *Dilophosaurus wetherilli* [61], and *Sarcosaurus woodi* [57]. The pubic peduncle is anteroventrally oriented, whereas the ischiadic peduncle is considerably more vertically directed, facing only slightly posteroverntrally. The suture between the ilium and pubis is completely unfused. The suture with the ischium is unfused along its posterior portion, but on its anterior portion, which is located across the antitrochanter and part of the acetabulum, the suture is closed and the elements are indistinguishably fused.

Pubis.

Both the left and the right pubes of NHMUK PV R 37591 are largely complete and in articulation with each other (Fig. 2C). Both elements lack the distal end of the pubic shaft, but the shaft extends further distally in the right element than the left. Overall, the preservation of the left element is superior to that of the right element since the surface of the latter is damaged in several places. Therefore, the description of the pubis is largely based on the left element. The shaft of the pubis is anteroventrally directed and elongate (Fig. 1A). Its extent is considerable but cannot be fully assessed because the distal end is missing on both sides. The longest preserved pubis, the right element, is 63.2 mm long. When including the imprint of the pubic shaft, which reaches further distally but likely does not represent the distal terminus of the pubes, the maximum length is 74.8 mm. The shaft is rod-like with a plate-like medial apron, which is lateromedially wide and
anteroposteriorly flat (Fig. 2B–C). The anterior surface of the shaft is convex and, correspondingly, the posterior surface is concave. As a result, the pubic shaft is slightly anteriorly curved in lateral view as in *Coelophysis bauri* (AMNH 7223, 7224), *Megapnosaurus rhodesiensis* [60], ‘*Syntarsus kayentakatae*’ [78], *Dracoraptor hanigani* (NMW 2015.5G.1–2015.5G.11), *Procompsognathus triassicus* (SMNS 12591), *Notatessaeraeraptor frickensis* (SMF 06-1), and *Gojirasaurus quayi* [65]. A higher degree of curvature occurs in *Eodromaeus murphi* (PVSJ 562). By contrast, the pubic shaft is straight in *Liliensternus liliensterni* (HMN MB.R.2175) and *Dilophosaurus wetherilli* [61]. Distally, the shaft gradually narrows mediolaterally. Because the distal end is missing, it cannot be determined whether *Pendraig orynys* possessed an expanded pubic boot. The pubic shaft meets its antimere distally, but it is unclear whether the shafts were also connected proximally or separated by a pubic foramen [74], since the shafts are covered by matrix on both sides proximally.

The anterior margin of the proximal portion of the pubis is smooth. The anterior portion of the acetabular contribution of the pubis is slightly rugose and a faint ridge is formed on its lateral margin (Fig. 1A). The pubis bears two openings on its ventrolateral surface proximally (Figs. 1A and 2B). The dorsal opening is the obturator foramen. It is oval and approximately four times longer anteroposteriorly than tall dorsoventrally. The obturator foramen occurs widely in archosauromorphs [70, 79] but is lost in most averostran theropods, which is attributable to a reduction in the ossification of the puboischiadic plate, resulting in the confluence the obturator foramen with the puboischiadic fenestra [74]. The considerably larger opening present ventral to the obturator foramen represents the pubic fenestra, which also occurs in *Megapnosaurus rhodesiensis* [60], *Segisaurus halli* [80, 81], *Coelophysis bauri* [62], and *Gojirasaurus quayi* [65]. The pubic plate of *Pendraig orynys* is well-ossified as it articulates with its antimere along its entire ventral margin. Among theropods this ventral median contact is a rarely preserved feature that has previously only been described or figured for *Megapnosaurus rhodesiensis* [60] and *Torvosaurus tanneri* [82]. A suture between the pubis and ilium can be clearly discerned. However, it is unclear whether a suture is also present between the pubis and ischium or whether these elements were fully fused, since several cracks obscure this region. A low tuberosity for the probable origin of the *M. ambiens* is present on the anterolateral surface of the bone in transition between the proximal end and the shaft.

**Ischium.**

Ischia are preserved on both sides of the pelvis of NHMUK PV R 37591. The right ischium comprises the ventral portion of the ischiadic plate, including a complete ventral margin, and the base of the ischiadic shaft (Fig. 1B). The left ischium also only preserves the base of the ischiadic shaft, but the
entire proximal part of the bone is preserved (Fig. 1A) and therefore the description of the ischium is
mostly based on this element. The maximum length of the left ischium, measured from the
distalmost preserved end of the shaft to the connection between the ischium and pubis on the
margin of the acetabulum is 26.6 mm. The base of the shaft of the ischium is posteroventrally
directed (Fig. 1A) and the shaft is considerably lateromedially narrower at its base than the pubis
(Fig. 2B). The ventral margin of the ischiadic plate connects its antimere along its anteroposterior
length and is continuous with the ventral margin of the pubic plate. At its posterior end, the ventral
margin bears a notch that separates it from the base of the ischiadic shaft (Fig. 1A). This notch
occurs widely among early neotheropods and has previously been considered as a synapomorphy
for the group [76]. The notch of *Pendraig orynys* is shallow as a result of the absence of a
posteroventrally oriented projection of the obturator plate. By contrast, this projection is present
and forms a deep, V-shaped or U-shaped notch in lateral view in *Megapnosaurus rhodesiensis*
(NHMB QG 1), *Dracoraptor hanigani* [83], *Dilophosaurus wetherilli* (UCMP 37302), and *Tachiraptor
admirabilis* [84]. There are no openings on the ischiadic plate, contrasting with the presence of an
ischial foramen in *Segisaurus halli* [81]. In contrast to the pubic plates, which are only connected at
their distalmost ventral margin, the ischiadic plates form a taller connection that occurs medially for
slightly more than half their dorsoventral height. The iliac peduncle of the ischium is clearly
separated by a deep concavity from the ventral margin of the acetabulum formed by the ischium.
The ventral margin bears a low but distinct ridge (Fig. 1A). The antitrochanter is largely formed by
the ischium. It is a flat rugose surface that is clearly demarcated by a rounded convex ventral ridge.

The isolated partial left ischium NHMUK PV R 37597 comprises the iliac peduncle and part of the
ischial plate (Fig. 5). The medial side of the specimen is fully exposed (Fig. 5A), whereas the lateral
side is largely covered by matrix, only exposing the iliac peduncle. The articular facet with the ilium is
anteroposteriorly elongate, oval, and concave (Fig. 5B). Anterolaterally it bears a clear rim that
demarcates the articular surface from the portion of the antitrochanter formed by the ischium. The
surface of the antitrochanter is slightly rugose and rounded ventrally. The acetabular margin of the
ischium bears a clear concavity ventral to the antitrochanter (Fig. 5A). The posterior margin of the
ischium is slightly concave and represents the transition from the iliac peduncle to the posterior
margin of the shaft of the ischium, which is otherwise not preserved. The ischial shaft is straight as
far as it is preserved and rod-like, forming a subtriangular cross-section with its counterpart where
they are broken off.

Femur.
Only the left femur of the holotype NHMUK PV R 37591 is preserved. Originally, this element was displaced and positioned lateroventrally to the right hemipelvis in the same block, but it had been prepared free of matrix by the time of the thesis of Warrener [41]. Based on its association, overall size, and morphology the femur can be confidently identified as belonging to the same individual as the pelvis and associated vertebrae. The femur is very well-preserved and comprises a complete proximal end and most of the shaft, only missing the distal end and the distalmost end of the shaft (Fig. 3). The preserved length of the femur is 86.3 mm. The proximal femoral head is inturned and would have been oriented anteromedially to articulate with the acetabulum of the pelvis, as in other early dinosaurs [85, 86]. The maximum width of the proximal head of the femur is 15.1 mm. On its ventral end the proximal head bears a clear lip, forming a distinctly concave emargination on the transition with the shaft (Fig. 3A-B), as is present in other dinosaurs [70]. Directly dorsal to this lip, a small, hook-shaped anteromedial tuber (sensu [70], = posteromedial tuber of [79]) projects from the femoral head medially (Fig. 3E), as occurs in other early neotheropods (e.g., Coelophysis bauri, Megapnosaurus rhodesiensis, Dilophosaurus wetherilli, Liliensternus liliensterni) [76]. In contrast, the posteromedial tuber (sensu [70], = posterior tuber of [79, 87]), positioned posterolaterally to the anteromedial tuber, is poorly developed, forming a slight convexity on the posteromedial margin of the proximal head. Posterolateral to this, the posteromedial margin of the femoral head is slightly depressed, representing the facies articularis antitrochanterica. The anterolateral margin of the femoral head is continuously convex along its length as a result of the presence of an anterolateral tuber (sensu [70], = anteromedial tuber of [79]). The proximal surface of the femur lacks a longitudinal groove, as occurs in skeletally mature specimens of Megapnosaurus rhodesiensis [53].

The greater or dorsolateral trochanter is a mound-like tuberosity positioned on the lateral surface of the femur distal to the proximal head (Fig. 3). Among early neotheropods, a distomedially directed ridge is present directly posteromedial to the greater trochanter in some, generally relatively mature, specimens of the coelophysoid taxa Megapnosaurus rhodesiensis, Coelophysis bauri [53], ‘Syntarsus’ kayentakatae (MNA V2526), and Segisaurus halli (UCMP 32101). This ridge was identified as an obturator ridge and considered to probably represent an attachment site for Mm. puboischiofemoralis externi by Raath [60]. A very distinct ridge positioned and oriented as in these taxa is present on the femur of Pendraig orynys (Fig. 3A), and we therefore refer to this structure as the obturator ridge. The obturator ridge is raised considerably, particularly on its posterolateral portion, and its surface is rugose. Another ridge that originates proximally to the obturator ridge, and which is oriented proximomedially, occurs in several specimens of Megapnosaurus rhodesiensis and Coelophysis bauri [53]. However, as in Segisaurus halli (UCMP 32101) and ‘Syntarsus’ kayentakatae (MNA V2526), this ridge is absent in Pendraig orynys. Directly distal to the proximal
head, a very large, rugose anterior trochanter that is subtriangular in anterior view projects on the anterolateral side of the femur (Fig. 3). The anterior trochanter is projected proximoanteriorly to proximolaterally from the shaft and gradually merges with the shaft except for its proximomedial margin, which is separated from the shaft by a shallow cleft (Fig. 3D). This cleft occurs widespread among neotheropods (e.g., *Dilophosaurus wetherilli* [61]; *Sarcosaurus woodi* [57]; *Coelophysis bauri* and *Megapnosaurus rhodesiensis* [53]; ‘*Syntarsus’ kayentakatae*: MNA V2526; *Liliensternus liliensterni*: HMM MB.R.2175), whereas it is absent in *Eodromaeus murphi* (PVSJ 562). This concavity opens onto a ridge on the posterolateral side of the anterior trochanter. This ridge, the trochanteric shelf, likely forms an attachment site for the *M. iliofemoralis*, and is well-developed in many early ornithodirans [54, 85, 88]. In *Pendraig orynys*, the trochanteric shelf is well-developed but only shortly projected, terminating on the posterolateral margin of the shaft. The most posterolateral region of the trochanteric shelf is damaged, thus whether it was connected to the *linea intermuscularis caudalis* (see below), as in other relatively skeletally mature early neotheropod specimens (e.g., *Megapnosaurus rhodesiensis* [53]), is unknown. The trochanteric shelf has a marked posterodistal orientation. A straight, mainly lateromedially oriented tuberosity extends along most of the posterior surface of the bone dorsal to the fourth trochanter. It was probably connected to the trochanteric shelf and the *linea intermuscularis caudalis* but the region of contact between the structures is damaged. This tuberosity probably represents the insertion scar of the *M. caudifemoralis brevis* and occurs in other skeletally mature individuals of early dinosauriforms [53].

The fourth trochanter is an elongate flange positioned on the posteromedial surface of the shaft (Fig. 3). It is a thin, 23.1 mm long, crest-like flange with a slightly convex anteromedial face and a concave posterolateral face. Proximally, the flange raises gradually, but on its distal end, which is slightly proximal to the mid-length of the shaft, the flange decreases in height more abruptly (Fig. 3C), but without forming the asymmetric fourth trochanter of most non-neotheropod dinosaurs (e.g., *Herrerasaurus ischigualastensis* [89]; *Eodromaeus murphi*: PVSJ 562; *Eoraptor lunensis* [90]). The fourth trochanter of *Pendraig orynys* is relatively well developed posteriorly, resembling the condition in *Liliensternus liliensterni* (HMM MB.R.2175), *Procompsognathus triassicus* (SMNS 12591), *Cryolophosaurus ellioti* [67], and *Dilophosaurus wetherilli* [61], but contrasting with the very low trochanter of *Sarcosaurus woodi* [57], *Megapnosaurus rhodesiensis* (NHMUK PV R9584, cast of NHMB QG 1), *Segisaurus halli* (UCMP 32101), and ‘*Syntarsus’ kayentakatae* (MCZ 9175, cast of MNA V2623). The fourth trochanter is mainly longitudinally oriented, but it slants slightly from proximomedially to distolaterally in posterior view. On the anteromedial surface of the femur there is a slightly rugose depression at the base of the fourth trochanter that is demarcated medially by a crescent-shaped ridge. This depression likely represents an insertion area for the *M. caudifemoralis*
The femoral shaft is long and slender and anteriorly curved along its entire length. The anterolateral and posteromedial surfaces of the shaft are clearly delineated by two ridges or intermuscular lines extending along the length of the shaft. The anteromedial *linea intermuscularis cranialis* probably demarcated the border between the *M. femorotibialis externus* and *M. femorotibialis internus* (Fig. 3C), whereas the posterolateral *linea intermuscularis caudalis* (Fig. 3D) probably separated the *M. femorotibialis externus* and the *M. adductor femoris* 1&2 [85]. The broken distal end of the femur reveals that the cortex of the shaft was thin (Fig. 3F), 0.8 mm thick, whereas the cross section of the femur is 8.5 mm long at its greatest extent. The broken distal end of the shaft reveals that it is oval in cross-section, being slightly transversely broader than anteroposteriorly deep, and filled by a crystalline matrix.

**Methods.**

**Phylogenetic analysis.**

*Pendraig orynys* was incorporated into the data matrix of Novas et al. [91], which represents the most recent iteration of the matrix originally published by Nesbitt et al. [88], which has also been modified in various other studies [57, 63, 83, 92-99]. Following Ezcurra et al. [57], ‘Velociraptor mongoliensis’, ‘Powellvenator podocitus holotype’, and ‘Lepidus praecisio combined’ were deactivated, whereas ‘Powellvenator podocitus’ and ‘Lepidus praecisio holotype’ remained active. Additionally, of the newly added terminals by Ezcurra et al. [57] ‘Sarcosaurus combined’, ‘Tachiraptor admirabilis’, and ‘Eoabelisaurus mefi’ remained active. Recent new information about non-dinosaurian avemetatarsalians is not included in this matrix [100] and the members of this part of the tree should be considered as outgroups without a proper test of their interrelationships here.

The data matrix was analysed under the equally weighted parsimony criterion using TNT 1.5 [101], with *Erythrosuchus africanus* selected as the outgroup. As in Novas et al. [91] the following characters were treated as additive: 9, 18, 30, 67, 128-129, 174, 184, 197, 207, 213, 219, 231, 236, 248, 253-254, 273, 329, 343, 345, 347, 349, 354, 366, 371, 374, 377–379, 383-384. Using the Traditional Search algorithm, a heuristic search of 1,000 replications of Wagner trees with random addition sequence was performed, followed by TBR branch swapping holding ten trees per replicate. Homoplasy indices were calculated with a script that does not take into account *a priori* deactivated terminals (see Supplementary Data – StatsB.run). Bremer and Bootstrap support values were calculated, the latter using a ‘Traditional search’ at 1,000 iterations.

**Femoral length estimation and ancestral state reconstruction**
To test whether *Pendraig orynys* might represent an insular dwarf as has been suggested for other reptiles of the fissure fills faunas [19-21], ancestral state reconstruction of the femoral length was performed on a sample of early theropods and closely related taxa to compare the relative size of *Pendraig orynys* in a quantitative phylogenetic framework. Even though femoral circumference is generally considered to represent the best proxy for body size [102], femur length was used since this measurement is available in a wide range of early theropod specimens and because it is expected to represent a reliable proxy for our relatively narrow phylogenetic sample (*sensu* [99]).

The only known femur of *Pendraig orynys* (NHMUK PV R 37591) is largely complete but the distal end is missing. We compiled a dataset of femoral measurements from several early theropods, composed of femoral length, maximal longitudinal width of the proximal head, maximal depth of the proximal head, and minimal femoral circumference (Supplementary Table 1). We subsequently performed regression analyses in the software environment R version 4.0.4 [103] with all values having been log-transformed. We used the predict function to estimate the femoral length and calculate confidence intervals for NHMUK PV R 37591.

Ancestral state reconstruction was performed on a dataset of femoral lengths of early theropods and closely related taxa, including the estimated femoral length of *Pendraig orynys*. The inclusion of taxa represented by immature specimens likely has a considerable effect on the outcome of body size analyses for early theropods, resulting in the underestimation of ancestral femoral lengths [99]. Therefore, in addition to the analysis including all taxa, we performed an alternative analysis in which we excluded theropod taxa that 1) were less mature than *Pendraig orynys* (a maximum maturity score lower than 19 based on the maturity assessment matrix of Griffin [53]) and 2) had a femoral length of less than 21 cm (for maturity scores of relevant taxa, see Supplementary Figure 11). Theropod taxa with a femoral length of over 21 cm were included, even when they are represented by immature specimens, because their inclusion was considered not to contribute to an underestimation of ancestral femoral lengths due to their large size and because early large-bodied theropods are exclusively known from immature specimens [56, 99]. Following these criteria, the taxa excluded for the alternative analysis are: *Panguraptor lufengensis*, *Lepidus praecisio*, *Dracoraptor hanigani*, and *Powellvenator podocitus*.

A total of six most parsimonious trees (MPTs) were found for the phylogenetic analysis (see below). Since the focus of our analysis is on Coelophysoidea, we performed the ancestral state reconstruction analyses on the four equally parsimonious resolutions of the position of *Pendraig orynys*, whereas we used the topology of the strict consensus for the rest of the tree. To time-calibrate the trees, the first and last occurrences (which for most theropods and early dinosaurs
represent stratigraphic uncertainty rather than true ranges) of all taxa were obtained from the literature, using the International Chronographic Chart [104] to determine the delimitations of the various geological stages (e.g., *Pendraig orynys*, earliest occurrence late Norian, latest occurrence possibly late Rhaetian; 214.7 to 201.3 million years ago). Branch lengths were calculated using the timetreephy() function from the paleotree package [105] under three different settings for minimum branch lengths (mbl), 1.0, 0.5, and 0.1 million years, to test for the influence of different parameter settings on our results. The analyses were performed using the function anc.ml() from the phytools package [106] to calculate ancestral states under a Brownian model of evolution using maximum likelihood.

**Results.**

Phylogenetic analysis.

The phylogenetic analysis found six MPTs of 1360 steps with a consistency index (CI) of 0.346 and a retention index (RI) of 0.676. *Pendraig orynys* is found within Coelophysidae but outside Coelophysidae (i.e., *Coelophysis*, *Procompsognathus*, their most recent common ancestor and all descendants) [51] in all MPTs. Within the strict consensus tree (SCT) generated from the MPTs it forms a polytomy together with *Powellvenator podocitus*, *Lucianovenator bonoi*, and a clade composed of ‘Syntarsus’ *kayentakatae* and Coelophysidae (Fig. 6). Among these MPTs, *Lucianovenator bonoi* and *Powellvenator podocitus* alternate as the sister taxon to the ‘Syntarsus’ *kayentakatae* + Coelophysidae clade. Three additional steps are required to force *Pendraig orynys* outside Coelophysoidea, one step for *Pendraig orynys* to be the sister taxon of the ‘Syntarsus’ *kayentakatae* + Coelophysidae clade, and five steps for it to be the sister taxon to or for it to be part of Coelophysidae. The following synapomorphies support the placement of *Pendraig orynys* within Coelophysoidea: presence of a flat dorsal margin of the ilium dorsal to the supra-acetabular rim (200 \( \rightarrow \) 1) and the presence of a rounded ridge or dorsolateral trochanter on the dorsolateral margin of the proximal portion of the femur (230 \( \rightarrow \) 2). The presence of elongate posterior dorsal vertebrae with a centrum length that is at least twice the height of their anterior articular surface (329 \( \rightarrow \) 2) is present in *Pendraig orynys* and represents a common synapomorphy for the clade composed of all coelophysoids except *Panguraptor lufengensis*.

Femoral length estimation.

We found that femoral length is significantly correlated with all other variables that we considered (maximal longitudinal width of the proximal head: \( p < 2.2 \times 10^{-10} \), maximal depth of the proximal head: \( p = 3.67 \times 10^{-6} \), and minimal femoral circumference: \( p = 7.173 \times 10^{-6} \)). Since maximal
longitudinal width of the proximal head has the most significant correlation with femoral length and is the most widely available measurement in the studied sample, we used this variable to estimate the femoral length of NHMUK PV R 37591 (Fig. 7). Based on this, the reconstructed femoral length of NHMUK PV R 37591 is 10.21 cm (lower 95% CI: 8.60 cm; upper 95% CI: 12.11 cm). The results of the ancestral state reconstruction analysis are discussed below.

Discussion.

Phylogenetic implications.

The scoring of the ontogenetic characters formulated by Griffin [53] suggests that the holotype NHMUK PV R 37591 of *Pendraig orynys* is immature with regards to certain skeletal features (Supplementary Figure 11A). It is therefore important to consider that skeletally immature specimens are often recovered in a different (often less derived) phylogenetic position than mature specimens of the same species (e.g., [99, 107, 108]). The phylogenetic analysis recovered *Pendraig orynys* as a non-coelophysid coelophysoid (Fig. 6), but with low support values for Coelophysoidea and its internal nodes. Nevertheless, the referral of *Pendraig orynys* to Coelophysoidea is supported by the presence of several typically coelophysoid character states, such as the flat dorsal margin of the ilium, the considerable anteroposterior elongation of the posterior dorsal vertebrae, and the distinct posterior rim on the ventral part of the postacetabular process of the ilium exposed in lateral view. Alongside *Procompsognathus triassicus* and possibly *Liliensternus liliennsterni*, *Pendraig orynys* represents a third Triassic coelophysoid taxon from Europe and the first unambiguous Triassic theropod from the United Kingdom.

The results of our analysis are incongruent with several previous phylogenetic studies of early neotheropods in the placement of *Dracoraptor hanigani* and *Lepidus praecisio* outside Coelophysoidea and the derived position of ‘Syntarsus’ kayentakatae within this clade. Previously, *Dracoraptor hanigani* from the Early Jurassic of Wales was recovered as a coelophysoid [57, 83], but it was found outside Coelophysoidea by Baron et al. [33] in a large polytomy among early Neotheropoda, and as the sister taxon to ‘Syntarsus’ kayentakatae in Langer et al. [38] and Baron et al. [39] in analyses that did not recover a monophyletic Coelophysoidea as it is historically considered. Here, *Dracoraptor hanigani* is found as a non-coelophysoid neotheropod in a polytomy with *Liliensternus liliennsterni* and a clade composed of all remaining averostran-line neotheropods (Fig. 6). The position of *Liliensternus liliennsterni* as an early diverging non-coelophysoid neotheropod in our analysis corresponds with several studies [83, 94, 95, 97], although other analyses recovered this species as one of the earliest diverging non-coelophysid coelophysoids [57, 63, 99]. *Lepidus praecisio* was previously considered a coelophysid coelophysoid [57, 94, 98, 99, 109], but was found
outside Coelophsysoidea by Marsh et al. [95], in which it was found as the sister taxon to all other non-coelophysoid neotheropods, and by Marsh and Rowe [61], in which it was found as the sister taxon to *Liliensternus liliensterni* in a clade that is part of a polytomy at the base of Neotheropoda. Here, the holotype of *Lepidus praecisio* was recovered outside Neotheropoda as the direct sister taxon to *Lepidus praecisio* in our analysis because of the uncertain taxonomic affinity of the referred material for this species [98]. *‘Syntarsus’ kayentakatae* is unambiguously considered as a coelophysoid theropod and represents one of best known taxa of the clade [75]. However, the position of *‘Syntarsus’ kayentakatae* within Coelophysoidea is somewhat uncertain and in recent other studies employing the Nesbitt et al. [88] matrix this taxon was recovered as quite distantly related to Coelophysidae (i.e., being more distantly related to *Coelaphysis bauri* and *Procompsognathus triassicus* than are *Panguraptor lufengensis*, *Lucianovenator bonoi*, and *Powellvenator podocitus*) [57, 63, 83, 94, 97, 99]. In contrast, in our analysis *‘Syntarsus’ kayentakatae* is recovered as the sister taxon to Coelophysidae (Fig. 6). The lack of consensus in early neotheropod phylogeny, including Coelophsysoidea, has been acknowledged and discussed in recent studies (e.g., [57, 99]) and can likely be attributed to large amounts of missing data for many early neotheropod taxa and the inclusion of taxa represented by immature ontogenetic stages [53, 99]. The holotype of *Lepidus praecisio* includes a particularly large amount of missing data (90.72%) and *Lepidus praecisio*, *Liliensternus liliensterni*, and *Dracoraptor hanigani* are represented by immature specimens (Supplementary Figure 11; Supplementary Table 2) [56]. The presence of taxa based on skeletally immature specimens or with unclear ontogenetic stage increases the proportion of missing data because ontogenetically variable characters should be scored as ambiguous. The more derived position of *‘Syntarsus’ kayentakatae* recovered in our analysis is, in part, a result of the scorings revised in our modified data matrix and the inclusion of the new species *Pendraig orynys*. Indeed, if the latter species is excluded *a priori* from the analysis, *‘Syntarsus’ kayentakatae* is recovered in multiple positions among non-coelophysid coelophysoids in the resultant MPTs. This result reflects the importance of adding new taxa with a novel combination of character states and the continuous revision of the data matrices in phylogenetic studies.

**Body size evolution of *Pendraig orynys* and other early theropods.**

Research on early theropod body size evolution has recently been reviewed by Griffin [99] and Griffin and Nesbitt [56]. Recent analyses using ancestral state reconstruction found the femoral length of the last common ancestor of Neotheropoda to be approximately 29 to 35 cm [99, 110, 111]. Lee et al. [112] found a considerably higher ancestral femoral length of 47.5 cm for *Neotheropoda*, but the dataset used in that analysis contained a comparatively smaller sample of early theropods. Our analyses reveal that different values used for the minimum branch length...
parameter (mbl, set at 0.1, 0.5, and 1.0 million years) have quite large implications for the reconstructed ancestral values. The analysis on the first of the four equally parsimonious trees with mbl set at 1.0 million years and including all sampled taxa (Fig. 8) recovered an ancestral femoral length of 24.2 cm for Neotheropoda (upper CI: 33.7 cm; lower CI: 17.3 cm) and 17.6 cm for Coelophysoidea (upper CI: 27.6 cm; lower CI: 11.2 cm) (Supplementary Table 3.1), whereas when an mbl of 0.1 million years is considered, the ancestral value for Neotheropoda is 39.6 cm (upper CI: 58.0 cm; lower CI: 27.1 cm) and that for Coelophysoidea is 14.9 cm (upper CI: 25.1 cm; lower CI: 8.8 cm) (Supplementary Table 3.3). For an mbl of 0.5 million years, the ancestral value for Neotheropoda is 29.7 cm (upper CI: 43.0 cm; lower CI: 20.5 cm) and for Coelophysoidea 16.4 cm (upper CI: 27.0 cm; lower CI: 9.9 cm) (Supplementary Table 3.4). When the femoral lengths of small-bodied neotheropod taxa represented by immature specimens are pruned (i.e., taxa with a maximum maturity score of 17 or less: Panguraptor lufengensis, Lepidus praecisio, Dracoraptor hanigani, and Powellvenator podocitus), the ancestral femoral length is 25.7 cm (upper CI: 36.2 cm; lower CI: 18.3 cm) for Neotheropoda and 21.1 cm (upper CI: 34.5 cm; lower CI: 12.9 cm) for Coelophysoidea when considering the first of the four equally parsimonious trees and with mbl set at 1.0 million years (Supplementary Table 3.2). The four equally parsimonious resolutions of the early coelophysoid relationships result in similar reconstructed femoral lengths for Neotheropoda and Coelophysoidea, with the ancestral estimates for the latter being between 17 and 18 cm when mbl is set at 1.0 million years and the femoral lengths of all sampled taxa are included (Supplementary Tables 3.1, 3.3, 3.4). Overall, the large discrepancy in reconstructed ancestral femoral lengths for Neotheropoda and Coelophysoidea between the different analyses, particularly between the analyses with different minimum branch lengths, and the wide confidence intervals for all values indicate that there is much uncertainty in approximating ancestral body sizes in early neotheropods, but our recovered values are broadly similar to the results of Irmis [110], Benson et al. [111], and Griffin [99].

Our results indicate that averostran-line neotheropods underwent a size increase already during the Triassic (Fig. 8; Supplementary Information). In contrast, the body size of coelophysoids is considerably smaller. This corresponds with the results of Griffin [99]. Size decreases occurred early in Coelophysoidea and ancestral values gradually increase in consecutive nodes from the clade encompassing Lucianovenator bonoi, ‘Syntarsus’ kayentakatae, and Coelophysidae onwards regardless of minimum branch length in the analyses encompassing all data (Supplementary Tables 3.1, 3.3, 3.4). In contrast, Griffin [99] found an initial increase in body size in the evolution of Coelophysoidea, which is attributable to the placement of Liliensternus liliensterni (and in one of the two analyses Gojirasaurus quayi) at the base of the clade in his phylogenetic analyses and the
absence of several coelophysoid taxa in that dataset (*Powellvenator podocitus, Procompsognathus triassicus, Segisaurus halli, Lucianovenator bonoi, Camposaurus arizonensis*, and the new taxon *Pendraig orynys*). In the two equally parsimonious topologies in which *Lucianovenator bonoi* is more distantly related to Coelophysidae, ancestral femoral length increases from the clade comprising ‘Syntarsus’ kayentakatae, and Coelophysidae onwards (Supplementary Tables 3.6, 3.7). In the analyses excluding *Panguraptor lufengensis, Lepidus praecisio, Dracoraptor hanigani*, and *Powellvenator podocitus*, the ancestral body size of Coelophysoidea is also reduced relative to the ancestral neotheropod condition and decreases somewhat further early in coelophysoid evolution and subsequently remains similar for subsequent nodes, only to increase again at the most apical node (Supplementary Table 3.2).

The ontogenetic assessment of the holotype of *Pendraig orynys* indicates that this specimen was not skeletally mature (i.e., likely had not reached asymptotic growth [56]) but that it is likely also not at an early ontogenetic stage (Supplementary Figure 11A). It therefore seems unlikely that *Pendraig orynys* would have increased much more in size and this species would thus have been considerably smaller than better known coelophysoids like *Coelophysis bauri, Megapnosaurus rhodesiensis*, and ‘Syntarsus’ kayentakatae. The ancestral femoral length for the closest node for *Pendraig orynys* is between 144% (Supplementary Table 3.3) and 195% (Supplementary Table 3.2) larger than for *Pendraig orynys*, thus indicating that the small size of *Pendraig orynys* is autapomorphic. However, *Procompsognathus triassicus, Segisaurus halli*, and, in the analyses in which this taxon is considered, *Powellvenator podocitus*, all independently underwent a similar size reduction based on our analyses (Fig. 8; Supplementary Information). Because its small size is not unique among Coelophysoidea and other coelophysoid taxa that underwent a similar size reduction were not restricted to insular environments, our dataset is ambiguous regarding insular dwarfism as a possible explanation of the reduced body size in *Pendraig orynys*. However, insular dwarfism in *Pendraig orynys* cannot be excluded, and further studies into the palaeohistology and body size evolution of other taxa from Pant-y-ffynnon and related fissure fill deposits are required to investigate the possibility that these faunas were subject to dwarfism or other aspects of the ‘Island Rule’.

Palaeoecology of *Pendraig orynys* and Pant-y-ffynnon.

The known dentitions of coelophysoid theropods are characterized by blade-like serrated maxillary and non-mesial dentary teeth, indicating a mostly macrophagous carnivorous diet for these taxa [60, 69, 75]. It therefore seems highly likely that *Pendraig orynys* had a similar dentition and diet even though no craniodental remains from Pant-y-ffynnon can unequivocally be attributed to this species. *Pendraig orynys* represents a second macrophagous predator known from Pant-y-ffynnon (Fig. 9),
the other being the non-crocodyliform crocodylomorph *Terrestrisuchus gracilis* [18]. Like *Pendraig orynys*, *Terrestrisuchus gracilis* was small-bodied (approximately 76 cm in total body length [18]) and had a gracile body plan. Other likely predators known from the Late Triassic and Early Jurassic fissure fill deposits of southwestern England and southern Wales were either similarly small-bodied: *Terrestrisuchus*-like unidentified crocodylomorphs from Cromhall and Ruthin Quarries [19, 32] and ‘*Agnosphytis cromhallensis*’ from Cromhall Quarry [32]; or most likely semi-aquatic (*‘Paleosaurus platyodon’*) [27]. Remains of the considerably larger-sized herbivorous sauropodomorph *Thecodontosaurus antiquus* have been preserved at the Durdham Down and Tytherington deposits [20, 27], but only remains of the smaller sauropodomorph *Pantydraco caducus*, which might represent an immature form of *Thecodontosaurus antiquus* [20], are known from Pant-y-ffynnon [28, 29]. Therefore, it is currently unclear whether predators at Pant-y-ffynnon simply did not exceed the size of *Pendraig orynys* and *Terrestrisuchus gracilis*, which could be attributable to a lack of resources to sustain larger predators as is typical in certain island environments [22], or whether larger-bodied predators in this ecosystem have not yet been discovered or preserved, possibly because taphonomic factors are biased against preservation of large-bodied animals at Pant-y-ffynnon and other fissure fill deposits.

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Figure captions.

Figure 1. Holotype NHMUK PV R 37591 pelvis and vertebrae of *Pendraig orynys* gen. et sp. nov. in (A) left lateral view, (B) right lateral view. Abbreviations: atr, antitrochanter; bf, brevis fossa; bfr, brevis fossa rim; bs, brevis shelf; dv, dorsal vertebra; iss, ischial shaft; nc, neural canal; no, notch; obf, obturator foramen; poap, postacetabular process; prap, preacetabular process; puf, pubic fenestra; pus, pubic shaft; ras, rib attachment scar; ri, rim; sac, supra-acetabular crest; sv, sacral vertebra.

Figure 2. Holotype NHMUK PV R 37591 pelvis and vertebrae of *Pendraig orynys* gen. et sp. nov. in (A) dorsal view, (B) ventral view, (C) anterior view, and (D) posterior view. Abbreviations: bf, brevis fossa; bfr, brevis fossa rim; diap, diapophysis; dv, dorsal vertebra; gr, groove; il, ilium; ipis, iliac peduncle of ischium; iss, ischiadic shaft; obf, obturator foramen; poap, postacetabular process; ppdl, paradiapophyseal lamina; prap, preacetabular process; puf, pubic fenestra; pus, pubic shaft; sac, supra-acetabular crest; sv, sacral vertebra; tp, transverse process; vl, ventral lamina.

Figure 3. Holotype NHMUK PV R 37591 left femur of *Pendraig orynys* gen. et sp. nov. in (A) posteromedial, (B) anterolateral, (C) anteromedial, (D) posterolateral, (E) proximal, and (F) distal view. Abbreviations: amt, anteromedial tuber; at, anterior trochanter; icfl, depression associated with the insertion of the *M. caudofemoralis longus*; gt, greater trochanter; lica, linea intermuscularis caudalis; lincr, linea intermuscularis cranialis; obr, obturator ridge; pmt, posteromedial tuber; ts, trochanteric shelf; 4th t, fourth trochanter.

Figure 4. Isolated mid to posterior dorsal vertebra NHMUK PV 37596 of *Pendraig orynys* gen. et sp. nov. in (A) right lateral view, (B) left lateral view, (C) ventral view, (D) dorsal view, (E) anterior view, and (F) posterior view. Abbreviations: aas, anterior articular surface; acpl, anterior centroparapophyseal lamina; ce, centrum; diap, diapophysis; nf, nutrient foramen; ns, neural spine; pacdf, parapophyseal centrodiapophyseal fossa; pacprf, parapophyseal centroprezygapophyseal fossa; pap, parapophysis; pas, posterior articular surface; pcldr, posterior centrodialaphyseal; pocdf, postzygapophyseal centrodialaphyseal fossa; podl, postzygodiapophyseal lamina; poz, postzygapophyseis; ppdl, paradiapophyseal lamina; prpl, prezygaparaphyseal lamina; prz, prezygapophysis; spozf, spinopostzygapophyseal fossa; sprzf, spinoprezygapophyseal fossa.

Figure 5. Isolated partial left ischium NHMUK PV R 37597 of *Pendraig orynys* gen. et sp. nov. in (A) medial and (B) dorsal view. Abbreviations: asil, articulation surface with ilium; atr, antitrochanter; ipis, iliac peduncle of ischium.
Figure 6. Strict consensus of six most parsimonious trees of the phylogenetic analysis. Bremer support, absolute bootstrap frequency, and GC bootstrap frequency values are indicated at each branch in that order.

Figure 7. \( \log_{10} \)-transformed bivariate plot of the longitudinal width of proximal head of the femur versus the femoral length of early theropods. The solid black line represents the linear regression described by the formula, and the red dotted lines represent the 95% confidence intervals.

Figure 8. Results of the ancestral state reconstruction of the \( \log_{10} \)-transformed femoral lengths. For the analysis figured here all sampled taxa were included and minimum branch length was set at 1.0 million years. The polytomy within Coelophysoidea in the strict consensus tree was manually resolved with one of the four equally parsimonious resolutions. The other analyses can be found in the Supplementary Information. The femoral lengths used for the analysis can be found in Supplementary Table 2. Reconstructed values for major nodes can be found in Table 3, and for all nodes in Supplementary Table 3.1. Node numbers used for Supplementary Table 3.1 are indicated for each node in Supplementary Figure 1.

Figure 9. Life reconstruction of *Pendraig orynys* gen. et sp. nov. amongst the fissures of Pant-y-ffynnon and three individuals of the rhynchocephalian lepidosaur *Clevosaurus cambrica* during the Late Triassic. Artwork by James Robbins.

Table 1. Vertebral measurements of NHMUK PV R 37591 and NHMUK PV 37596. Measurements were taken with a Sealey electronic vernier calliper. Values preceded by a tilde (~) indicate an approximated value because a measurement was hampered, either by poor preservation, or by the relevant structure being partially covered. Abbreviations: dv, dorsal vertebra; sv, sacral vertebra.

|               | dv1 | dv2 | sv1 | sv2 | sv3 | sv4 | NHMUK PV 37596 |
|---------------|-----|-----|-----|-----|-----|-----|-----------------|
| Centrum length| -   | 14.7 mm | -   | 13.3 mm | 11.1 mm | -   | 14.6 mm |
| Neural spine height | -   | -   | -   | -   | -   | -   | 5.0 mm |
| Neural spine length | -   | -   | -   | -   | -   | -   | 14.3 mm |
| Width of diapophysis/transverse processes (+ rib) | -   | 9.9 mm | -   | 5.39 mm | 6.2 mm | 6.5 mm | -   | 7.4 mm |
| Anterior articular surface centrum height | -   | 6.4 mm | -   | 5.2 mm | 4.7 mm | -   | 5.7 mm |
Table 2. Measurements of the appendicular skeleton of NHMUK PV R 37591. Measurements were taken with a Sealey electronic vernier calliper. The circumference of the femoral shaft was measured by running a piece of string around the shaft and subsequently measuring the length of the amount of string with the calliper. Values in parentheses represent incomplete values, due to the relevant structure being incompletely preserved. Abbreviations: max, maximum.

| Measurement                                      | Value       | Value       | Value       | Value       | Value       | Value       |
|--------------------------------------------------|-------------|-------------|-------------|-------------|-------------|-------------|
| Posterior articular surface centrum height       | 7.0 mm      | 6.4 mm      | 4.7 mm      | 4.2 mm      | 5.8 mm      |
| Anteroposterior width transverse proces + rib    | n/a         | n/a         | 3.7 mm      | 5.7 mm      | n/a         | n/a         |
| distal end                                       |             |             |             |             |             |             |

max. length left ilium across iliac blade          | 55.8 mm     |
max. length left ilium across peduncles            | 26.0 mm     |
max. length left acetabulum                        | 16.7 mm     |
max. dorsoventral height left acetabulum           | 17.6 mm     |
max. length right pubis (excluding imprint)        | (63.2 mm)   |
max. length right pubis (including imprint)        | (74.8 mm)   |
max. length left ischium                           | (26.6 mm)   |
max. length left femur                             | (86.3 mm)   |
max. width proximal head left femur                | 15.1 mm     |
min. circumference shaft of left femur             | 25.08 mm    |

Table 3. Ancestral state values (in cm) for major nodes for the analysis shown in Figure 8.

| Ancestral estimate | Variance | Lower 95% Confidence Interval | Upper 95% Confidence Interval |
|--------------------|----------|-----------------------------|-------------------------------|
| Dinosauria         | 15.038   | 10.787                      | 20.964                        |
| Theropoda          | 17.679   | 13.542                      | 23.080                        |
| Neotheropoda       | 24.168   | 17.331                      | 33.703                        |
| Non-coelophysoid neotheropods | 30.899 | 22.653                      | 42.146                        |
| Averostra          | 60.474   | 44.309                      | 82.536                        |
| Coelophysoidea     | 17.585   | 11.191                      | 27.631                        |
|                       | Value 1 | Value 2 | Value 3 | Value 4 |
|-----------------------|---------|---------|---------|---------|
| Coelaphysoidea excluding Panguraptor | 16.285  | 1.021   | 10.658  | 24.882  |
| Coelophysidae          | 17.118  | 1.015   | 11.891  | 24.643  |

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Figure 1. Holotype NHMUK PV R 37591 pelvis and vertebrae of Pendraig orynys gen. et sp. nov. in (A) left lateral view, (B) right lateral view. Abbreviations: atr, antitrochanter; bf, brevis fossa; bfr, brevis fossa rim; bs, brevis shelf; dv, dorsal vertebra; iss, ischial shaft; nc, neural canal; no, notch; obf, obturator foramen; poap, postacetabular process; prap, preacetabular process; puf, pubic fenestra; pus, pubic shaft; ras, rib attachment scar; ri, rim; sac, supra-acetabular crest; sv, sacral vertebra.
Figure 2. Holotype NHMUK PV R 37591 pelvis and vertebrae of Pendraig orynys gen. et sp. nov. in (A) dorsal view, (B) ventral view, (C) anterior view, and (D) posterior view. Abbreviations: bf, brevis fossa; bfr, brevis fossa rim; diap, diapophysis; dv, dorsal vertebra; gr, groove; il, ilium; ipis, iliac peduncle of ischium; iss, ischiadic shaft; obf, obturator foramen; poap, postacetabular process; ppdl, paradiapophyseal lamina; prap, preacetabular process; puf, pubic fenestra; pus, pubic shaft; sac, supra-acetabular crest; sv, sacral vertebra; tp, transverse process; vl, ventral lamina.
Figure 3. Holotype NHMUK PV R 37591 left femur of Pendraig orynys gen. et sp. nov. in (A) posteromedial, (B) anterolateral, (C) anteromedial, (D) posterolateral, (E) proximal, and (F) distal view. Abbreviations: amt, anteromedial tuber; at, anterior trochanter; icfl, depression associated with the insertion of the M. caudofemoralis longus; gt, greater trochanter; lica, linea intermuscularis caudalis; lincr, linea intermuscularis cranialis; obr, obturator ridge; pmt, posteromedial tuber; ts, trochanteric shelf; 4th t, fourth trochanter.
Figure 4. Isolated mid to posterior dorsal vertebra NHMUK PV 37596 of Pendraig orynys gen. et sp. nov. in (A) right lateral view, (B) left lateral view, (C) ventral view, (D) dorsal view, (E) anterior view, and (F) posterior view. Abbreviations: aas, anterior articular surface; acpl, anterior centroparapophyseal lamina; ce, centrum; diap, diapophysis; nf, nutrient foramen; ns, neural spine; pacdf, parapophyseal centrodiaaphyseal fossa; pacprf, parapophyseal centroprezygapophyseal fossa; pap, parapophysis; pas, posterior articular surface; pcdl, posterior centrodiaaphyseal; pocdf, postzygapophyseal centrodiaaphyseal fossa; podl, postzygapophyseal lamina; poz, postzygapophysis; ppdl, paradiapophyseal lamina; prpl, prezygaparaphyseal lamina; prz, prezygapophysis; spozf, spinopostzygapophyseal fossa; sprzf, spinoprezygapophyseal fossa.
Figure 5. Isolated partial left ischium NHMUK PV R 37597 of Pendraig orynys gen. et sp. nov. in (A) medial and (B) dorsal view. Abbreviations: asil, articulation surface with ilium; atr, antitrochanter; ipis, iliac peduncle of ischium.
Coelophysidae indet.
Coelophysis bauri
Dilophosaurus wetherilli
Eodromaeus murphi
Liliensternus liliensterni
Megapnosaurus rhodesiensis
'Syntarsus' kayentakatae
Pendraig orynys (estimated)

\[ y = 0.845x + 1.013 \]

\[ r^2 = 0.968, p < 2.2 \times 10^{-16} \]
Figure 9. Life reconstruction of Pendraig orynys gen. et sp. nov. amongst the fissures of Pant-y-ffynnon and three individuals of the rhynchocephalian lepidosaur Clevosaurus cambrica during the Late Triassic. Artwork by James Robbins.

322x239mm (300 x 300 DPI)
This manuscript presents a thorough comparative description of a new theropod dinosaur and places it into a phylogenetic hypothesis using a relevant and recent character matrix. The small size of the holotype individual is striking, so the authors also conduct an ancestral state reconstruction for body size among early theropod dinosaurs and also attempt to take the individual’s ontogenetic status into account to be sure that the small size does not simply stem from the individual’s immaturity.

The manuscript is well-written and thorough, the comparative descriptions sound, the figures are clear and informative, and the analyses all appear to be properly conducted (but see below for problems with the R code). In my opinion the manuscript is largely sound and can be accepted for publication with moderate revision. I have attached a PDF with my minor edits and comments.

Major Comments

1) Why are the eleven supplementary figures provided as separate files, with yet another Word file for the captions? It would be much easier to include all figures with associated captions as one PDF file. Also, in Table S2 in the “Juvenile” column, there are several different terms used for maturity assessment, including juvenile, non-juvenile, subadult, immature, etc. Sometimes these seem to be synonymous, but their usage at other times appears to be mutually exclusive. For example, some taxa are listed as “SUBADULT/IMMATURE” and others are just listed as “IMMATURE”. Could you provide more explanation for these maturity categories?

2) When running the R code, I experienced an error code that prevented me from continuing to evaluate the rest of the code. The error occurred on line 42, on the anc.ML() command, and read: “Error in optim(c(sig2, a, y, rep(mean(x), length(xx))), fn = likelihood, : non-finite value supplied by optim”.

All the underlying data looked sound to me; I saw no obvious issues with the way the data was input, the tree file, etc. It may be the issue is with my version of R or R Studio, because I just updated both two days ago, but this affects repeatability and is something the authors should be aware of.

3) I appreciate that the authors take the body size of the type individual into account when evaluating possible small body size. This is done in a clear way using character state transformations that have been useful in other early theropods, particularly Coelophysis. I agree with the authors’ assessment that this individual does not display the features we might expect of either a very skeletally mature or immature individual, and the character states instead suggest that this individual is in a middling ‘gray zone’ of ontogeny. Indeed, there is no reasonably complete specimen of Coelophysis that has been scored with a consistent combination of character states (data from Griffin & Nesbitt 2016, Griffin 2018), making direct comparison with Coelophysis character states and femoral lengths difficult. This, combined with the fact that their scoring of Panguraptor ontogenetic character state combinations that contradict any reconstructed ontogenetic sequence of Coelophysis (very interesting finding, by
the way), strongly suggests that there is even more variation in ontogenetic trajectories among Coelophysoids than has presently been reconstructed.

Because of the large amount of ontogenetic variation known from other coelophysoids, combined with the fact that most of the size variation in Coelophysis is known precisely from this ontogenetic gray zone, I disagree with the authors’ statement that this individual was likely near maximum body size and would not have gotten much larger. Instead, I think that there is not enough evidence to say one way or another.

Although there is no direct comparison between the character states of Pendraig and Coelophysis or Megapnosaurus, some examples from individuals roughly the size of Pendraig that also display similarly mature character states may be informative:

-- The smallest known individual of Megapnosaurus (NHMZ QG 45) possesses fused sacral neural spines (character 1-1; and therefore probably at least some fused sacral centra, although these are not able to be scored) and a small trochanteric shelf (14-1; 15-0), despite its extremely small size (femoral head 1.5 cm; reconstructed femoral length ~11.2 cm).
-- Coelophysis bauri (TMP 1984.063.0001 #13; reconst. femur length ~10.9 cm) has fused its pubis to the ilium (8-1) and ischium (10-1), but the ilium and ischium remain unfused (9-1).
-- Coelophysis bauri (SMP 858; femoral head 1.29 cm, reconst. femur length ~10.2 cm) possesses five fused sacrals (2-2), a fused pubis (8-1), a trochanteric shelf (14-1), a mound-like dorsolateral trochanter (16-1), a cranial intermuscular line (17-1), a caudal intermuscular line (18-1), and an ‘anterolateral scar’ (19-1).
-- Coelophysis bauri (CMNH 10971 #3; femur length 10.94 cm) possesses five fused sacrals (2-2), a fused pubis (8-1), a trochanteric shelf (14-1), a mound-like dorsolateral trochanter (16-1), a cranial intermuscular line (17-1), a caudal intermuscular line (18-1), and an ‘anterolateral scar’ (19-1).

There are of course smaller individuals of Coelophysis that display more immature character states as well. But my point here is that finding an individual of Coelophysis that displays a similar body size and similar ontogenetic character states is not unprecedented. Because we know that Coelophysis can reach much larger sizes (~25 cm femoral length), then with a sample size of 1, this is not great evidence that Pendraig’s maximum size is close to what this individual’s is; this taxon could just happen to be represented by one of those more mature-looking but anomalously small individuals also found in other coelophysoids. Therefore, although the data are consistent with Pendraig having a small maximum body size, I do not think the data support saying that it did have a small maximum body size.

4) This brings me to my suggestion that the best way to resolve this issue of maturity and body size is by histologically sampling the individual. I understand that the authors probably have qualms about destructively sampling a holotype and only known specimen (barring the referred vertebra) of a taxon, but I do have two ideas that may alleviate some concerns.

I notice in Figure 3 that the femur is already somewhat damaged at midshaft. I suggest that, instead of sampling the entire cross-section of the femoral shaft, you break off a small piece of already-damaged cortex from this midshaft region and histologically sample that (see picture below to see what I mean). I have successfully used this technique when I did not want to damage the full specimen but just sampled a portion that was already damaged, including on
a femur of *Dromomeran romeri* (Griffin et al. 2019, PeerJ), and on a femur of Coelophysis (CMNH 10971; Barta et al. in prep). Although a full cortical sample is ideal, with a partial cortex you can still see, for example, LAGs, LAG spacing, an EFS if present, etc. I used this method to find an EFS in the Coelophysis individual referenced above.

Another option, and slightly more heterodox, would be attempting to sample the distalmost preserved end of the ischium, which is roughly midshaft. Pelvic elements are not often sampled, but in my experience any long, somewhat tubular endochondral bone preserves a record of growth and can useful for histological maturity assessment when sampled near midshaft. I have seen this work on an immature Tyrannosaurid pubis (pers. obs.), metatarsals (McLain et al. 2018, Palaeons), and hyoid elements (pers. obs., submitted to be a 2021 SVP poster). A 2011 Master’s thesis showed that the midshaft of the Alligator pubis is skeletochronologically informative, and the ischium did not work only because it is platelike, not elongate, which is not an issue for Pendraig (Garcia 2011, “Skeletochronology of the American Alligator (Alligator Mississipiensis): Examination of the Utility of Elements for Histological Study”, Florida State University). The ischium of Pendraig is broken at roughly midshaft, so only ~1 cm of the ischium would need to be removed to make a histological section, causing minimal damage to the specimen. In fact, a combination of sampling from a femoral fragment and the ischium would be a good multi-elemental way to assess maturity and back up the assessment made by morphology, making the assessment supported by multiple lines of evidence.

I do not hinge my final approval on whether histological sampling is conducted on this specimen, and I think the authors can incorporate the concerns from my comment #3 without including histology. I know that it is not always possible or desirable to destructively sample a holotype. However, I do think that it would make the paper stronger, more convincing, and more citable, and therefore I recommend the authors add this to their study, if it is possible.

The authors are free to contact me with any questions, requests for clarification, or concerns.

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**Modified figures showing suggested sampling locations on next two pages:**
Appendix C

Pendraig orynys, a new small-sized coelophysoid theropod from the Late Triassic of Wales

| Journal:     | Royal Society Open Science |
|--------------|-----------------------------|
| Manuscript ID| RSOS-210915                 |
| Article Type:| Research                    |
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| Keywords:    | Pendraig, Coelophysoidea, Theropoda, Triassic, Body size evolution, Osteology |
| Subject Category: | Organismal and Evolutionary Biology |
Author-supplied statements

Relevant information will appear here if provided.

Ethics

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

Statement (if applicable):
CUST_IF_YES ETHICS : No data available.

Data

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

Statement (if applicable):
All data are provided for initial review as supplementary material.

Zip folders are provided for the R code and associated data files for both the regression and ancestral state reconstruction analyses. The initial code for the ancestral state reconstruction is provided for the analysis figured in Figure 8. The parameters can easily be changed manually by reviewers familiar with R to perform the analyses under the various settings provided in the Supplements. Different MPTs and the femoral lengths used for the conservative analyses are provided in the zip folder and minimum branch length can easily be adjusted from 1.0 to 0.5 and 0.1 in the code.

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):
SNFS, MDE, RJB, and SCRM designed the study. SNFS and MDE contributed to data collection. SNFS, MDE, and RJB analysed the data. SNFS made the figures and wrote the majority of the manuscript. All authors contributed to the writing and reviewing of the manuscript.
Pendraig orynys, a new small-sized coelophysoid theropod from the Late Triassic of Wales

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Abstract.

We describe a new genus and species of small-bodied coelophysoid theropod dinosaur, Pendraig orynys gen. et sp. nov, from the Late Triassic fissure fill deposits of Pant-y-ffynnon in southern Wales. The species is represented by the holotype, consisting of an articulated pelvic girdle, sacrum and posterior dorsal vertebrae, and an associated left femur, and by two referred specimens, comprising an isolated dorsal vertebra and a partial left ischium. Our phylogenetic analysis recovers Pendraig orynys as a non-coelophysid coelophysoid theropod, representing the first named unambiguous theropod from the Triassic of the United Kingdom. Recently it has been suggested that the faunas of Pant-y-ffynnon and other nearby Late Triassic to Early Jurassic fissure fill localities might have been subjected to insular dwarfism. To test this hypothesis for Pendraig orynys, we performed an ancestral state reconstruction analysis of body size in early neotheropods. Although our results indicate that a reduced body size is autapomorphic for Pendraig orynys, some other coelophysoid taxa show a similar size reduction, and there is therefore ambiguous evidence to indicate that this species was subjected to dwarfism. Our analyses further indicate that, in contrast to averostran-line neotheropods, which increased in body size during the Triassic, coelophysoids underwent a body size decrease early in their evolution.

Introduction.

The Late Triassic and Early Jurassic fissure fill deposits of southwestern England and southern Wales were formed as Mississippian Carboniferous Limestone exposed at the land surface that underwent karstic weathering processes and faulting [1, 2]. Previously, the putative Triassic age of the sediments was largely assessed as such on their basic lack of mammal remains and their occurrence...
in generally wider, distinctly solution-etched karstic features; they were considered to be representative of an upland environment (e.g., [2]). Other fissures containing generally less diverse vertebrate assemblages, but including extensive mammalian remains, and occurring in more restricted slot-like openings in the limestone were regarded as representative of island communities – most specifically Early Jurassic as corroborated by palynomorphs [3, 4]. Since then, many new discoveries have been made and evidence has been presented to suggest that at least some of the putative Triassic fissure fills were subject to the influences of marine transgressions and they are now considered to have been distributed among various nearshore islands [5-9]. Dating the fissure fills has continued to prove difficult due to their depositional setting, but some recent revisions, including faunal comparisons and palynological analyses, now argue that they are between early Rhaetian and early Sinemurian in age [1, 6, 10]. Yet doubt still remains and others [11, 12] continue to contend that some of the assemblages date back to the Norian and were filled at a time when the area was probably more akin to a broad sabkha-type environment.

Due to their unique preservational setting, a rich assemblage of mostly small-bodied vertebrates has been recovered from the fissure fills, which has provided important insights into the early evolution of major tetrapod groups such as mammaliaforms, rhynchocephalians, crocodylomorphs, and dinosaurs, as well as enigmatic diapsid groups such as kuehneosaurids (e.g., [13-18]). It has been suggested that taxa known from the fissure fills are smaller than their close relatives [19-21]. Although this has not been tested quantitatively, it has tentatively been attributed to insular dwarfism, which is a manifestation of the biogeographical concept known as the ‘Island Rule’ [22, 23]. However, most of the specimens are preserved as isolated fragments, meaning that the taxonomic status and phylogenetic position of much of the material has remained controversial.

Among the fissure fills faunas, archosaurs are represented by aetosaurs, phytosaurs, an enigmatic pseudosuchian, crocodylomorphs, sauropodomorph dinosaurs, and theropod dinosaurs, many of which have not been formally described (e.g., [1, 6, 24]). *Thecodontosaurus antiquus* and *Pantydraco caducus*, two sauropodomorph dinosaurs, represent the best studied archosaurs from the fissure fills. *Thecodontosaurus antiquus* was the fourth British dinosaur to be described [25, 26] and is represented by mostly isolated remains from Durdham Down Quarry in Bristol and Tytherington Quarry (?Rhaetian) [20, 27]. *Pantydraco caducus* is known from the putatively coeval Pant-y-ffynnon Quarry and is represented by a partial articulated skeleton including most of the skull, as well as a few partial skeletons and isolated elements [28, 29]. The material of *Pantydraco caducus* is considerably smaller than that described for *Thecodontosaurus antiquus*, and it was originally described and identified as *Thecodontosaurus* sp. [30]. The Pant-y-ffynnon specimens were subsequently referred to *Thecodontosaurus caducus* [29] and later *Pantydraco caducus* [31] and
considered to differ from *Thecodontosaurus antiquus* in the morphology of the cervical vertebrae, ilium, and humerus. Although *Pantydraco caducus* has been described in detail [28, 29], its taxonomic status is contentious, since the observed morphological differences with *Thecodontosaurus antiquus* are minor and could be attributable to taphonomic deformation or ontogenetic variation, and *Pantydraco caducus* might represent an early ontogenetic stage of *Thecodontosaurus antiquus* [20].

Crocodylomorphs are currently represented by a single taxon, *Terrestrisuchus gracilis*, a gracile non-crocodyliform crocodylomorph known from several partially articulated and many disarticulated specimens from Pant-y-ffynnon Quarry [18]. However, extensive crocodylomorph material is also known from Cromhall Quarry and might represent two separate species, both different from *Terrestrisuchus gracilis* [32], but this material has not yet been studied in detail. Cromhall Quarry has also yielded isolated material, comprising an ilium, maxilla, humerus, two astragali, and a tooth that were interpreted to represent a single dinosauriform taxon, ‘*Agnosphytis cromhallensis*’ [32]. The ‘*Agnosphytis cromhallensis*’ specimens were inferred to represent a single taxon because of the absence of additional archosauroid material among the Cromhall Quarry specimens, except for confidently identified crocodylomorph and ‘rauisuchian’ remains. However, the astragalus possessed several dinosaurian traits, the holotype specimen, an ilium, appeared similar to sauropodomorphs, and the maxilla had features present in non-dinosaurian dinosauriforms; consequently, it was suggested that ‘*Agnosphytis cromhallensis*’ might represent a chimera and a *nomen dubium* [33-37]. The original hypodigm of ‘*Agnosphytis cromhallensis*’ was recovered as a silesaurid in the analysis of Baron et al. [33] and in subsequent revisions of this analysis in a large polytomy at the base of Saurischia [38] or as the sister taxon to Herrerasauridae and Dinosauria [39]. Recently, an enigmatic pseudosuchian archosaur of equivocal phylogenetic affinity, *Aenigmaspina pantyffynnonensis*, has been described from Pant-y-ffynnon based on two complementary blocks comprising semi-articulated vertebrae, ribs, osteoderms, a scapula, and a number of fragments including skull bones, in addition to several fragmentary remains [24]. Additional fragmentary archosaur remains have also been identified from various fissure fills localities. These include a single aetosaur scute from Cromhall Quarry [40] and a phytosaur tooth and a possible humerus from Durdham Down Quarry assigned to ‘*Paleosaurus platyodon*’, which is now considered to represent a *nomen dubium* [27].

Finally, a theropod has been reported from Pant-y-ffynnon Quarry. It was originally described in the unpublished PhD thesis of Warrener [41] and interpreted as a coelurosaur. In it, an articulated pelvic girdle, associated with the two posteriormost dorsal vertebrae and four sacral vertebrae, a largely complete femur, an isolated dorsal vertebra, and a partial ischium were referred to the unnamed theropod. Additionally, it was suggested that three phalanges, including one ungual, and a
metapodial that were associated with the other remains could possibly be referred to the same taxon. Subsequently, the Pant-y-ffynnon theropod was briefly described and interpretative drawings of the pelvic girdle and femur were presented by Rauhut and Hungerbühler [42]. Therein, the material was assigned to *Syntarsus* sp. and considered to be closely related to the coelophysoid theropods ‘*Syntarsus’ rhodesiensis* (now *Megapnosaurus rhodesiensis*) and *Procompsognathus triassicus*. The Pant-y-ffynnon theropod was also mentioned by Galton and Kermack [28] and therein referred to as *Coelophysis* without providing further justification for this assignment. Recently it was reported that the material could not be located within the NHMUK collections [43]. However, the articulated partial pelvic girdle and vertebrae, as well as the femur and complete isolated dorsal vertebra referred to the theropod by Warrener [41] have now been relocated. Here, we provide the first detailed comparative description of this new taxon. We incorporate it in a phylogenetic analysis and compare its relative body size to other early theropod dinosaurs to examine whether the small size of the taxon might be a consequence of island dwarfism, as has been suggested for other elements of the fissure fills faunas [19-21].

**Systematic Palaeontology.**

Archosauria Cope, 1869-1870 [44] [Gauthier & Padian, 2020] [45]

Dinosauria Owen, 1842 [46] [Langer, Novas, Bittencourt, Ezcurra & Gauthier, 2020] [47]

Theropoda Marsh, 1881 [48] [Naish, Cau, Holtz, Fabbri & Gauthier, 2020] [49]

Neotheropoda Bakker, 1986 [50], *sensu* Sereno, 1998 [51]

Coelophysoidea Nopcsa, 1928 [52], *sensu* Sereno, 1998 [51]

**Pendraig orynys** gen. et sp. nov.

**Etymology.** *Pendraig* from the Welsh *Pen* (‘head’, ‘chief’ or ‘top’) and *Draig* (‘dragon’), literally meaning ‘chief dragon’ but used in a figurative sense in Medieval Welsh to mean ‘chief warrior’. The anglicised form, Pendragon, was the epithet of Uther, father of King Arthur in medieval legend. *Orynys*, from the Welsh ‘o’r ynys’, meaning ‘of the island’.

**Diagnosis.** *Pendraig orynys* is a small-sized non-averostran theropod (estimated femoral length: 10.21 cm; lower 95% CI: 8.60 cm; upper 95% CI: 12.08 cm; see below) that differs from other dinosaurs in the following unique combination of character states present in the holotype (autapomorphies indicated with an asterisk): posteiormost dorsal vertebrae with a strongly elongated centrum (c. length c. 2.6 times its anterior height), ilium with a distinctly anteroventrally slanting dorsal margin of the preacetabular process, and posterodorsal margin of the postacetabular
process curving abruptly posteroventrally and, as a result, the posteroventral end of the process is formed by an acute angle of approximately 65 degrees in lateral view*; pubis with pubic fenestra; ischium with well-developed obturator plate but without posteroventral projection forming a deep U-shaped or V-shaped notch with the shaft; and femur with fourth trochanter posteriorly developed to a height similar to the mid-depth of the shaft at that level. In addition, the referred middle-posterior dorsal vertebra differs from other early neotheropods in the absence of an accessory hyposphene-hypantrum articulation, and the presence of an anteriorly expanded neural spine*.

Holotype. NHMUK PV R 37591: An articulated vertebral series and pelvic girdle comprising the two posteriormost dorsal vertebrae missing most of the neural spines, three sacral vertebrae and a small fragment of the centrum of the fourth sacral, a complete left ilium, a largely complete left pubis missing the distal end, a left ischium missing most of the distal portion, a largely complete right pubis missing the distal end, and a right ischium missing most of the dorsal and distal portions (field number P77/1) (Figs. 1 and 2). Additionally, a left femur was found disarticulated from the left hemipelvis in the same block (field number P76/1). It has been completely freed from the matrix and is confidently referred to the same individual as the vertebral column and pelvis (Fig. 3).

Referred material. NHMUK PV R 37596 (field number P83/1): A complete middle to posterior dorsal vertebra completely freed from matrix (Fig. 4). NHMUK PV R 37597 (field number P65/66b): the proximal end of a left ischium preserving the articular facet with the left ilium (Fig. 5). A counterslab to this specimen, listed as field number P65/66a and comprising the base of the distal portion and part of the proximal expansion of the ischium, was described and figured in the unpublished PhD thesis of Warrener (1983). However, there is no record of this specimen in the collections at NHMUK and is therefore not considered here.

Locality and horizon. Fissure fills of Pant-y-ffynnon Quarry, southern Wales; earliest occurrence possibly late Norian, latest occurrence possibly late Rhaetian; 214.7 to 201.3 million years ago [1].

Remarks. Additional material from Pant-y-ffynnon, comprising two isolated non-ungual phalanges (field numbers P65/30 and P65/49), an isolated metapodial (field number P65/23), and an isolated ungual (field number P65/45), were considered to possibly be conspecific with *Pendraig orynys* by Warrener [41] and interpretative drawings of these elements were provided therein. These elements cannot be confidently attributed to any other known taxa known from Pant-y-ffynnon and were likely recovered from the same block as the partial left ischium of *Pendraig orynys* (field number P65/66b) as indicated by the shared number 65 in their field number. The location of these elements is currently unknown and there is no record of them in the NHMUK collections. Since these
elements do not exhibit diagnostic theropod features, there is currently insufficient support for an unequivocal attribution of this material to *Pendraig orynys*.

**Ontogenetic assessment.** The limited material currently referable to *Pendraig orynys* limits interpretations of intraspecific variation related to ontogeny, and therefore a comprehensive assessment of maturity cannot be provided. However, we approximate the ontogenetic stage of the holotype NHMUK PV R 37591 by scoring it for the maturity assessment matrix that has been formulated for early theropods (*Coelophysis bauri* and *Megapnosaurus rhodesiensis*) and a non-dinosaurian dinosauriform (*Asilisaurus kongwe*) [53-55]. Based on the results of our phylogenetic analysis (see below), these taxa provide a narrow phylogenetic bracket, and the characters are therefore likely suitable for approximating the maturity of *Pendraig orynys* (see also [56]). However, it is important consider that it cannot be confidently ascertained whether all characters that were scored are truly ontogenetically dependent for this specific taxon. Out of 32 characters of the maturity assessment matrix, 16 could be scored for NHMUK PV R 37591. Eight characters were scored as mature (1) and another eight were scored as immature (0). None of the characters considered highly informative of maturity (see figure 22a in [53]) are scored as 1, nor are any of the characters considered highly informative of immaturity scored as 0. Of the sequence order of mature state attainment (between 1 and 29) [53, 56], NHMUK PV R 37591 has a relative minimum maturity of 5 based on the presence of a mound-like dorsolateral trochanter on the femur (16-1), the presence of the *linea intermuscularis caudalis* on the femur (18-1), and the presence of an obturator ridge on the femur (20-1), and a maximum maturity of 19 based on the co-ossification of less than four sacral vertebrae (2-0), the absence of co-ossification between the ilium and pubis (8-0), the absence of an ‘anterolateral scar’ on the femur (19-0), and the presence of a gracile and thin fourth trochanter of the femur (23-0). The relative maximum maturity indicates that the holotype of *Pendraig orynys* was likely not fully skeletally mature, but the relatively large number of characters scored as 1 indicates that it likely also did not represent an early ontogenetic stage. For example, the holotype of *Pendraig orynys* is interpreted as more skeletally mature than the type specimens of *Liliensternus liliensterni* and as mature as or potentially more mature than the holotype of *Gojirasaurus quayi* [56], which are considerably larger than the new taxon.

**Morphological description and comparisons.**

Here we describe in detail the holotype and referred specimens of *Pendraig orynys* and compare it exhaustively with other non-averostran neotheropods and the early theropod *Eodromaeus murphi*, which has been found as the sister taxon to Neotheropoda in recent analyses (e.g., [57, 58]).

Axial skeleton.
Four largely complete vertebrae are preserved in the holotype specimen NHMUK PV R 37591 (Fig. 2A). Additionally, a partial vertebra is preserved at the anterior end of the preserved vertebral column and a tiny fragment of a sacral vertebra is preserved at the posterior end of the column. The anterior two vertebrae are identified as dorsal vertebrae and the other four as sacral vertebrae based on the presence of articulations with the ilia, as is explained in more detail below. The isolated dorsal vertebra NHMUK PV R 37596 (Fig. 4) was not associated with NHMUK PV R 37591 and thus cannot unequivocally be referred to the same individual. However, as is explained below, NHMUK PV R 37596 can be relatively confidently referred to *Pendraig orynys* based on a strong morphological overlap with NHMUK PV R 37591 and because both specimens were recovered from the same locality.

Dorsal vertebrae.

The most anterior vertebra of the articulated vertebral series preserved in NHMUK PV R 37591 comprises a partial centrum and neural arch, which preserves the left diapophysis (Figs. 1B and 2A, C). The neural spine and anterior portion of the vertebra are completely missing. The right side of the specimen is damaged and partly missing. The centrum is only exposed on its broken right lateral side. There is no visible suture between the centrum and neural arch. On the left side the diapophysis is complete and has an anteroposteriorly elongate, oval articular facet (Fig. 1A). The process reaches less far laterally than the diapophysis of the succeeding vertebra (Fig. 2A). In dorsal view, the diapophysis is sub-trapezoidal, with the posterior margin of the diapophysis being slightly concave and the anterior margin being anteriorly curved at its base. This almost certainly represents the paradiapophyseal lamina (*sensu* [59]) that connected the diapophysis to the parapophysis — which is not preserved—, as occurs in the middle-posterior dorsal vertebrae of other early neotheropods (e.g., *Megapnosaurus rhodesiensis* [60]; *Liliensternus liliensterni*: HMN MB.R.2175; *Dilophosaurus wetherilli* [61]). The left postzygapophysis is poorly preserved and its morphology cannot therefore be inferred, but it is still in articulation with the corresponding prezygapophysis of the succeeding dorsal vertebra.

The last dorsal vertebra of NHMUK PV R 37591 comprises a complete centrum and a neural arch missing the neural spine, right diapophysis, and right postzygapophysis (Figs. 1B and 2A). Its centrum is 14.7 mm long, being 2.63 times the height of its anterior surface (Table 1). This ratio matches that of at least some specimens of *Coelophysis bauri* (e.g., [62]: ratio = 1.98–2.87, D11–D13 of AMNH 7228 based on the posterior height of the centrum) and is slightly proportionally longer than those of the posterior dorsal vertebrae of *Eodromaeus murphi* (PVSJ 562: ratio = 2.0–2.18), *Panguraptor lufengensis* ([63], fig. 1: ratio = c. 2.0–2.11 in the last two dorsal vertebrae), and *Megapnosaurus*
rhodesiensis ([60]: ratio = 2.10, D13 of NHMB QG 1). By contrast, these vertebrae are considerably proportionally shorter in Liliensternus liliensterni (HMN MB.R.2175: 2.22–2.24: ratio = 1.58–1.67, posterior dorsal vertebrae), Lucianovenator bonoi (PVSJ 906: ratio = 1.63, last dorsal vertebra), Lophostropheus airelensis ([64]: ratio = 1.32, last dorsal vertebra), Dracoraptor hanigani (NMW 2015.5G.1–2015.5G.11: ratio = 1.63–1.75, middle–posterior dorsal vertebrae), Cryolophosaurus elliott (FMNH PR1821: ratio 1.07, posterior dorsal vertebra), Dilophosaurus wetherilli ([61]: ratio = 1.16–1.52, D10, D11 and D13 of UCMP 37302; ratio = 1.19 D14 of UCMP 77270), and Sarcosaurus woodi ([57]: ratio = c. 1.9, middle–posterior dorsal vertebra of WARMS G678). The ventral surface of the centrum is anteroposteriorly concave and lacks a ventral keel (Fig. 1B). The centrum is amphiplatyan with very slightly concave anterior and posterior articular surfaces. As in the preceding vertebra, no visible suture is present between the centrum and neural arch. The lateral surface of the centrum bears an anteroposteriorly elongate but shallow fossa just ventral to the articulation with the neural arch, which is a common condition in the middle–posterior dorsal vertebrae of early neotheropods (e.g., Liliensternus liliensterni: HMN MB.R.2175; Procompsognathus triassicus: SMNS 12591; Lucianovenator bonoi: PVSJ 906; Lophostropheus airelensis [64]; Sarcosaurus woodi [57]). The last dorsal vertebra possessed only a single articular facet for the rib on each side, located at the end of a transversely wide, wing-like transverse process (Fig. 2A). In dorsal view, its posterior margin is concave and its anterior margin appears to be somewhat sinusoidal. There is no distinct fossa on the dorsal surface of the base of the transverse process. The articular surfaces of the prezygapophyses face dorsomedially. The articular surface of the left postzygapophysis is poorly preserved. No hyposphene articular surface is preserved, but this region is poorly preserved. The prezygapophyses diverge from each other in dorsal view and their tips are well separated from the median line, contrasting with the sub-parallel prezygapophyses of Sarcosaurus woodi [57].

The isolated dorsal vertebra NHMUK PV 37596 is virtually complete, undistorted, and freed from matrix (Fig. 4). The centrum is 14.6 mm long and 2.59 times longer than the height of its anterior articular surface (Table 1). The elongation of this centrum matches or closely resembles that of the middle dorsal vertebrae of the coelophysids Coelophysis bauri (e.g., NMV P231382: c. 2.6, middle dorsal vertebra), Megapnosaurus rhodesiensis ([60]: 2.33–2.64, D6 and D7 of NHMB QG 1), and Procompsognathus triassicus (SMNS 12591: 2.70–2.91, D7 and D8), whereas in other early neotheropods the middle–posterior dorsal vertebrae are proportionally shorter (e.g., Liliensternus liliensterni, Gojirasaurus quayi; Dilophosaurus wetherilli, Dracoraptor hanigani, Cryolophosaurus elliott; Sarcosaurus woodi) [57, 61, 65–67]. The ventral surface of NHMUK PV 37596 is concave in lateral view and there is no ventral keel. A single nutrient foramen can be observed close to the anterior end of the centrum on its right ventrolateral side. The anterior and posterior articular
surfaces of the centrum are both very slightly concave and transversely broader than tall, resembling the condition in *Gojirasaurus quayi* [65]. By contrast, the centrum is taller than broad in the posterior dorsal vertebrae of *Megapnosaurus rhodesiensis* ([60]: table 6), *Sarcosaurus woodi* (only the anterior surface is preserved) [57], *Cryolophosaurus ellioti* [67], and *Dilophosaurus wetherilli* [61], approximately as broad as tall in *Liliensternus liliensterni* (HMN MB.R.2175), and both conditions occur in *Eodromaeus murphi* (PVSJ 562). The lateral surfaces of the centrum bear a shallow fossa directly ventral to the connection to the neural arch, as occurs in NHMUK PV R 37591 and other early neotheropods (see above). The neurocentral suture is closed along most of its extension, being only visible on the most posterior region of the neural arch peduncle on both sides of the bone.

The diapophysis is placed on a wide sub-trapezoidal or wing-like transverse process (Fig. 4D). In dorsal view, the posterior margin of this process is mainly laterally oriented and slightly concave, whereas the anterior margin is anteromedially to posterolaterally oriented and somewhat sinusoidal. The anteroposteriorly long base of the transverse process and strong posterolateral slating of its anterior margin resemble the condition in the middle dorsal vertebrae of *Eodromaeus murphi* (PVSJ 562) and the coelophysids *Coelophysis bauri* (AMNH 7224), *Megapnosaurus rhodesiensis* [60], and *Procompsognathus triassicus* (SMNS 12591). The parapophysis is placed on a strongly developed, narrow and rod-like stalk, but it is considerably less extended laterally than the diapophysis, resembling the condition in the middle-posterior dorsal vertebrae of at least some other early neotheropods (e.g., *Liliensternus liliensterni*: HMN MB.R.2175; *Megapnosaurus rhodesiensis* [60]). Both processes are positioned fully on the neural arch and are connected through a thin paradiapophyseal lamina (*sensu* [59]). The diapophysis is located slightly dorsal to the parapophysis (Fig. 4A-B). The articular facet of the diapophysis is oval and anteroposteriorly elongated, whereas the facet of the parapophysis is subcircular. The parapophyseal centrodiapophyseal fossa ventral to the diapophysis is shallow, whereas the parapophyseal centroprezygapophyseal and postzygapophyseal centrodiapophyseal fossae are very deep and framed by pronounced and thin laminae (*sensu* [68]). The laminae framing the parapophyseal prezygapophyseal fossa are the prezygaparapophyseal lamina dorsally and the anterior centroparapophyseal lamina ventrally, whereas the postzygapophyseal centrodiapophyseal fossa is framed by the postzygodiapophyseal lamina dorsally and the posterior centrodiapophyseal lamina ventrally (*sensu* [59]). This pattern of laminae and fossae matches that of a posterior dorsal vertebra of *Liliensternus liliensterni* (HMN MB.R.2175 2.22). There are no pneumatic foramina within the fossae. The transition between the transverse process of the diapophysis and the neural spine forms an angle of approximately 90 degrees, and there is no fossa present in this region. The
postzygapophyses are closely placed together and their articulation facets face ventrolaterally. A hyposphene is absent between the postzygapophyses and therefore there is no accessory intervertebral articulation (Fig. 4F), contrasting with its presence in the middle-posterior dorsal vertebrae of *Eodromaeus murphi* (*PVSJ* 562), *Megapnosaurus rhodesiensis* [60], *Gojirasaurus quayi* [65], *Cryolophosaurus ellioti* [67], *Sarcosaurus woodi* [57], and *Dilophosaurus wetherilli* [61]. The articulation facets of the prezygapophyses face dorsomedially (Fig. 4E). Both the spinoprezygapophyseal and spinopostzygapophyseal fossae are very narrow slit-like openings between the pre- and postzygapophyses, respectively [68], and they do not extend onto the surface of the neural spine. The spinopostzygapophyseal fossa is considerably larger than the spinoprezygapophyseal one.

The neural spine is proportionally low, being 0.4 times taller than anteroposteriorly long at its base, resembling the condition in the middle and posterior — but not the posteriormost — dorsal vertebrae of *Coelophysis bauri* (AMNH 7224) and *Megapnosaurus rhodesiensis* [60]. By contrast, *Eodromaeus murphi* and other early neotheropods (e.g., *Dilophosaurus wetherilli* [61]; *Gojirasaurus quayi* [65]; *Panguraptor lufengensis* [63]) have proportionally taller middle-posterior dorsal neural spines (ratio >0.5). The anterior margin of the neural spine is located at the level of the parapophysis (Fig. 4A-B). It curves from its base into an anterodorsal direction and subsequently becomes posterodorsally oriented distally. The posterior margin of the neural spine is notched proximally as a result of strongly anterior bowing in lateral view. Distally, the posterior margin is posterodorsally directed and convex. The posterior end of the neural spine is slightly further extended posteriorly than the postzygapophyses. The presence of middle-posterior dorsal vertebrae with a curved posterior margin of the neural spine that overhangs the postzygapophysis also occurs in *Coelophysis bauri* (NMV P231382), *Procompsognathus triassicus* (SMNS 12591), and *Dilophosaurus wetherilli* [61]. In some other early theropods the neural spine also extends posteriorly close to or beyond the level of the postzygapophysis, but the posterior margin of the spine is straight (e.g., *Eodromaeus murphi*: *PVSJ* 562; *Gojirasaurus quayi* [65]). The distal margin of the neural spine is not transversely expanded (Fig. 4E-F). Most of the distal margin is straight and slightly anteroventrally directed in lateral view. Posteriorly, the distal margin is convex, sloping down towards the posterior margin. The neural spine is 14.3 mm long and 5.0 mm tall (Table 1). Its left lateral surface is largely missing (Fig. 4B).

Compared to NHMUK PV R 37596, only few morphological features of the posterior dorsal vertebrae can be deduced from the articulated vertebral series of NHMUK PV R 37591. Nevertheless, the overall size, as well as the relative proportions of the vertebral centrum of NHMUK PV 37596 correspond with that of the posteriormost dorsal vertebra of NHMUK PV R 37591 (e.g., centrum
length versus anterior height ratio). Both vertebrae also lack a ventral keel and possess a similar curvature of the ventral margin of the centrum and are amphiplatyan. Furthermore, the diapophysis of NHMUK PV R 37596 has a similar wing shape and concave posterior margin as the penultimate and last dorsal vertebrae of NHMUK PV R 37591. Based on the position of the parapophysis, which is completely located on the neural arch (Fig. 4A-B), NHMUK PV 37596 can be interpreted as a middle to posterior dorsal vertebra [60, 61, 69].

Sacral vertebrae.

The first sacral vertebra of NHMUK PV R 37591 is disarticulated from the rest of the vertebral column and has shifted approximately 90 degrees so that its posterior articular facet faces in a right lateral direction relative to the rest of the vertebral column (Fig. 1B). Therefore, the first sacral centrum was not fused to adjacent vertebrae. However, based on its position in the vertebral column and the width of its complete, wing-like right transverse process-rib, it most likely would have attached to the preacetabular process of the ilium (Fig. 2A). This element is therefore interpreted as a dorsosacral vertebra, and functionally, as the first vertebra of the sacrum. The left transverse process-rib is incomplete distally. The neural spine is broken, and its height can therefore not be assessed. However, the base of the spine is preserved, revealing that the spine arose along the entire length of the neural arch. The neural arch is fused to the centrum along its entire anteroposterior length. Its lateral surfaces are lateromedially very thin and markedly laterally convex on both sides, extending considerably further laterally at their mid-height than the centrum. The neural arch encloses a very large neural canal that is virtually circular in cross-section (Fig. 1B). The centrum is small relative to the size of the vertebra and considerably lateromedially wider than dorsoventrally tall. It has a concave posterior articular surface. The transition between the neural arch and centrum is demarcated by a clear anteroposteriorly directed groove in lateral view (Fig. 2D). The length of the vertebra cannot be measured because the anterior end is covered in matrix. The right prezygapophysis is visible and has a similar morphology to that of the preceding vertebra and that of NHMUK PV 37596.

The centra of the subsequent two vertebrae of NHMUK PV R 37591 are fused, but their margins can be deduced from slight dorsoventral expansions that demarcate the articulations (Fig. 2B). It is unclear whether the zygapophyses are also fused between the two vertebrae since they are insufficiently preserved. The second sacral centrum is longer (13.3 mm) than the centrum of the third sacral (11.1 mm; Table 1), a condition that also occurs in Lucianovenator bonoi (PVSJ 906). Both vertebrae preserve the centrum and the left side of the neural arches. The position of the second sacral vertebra matches that of the first primordial sacral of archosauriforms with two sacral
vertebrae. The third sacral probably represents an “inserted” sacral (sensu [70]) because its rib articulates with the ilium anteriorly to the level of the base of the ischiadic peduncle, where the second primordial sacral vertebra articulates in earlier archosauriforms [70]. Only the left prezygapophysis of the second sacral vertebra is partially preserved, and its articular surface faces dorsomedially. The left ribs of both vertebrae are fused to the left ilium, as occurs in skeletally mature individuals of other early neotheropods [71, 72]. The right side of the neural arch and the neural spine are completely missing. The vertebral centra are dorsoventrally shorter than in the preceding vertebrae; the anterior articular surface of the centrum of the second sacral is 5.2 mm tall, whereas that of the posteriormost dorsal vertebra is 6.4 mm (Table 1), and the dorsal surfaces of the centra are gently concave (Fig. 2D). The ventral margins of the centra are slightly anteroposteriorly concave, but considerably less so than the posteriormost dorsal vertebra (Fig. 1B).

The transverse processes of both vertebrae are fused to their corresponding ribs and are somewhat dorsolaterally extended, in the third sacral vertebra more so than in the second (Fig. 2A). The fused transverse process and rib of the second sacral vertebra taper slightly distally and have a concave posterior margin and a straight anterior margin. The anteroposterior width of the fused process and rib at their distal end is 3.7 mm. Matrix supports the transverse process of the second sacral vertebra ventrally, and it is therefore not possible to discern its thickness, nor the presence of a ventral lamina. The combined transverse process and rib of the third sacral vertebra is anteroposteriorly 5.7 mm wide at its distal end and therefore wider than that of the second sacral (Table 1). It broadens distally and has a concave posterior margin and a slightly convex anterior margin. This transverse process has mostly been freed from the surrounding matrix and is dorsoventrally thin. A very thin, ventrally directed lamina is projected from the anterior margin of the transverse process (Fig. 2D), giving the entire process an L-shape in lateral view. The ventral extent of this lamina cannot be discerned because its ventral section is surrounded by matrix. The attachment sites on the medial surface of the ilium for the second and third sacral ribs are positioned on an anteroposteriorly directed rim that extends further posterior to these attachment sites (Fig. 1B). This rim terminates posteriorly at a dorsoventrally oriented thickening of the medial surface of the ilium. This thickening connects the rim with the ridge that forms the dorsomedial margin of the brevis fossa. This thickening represents an attachment site scar for the fourth sacral rib.

A small fragment of the centrum of the fourth sacral vertebra is preserved and fused to the centrum of the third sacral of NHMUK PV R 37591. The second, third and fourth sacral centra form a straight structure in lateral view, resembling Lucianovenator bonoi (PVSJ 899), Coelophysis bauri (CMNH 10971), and Megapnosaurus rhodesiensis [60], but contrasting with the dorsally arched sacrum of
‘Syntarsus’ kayentakatae (TMM 43688-1). There are no visible additional attachment site scars preserved on the medial surface of the ilium. Nevertheless, the presence of another posterior sacral vertebra cannot be ruled out. Therefore, *Pendraig orynys* possessed at least four sacral vertebrae.

Appendicular skeleton.

The pelvic girdle of NHMUK PV R 37591 comprises a complete left hemipelvis excluding the distal ends of the left pubis and ischium, as well as a largely complete right pubis and ischium (Fig. 1). In addition, a partial left ischium, NHMUK PV R 37597 (Fig. 5), comprising the iliac peduncle and part of the ischial plate, can be confidently assigned to *Pendraig orynys* based on the presence and shape of the antitrochanter and the concavity on the acetabular rim, which are in correspondence with the morphology of the left ischium of NHMUK PV R 37591. NHMUK PV R 37597 is slightly larger than the holotype. Finally, a largely complete left femur (Fig. 3) is referred to the same individual as the articulated pelvic girdle and vertebral series and together comprise the holotype (NHMUK PV R 37591) of *Pendraig orynys* (see Systematic Palaeontology section). Measurements of the appendicular skeleton of NHMUK PV R 37591 are provided in Table 2.

Ilium.

The left ilium of NHMUK PV R 37591 is completely preserved, with exception of some damage on the posterior end of the postacetabular process, and in articulation with the left pubis and ischium, and with the second and third sacral ribs (Figs. 1 and 2). The dorsal margin of the iliac blade is straight to slightly convex on its middle and posterior portions, which comprises the section dorsal to the supraacetabular crest and the elongate postacetabular process (Fig. 1A). Anteriorly, the dorsal margin of the preacetabular process is more distinctly convex and forms a relatively abrupt anteroventral transition to the anterior margin of the preacetabular process, resembling the condition in *Sarcosaurus woodi* [57]. By contrast, the dorsal margin of the preacetabular process is straight or only slightly convex in other non-averostran neotheropods (e.g., *Coelophysis bauri*: USNM 529376; *Liliensternus liliensterni*: HMN MB.R.2175; *Lucianovenator bonoi*: PVSJ 906; *Coelophysis* sp.: UCMP 129618; *Notatesseraeraptor frickensis* [73]; *Megapnosaurus rhodesiensis*: NHMB QG 1; *Dilophosaurus wetherilli* [61]). The dorsal margin of the iliac blade of *Pendraig orynys* possesses a somewhat thickened, mostly flat surface that faces slightly laterally. This flat surface extends along most of the bone, with exception of the anteriormost region of the preacetabular process and starts to taper anteriorly at the mid-length of this process. On the posterior region of the iliac blade, this flat surface extends ventrally as a raised region to occupy the entire dorsoventral height of the lateral surface of the posterior end of the postacetabular process. It has been inferred that the anterior rim of this raised surface probably delimited the attachment site of the *M. iliofemoralis* [72,
This same condition occurs in *Coelophysis bauri* (USNM 529376), *Lucianovenator bonoi* (PVSJ 899, 906), *Coelophysis* sp. (UCMP 129618), ‘*Syntarsus’ kayentakatae* [75], and *Megapnosaurus rhodesiensis* (NHMB QG 1), but not in other early neotheropods [72]. The anterior margin of the preacetabular process is continuously rounded and extends considerably further anterior than the pubic peduncle of the ilium, as occurs in other neotheropods [76]. The preacetabular process is transversely very thin (i.e., laminar) and slightly medially curved in dorsal view. The ventral margin of the preacetabular process is slightly convex and oriented somewhat anteroventrally to posterodorsally. However, the overall orientation of the preacetabular process is anteriorly facing and a broad gap separates it from the pubic peduncle. This morphology corresponds to that of most theropods, but contrasts with the anteroventrally directed processes of *Sarcosaurus woodi* and some ceratosaurs (e.g., *Ceratosaurus nasicornis*, *Eoabelisaurus mefi*) [57]. At its posterodorsal end, the postacetabular process curves abruptly posteroventrally and the posteroventral end of the process is formed by an acute angle of approximately 65 degrees in lateral view. By contrast, the posteroventral corner of the postacetabular process is approximately right-angled or slightly acute in other non-averostran neotheropods (e.g., *Coelophysis bauri*: USNM 529376; *Liliensternus liliensterni*: HMN MB.R.2175; *Lucianovenator bonoi*: PVSJ 906; *Coelophysis* sp.: UCMP 129618; ‘*Syntarsus’ kayentakatae*: Tykoski 2005; *Megapnosaurus rhodesiensis*: NHMB QG 1; *Dilophosaurus wetherilli*: Marsh & Rowe 2020; *Sarcosaurus woodi*: NHMUK PV R4840). A notch on the posterior end of the postacetabular process, as has been described for various coelophysoid taxa (e.g., *Coelophysis bauri*, *Coelophysis* sp., *Megapnosaurus rhodesiensis*, ‘*Syntarsus’ kayentakatae’ [72], is absent. In dorsal view the ilium is oriented approximately straight anteroposteriorly (Fig. 2A) and the postacetabular process expands gradually laterally towards its posterior end, resembling the condition in *Liliensternus liliensterni* (HMN MB.R.2175), *Lucianovenator bonoi* (PVSJ 906), and *Dilophosaurus wetherilli* (UCMP 37302). By contrast, the the postacetabular process is distinctly more laterally expanded, extending beyond the level of the outer rim of the supra-acetabular crest in dorsal view, in *Coelophysis bauri* (USNM 529376), *Coelophysis* sp. (UCMP 129618), and *Megapnosaurus rhodesiensis* [60].

The lateral surface of the iliac blade is concave along its entire anteroposterior length. A shallow, not well-rimmed fossa is present immediately dorsal to the supra-acetabular crest and this region lacks the vertical ridge present in *Lophostropheus airelensis* [64, 77]. The ventral margin of the postacetabular process is formed by a distinct and sharp brevis shelf (Fig. 1A). The concave portion of the postacetabular process positioned medioventrally to this shelf is the brevis fossa [74]. This fossa is inferred to have formed the attachment site for the *M. caudofemoralis brevis* and is mediadorsally framed by a distinct ridge (Fig. 1B). The brevis fossa is only visible in lateral view in its anterior
portion. The remainder of the fossa faces ventrally or medioventrally and is obscured by the brevis shelf in lateral view, a condition typical of neotheropods [70].

The acetabulum is fully perforated and mostly formed by the ilium (Fig. 1A). On the posterior surface of the acetabulum a well posteriorly delimited, crescent-shaped rugosity is present, which represents the antitrochanter. The dorsal portion of the antitrochanter is positioned on the ilium, whereas most of its surface is present on the ischial portion of the acetabular margin. The development of this antitrochanter closely resembles those observed in Megapnosaurus rhodesiensis (NHMB QG 1), Coelophysis bauri (USNM 529376), Coelophysis sp. (UCMP 129618), ‘Syntarsus’ kayentakatae [72], and Lucianovenator bonoi (PVSJ 906). Dorsally, the acetabulum is framed by a pronounced supra-acetabular crest, which projects laterally and slightly ventrally (Figs. 1A and 2C). The rim of the crest extends close to the connection with the pubis anteriorly and to the origin of the brevis shelf posteriorly. However, the supra-acetabular crest and the brevis shelf do not form the continuous, well-laterally developed ridge present in Megapnosaurus rhodesiensis (NHMB QG 1), Coelophysis bauri (USNM 529376), Lophostropheus airelensis [77], Procompsognathus triassicus (SMNS 12591), ‘Syntarsus’ kayentakatae [72], and Lucianovenator bonoi (PVSJ 906). The condition of Pendraig orynys resembles that of Liliensternus liliesterni (HMN MB.R.2175), Coelophysis sp. (UCMP 129618), Dilophosaurus wetherilli [61], and Sarcosaurus woodi [57]. The pubic peduncle is anteroventrally oriented, whereas the ischiadic peduncle is considerably more vertically directed, facing only slightly posteroventrally. The suture between the ilium and pubis is completely unfused. The suture with the ischium is unfused along its posterior portion, but on its anterior portion, which is located across the antitrochanter and part of the acetabulum, the suture is closed and the elements are indistinguishably fused.

Pubis.

Both the left and the right pubes of NHMUK PV R 37591 are largely complete and in articulation with each other (Fig. 2C). Both elements lack the distal end of the pubic shaft, but the shaft extends further distally in the right element than the left. Overall, the preservation of the left element is superior to that of the right element since the surface of the latter is damaged in several places. Therefore, the description of the pubis is largely based on the left element. The shaft of the pubis is anteroventrally directed and elongate (Fig. 1A). Its extent is considerable but cannot be fully assessed because the distal end is missing on both sides. The longest preserved pubis, the right element, is 63.2 mm long. When including the imprint of the pubic shaft, which reaches further distally but likely does not represent the distal terminus of the pubes, the maximum length is 74.8 mm. The shaft is rod-like with a plate-like medial apron, which is lateromedially wide and
anteroposteriorly flat (Fig. 2B–C). The anterior surface of the shaft is convex and, correspondingly, the posterior surface is concave. As a result, the pubic shaft is slightly anteriorly curved in lateral view as in *Coelophysis bauri* (AMNH 7223, 7224), *Megapnosaurus rhodesiensis* [60], ‘Syntarsus’ *kayentakatae* [78], *Dracoraptor hanigani* (NMW 2015.5G.1–2015.5G.11), *Procompsognathus triassicus* (SMNS 12591), *Notatessaeraptor frickensis* (SMF 06-1), and *Gojirasaurus quayi* [65]. A higher degree of curvature occurs in *Eodromaeus murphi* (PVSJ 562). By contrast, the pubic shaft is straight in *Liliensternus liliensterni* (HMN MB.R.2175) and *Dilophosaurus wetherilli* [61]. Distally, the shaft gradually narrows mediolaterally. Because the distal end is missing, it cannot be determined whether *Pendraig orynys* possessed an expanded pubic boot. The pubic shaft meets its antimere distally, but it is unclear whether the shafts were also connected proximally or separated by a pubic foramen [74], since the shafts are covered by matrix on both sides proximally.

The anterior margin of the proximal portion of the pubis is smooth. The anterior portion of the acetabular contribution of the pubis is slightly rugose and a faint ridge is formed on its lateral margin (Fig. 1A). The pubis bears two openings on its ventrolateral surface proximally (Figs. 1A and 2B). The dorsal opening is the obturator foramen. It is oval and approximately four times longer anteroposteriorly than tall dorsoventrally. The obturator foramen occurs widely in archosauromorphs [70, 79] but is lost in most averostran theropods, which is attributable to a reduction in the ossification of the puboischiadic plate, resulting in the confluence the obturator foramen with the puboischiadic fenestra [74]. The considerably larger opening present ventral to the obturator foramen represents the pubic fenestra, which also occurs in *Megapnosaurus rhodesiensis* [60], *Segisaurus hallii* [80, 81], *Coelophysis bauri* [62], and *Gojirasaurus quayi* [65]. The pubic plate of *Pendraig orynys* is well-ossified as it articulates with its antimere along its entire ventral margin. Among theropods this ventral median contact is a rarely preserved feature that has previously only been described or figured for *Megapnosaurus rhodesiensis* [60] and *Torvosaurus tanneri* [82]. A suture between the pubis and ilium can be clearly discerned. However, it is unclear whether a suture is also present between the pubis and ischium or whether these elements were fully fused, since several cracks obscure this region. A low tuberosity for the probable origin of the *M. ambiens* is present on the anterolateral surface of the bone in transition between the proximal end and the shaft.

**Ischium.**

Ischia are preserved on both sides of the pelvis of NHMUK PV R 37591. The right ischium comprises the ventral portion of the ischiadic plate, including a complete ventral margin, and the base of the ischiadic shaft (Fig. 1B). The left ischium also only preserves the base of the ischiadic shaft, but the
The entire proximal part of the bone is preserved (Fig. 1A) and therefore the description of the ischium is mostly based on this element. The maximum length of the left ischium, measured from the distalmost preserved end of the shaft to the connection between the ischium and pubis on the margin of the acetabulum is 26.6 mm. The base of the shaft of the ischium is posteroventrally directed (Fig. 1A) and the shaft is considerably lateromedially narrower at its base than the pubis (Fig. 2B). The ventral margin of the ischiadic plate connects its antimere along its anteroposterior length and is continuous with the ventral margin of the pubic plate. At its posterior end, the ventral margin bears a notch that separates it from the base of the ischiadic shaft (Fig. 1A). This notch occurs widely among early neotheropods and has previously been considered as a synapomorphy for the group [76]. The notch of *Pendraig orynys* is shallow as a result of the absence of a posteroventrally oriented projection of the obturator plate. By contrast, this projection is present and forms a deep, V-shaped or U-shaped notch in lateral view in *Megapnosaurus rhodesiensis* (NHMB QG 1), *Dracoraptor hanigani* [83], *Dilophosaurus wetherilli* (UCMP 37302), and *Tachiraptor admirabilis* [84]. There are no openings on the ischiadic plate, contrasting with the presence of an ischial foramen in *Segisaurus halli* [81]. In contrast to the pubic plates, which are only connected at their distalmost ventral margin, the ischiadic plates form a taller connection that occurs medially for slightly more than half their dorsoventral height. The iliac peduncle of the ischium is clearly separated by a deep concavity from the ventral margin of the acetabulum formed by the ischium. The ventral margin bears a low but distinct ridge (Fig. 1A). The antitrochanter is largely formed by the ischium. It is a flat rugose surface that is clearly demarcated by a rounded convex ventral ridge.

The isolated partial left ischium NHMUK PV R 37597 comprises the iliac peduncle and part of the ischial plate (Fig. 5). The medial side of the specimen is fully exposed (Fig. 5A), whereas the lateral side is largely covered by matrix, only exposing the iliac peduncle. The articular facet with the ilium is anteroposteriorly elongate, oval, and concave (Fig. 5B). Anterolaterally it bears a clear rim that demarcates the articular surface from the portion of the antitrochanter formed by the ischium. The surface of the antitrochanter is slightly rugose and rounded ventrally. The acetabular margin of the ischium bears a clear concavity ventral to the antitrochanter (Fig. 5A). The posterior margin of the ischium is slightly concave and represents the transition from the iliac peduncle to the posterior margin of the shaft of the ischium, which is otherwise not preserved. The ischial shaft is straight as far as it is preserved and rod-like, forming a subtriangular cross-section with its counterpart where they are broken off.

**Femur.**
Only the left femur of the holotype NHMUK PV R 37591 is preserved. Originally, this element was displaced and positioned lateroventrally to the right hemipelvis in the same block, but it had been prepared free of matrix by the time of the thesis of Warrener [41]. Based on its association, overall size, and morphology the femur can be confidently identified as belonging to the same individual as the pelvis and associated vertebrae. The femur is very well-preserved and comprises a complete proximal end and most of the shaft, only missing the distal end and the distalmost end of the shaft (Fig. 3). The preserved length of the femur is 86.3 mm. The proximal femoral head is inturned and would have been oriented anteromedially to articulate with the acetabulum of the pelvis, as in other early dinosaurs [85, 86]. The maximum width of the proximal head of the femur is 15.1 mm. On its ventral end the proximal head bears a clear lip, forming a distinctly concave emargination on the transition with the shaft (Fig. 3A-B), as is present in other early neotheropods (e.g., Coelophysis bauri, Megapnosaurus rhodesiensis, Dilophosaurus wetherilli, Liliensternus liliensterni) [76]. In contrast, the postero medial tuber (sensu [70], = posteromedial tuber of [79]) projects from the femoral head medially (Fig. 3E), as occurs in other early neotheropods (e.g., Coelophysis bauri, Megapnosaurus rhodesiensis, Dilophosaurus wetherilli, Liliensternus liliensterni) [76]. In contrast, the posteromedial tuber (sensu [70], = posterior tuber of [79, 87]), positioned posterolaterally to the anteromedial tuber, is poorly developed, forming a slight convexity on the posteromedial margin of the proximal head. Posterolateral to this, the posteromedial margin of the femoral head is slightly depressed, representing the facies articularis antitrochanterica. The anterolateral margin of the femoral head is continuously convex along its length as a result of the presence of an anterolateral tuber (sensu [70], = anteromedial tuber of [79]). The proximal surface of the femur lacks a longitudinal groove, as occurs in skeletally mature specimens of Megapnosaurus rhodesiensis [53].

The greater or dorsolateral trochanter is a mound-like tuberosity positioned on the lateral surface of the femur distal to the proximal head (Fig. 3). Among early neotheropods, a distomedially directed ridge is present direct posteromedially to the greater trochanter in some, generally relatively mature, specimens of the coelophysoid taxa Megapnosaurus rhodesiensis, Coelophysis bauri [53], ‘Syntarsus’ kayentakatae (MNA V2526), and Segisaurus halli (UCMP 32101). This ridge was identified as an obturator ridge and considered to probably represent an attachment site for Mm. puboischiofemoralis externi by Raath [60]. A very distinct ridge positioned and oriented as in these taxa is present on the femur of Pendraig orynys (Fig. 3A), and we therefore refer to this structure as the obturator ridge. The obturator ridge is raised considerably, particularly on its posterolateral portion, and its surface is rugose. Another ridge that originates proximally to the obturator ridge, and which is oriented proximomedially, occurs is several specimens of Megapnosaurus rhodesiensis and Coelophysis bauri [53]. However, as in Segisaurus halli (UCMP 32101) and ‘Syntarsus’ kayentakatae (MNA V2526), this ridge is absent in Pendraig orynys. Directly distal to the proximal
head, a very large, rugose anterior trochanter that is subtriangular in anterior view projects on the anterolateral side of the femur (Fig. 3). The anterior trochanter is projected proximoanteriorly to proximolaterally from the shaft and gradually merges with the shaft except for its proximomedial margin, which is separated from the shaft by a shallow cleft (Fig. 3D). This cleft occurs widespread among neotheropods (e.g., *Dilophosaurus wetherilli* [61]; *Sarcosaurus woodi* [57]; *Coelophysis bauri* and *Megapnosaurus rhodesiensis* [53]; ‘*Syntarsus*’ *kayentakatae*: MNA V2526; *Liliiensternus liliensterni*: HMN MB.R.2175), whereas it is absent in *Eodromaeus murphi* (PVSJ 562). This concavity opens onto a ridge on the posterolateral side of the anterior trochanter. This ridge, the trochanteric shelf, likely forms an attachment site for the *M. iliofemoralis*, and is well-developed in many early ornithodirans [54, 85, 88]. In *Pendraig orynys*, the trochanteric shelf is well-developed but only shortly projected, terminating on the posterolateral margin of the shaft. The most posterolateral region of the trochanteric shelf is damaged, thus whether it was connected to the *linea intermuscularis caudalis* (see below), as in other relatively skeletally mature early neotheropod specimens (e.g., *Megapnosaurus rhodesiensis* [53]), is unknown. The trochanteric shelf has a marked posterodistal orientation. A straight, mainly lateromedially oriented tuberosity extends along most of the posterior surface of the bone dorsal to the fourth trochanter. It was probably connected to the trochanteric shelf and the *linea intermuscularis caudalis* but the region of contact between the structures is damaged. This tuberosity probably represents the insertion scar of the *M. caudifemoralis brevis* and occurs in other skeletally mature individuals of early dinosauriforms [53].

The fourth trochanter is an elongate flange positioned on the posteromedial surface of the shaft (Fig. 3). It is a thin, 23.1 mm long, crest-like flange with a slightly convex anteromedial face and a concave posterolateral face. Proximally, the flange raises gradually, but on its distal end, which is slightly proximal to the mid-length of the shaft, the flange decreases in height more abruptly (Fig. 3C), but without forming the asymmetric fourth trochanter of most non-neotheropod dinosaurs (e.g., *Herrerasaurus ischigualastensis* [89]; *Eodromaeus murphi*: PVSJ 562; *Eoraptor lunensis* [90]). The fourth trochanter of *Pendraig orynys* is relatively well developed posteriorly, resembling the condition in *Liliiensternus liliensterni* (HMN MB.R.2175), *Procompsognathus triassicus* (SMNS 12591), *Cryolophosaurus ellioti* [67], and *Dilophosaurus wetherilli* [61], but contrasting with the very low trochanter of *Sarcosaurus woodi* [57], *Megapnosaurus rhodesiensis* (NHMUK PV R9584, cast of NHMB QG 1), *Segisaurus halli* (UCMP 32101), and ‘*Syntarsus*’ *kayentakatae* (MCZ 9175, cast of MNA V2623). The fourth trochanter is mainly longitudinally oriented, but it slants slightly from proximomedially to distolaterally in posterior view. On the anteromedial surface of the femur there is a slightly rugose depression at the base of the fourth trochanter that is demarcated medially by a crescent-shaped ridge. This depression likely represents an insertion area for the *M. caudifemoralis*
*longus*. The femoral shaft is long and slender and anteriorly curved along its entire length. The anterolateral and posteromedial surfaces of the shaft are clearly delineated by two ridges or intermuscular lines extending along the length of the shaft. The anteromedial *linea intermuscularis cranialis* probably demarcated the border between the *M. femorotibialis externus* and *M. femorotibialis internus* (Fig. 3C), whereas the posterolateral *linea intermuscularis caudalis* (Fig. 3D) probably separated the *M. femorotibialis externus* and the *M. adductor femoris* 1&2 [85]. The broken distal end of the femur reveals that the cortex of the shaft was thin (Fig. 3F), 0.8 mm thick, whereas the cross section of the femur is 8.5 mm long at its greatest extent. The broken distal end of the shaft reveals that it is oval in cross-section, being slightly transversely broader than anteroposteriorly deep, and filled by a crystalline matrix.

**Methods.**

Phylogenetic analysis.

*Pendraig orynys* was incorporated into the data matrix of Novas et al. [91], which represents the most recent iteration of the matrix originally published by Nesbitt et al. [88], which has also been modified in various other studies [57, 63, 83, 92-99]. Following Ezcurra et al. [57], ‘Velociraptor mongoliensis’, ‘Powellvenator podocitus holotype’, and ‘Lepidus praecisio combined’ were deactivated, whereas ‘*Powellvenator podocitus*’ and ‘*Lepidus praecisio holotype*’ remained active. Additionally, of the newly added terminals by Ezcurra et al. [57] ‘*Sarcosaurus combined*’, ‘*Tachiraptor admirabilis*’, and ‘*Eoabelisaurus mefi*’ remained active. Recent new information about non-dinosaurian avemetatarsalians is not included in this matrix [100] and the members of this part of the tree should be considered as outgroups without a proper test of their interrelationships here.

The data matrix was analysed under the equally weighted parsimony criterion using TNT 1.5 [101], with *Erythrosuchus africanus* selected as the outgroup. As in Novas et al. [91] the following characters were treated as additive: 9, 18, 30, 67, 128-129, 174, 184, 197, 207, 213, 219, 231, 236, 248, 253-254, 273, 329, 343, 345, 347, 349, 354, 366, 371, 374, 377–379, 383-384. Using the Traditional Search algorithm, a heuristic search of 1,000 replications of Wagner trees with random addition sequence was performed, followed by TBR branch swapping holding ten trees per replicate. Homoplasy indices were calculated with a script that does not take into account *a priori* deactivated terminals (see Supplementary Data – StatsB.run). Bremer and Bootstrap support values were calculated, the latter using a ‘Traditional search’ at 1,000 iterations.

Femoral length estimation and ancestral state reconstruction
To test whether *Pendraig orynys* might represent an insular dwarf as has been suggested for other reptiles of the fissure fills faunas [19-21], ancestral state reconstruction of the femoral length was performed on a sample of early theropods and closely related taxa to compare the relative size of *Pendraig orynys* in a quantitative phylogenetic framework. Even though femoral circumference is generally considered to represent the best proxy for body size [102], femur length was used since this measurement is available in a wide range of early theropod specimens and because it is expected to represent a reliable proxy for our relatively narrow phylogenetic sample (*sensu* [99]).

The only known femur of *Pendraig orynys* (NHMUK PV R 37591) is largely complete but the distal end is missing. We compiled a dataset of femoral measurements from several early theropods, composed of femoral length, maximal longitudinal width of the proximal head, maximal depth of the proximal head, and minimal femoral circumference (Supplementary Table 1). We subsequently performed regression analyses in the software environment R version 4.0.4 [103] with all values having been log-transformed. We used the predict function to estimate the femoral length and calculate confidence intervals for NHMUK PV R 37591.

Ancestral state reconstruction was performed on a dataset of femoral lengths of early theropods and closely related taxa, including the estimated femoral length of *Pendraig orynys*. The inclusion of taxa represented by immature specimens likely has a considerable effect on the outcome of body size analyses for early theropods, resulting in the underestimation of ancestral femoral lengths [99]. Therefore, in addition to the analysis including all taxa, we performed an alternative analysis in which we excluded theropod taxa that 1) were less mature than *Pendraig orynys* (a maximum maturity score lower than 19 based on the maturity assessment matrix of Griffin [53]) and 2) had a femoral length of less than 21 cm (for maturity scores of relevant taxa, see Supplementary Figure 11). Theropod taxa with a femoral length of over 21 cm were included, even when they are represented by immature specimens, because their inclusion was considered not to contribute to an underestimation of ancestral femoral lengths due to their large size and because early large-bodied theropods are exclusively known from immature specimens [56, 99]. Following these criteria, the taxa excluded for the alternative analysis are: *Panguraptor lufengensis*, *Lepidus praecisio*, *Dracoraptor hanigani*, and *Powellvenator podocitus*.

A total of six most parsimonious trees (MPTs) were found for the phylogenetic analysis (see below). Since the focus of our analysis is on Coelophysoidea, we performed the ancestral state reconstruction analyses on the four equally parsimonious resolutions of the position of *Pendraig orynys*, whereas we used the topology of the strict consensus for the rest of the tree. To time-calibrate the trees, the first and last occurrences (which for most theropods and early dinosaurs
of all taxa were obtained from the literature, using the International Chronographic Chart [104] to determine the delimitations of the various geological stages (e.g., *Pendraig orynys*, earliest occurrence late Norian, latest occurrence possibly late Rhaetian; 214.7 to 201.3 million years ago). Branch lengths were calculated using the `timepaleophy()` function from the paleotree package [105] under three different settings for minimum branch lengths (mbl), 1.0, 0.5, and 0.1 million years, to test for the influence of different parameter settings on our results. The analyses were performed using the function `anc.ml()` from the phytools package [106] to calculate ancestral states under a Brownian model of evolution using maximum likelihood.

**Results.**

**Phylogenetic analysis.**

The phylogenetic analysis found six MPTs of 1360 steps with a consistency index (CI) of 0.346 and a retention index (RI) of 0.676. *Pendraig orynys* is found within Coelophysoidea but outside Coelophysidae (i.e., *Coelophysis*, *Procompsognathus*, their most recent common ancestor and all descendants) [51] in all MPTs. Within the strict consensus tree (SCT) generated from the MPTs it forms a polytomy together with *Powellvenator podocitus*, *Lucianovenator bonoi*, and a clade composed of ‘Syntarsus’ *kayentakatae* and Coelophysidae (Fig. 6). Among these MPTs, *Lucianovenator bonoi* and *Powellvenator podocitus* alternate as the sister taxon to the ‘Syntarsus’ *kayentakatae* + Coelophysidae clade. Three additional steps are required to force *Pendraig orynys* outside Coelophysoidea, one step for *Pendraig orynys* to be the sister taxon of the ‘Syntarsus’ *kayentakatae* + Coelophysidae clade, and five steps for it to be the sister taxon to or for it to be part of Coelophysidae. The following synapomorphies support the placement of *Pendraig orynys* within Coelophysoidea: presence of a flat dorsal margin of the ilium dorsal to the supra-acetabular rim (200 → 1) and the presence of a rounded ridge or dorsolateral trochanter on the dorsolateral margin of the proximal portion of the femur (230 → 2). The presence of elongate posterior dorsal vertebrae with a centrum length that is at least twice the height of their anterior articular surface (329 → 2) is present in *Pendraig orynys* and represents a common synapomorphy for the clade composed of all coelophysoids except *Panguraptor lufengensis*.

**Femoral length estimation.**

We found that femoral length is significantly correlated with all other variables that we considered (maximal longitudinal width of the proximal head: \( p < 2.2 \times 10^{-16} \), maximal depth of the proximal head: \( p = 3.67 \times 10^{-6} \), and minimal femoral circumference: \( p = 7.173 \times 10^{-6} \)).
longitudinal width of the proximal head has the most significant correlation with femoral length and is the most widely available measurement in the studied sample, we used this variable to estimate the femoral length of NHMUK PV R 37591 (Fig. 7). Based on this, the reconstructed femoral length of NHMUK PV R 37591 is 10.21 cm (lower 95% CI: 8.60 cm; upper 95% CI: 12.11 cm). The results of the ancestral state reconstruction analysis are discussed below.

Discussion.

Phylogenetic implications.

The scoring of the ontogenetic characters formulated by Griffin [53] suggests that the holotype NHMUK PV R 37591 of *Pendraig orynys* is immature with regards to certain skeletal features (Supplementary Figure 11A). It is therefore important to consider that skeletally immature specimens are often recovered in a different (often less derived) phylogenetic position than mature specimens of the same species (e.g., [99, 107, 108]). The phylogenetic analysis recovered *Pendraig orynys* as a non-coelophysid coelophysoid (Fig. 6), but with low support values for Coelophysoidea and its internal nodes. Nevertheless, the referral of *Pendraig orynys* to Coelophysoidea is supported by the presence of several typically coelophysoid character states, such as the flat dorsal margin of the ilium, the considerable anteroposterior elongation of the posterior dorsal vertebrae, and the distinct posterior rim on the ventral part of the postacetabular process of the ilium exposed in lateral view. Alongside *Procompsognathus triassicus* and possibly *Liliensternus liliensterni, Pendrag orynys* represents a third Triassic coelophysoid taxon from Europe and the first unambiguous Triassic theropod from the United Kingdom.

The results of our analysis are incongruent with several previous phylogenetic studies of early neotheropods in the placement of *Dracoraptor hanigani* and *Lepidus praecisio* outside Coelophysoidea and the derived position of ‘*Syntarsus*’ kayentakatae’ within this clade. Previously, *Dracoraptor hanigani* from the Early Jurassic of Wales was recovered as a coelophysoid [57, 83], but it was found outside Coelophysoidea by Baron et al. [33] in a large polytomy among early Neotheropoda, and as the sister taxon to ‘*Syntarsus*’ kayentakatae’ in Langer et al. [38] and Baron et al. [39] in analyses that did not recover a monophyletic Coelophysoidea as it is historically considered. Here, *Dracoraptor hanigani* is found as a non-coelophysid neotheropod in a polytomy with *Liliensternus liliensterni* and a clade composed of all remaining averostran-line neotheropods (Fig. 6). The position of *Liliensternus liliensterni* as an early diverging non-coelophysid neotheropod in our analysis corresponds with several studies [83, 94, 95, 97], although other analyses recovered this species as one of the earliest diverging non-coelophysid coelophysoids [57, 63, 99]. *Lepidus praecisio* was previously considered a coelophysid coelophysoid [57, 94, 98, 99, 109], but was found
outside Coelophysoidea by Marsh et al. [95], in which it was found as the sister taxon to all other non-coelophysoid neotheropods, and by Marsh and Rowe [61], in which it was found as the sister taxon to Liliensternus liliensterni in a clade that is part of a polytomy at the base of Neotheropoda. Here, the holotype of Lepidus praecisio was recovered outside Neotheropoda as the direct sister taxon to this clade (Fig. 6). We included only the holotype of Lepidus praecisio in our analysis because of the uncertain taxonomic affinity of the referred material for this species [98]. ‘Syntarsus’ kayentakatae is unambiguously considered as a coelophysoid theropod and represents one of best known taxa of the clade [75]. However, the position of ‘Syntarsus’ kayentakatae within Coelophysoidea is somewhat uncertain and in recent other studies employing the Nesbitt et al. [88] matrix this taxon was recovered as quite distantly related to Coelophysidae (i.e., being more distantly related to Coelophysis bauri and Procompsognathus triassicus than are Panguraptor lufengensis, Lucianovenator bonoi, and Powellvenator podocitus) [57, 63, 84, 94, 97, 99]. In contrast, in our analysis ‘Syntarsus’ kayentakatae is recovered as the sister taxon to Coelophysidae (Fig. 6). The lack of consensus in early neotheropod phylogeny, including Coelophysoidea, has been acknowledged and discussed in recent studies (e.g., [57, 99]) and can likely be attributed to large amounts of missing data for many early neotheropod taxa and the inclusion of taxa represented by immature ontogenetic stages [53, 99]. The holotype of Lepidus praecisio includes a particularly large amount of missing data (90.72%) and Lepidus praecisio, Liliensternus liliensterni, and Dracoraptor hanigani are represented by immature specimens (Supplementary Figure 11; Supplementary Table 2) [56]. The presence of taxa based on skeletally immature specimens or with unclear ontogenetic stage increases the proportion of missing data because ontogenetically variable characters should be scored as ambiguous. The more derived position of ‘Syntarsus’ kayentakatae recovered in our analysis is, in part, a result of the scorings revised in our modified data matrix and the inclusion of the new species Pendraig orynys. Indeed, if the latter species is excluded a priori from the analysis, ‘Syntarsus’ kayentakatae is recovered in multiple positions among non-coelophysid coelophysoids in the resultant MPTs. This result reflects the importance of adding new taxa with a novel combination of character states and the continuous revision of the data matrices in phylogenetic studies.

Body size evolution of Pendraig orynys and other early theropods.

Research on early theropod body size evolution has recently been reviewed by Griffin [99] and Griffin and Nesbitt [56]. Recent analyses using ancestral state reconstruction found the femoral length of the last common ancestor of Neotheropoda to be approximately 29 to 35 cm [99, 110, 111]. Lee et al. [112] found a considerably higher ancestral femoral length of 47.5 cm for Neotheropoda, but the dataset used in that analysis contained a comparatively smaller sample of early theropods. Our analyses reveal that different values used for the minimum branch length
parameter (mbl, set at 0.1, 0.5, and 1.0 million years) have quite large implications for the reconstructed ancestral values. The analysis on the first of the four equally parsimonious trees with mbl set at 1.0 million years and including all sampled taxa (Fig. 8) recovered an ancestral femoral length of 24.2 cm for Neotheropoda (upper CI: 33.7 cm; lower CI: 17.3 cm) and 17.6 cm for Coelophysoidea (upper CI: 27.6 cm; lower CI: 11.2 cm) (Supplementary Table 3.1), whereas when an mbl of 0.1 million years is considered, the ancestral value for Neotheropoda is 39.6 cm (upper CI: 58.0 cm; lower CI: 27.1 cm) and that for Coelophysoidea is 14.9 cm (upper CI: 25.1 cm; lower CI: 8.8 cm) (Supplementary Table 3.3). For an mbl of 0.5 million years, the ancestral value for Neotheropoda is 29.7 cm (upper CI: 43.0 cm; lower CI: 20.5 cm) and for Coelophysoidea 16.4 cm (upper CI: 27.0 cm; lower CI: 9.9 cm) (Supplementary Table 3.4). When the femoral lengths of small-bodied neotheropod taxa represented by immature specimens are pruned (i.e., taxa with a maximum maturity score of 17 or less: Panguraptor lufengensis, Lepidus praecisio, Dracoraptor hanigani, and Powellvenator podocitus), the ancestral femoral length is 25.7 cm (upper CI: 36.2 cm; lower CI: 18.3 cm) for Neotheropoda and 21.1 cm (upper CI: 34.5 cm; lower CI: 12.9 cm) for Coelophysoidea when considering the first of the four equally parsimonious trees and with mbl set at 1.0 million years (Supplementary Table 3.2). The four equally parsimonious resolutions of the early coelophysoid relationships result in similar reconstructed femoral lengths for Neotheropoda and Coelophysoidea, with the ancestral estimates for the latter being between 17 and 18 cm when mbl is set at 1.0 million years and the femoral lengths of all sampled taxa are included (Supplementary Tables 3.1, 3.3, 3.4). Overall, the large discrepancy in reconstructed ancestral femoral lengths for Neotheropoda and Coelophysoidea between the different analyses, particularly between the analyses with different minimum branch lengths, and the wide confidence interval ranges for all values indicate that there is much uncertainty in approximating ancestral body sizes in early neotheropods, but our recovered values are broadly similar to the results of Irmis [110], Benson et al. [111], and Griffin [99].

Our results indicate that averostran-line neotheropods underwent a size increase already during the Triassic (Fig. 8; Supplementary Information). In contrast, the body size of coelophysoids is considerably smaller. This corresponds with the results of Griffin [99]. Size decreases occurred early in Coelophysoidea and ancestral values gradually increase in consecutive nodes from the clade encompassing Lucianovenator bonoi, ‘Syntarsus’ kayentakatae, and Coelophysidae onwards regardless of minimum branch length in the analyses encompassing all data (Supplementary Tables 3.1, 3.3, 3.4). In contrast, Griffin [99] found an initial increase in body size in the evolution of Coelophysoidea, which is attributable to the placement of Liliensternus liliensterni (and in one of the two analyses Gojirasaurus quayi) at the base of the clade in his phylogenetic analyses and the
absence of several coelophysoid taxa in that dataset (*Powellvenator podocitus*, *Procompsognathus triassicus*, *Segisaurus halli*, *Lucianovenator bonoi*, *Camposaurus arizonensis*, and the new taxon *Pendraig orynys*). In the two equally parsimonious topologies in which *Lucianovenator bonoi* is more distantly related to Coelophysidae, ancestral femoral length increases from the clade comprising ‘Syntarsus’ *kayentakatae*, and Coelophysidae onwards (Supplementary Tables 3.6, 3.7). In the analyses excluding *Panguraptor lufengensis*, *Lepidus praecisio*, *Dracoraptor hanigani*, and *Powellvenator podocitus*, the ancestral body size of Coelophysoidea is also reduced relative to the ancestral neotheropod condition and decreases somewhat further early in coelophysoid evolution and subsequently remains similar for subsequent nodes, only to increase again at the most apical node (Supplementary Table 3.2).

The ontogenetic assessment of the holotype of *Pendraig orynys* indicates that this specimen was not skeletally mature (i.e., likely had not reached asymptotic growth [56]) but that it is likely also not at an early ontogenetic stage (Supplementary Figure 11A). It therefore seems unlikely that *Pendraig orynys* would have increased much more in size and this species would thus have been considerably smaller than better known coelophysoids like *Coelophysis bauri*, *Megapnosaurus rhodesiensis*, and ‘Syntarsus’ *kayentakatae*. The ancestral femoral length for the closest node for *Pendraig orynys* is between 144% (Supplementary Table 3.3) and 195% (Supplementary Table 3.2) larger than for *Pendraig orynys*, thus indicating that the small size of *Pendraig orynys* is autapomorphic. However, *Procompsognathus triassicus*, *Segisaurus halli*, and, in the analyses in which this taxon is considered, *Powellvenator podocitus*, all independently underwent a similar size reduction based on our analyses (Fig. 8; Supplementary Information). Because its small size is not unique among Coelophysoidea and other coelophysoid taxa that underwent a similar size reduction were not restricted to insular environments, our dataset is ambiguous regarding insular dwarfism as a possible explanation of the reduced body size in *Pendraig orynys*. However, insular dwarfism in *Pendraig orynys* cannot be excluded, and further studies into the palaeohistology and body size evolution of other taxa from Pant-y-ffynnon and related fissure fill deposits are required to investigate the possibility that these faunas were subject to dwarfism or other aspects of the ‘Island Rule’.

Palaeoecology of *Pendraig orynys* and Pant-y-ffynnon.

The known dentitions of coelophysoid theropods are characterized by blade-like serrated maxillary and non-mesial dentary teeth, indicating a mostly macrophagous carnivorous diet for these taxa [60, 69, 75]. It therefore seems highly likely that *Pendraig orynys* had a similar dentition and diet even though no craniodental remains from Pant-y-ffynnon can unequivocally be attributed to this species. *Pendraig orynys* represents a second macrophagous predator known from Pant-y-ffynnon (Fig. 9),
the other being the non-crocodyliform crocodylomorph *Terrestrisuchus gracilis* [18]. Like *Pendraig orynys*, *Terrestrisuchus gracilis* was small-bodied (approximately 76 cm in total body length [18]) and had a gracile body plan. Other likely predators known from the Late Triassic and Early Jurassic fissure fill deposits of southwestern England and southern Wales were either similarly small-bodied: *Terrestrisuchus*-like unidentified crocodylomorphs from Cromhall and Ruthin Quarries [19, 32] and ‘*Agnosphytis cromhallensis*’ from Cromhall Quarry [32]; or most likely semi-aquatic (*'Paleosaurus platyodon’*) [27]. Remains of the considerably larger-sized herbivorous sauropodomorph *Thecodontosaurus antiquus* have been preserved at the Durdham Down and Tythepton deposits [20, 27], but only remains of the smaller sauropodomorph *Pantydraco caducus*, which might represent an immature form of *Thecodontosaurus antiquus* [20], are known from Pant-y-ffynnon [28, 29]. Therefore, it is currently unclear whether predators at Pant-y-ffynnon simply did not exceed the size of *Pendraig orynys* and *Terrestrisuchus gracilis*, which could be attributable to a lack of resources to sustain larger predators as is typical in certain island environments [22], or whether larger-bodied predators in this ecosystem have not yet been discovered or preserved, possibly because taphonomic factors are biased against preservation of large-bodied animals at Pant-y-ffynnon and other fissure fill deposits.

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Figure captions.

Figure 1. Holotype NHMUK PV R 37591 pelvis and vertebrae of *Pendraig orynys* gen. et sp. nov. in (A) left lateral view, (B) right lateral view. Abbreviations: atr, antitrochanter; bf, brevis fossa; bfr, brevis fossa rim; bs, brevis shelf; dv, dorsal vertebra; iss, ischial shaft; nc, neural canal; no, notch; obf, obturator foramen; poap, postacetabular process; prap, preacetabular process; puf, pubic fenestra; pus, pubic shaft; ras, rib attachment scar; ri, rim; sac, supra-acetabular crest; sv, sacral vertebra.

Figure 2. Holotype NHMUK PV R 37591 pelvis and vertebrae of *Pendraig orynys* gen. et sp. nov. in (A) dorsal view, (B) ventral view, (C) anterior view, and (D) posterior view. Abbreviations: bf, brevis fossa; bfr, brevis fossa rim; diap, diapophysis; dv, dorsal vertebra; gr, groove; il, ilium; ipis, iliac peduncle of ischium; iss, ischiadic shaft; obf, obturator foramen; poap, postacetabular process; ppdl, paradiapophyseal lamina; prap, preacetabular process; puf, pubic fenestra; pus, pubic shaft; sac, supra-acetabular crest; sv, sacral vertebra; tp, transverse process; vl, ventral lamina.

Figure 3. Holotype NHMUK PV R 37591 left femur of *Pendraig orynys* gen. et sp. nov. in (A) posteromedial, (B) anterolateral, (C) anteromedial, (D) posterolateral, (E) proximal, and (F) distal view. Abbreviations: amt, anteromedial tuber; at, anterior trochanter; icfl, depression associated with the insertion of the *M. caudofemoralis longus*; gt, greater trochanter; lica, linea intermuscularis caudalis; lincr, linea intermuscularis cranialis; obr, obturator ridge; pmt, posteromedial tuber; ts, trochanteric shelf; 4th t, fourth trochanter.

Figure 4. Isolated mid to posterior dorsal vertebra NHMUK PV 37596 of *Pendraig orynys* gen. et sp. nov. in (A) right lateral view, (B) left lateral view, (C) ventral view, (D) dorsal view, (E) anterior view, and (F) posterior view. Abbreviations: aas, anterior articular surface; acpl, anterior centroparapophyseal lamina; ce, centrum; diap, diapophysis; nf, nutrient foramen; ns, neural spine; pacdf, parapophyseal centrodiapophyseal fossa; pacprf, parapophyseal centroprezygapophyseal fossa; pap, parapophysis; pas, posterior articular surface; pcdl, posterior centrodiaophyseal; pocdf, postzygapophyseal centrodiaophyseal fossa; podl, postzygodiapophyseal lamina; poz, postzygapophysis; ppdl, paradiapophyseal lamina; prpl, prezygaparaphyseal lamina; prz, prezygapophysis; spozf, spinopostzygapophyseal fossa; sprzf, spinoprezygapophyseal fossa.

Figure 5. Isolated partial left ischium NHMUK PV R 37597 of *Pendraig orynys* gen. et sp. nov. in (A) medial and (B) dorsal view. Abbreviations: asil, articulation surface with ilium; atr, antitrochanter; ipis, iliac peduncle of ischium.
Figure 6. Strict consensus of six most parsimonious trees of the phylogenetic analysis. Bremer support, absolute bootstrap frequency, and GC bootstrap frequency values are indicated at each branch in that order.

Figure 7. Log$_{10}$-transformed bivariate plot of the longitudinal width of proximal head of the femur versus the femoral length of early theropods. The solid black line represents the linear regression described by the formula, and the red dotted lines represent the 95% confidence intervals.

Figure 8. Results of the ancestral state reconstruction of the log$_{10}$-transformed femoral lengths. For the analysis figured here all sampled taxa were included and minimum branch length was set at 1.0 million years. The polytomy within Coelophysoidea in the strict consensus tree was manually resolved with one of the four equally parsimonious resolutions. The other analyses can be found in the Supplementary Information. The femoral lengths used for the analysis can be found in Supplementary Table 2. Reconstructed values for major nodes can be found in Table 3, and for all nodes in Supplementary Table 3.1. Node numbers used for Supplementary Table 3.1 are indicated for each node in Supplementary Figure 1.

Figure 9. Life reconstruction of *Pendraig orynys* gen. et sp. nov. amongst the fissures of Pant-yffynnon and three individuals of the rhynchocephalian lepidosaur *Clevosaurus cambrica* during the Late Triassic. Artwork by James Robbins.

Table 1. Vertebral measurements of NHMUK PV R 37591 and NHMUK PV 37596. Measurements were taken with a Sealey electronic vernier calliper. Values preceded by a tilde (¶) indicate an approximated value because a measurement was hampered, either by poor preservation, or by the relevant structure being partially covered. Abbreviations: dv, dorsal vertebra; sv, sacral vertebra.

|                  | dv1 | dv2 | sv1 | sv2 | sv3 | sv4 | NHMUK PV 37596 |
|------------------|-----|-----|-----|-----|-----|-----|----------------|
| Centrum length   |     | 14.7 mm |     | 13.3 mm | 11.1 mm |     | 14.6 mm |
| Neural spine height |     |     |     |     |     |     | 5.0 mm |
| Neural spine length |     |     |     |     |     |     | 14.3 mm |
| Width of diapophysis/transverse processes (+ rib) |     | 9.9 mm |    ¶5.39 mm | 6.2 mm | 6.5 mm |     | 7.4 mm |
| Anterior articular surface centrum height |     | 6.4 mm |     | 5.2 mm | 4.7 mm |     | 5.7 mm |
Table 2. Measurements of the appendicular skeleton of NHMUK PV R 37591. Measurements were taken with a Sealey electronic vernier calliper. The circumference of the femoral shaft was measured by running a piece of string around the shaft and subsequently measuring the length of the amount of string with the calliper. Values in parentheses represent incomplete values, due to the relevant structure being incompletely preserved. Abbreviations: max, maximum.

| Measurement                                              | Value   |
|----------------------------------------------------------|---------|
| max. length left ilium across iliac blade                | 55.8 mm |
| max. length left ilium across peduncles                  | 26.0 mm |
| max. length left acetabulum                              | 16.7 mm |
| max. dorsoventral height left acetabulum                 | 17.6 mm |
| max. length right pubis (excluding imprint)              | (63.2 mm) |
| max. length right pubis (including imprint)              | (74.8 mm) |
| max. length left ischium                                 | (26.6 mm) |
| max. length left femur                                   | (86.3 mm) |
| max. width proximal head left femur                      | 15.1 mm |
| min. circumference shaft of left femur                   | 25.08 mm |

Table 3. Ancestral state values (in cm) for major nodes for the analysis shown in Figure 8.

| Ancestral estimate | Variance | Lower 95% Confidence Interval | Upper 95% Confidence Interval |
|--------------------|----------|-------------------------------|-------------------------------|
| Dinosauria         | 15.038   | 1.013                         | 10.787                        | 20.964                        |
| Theropoda          | 17.679   | 1.008                         | 13.542                        | 23.080                        |
| Neotheropoda       | 24.168   | 1.013                         | 17.331                        | 33.703                        |
| Non-coelophysoid neotheropods | 30.899   | 1.011                         | 22.653                        | 42.146                        |
| Averostra          | 60.474   | 1.011                         | 44.309                        | 82.536                        |
| Coelophysoidea     | 17.585   | 1.023                         | 11.191                        | 27.631                        |
Coelaphysoidea excluding Panguraptor

|                |     |     |     |     |
|----------------|-----|-----|-----|-----|
| Coelophysidae  | 17.118 | 1.015 | 11.891 | 24.643 |

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Figure 1. Holotype NHMUK PV R 37591 pelvis and vertebrae of Pendraig orynys gen. et sp. nov. in (A) left lateral view, (B) right lateral view. Abbreviations: atr, antitrochanter; bf, brevis fossa; bfr, brevis fossa rim; bs, brevis shelf; dv, dorsal vertebra; iss, ischial shaft; nc, neural canal; no, notch; obf, obturator foramen; poap, postacetabular process; prap, preacetabular process; puf, pubic fenestra; pus, pubic shaft; ras, rib attachment scar; ri, rim; sac, supra-acetabular crest; sv, sacral vertebra.
Figure 2. Holotype NHMUK PV R 37591 pelvis and vertebrae of Pendraig orynys gen. et sp. nov. in (A) dorsal view, (B) ventral view, (C) anterior view, and (D) posterior view. Abbreviations: bf, brevis fossa; bfr, brevis fossa rim; diap, diapophysis; dv, dorsal vertebra; gr, groove; il, ilium; ipis, iliac peduncle of ischium; iss, ischiadic shaft; obf, obturator foramen; poap, postacetabular process; ppdl, paradiapophyseal lamina; prap, preacetabular process; puf, pubic fenestra; pus, pubic shaft; sac, supra-acetabular crest; sv, sacral vertebra; tp, transverse process; vl, ventral lamina.
Figure 3. Holotype NHMUK PV R 37591 left femur of Pendraig orynys gen. et sp. nov. in (A) posteromedial, (B) anterolateral, (C) anteromedial, (D) posterolateral, (E) proximal, and (F) distal view. Abbreviations: amt, anteromedial tuber; at, anterior trochanter; icfl, depression associated with the insertion of the M. caudofemoralis longus; gt, greater trochanter; lica, linea intermuscularis caudalis; lincr, linea intermuscularis cranialis; obr, obturator ridge; pmt, posteromedial tuber; ts, trochanteric shelf; 4th t, fourth trochanter.
Figure 4. Isolated mid to posterior dorsal vertebra NHMUK PV 37596 of Pendraig orynys gen. et sp. nov. in (A) right lateral view, (B) left lateral view, (C) ventral view, (D) dorsal view, (E) anterior view, and (F) posterior view. Abbreviations: aas, anterior articular surface; acpl, anterior centroparapophyseal lamina; ce, centrum; diap, diapophysis; nf, nutrient foramen; ns, neural spine; pacdf, parapophyseal centrodiaophyseal fossa; pacprf, parapophyseal centroprezygapophyseal fossa; pap, parapophysis; pas, posterior articular surface; pcdl, posterior centrodiaphyseal lamina; podl, paradiaphyseal lamina; poz, postzygapophysis; prpl, prezygaparaphyseal lamina; prz, prezygapophysis; spozf, spinopostzygapophyseal fossa; sprzf, spinoprezygapophyseal fossa.
Figure 5. Isolated partial left ischium NHMUK PV R 37597 of Pendraig orynys gen. et sp. nov. in (A) medial and (B) dorsal view. Abbreviations: asil, articulation surface with ilium; atr, antitrochanter; ipis, iliac peduncle of ischium.
 Taxon

- Coelophysidae indet.
- Coelophysis bauri
- Dilophosaurus wetherilli
- Eodromaeus murphi
- Liliensternus liliensterni
- Megapnosaurus rhodesiensis
- 'Syntarsus' kayentakatae
- Pendraig orynys (estimated)

\[
y = 0.845x + 1.013 \\
\text{ } \quad r^2 = 0.968, p < 2.2 \times 10^{-16}
\]
Figure 9. Life reconstruction of Pendraig orynys gen. et sp. nov. amongst the fissures of Pant-y-ffynnon and three individuals of the rhynchocephalian lepidosaur Clevosaurus cambrica during the Late Triassic. Artwork by James Robbins.

322x239mm (300 x 300 DPI)
Appendix D

Dear Drs. Botha and Padian,

Please find our response to your recommendations and those of the reviewers below indicated in bold and in the annotated PDFs, which we have uploaded separately.

Kind regards, also on behalf of my co-authors,

Dr. Stephan Spiekman

Dear Dr Spiekman

The Editors assigned to your paper RSOS-210915 "Pendraig orynys, a new small-sized coelophysoid theropod from the Late Triassic of Wales" 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 manuscript will be sent back to one or more of the original reviewers for assessment. If the original reviewers are not available, we may invite new reviewers.

Please submit your revised manuscript and required files (see below) no later than 21 days from today's (ie 16-Jul-2021) date. Note: the ScholarOne system will 'lock' if submission of the revision is attempted 21 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.

Please note article processing charges apply to papers accepted for publication in Royal Society Open Science (https://royalsocietypublishing.org/rsos/charges). Charges will also apply to papers transferred to the journal from other Royal Society Publishing journals, as well as papers submitted as part of our collaboration with the Royal Society of Chemistry (https://royalsocietypublishing.org/rsos/chemistry). Fee waivers are available but must be requested when you submit your revision (https://royalsocietypublishing.org/rsos/waivers).

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.

Kind regards,
Royal Society Open Science Editorial Office
Royal Society Open Science
openscience@royalsociety.org

on behalf of Dr Jennifer Botha (Associate Editor) and Kevin Padian (Subject Editor)
Associate Editor Comments to Author (Dr Jennifer Botha):
Associate Editor: 1
Comments to the Author:
This is a good paper, well worth publishing. However, there are some corrections necessary before the paper can be accepted for publication. Two important points worth noting specifically (1) one of the reviewers tested the code and was unable to replicate the results - the code needs to be checked for errors and (2) the interpretation that this individual is a small taxon as opposed to being a juvenile requires further evidence, and reviewer one makes a good case for thin sectioning part of the femur to check for the presence of an EFS. Otherwise there is simply not enough evidence for small size. I encourage the authors to look seriously into this suggestion.

We have responded to these issues below where they were raised by the reviewers.

Reviewer comments to Author:
Reviewer: 1
Comments to the Author(s)
This manuscript presents a thorough comparative description of a new theropod dinosaur and places it into a phylogenetic hypothesis using a relevant and recent character matrix. The small size of the holotype individual is striking, so the authors also conduct an ancestral state reconstruction for body size among early theropod dinosaurs and also attempt to take the individual's ontogenetic status into account to be sure that the small size does not simply stem from the individual's immaturity.

The manuscript is well-written and thorough, the comparative descriptions sound, the figures are clear and informative, and the analyses all appear to be properly conducted (but see below for problems with the R code). In my opinion the manuscript is largely sound and can be accepted for publication with moderate revision. I have attached a PDF with my minor edits and comments.

Major Comments

1) Why are the eleven supplementary figures provided as separate files, with yet another Word file for the captions? It would be much easier to include all figures with associated captions as one PDF file. Also, in Table S2 in the “Juvenile” column, there are several different terms used for maturity assessment, including juvenile, non-juvenile, subadult, immature, etc. Sometimes these seem to be synonymous, but their usage at other times appears to be mutually exclusive. For example, some taxa are listed as “SUBADULT/IMMATURE” and others are just listed as “IMMATURE”. Could you provide more explanation for these maturity categories?

We now provide a single PDF file that includes all Supplementary Figures and their corresponding captions. The dataset provided in Table S2 is part of a large dataset compiled for a separate study.
For the purposes of this study, we have now modified all identifiers of a non-mature state to “immature”.

2) When running the R code, I experienced an error code that prevented me from continuing to evaluate the rest of the code. The error occurred on line 42, on the anc.ML() command, and read: “Error in optim(c(sig2, a, y, rep(mean(x), length(xx))), fn = likelihood, : non-finite value supplied by optim”.

All the underlying data looked sound to me; I saw no obvious issues with the way the data was input, the tree file, etc. It may be the issue is with my version of R or R Studio, because I just updated both two days ago, but this affects repeatability and is something the authors should be aware of.

We ran the code on three different machines and in all cases we did not encountered any error. As the reviewer stated, the errors he experienced are most likely attributable to having an older version of R and R Studio installed. Under the latest versions of R (4.1.0) and R Studio (1.4.1717) the code should work fine.

3) I appreciate that the authors take the body size of the type individual into account when evaluating possible small body size. This is done in a clear way using character state transformations that have been useful in other early theropods, particularly Coelophysis. I agree with the authors’ assessment that this individual does not display the features we might expect of either a very skeletally mature or immature individual, and the character states instead suggest that this individual is in a middling ‘gray zone’ of ontogeny. Indeed, there is no reasonably complete specimen of Coelophysis that has been scored with a consistent combination of character states (data from Griffin & Nesbitt 2016, Griffin 2018), making direct comparison with Coelophysis character states and femoral lengths difficult. This, combined with the fact that their scoring of Panguraptor ontogenetic character state combinations that contradict any reconstructed ontogenetic sequence of Coelophysis (very interesting finding, by the way), strongly suggests that there is even more variation in ontogenetic trajectories among Coelophysoids than has presently been reconstructed. Because of the large amount of ontogenetic variation known from other coelophysoids, combined with the fact that most of the size variation in Coelophysis is known precisely from this ontogenetic gray zone, I disagree with the authors’ statement that this individual was likely near maximum body size and would not have gotten much larger. Instead, I think that there is not enough evidence to say one way or another.

Although there is no direct comparison between the character states of Pendraig and Coelophysis or Megapnosaurus, some examples from individuals roughly the size of Pendraig that also display similarly mature character states may be informative:

-- The smallest known individual of Megapnosaurus (NHMZ QG 45) possesses fused sacral neural spines (character 1-1; and therefore probably at least some fused sacral centra, although these are not able to be scored) and a small trochanteric shelf (14-1; 15-0), despite its extremely small size (femoral head 1.5 cm; reconstructed femoral length ~11.2 cm).

-- Coelophysis bauri (TMP 1984.063.0001 #13; reconst. femur length ~10.9 cm) has fused its pubis to the ilium (8-1) and ischium (10-1), but the ilium and ischium remain unfused (9-1).

-- Coelophysis bauri (SMP 858; femoral head 1.29 cm, reconst. femur length ~10.2 cm) possesses five fused sacrals (2-2), a fused pubis (8-1), a trochanteric shelf (14-1), a mound-like dorsolateral trochanter (16-1), a cranial intermuscular line (17-1), a caudal intermuscular
line (18-1), and an ‘anterolateral scar’ (19-1).
-- Coelophysis bauri (CMNH 10971 #3; femur length 10.94 cm) possesses five fused sacrals (2-2), a fused pubis (8-1), a trochanteric shelf (14-1), a mound-like dorsolateral trochanter (16-1), a cranial intermuscular line (17-1), a caudal intermuscular line (18-1), and an ‘anterolateral scar’ (19-1).

There are of course smaller individuals of Coelophysis that display more immature character states as well. But my point here is that finding an individual of Coelophysis that displays a similar body size and similar ontogenetic character states is not unprecedented. Because we know that Coelophysis can reach much larger sizes (~25 cm femoral length), then with a sample size of 1, this is not great evidence that Pendraig’s maximum size is close to what this individual’s is; this taxon could just happen to be represented by one of those more mature-looking but anomalously small individuals also found in other coelophysoids. Therefore, although the data are consistent with Pendraig having a small maximum body size, I do not think the data support saying that it did definitively have a small maximum body size.

We appreciate the reviewer’s comments on this subject as we based our assessment of the ontogenetic stage of Pendraig on the maturity matrix he developed. We have modified this part of the discussion according to these comments. We now no longer claim that the analysis based on the maturity matrix shows that Pendraig was smaller than Coelophysis and Megapnosaurus. But since the reviewer also indicates that specimens of Coelophysis and Megapnosaurus with a similar size and degree of maturity as the holotype of Pendraig represent exceptions rather than the rule (i.e., anomalies), we do point out that the analysis at least hints at a smaller body size for Pendraig. We additionally point out, based on the reviewer’s comments, that the absence of a hyposphene-hypantrum articulation in the dorsal vertebrae provides an alternative line of evidence that suggests that Pendraig was smaller than the aforementioned taxa. This articulation occurs in all known theropod taxa with a femoral length >170 mm and its clear absence in Pendraig thus suggests that this taxon very likely had a smaller femur length than this threshold value and was therefore considerably smaller than the largest known specimens of Coelophysis and Megapnosaurus.

4) This brings me to my suggestion that the best way to resolve this issue of maturity and body size is by histologically sampling the individual. I understand that the authors probably have qualms about destructively sampling a holotype and only known specimen (barring the referred vertebra) of a taxon, but I do have two ideas that may alleviate some concerns. I notice in Figure 3 that the femur is already somewhat damaged at midshaft. I suggest that, instead of sampling the entire cross-section of the femoral shaft, you break off a small piece of already-damaged cortex from this midshaft region and histologically sample that (see picture in attached file to see what I mean). I have successfully used this technique when I did not want to damage the full specimen but just sampled a portion that was already damaged, including on a femur of Dromomeron romeri (Griffin et al. 2019, PeerJ), and on a femur of Coelophysis (CMNH 10971; Barta et al. in prep). Although a full cortical sample is ideal, with a partial cortex you can still see, for example, LAGs, LAG spacing, an EFS if present, etc. I used this method to find an EFS in the Coelophysis individual referenced above.

Another option, and slightly more heterodox, would be attempting to sample the distalmost preserved end of the ischium, which is roughly midshaft. Pelvic elements are not often sampled, but in my experience any long, somewhat tubular endochondral bone preserves a record of growth and can useful for histological maturity assessment when sampled near
midshaft. I have seen this work on an immature Tyrannosaurid pubis (pers. obs.), metatarsals (McLain et al. 2018, Palaios), and hyoid elements (pers. obs., submitted to be a 2021 SVP poster). A 2011 Master's thesis showed that the midshaft of the Alligator pubis is skeletallychronologically informative, and the ischium did not work only because it is platelike, not elongate, which is not an issue for Pendraig (Garcia 2011, “Skeletallychronology of the American Alligator (Alligator Mississippiensis): Examination of the Utility of Elements for Histological Study”, Florida State University). The ischium of Pendraig is broken at roughly midshaft, so only ~1 cm of the ischium would need to be removed to make a histological section, causing minimal damage to the specimen. In fact, a combination of sampling from a femoral fragment and the ischium would be a good multi-elemental way to assess maturity and back up the assessment made by morphology, making the assessment supported by multiple lines of evidence.

I do not hinge my final approval on whether histological sampling is conducted on this specimen, and I think the authors can incorporate the concerns from my comment #3 without including histology. I know that it is not always possible or desirable to destructively sample a holotype. However, I do think that it would make the paper stronger, more convincing, and more citable, and therefore I recommend the authors add this to their study if it is possible.

Destructive sampling of this specimen (whether taking a full section or breaking parts off) has been declined by the NHM. The specimen is the holotype and only known specimen of this genus and species. The NHM’s destructive sampling procedures indicate that, in general, destructive sampling of holotypes should not be carried out unless there is a very realistic likelihood that the results will significantly improve our knowledge and understanding of the specimen, and we do not think that is likely here. Previous attempts have been made to histologically sample several specimens from Pant-y-fyny non quarry with poor results which have precluded publication of these studies. It is not unlikely, therefore, that we could cut a thin section from this holotype and it would reveal that taphonomic effects have destroyed or overprinted the bone fabric, precluding us from obtaining the ontogenetic information we seek. Furthermore, histological sectioning is unlikely to actually tell us more than we have already determined from a skeletal assessment of maturity. The histological characteristic usually used to indicate maturity in dinosaurs, an external fundamental system, is rarely found, suggesting that the vast majority of dinosaur specimens that have ever been sectioned either die before they attain maximum body size, or that not all dinosaurs developed an EFS. It is more likely that we would conclude from any histological study that the specimen was not a juvenile, but not fully grown, which is what we have determined from our skeletal investigation anyway: histology will not shed light on the final body size of the taxon. If there were many specimens of this genus (as there are for Coelophysis, for example) we would definitely have attempted histological sectioning, but as it is, we can’t justify destructively sampling this specimen given the likelihood of little advance in our knowledge.

The authors are free to contact me with any questions, requests for clarification, or concerns.

Chris Griffin
chris.griffin@yale.edu

See attached file "Spiekman et al_2021_Pendraig orynys_GriffinMajorComments.docx" for the modified figures referenced above, showing suggested locations for histological sampling.
Reviewer: 2

Comments to the Author(s)
I congratulate the authors on what is a well-researched and well-written manuscript. The description is a good length and provides sufficient comparisons, the assessment and subsequent discussion of skeletal maturity in the new taxon is welcome and justified, and the figures appropriately provide the reader with visual representations of important anatomical characteristics. I conducted the phylogenetic analysis in TNT and have no concerns about that treatment or the subsequent regressions and ancestral state reconstructions (but see below for some comments on interpretation). I have attached my grammar and syntax edits/comments in a marked-up PDF, but I outline some of the important comments and suggested changes below. Thank you for the opportunity to review this work; it's an important new taxon that says a lot about the diversity of the uppermost western European Triassic and I think will eventually help stabilize this part of the tree.

Page 2, line 47: I would characterize this not necessarily as discrete body size reduction but rather maintaining the plesiomorphic condition of smaller body sizes among dinosauromorphs/pterosauromorphs. See PDF for further comments later in the discussion.

Early small-sized ornithodirans (e.g., pterosauromorphs, Lagosuchus) have been also included in our ancestral body size analyses. Our reconstructions found an increase of body size among dracohors/dinosaurs from the condition present in early ornithodirans, and a body size reduction among coelophysids from the ancestral condition of Dinosauria and from that of Neotheropoda (the closest ancestral node). So, we think that the interpretation of coelophysids as maintaining a plesiomorphic small size is not supported by the results of the analyses. However, because observed changes are relatively small, we have nuanced our statement in the text by writing that "coelophysoids underwent a small body size decrease early in their evolution".

Page 5, line 25: Please add Intuitional Abbreviations section where appropriate.

We have now added an institutional abbreviations section. Thank you for pointing this out!

Page 12, line 31: I personally avoid the word “fused” in these contexts because it can mean different things to different workers in morphological/developmental frameworks. Consider using “coossified”?

We have replaced fused with co-ossified throughout the text when two or more bony structures have grown or ossified together. When specifically talking about the absence or presence of visible sutures, we have maintained the term fused (e.g., whether or not there is a visible suture between the pubis and ischium).

Page 14, line 48: Please refer to the ‘Padian theropod’ as PEFO 21373/UCMP 129618 throughout; fossils from federal lands in the US must be first referenced by their federal catalogue number and then by an auxiliary number (if necessary, which in this case I think is since most people know the specimen by its UCMP number).

We have now refer to both numbers for this specimen.
Page 19, line 46: The holotype of kayentakatae is MNA V2623, is that what you mean here and a few other places?

We have corrected this typing error throughout the manuscript.

Page 21, line 29: Did your matrix (or that of Novas et al., 2021 for that matter) include modifications/scorings from Marsh and Rowe, 2020? I’m not asking you to redo analyses, just wanted to clarify. That could be one reason for some different tree topologies between your results and those of Marsh and Rowe, 2020 when it comes to Lepidus and/or kayentakatae. By the way, at some point we really need to score Sinosaurus and Shuangbaisaurus into this thing but I think they'll still fall up-tree from coelophysoids.

No, it didn’t. The modifications from Marsh and Rowe (2020) were not included in the matrix of Novas et al. (2021), nor here. However, this version of the data matrix and the changes of Marsh and Rowe (2020) will be integrated together in a project that it is currently being lead by one of the authors of this manuscript (see preliminary results in Ezcurra et al. 2021. A REVISION OF COELOPHYSOID THEROPOD SPECIMENS FROM PETRIFIED FOREST NATIONAL PARK, ARIZONA (USA), REVEALS A NEW SPECIES FROM THE UPPER TRIASSIC CHINLE FORMATION. Libro de Resúmenes de las 34 Jornadas Argentinas de Paleontología de Vertebrados: 39-40).

Sinosaurus and its possible synonym Shuangbaisaurus are very up-tree in comparison to coelophysoids, they could even be averostrans. We need a single dataset that includes all these taxa and one of the authors is working on that (MDE).

Page 21, line 36: I was going to ask about this... I agree it probably doesn't change anything in the part of the tree you're looking at, but at some point those modifications should be incorporated into this matrix for it to be even more useful/up to date.

Yes, we agree, one of us (MDE) is working to incorporate all these new information into a single dataset.

Page 26, line 49: “Size decreases occurred early in Coelophysoidea and ancestral values gradually increase in consecutive nodes” - I'm not sure you can say this with what is displayed in Fig. 8 (by the way, the next 1.5 pages of text rely heavily on supplemental data). Coelophysoid size was already within the range of most other dinosauriforms, and it only decreases three times (independently?) in Pendraig, Powellvenator, and Procompsognathus with what is shown in this non-supplemental figure. It's surprising to me that Segisaurus doesn't show up as markedly smaller in Fig. 8. If there are data that are better displayed in the Supplement that you find yourself citing often, I suggest incorporating them into Fig. 8.

We agree with the reviewer that the size fluctuations within Coelophysoidea are not remarkably strong when compared to broader dinosauriform evolution. However, we still think it is worthwhile to point out that the earliest nodes within Coelophysoidea indicate a slight size decrease relative to the ancestral neotheropod size (a decrease that is statistically supported since it is larger than the corresponding variances for these nodes) and that these values gradually increase slightly in subsequent nodes. We have modified this sentence to state that "Minor size
decreases occurred early in Coelophysoidea and ancestral values gradually increase slightly in consecutive nodes...”.

We agree with the reviewer that this section of the text refers a lot to the Supplementary Tables. We have tried to negate this by presenting an additional image in Figure 8 showing the nodal values and CIs for the region of interest in the tree. However, we nevertheless still refer to the Supplementary Tables in the text. We think this is relevant, because it indicates that, regardless of which parameters are used, our analyses show the same general patterns in body size evolution. We consider the tables to be too extensive to completely list them in the main text of our manuscript.

Although the femur length of *Segisaurus* is quite small (14.29 cm), it is still quite a bit larger than that of *Pendraig* (10.21 cm), *Powellvenator* (9.39 cm), and *Procompsognathus* (9.3 cm). This explains why it is found as less small (i.e. less cyan colored) than these other taxa. Also note that the branch length for this taxon specifically is quite long, which has an influence on length of the closest ancestral node, which will be longer than if the branch would be shorter.

Page 27, line 41: “…our dataset is ambiguous regarding insular dwarfism as a possible explanation of the reduced body size in *Pendraig orynys*. However, insular dwarfism in *Pendraig orynys* cannot be excluded...” - Agreed, but in reality your analyses did not test the hypothesis that insular dwarfism occurred, but rather that body size was changing across the tree in a strictly quantitative way. It can’t be excluded because that’s not actually what was tested. I think the way you frame your discussion is fine, just be aware of that subtle but important distinction. You didn’t test the hypothesis of island dwarfism, you tested the hypothesis that a systematic decrease in body size occurred that may or may not be the result of island dwarfism.

We state in the sentence above the one quoted by the reviewer that “Because its small size is not unique among Coelophysoidea and other coelophysoid taxa that underwent a similar size reduction were not restricted to insular environments, our dataset is ambiguous regarding insular dwarfism as a possible explanation of the reduced body size in *Pendraig milnerae*. “ We wanted to test how body sizes change throughout early neotheropod evolution to see whether *Pendraig* represents an anomalously small taxon. If this were to be the case, insular dwarfism could be a potential explanation for this anomaly. If *Pendraig* was not found to be small at all, then this would suggest against the possibility of insular dwarfism for this taxon. This was our approach to investigating this issue. However, the results are ambiguous when it comes to the question of whether *Pendraig* was anomalously small. Since the reviewer sees no real fault with the way we framed this discussion, and we had already stated that insular dwarfism was one possible explanation of reduced body size, we have maintained it.

Page 28, line 22: “… which could be attributable to a lack of resources to sustain larger predators as is typical in certain island environments...” - Be very careful here to avoid circular reasoning. You can’t use the fact that there are no large-bodied predator fossils as a line of evidence to support island dwarfism, and then also go on to say that island dwarfism caused a lack of large-bodied predators. For what it’s worth, I think taphonomic filters are almost certainly at play here. The fossil record is actually pretty bad and the fact that we can use it to say anything at all is always so incredible to me.
We agree that the statement “which could be attributable to a lack of resources to sustain larger predators as is typical in certain island environments” represents a form of circular reasoning, so we have removed it from the text.

Again, this is overall a very well-written and important contribution and I congratulate the authors on a good piece of work. Please consider my thoughts and let me know if you have any questions or want any clarifications.

Adam Marsh