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1 ***Scleromochlus* and the early evolution of Pterosauroomorpha**

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26 Pterosaurs, the first vertebrates to evolve powered flight, were key components of  
27 Mesozoic terrestrial ecosystems, from their sudden appearance in the Late Triassic until  
28 their demise at the end of the Cretaceous<sup>1-6</sup>. However, the origin and early evolution of  
29 pterosaurs are poorly understood, due to a substantial stratigraphic and morphological  
30 gap between these reptiles and their closest relatives<sup>6</sup>, Lagerpetidae<sup>7</sup>. *Scleromochlus*  
31 *taylori*, a tiny reptile from the early Late Triassic of Scotland discovered over a century  
32 ago, was hypothesized to be a key taxon closely related to pterosaurs<sup>8</sup>, but its poor  
33 preservation has limited prior studies and resulted in controversy over its phylogenetic  
34 position, with some even doubting its identification as an archosaur<sup>9</sup>. Here we use  
35 micro-computed tomographic scans to provide the first accurate whole skeleton  
36 reconstruction and a revised diagnosis of *Scleromochlus*, revealing new anatomical  
37 details that conclusively identify it as a close pterosaur relative<sup>1</sup> within  
38 Pterosauroomorpha (the lagerpetid + pterosaur clade). *Scleromochlus* is anatomically  
39 more similar to lagerpetids than to pterosaurs and retains numerous features that were  
40 likely present in very early diverging members of Avemetatarsalia (bird-line  
41 archosaurs). These results support the hypothesis that the first flying reptiles evolved  
42 from tiny, likely facultatively bipedal, cursorial ancestors<sup>1</sup>.

43 Pterosaurs were iconic components of Mesozoic (~252–66 million years ago) ecosystems and  
44 the first group of vertebrates to achieve powered flight, with a fossil record spanning over  
45 150 million years, from the Late Triassic until the end of the Cretaceous<sup>2–3,6</sup>. However, our  
46 understanding of the origin and early evolution of pterosaurs is hindered by major  
47 stratigraphic and morphological gaps between these highly modified reptiles and their closest  
48 relatives<sup>6–7</sup>. Even at the time of their first appearance ~220 million years ago (middle Norian,  
49 Late Triassic), the pterosaur body plan was so specialized that the identity of their closest  
50 relatives has long been mysterious<sup>2–3,6–7</sup>. Recently, lagerpetids – a group of small-bodied,  
51 terrestrial archosaurs previously thought to be close to dinosaur ancestry – were shown to be  
52 the sister taxon of pterosaurs, together forming Pterosauroomorpha<sup>7</sup>. This discovery reduced  
53 the anatomical distance between pterosaurs and their close relatives but left unanswered  
54 many questions regarding the tempo and mode of the morphological transformations  
55 occurring during the origin of pterosauromorphs<sup>6</sup>.

56 *Scleromochlus taylori*, known from seven articulated skeletons from the Upper  
57 Triassic Lossiemouth Sandstone Formation of Scotland<sup>1,4–5,8,12</sup>, has been considered central to  
58 resolving the origin of pterosaurs<sup>1,4,5,8</sup>. However, the anatomy and phylogenetic position of  
59 this reptile have been controversial because its small size – less than 20 cm in **total length** –  
60 **and unusual** preservation mode, as voids in sandstone, have made interpreting its osteology  
61 challenging<sup>1,4–5,8,12</sup>. Previous anatomical **studies** of *Scleromochlus* have relied primarily on  
62 casts of natural moulds of the skeletons. While such casts were long necessary, their ability to  
63 capture tiny, but crucial, anatomical details has been questioned and the reliability of the  
64 interpretations based upon them are debated<sup>14–5,9,13–14</sup>.

65 Since its discovery in 1907<sup>12</sup>, the anatomy of *Scleromochlus* has been redescribed in  
66 detail four times<sup>1,5,8–9</sup>, in addition to many other discussions on its mode of life and  
67 relationships (e.g.<sup>3–4,13</sup> among others, Supplementary Information). Thanks to these studies,

68 the general anatomy of *Scleromochlus* is well-known: it had a large head, short neck, gracile  
69 body and long hind limbs. Many other phylogenetically critical details are still unclear, such  
70 as the orientation of the quadrate, presence/absence of the mandibular fenestra, relative  
71 lengths of the forelimb segments, proportions of the torso, interpretation of the ankle, length  
72 of the tail, and whether the body was covered in osteoderms. Before synapomorphy-based  
73 studies, *Scleromochlus* was usually considered to be either a dinosaur<sup>12</sup> or a crocodile-line  
74 pseudosuchian<sup>8</sup> (see Supplementary Information); since the advent of phylogenetic analyses  
75 based on cladistic principles, *Scleromochlus* has been recovered as either a non-archosaurian  
76 archosauromorph<sup>9</sup> or more frequently as an avemetatarsalian<sup>5,15</sup>, close either to  
77 dinosauromorphs<sup>4-5,15</sup> or pterosaurs<sup>1,4-5,7,15,17</sup> (Supplementary Information).

78 Here, using microcomputed tomographic ( $\mu$ CT) techniques, we provide substantial  
79 new, formerly inaccessible, information on the anatomy of *Scleromochlus*, including critical  
80 regions and previously unknown elements. This approach allowed us to construct a revised  
81 taxonomic diagnosis, clarify the phylogenetic relationships of *Scleromochlus* and build the  
82 first accurate three-dimensional skeletal reconstruction of this pivotal taxon (Figs. 1–4,  
83 [Extended Data Figs. 1–2](#), [Supplementary Information videos 1–6](#)).

84 Our  $\mu$ CT data demonstrates that prior knowledge of *Scleromochlus* anatomy was  
85 incomplete and, in some cases, misleading. Traditional casting techniques failed to  
86 adequately capture crucial details of the skull, mandible, long bones and ribs, and did not  
87 provide access to important sections of the skeleton (e.g. tail, manus, pes). The  $\mu$ CT scans  
88 greatly increase the available information from all seven known individuals (Fig. 1), enabling  
89 us to demonstrate that *Scleromochlus* possesses cranial and postcranial character states  
90 diagnostic of pterosauromorphs (Fig. 2) and a previously unrecognised series of features that  
91 are common in early bird-line archosaurs.

92           **Description.** None of the *Scleromochlus* specimens are highly distorted but most  
93 display at least some post-mortem disarticulation<sup>5,9,13</sup> (i.e. displaced or missing small body  
94 parts) and compression (**Supplementary Information**). Previous authors proposed that the  
95 cranium had a long, low profile in life<sup>5,9</sup>, and this observation was used to support the  
96 hypothesis that *Scleromochlus* is a doswelliid<sup>9</sup> – a stem archosaur just outside the crown  
97 group. However,  $\mu$ CT data show that disarticulation and flattening of the skeletons was  
98 underestimated in previous studies, suggesting that the skulls were dorsoventrally  
99 compressed taphonomically and would have been considerably deeper in life. Skull length is  
100 ~50% that of the presacral vertebral column, as in early pterosaurs<sup>1,4-5,8</sup> (and potentially  
101 lagerpetids), but unlike those of other early avemetatarsalians, which have proportionally  
102 smaller heads<sup>15</sup>. The maxilla has an anterior process that tapers to a point and a concave  
103 anterior margin, which is a synapomorphy of pterosauriforms<sup>7</sup> (Figs. 1a, 2a–c). A newly  
104 imaged quadrate has a weakly concave posterior surface (Fig. 1b) and is vertically<sup>9</sup> to slightly  
105 posteroventrally-to-anterodorsally oriented as in most Triassic archosaurs, contrary to  
106 previous assessments<sup>5,12</sup> of an anteroventrally-to-posterodorsally oriented quadrate similar to  
107 those characterising early pterosaurs<sup>6-7</sup> and some aetosaurs<sup>16</sup>. The basioccipital neck is very  
108 short, as in lagerpetids and early pterosaurs<sup>7</sup>.  $\mu$ CT data confirm the debated<sup>5,9</sup> presence of a  
109 well-developed external mandibular fenestra (Fig. 1b), as in most archosauriforms<sup>17-19</sup> and,  
110 uniquely amongst pterosaurs, the Triassic taxon *Austriadraco dallavecchiai*<sup>20</sup>. The  
111 retroarticular process of the lower jaw extends well posterior to the glenoid fossa<sup>6</sup>, as in many  
112 early pterosaurs<sup>6,20</sup>, rather than being short<sup>9</sup> (Fig. 1b).

113           In the vertebral column, the short cervical centra<sup>4,8</sup> result in a neck that is  
114 proportionately shorter than those of pterosaurs, aphanosaurs, and other early  
115 avemetatarsalians<sup>15,21</sup>. The centra of the dorsal vertebrae<sup>5,12</sup> increase in length from the  
116 shoulders to the pelvis (Fig. 1c). The middle and posterior dorsal centra are uniquely

117 elongated for an archosaur (see Table 4 in<sup>23</sup>), with a centrum length/height ratio of >2.5,  
118 contributing to a torso that is similar in proportional length to those of silesaurids and  
119 aphanosaurs<sup>15,21–22</sup>, a similarity that may not be immediately noticeable because of the  
120 extreme elongation of the limbs in *Scleromochlus*. The dorsal ribs are 3–4 times longer than  
121 previous estimates (Fig. 1c), showing that the torso is deep, and not dorsoventrally flattened<sup>9</sup>.  
122 The number of sacral vertebrae is unclear but it is likely that there were either two, or no  
123 more than three, based on the lengths of the centra relative to the ilium. The tail of  
124 *Scleromochlus* has a minimum of ~50 caudal vertebrae, based on newly exposed caudal  
125 segments in three specimens. This corroborates earlier research<sup>8,12</sup> and a recent redescription<sup>9</sup>,  
126 and contrasts with other assessments that reported an unusually short tail<sup>4–5</sup>. We did not find  
127 evidence for any three-dimensional structures dorsal to the vertebrae that would indicate the  
128 presence of osteoderms; the two-dimensional structures previously identified as  
129 osteoderms<sup>5,9,13</sup> may be integument impressions instead.

130         The scapular blade is thin<sup>5,9,12</sup> and long, with an anteriorly concave margin and a  
131 weakly flared distal end (Fig. 1e). The limbs are comparatively longer and **slenderer** than  
132 those of any other Triassic avemetatarsalian<sup>23–24</sup>. The humerus has a straight shaft, a small  
133 deltopectoral crest, an expanded distal end, and is confirmed as longer than either the radius  
134 or ulna (Fig. 1e–f; Extended Data Fig. 2, Extended Data Table 1), as in lagerpetids, but unlike  
135 pterosaurs<sup>7</sup>. The metacarpus of *Scleromochlus* is short, less than 10% of total humeral length,  
136 and the manus is small (Fig. 1f–g, Extended Data Fig. 2, Extended Data Table 1), which is  
137 distinct from the elongated hands of other pterosauiromorphs<sup>7</sup>. The ilium is similar to those of  
138 lagerpetids in its relatively small size compared to the length of the hindlimb, and has an  
139 expanded pre-pubic peduncle that is dorsally concave above the acetabulum<sup>7</sup> and extends  
140 anteriorly beyond a pre-acetabular process, which is not as well developed as those in  
141 pterosaurs (Fig. 1i). The femur has a hook-shaped proximal head<sup>4</sup>, which *Scleromochlus*

142 shares with lagerpetids and the earliest-branching pterosaurs<sup>7</sup> (Figs. 1i, 2f–i), and the distal  
143 end has a bulbous crista tibiofibularis that is diagnostic of Lagerpetidae<sup>7,11,25–26</sup> (Fig. 2h–m).

144 Interpretations of the ankle structure in *Scleromochlus* have been central to  
145 consideration of its phylogenetic affinities<sup>1,4–5,9,12</sup>. However, even with  $\mu$ CT data, we could  
146 not satisfactorily clarify the morphology of the ankle components. We therefore opt for a  
147 conservative approach and recommend that ambiguous characters of the ankle should be left  
148 unscored in phylogenetic analyses. Nonetheless, we also consider previous interpretations of  
149 the ankle morphology in our phylogenetic analyses by adopting three separate scoring  
150 strategies for *Scleromochlus* (Methods) (Fig. 3, Extended Data Figs. 3–7, Supplementary  
151 Information): (i) advanced fused mesotarsal ankle<sup>1</sup>– but with an astragalocalcaneum that is  
152 unfused to the tibia and fibula (the latter feature cannot be positively assessed in casts, but  
153 there is separation between the proximal tarsals and the distal end of the tibia in the casts and  
154  $\mu$ CT data), similar to the condition in lagerpetids<sup>7</sup>; (ii) “intermediate” mesotarsal ankle<sup>5</sup> with  
155 a separate astragalus and calcaneum; and (iii) crurotarsal ankle<sup>8,9,12</sup>, the most plesiomorphic  
156 option, as in crocodile-line archosaurs (Fig. 3b–g) (see Phylogenetic analyses below and  
157 Supplementary Information). We do not see any evidence of four distal tarsals capping the  
158 metatarsals in any specimen using  $\mu$ CT data and interpret the previously reported presence of  
159 four distal tarsals in NHMUK PV R3556<sup>5,9</sup> as the proximal ends of the metatarsals.

160 The complete pes, described here for the first time, further underlines similarities with  
161 lagerpetids (e.g. *Lagerpeton*<sup>27</sup>) (Figs. 1k–l, 2n–p). The foot is proportionally longer than  
162 previously reported, and the combined length of the metatarsal + longest digit (IV) surpasses  
163 that of the tibia. The proximal and distal pedal phalanges are elongated and subequal in size.  
164 The pedal digits decrease in length from IV to I, and digit III is slightly angled relative to the  
165 midline, as also occurs in *Lagerpeton*<sup>28</sup>. Because metatarsals I–IV are closely appressed and  
166 subequal in length<sup>1,5,8–9,12</sup>, the metatarsal-phalangeal joints I–IV are aligned, so that digits I

167 and II are more prominent in *Scleromochlus* than *Lagerpeton*<sup>27</sup>. The pes has a phalangeal  
168 formula of 2-3-4-5-0, as in *Lagerpeton* and early dinosauromorphs<sup>28</sup>, differing from the 2-3-  
169 4-5-2 formula of early pterosaurs<sup>28</sup> (Fig. 2n–p). The pedal unguals are similar to those of  
170 *Lagerpeton*: triangular in cross-section, mediolaterally compressed and, unlike those of most  
171 early pterosaurs<sup>6–7</sup>, lack recurvature and ventral tubercles (Fig. 1l).

172 **Phylogenetic analyses.** New anatomical information from the  $\mu$ CT scans was used to  
173 re-score *Scleromochlus* in the largest and best documented phylogenetic data matrix of  
174 Permian–Triassic archosauromorphs<sup>7</sup>. This dataset includes taxa relevant to all of the  
175 previously hypothesized phylogenetic positions of *Scleromochlus* and has the largest  
176 available sampling of early pterosauromorphs<sup>7</sup> (Methods). Maximum parsimony and  
177 Bayesian inference analyses place *Scleromochlus* in Archosauria, Avemetatarsalia and  
178 Ornithodira, and its position in Pterosauroomorpha is strongly supported by a minimum of  
179 eight unambiguous synapomorphies: the base of the ascending process of the maxilla is  
180 concave (Character 59, state 1); the occipital neck is extremely short (Character 231, state 1);  
181 the metacarpal I is slender (distal end width versus total length <0.33) (Character 448, state  
182 0); presence of a concavity on the dorsal margin of the iliac blade (Character 466, state 2); the  
183 pubis is less than 50% the length of the femur (Character 472, state 0/1); the femoral head is  
184 distinctly in-turned with respect to the shaft (Character 492, state 1) and ‘hook-shaped’  
185 (Character 800, state 1); and the length of metatarsal V is less than half length of metatarsal  
186 III (Character 823, state 1). *Scleromochlus* also shares the following ambiguous  
187 synapomorphy with pterosauromorphs: the skull total length is over half the length of the  
188 presacral vertebral column (Character 2, state 1). All analyses, except one, recover  
189 *Scleromochlus* in Lagerpetidae, as the earliest diverging species within the group (Fig. 3,  
190 Extended Data Figs. 3–6, Supplementary Information). In the maximum parsimony analysis  
191 hypothesis where a ‘crurotarsal ankle’<sup>8–9</sup> interpretation is scored, we find *Scleromochlus* as

192 the sister taxon to Pterosauria and Lagerpetidae (Supplementary Information). Regardless,  
193 *Scleromochlus* is not excluded from Avemetatarsalia even when scored as possessing a  
194 crurotarsal ankle – a suite of character states that is also present in aphanosaurs and some  
195 dinosauriforms<sup>15</sup> (as well as pseudosuchians). In sum, there is strong evidence placing  
196 *Scleromochlus* close to the origin of Pterosauroomorpha, and the taxon has a combination of  
197 plesiomorphic features that are widespread in early avemetatarsalian groups (aphanosaurs and  
198 silesaurids), as well as derived character states that are either diagnostic of pterosauromorphs,  
199 lagerpetids or unique to *Scleromochlus*.

200 **Mode of life.** Debate about the locomotor abilities of *Scleromochlus* has confounded  
201 our understanding of the lifestyles of close pterosaur relatives. *Scleromochlus* has been  
202 described as a digitigrade bipedal runner or leaping saltator<sup>5,12</sup>, a sprawling (semi-)digitigrade  
203 quadruped, and a frog-like hopper<sup>9</sup>, among other locomotor modes. Below we focus on the  
204 osteological features supporting or refuting each hypothesis, stressing that all functional  
205 inferences should be verified through comprehensive biomechanical testing<sup>29</sup>.

206  $\mu$ CT data show that features considered to support quadrupedality, a sprawling  
207 posture and frog-like hopping<sup>9</sup> either derive from misinterpretations of incomplete data (e.g.  
208 short ribs, flattened torso and head, stiff osteoderm cuirass covering the sacrum, none of  
209 which are present, as shown here), are ambiguous (e.g. ankle structure, narrow foot), or do  
210 not appropriately account for disarticulation and taphonomy (the specimens are not likely  
211 preserved in *in-vivo* resting poses, as postulated<sup>9</sup>). *Scleromochlus* also lacks unambiguous  
212 adaptations for climbing/arboreal behaviour (e.g. recurved claws, elongated fingers), as  
213 shown by its slender limbs, small hands and straight pedal claws<sup>7</sup> — **but note** that small  
214 tetrapods can climb without possessing distinct adaptations for this behaviour. The small  
215 pelvic girdle is unsuitable for saltatorial (= leaping) behaviour<sup>5,12</sup>, which generally requires a  
216 reinforced pelvis and enlarged muscle attachments, even in tiny taxa (e.g. birds, frogs,



217 jerboas). Furthermore, other features occasionally used to support saltatorial/hopping  
218 locomotion (e.g. a comparatively short trunk, proportions of the hind limb segments,  
219 asymmetrical foot) are also common traits of bipedal runners<sup>33</sup>. We conclude that the hind  
220 limb morphology and proportions of *Scleromochlus* better support the view that it was  
221 digitigrade<sup>1,23,30</sup>, and we were unable to verify traits previously argued to support a  
222 plantigrade foot posture (e.g. crurotarsal ankle<sup>8,9</sup>, narrow feet<sup>9</sup>, lack of metatarsal  
223 adaptations<sup>9</sup>, hip and femur adaptations<sup>9</sup>).

224         However, even with these new data, uncertainty remains over the posture of  
225 *Scleromochlus* because of its unusual body plan. In particular, the forelimb/hind limb ratio  
226 (~0.59, similar to the value reported by<sup>23</sup>) falls between those of quadrupedal and bipedal  
227 archosauromorphs<sup>1,31</sup>, as does the difference between its femoral and humeral diameters<sup>32</sup>.  
228 The elongate centra of the mid-posterior dorsal vertebrae suggest quadrupedality<sup>23</sup>, but the  
229 ratios between the hind limb/trunk (~1.6–1.9), and forelimb and hind limb segments to gleno-  
230 acetabular distance (~2.41) imply a posteriorly positioned centre of mass, which characterises  
231 bipedal archosaurs<sup>23,33</sup>. The ratio between metatarsal and femoral lengths (~0.60) is firmly in  
232 the range of efficient runners<sup>31</sup>. Individually these metrics can be confusing, but their co-  
233 occurrence is phylogenetically and functionally informative<sup>23</sup>. Overall, we conclude that  
234 *Scleromochlus* was a gracile, digitigrade ground-dwelling runner<sup>1</sup>, capable of moving in an at  
235 least facultative bipedal posture.

236         **Palaeoecological implications.** Because it is the oldest known non-pterosaur  
237 pterosauiromorph from the Northern Hemisphere, *Scleromochlus* is fundamental to  
238 understanding early pterosauiromorph evolution. Lagerpetids and pterosaurs rarely co-occur  
239 in the same localities<sup>11</sup>: most early pterosaurs are found in the Norian–Rhaetian low-latitude  
240 coastal habitats of the Northern Tethyan region, with the exceptions of a yet undescribed  
241 pterosaur from the **upper** Chinle Formation of North America<sup>34</sup>, *Caelestiventus*<sup>35</sup> from desert

242 deposits in North America, *Arcticodactylus* from fluvial facies in Greenland<sup>20,36</sup>, *Yelaphomte*  
243 and *Pachagnathus* from floodplain/alluvial sediments in Argentina<sup>37</sup>. By contrast, lagerpetids  
244 have a wider latitudinal and geographical spread<sup>11</sup>, and occur earlier in the stratigraphic  
245 record (e.g. Ladinian–Carnian for *Kongonaphon*)<sup>26</sup>. The minimal geographical overlap of the  
246 two groups, even during their long stratigraphic overlap in the Norian–Rhaetian, could  
247 indicate latitudinal partitioning linked to climate preferences or tolerances. As currently  
248 known, the distribution of Triassic pterosauroforms implies the possibility that climate  
249 shaped the early evolution of the clade, and that the biogeographical expansion of the group  
250 might have been enabled by the removal of low latitude climatic barriers, such as those  
251 following the onset of the Carnian Pluvial Event<sup>38–40</sup>. However, the uneven geographical and  
252 temporal sampling of pterosauroforms, uncertainties in climate models and proxy data  
253 (e.g.<sup>10,41–43</sup>), taphonomy<sup>44</sup> and other sampling biases<sup>45</sup>, will need to be addressed in order to  
254 test these hypotheses rigorously.

255         **Conclusions.** New  $\mu$ CT scans have revealed novel anatomical features that  
256 conclusively place *Scleromochlus* within Pterosauroforma, establishing the importance of  
257 this historic taxon for understanding the early evolution of the clade. The available evidence  
258 suggests that *Scleromochlus* is more closely related to lagerpetids than to pterosaurs, and that  
259 it lacks adaptations for either flying, arboreality or a saltatorial lifestyle. Instead, its unusual  
260 proportions and hind limb morphology support the hypothesis that the common ancestor of  
261 pterosaurs and lagerpetids was a tiny, likely digitigrade, ground-dwelling (potentially  
262 bipedal) runner<sup>1</sup> rather than a sprawling quadruped, frog-like hopper or saltator<sup>9</sup>. The lack of  
263 flight-related adaptations in *Scleromochlus* and lagerpetids suggests that the evolution of the  
264 distinctive pterosaurian body-plan remains to be found in the ~18 Mya gap between the first  
265 pterosaurs and the origin of pterosauroforms<sup>7</sup>.

266

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392 **Figures**

393 **Figure 1. Newly revealed anatomical features of *Scleromochlus taylori*.** **a**, NHMUK PV  
394 R3557, skull in dorsolateral view. **b**, NHMUK PV R3557, right quadrate (blue), posterior  
395 lower jaw (green) and ceratobranchial bone (purple) in posterodorsal view. **c**, NHMUK PV  
396 R3557, torso and rib cage in ventral view. **d**, NHMUK PV R3556, caudal vertebrae in lateral  
397 view (mirrored). **(e)** NHMUK PV R3556, distal end of the left humerus in oblique posterior-  
398 medial view and dorsal view of the left scapula. **f**, NHMUK PV R3557, right forearm and  
399 hand in medial view. **g**, reconstruction of the hand (composite) in dorsal view. **h**, NHMUK  
400 PV R3557, partially exposed left ilium in lateral view. **i**, NHMUK PV R3557, proximal right  
401 femur in medial view. **j**, NHMUK PV R3146, distal end of the right femur in distal view. **k**,  
402 NHMUK PV R3914, right hindlimb in ventral view. **l**, NHMUK PV R3914, details of the last  
403 phalanges and unguals of pedal digit II and III in lateral view. **m** Skeletal reconstruction of  
404 *Scleromochlus taylori*, red shading indicates areas that most benefited from  $\mu$ CT data. Scale  
405 bars equal 10 mm (**a, c, e, f, h**); 5 mm (**b, k, l**); 2 mm (**i, j**). See Methods for abbreviations.

406

407 **Figure 2. Comparisons of selected features of *Scleromochlus taylori* and**

408 **pterosauromorphs.** **a–c**, Right maxilla in lateral view: **a**, *Scleromochlus taylori* (NHMUK  
409 PV R3557); **b**, *Kongonaphon kely* (UA 10618); **c**, *Raeticodactylus filisurensis* (BNM 14524).  
410 **d–g**, Proximal end of the right femur in posteromedial view: **d**, *Scleromochlus taylori*  
411 (NHMUK PV R3557); **e**, *Lagerpeton chanarensis* (PVL 4619); **f**, *Dromomeron gregorii*  
412 (TMM-31100-1306); **g**, *Raeticodactylus filisurensis* (BNM 14524, reversed). **h–m**, Distal  
413 ends of the right femora of pterosauriforms in posterior (**h**) and distal views (**i–m**): **h**,  
414 *Scleromochlus taylori* (NHMUK PV R3146); **i**, *Scleromochlus taylori* (NHMUK PV R3557);  
415 **j**, *Scleromochlus taylori* (NHMUK PV R3556); **k**, *Lagerpeton chanarensis* (PVL 4619); **l**,  
416 *Dromomeron gregorii* (TMM-31100-1306); **m**, *Dromomeron romeri* (GR 218). (**n–p**)

417 Pterosauiromorph left foot in dorsal view: **n**, *Scleromochlus taylori*; **o**, *Lagerpeton*  
418 *chanarensis* (redrawn from<sup>26</sup>); **p**, generic Triassic pterosaur (redrawn from<sup>39</sup>). Scale bars  
419 equal 10 mm (**a–c**, **e–g**, **n–p**), 2 mm (**d**, **h–j**). See Methods for abbreviations.

420

421 **Figure 3. Time-calibrated strict consensus tree focused on Pterosauiromorpha and**  
422 **different positions of *Scleromochlus taylori* based upon interpretations of the**

423 **phylogenetic scores for the ankle. a**, time calibrated strict consensus tree of Archosauria  
424 focused on Pterosauiromorpha (for complete versions and branch support values, see

425 **Extended Data Figs. 3–7). b–c**, advanced mesotarsal ankle interpretation (= fused

426 astragalocalcaneum). **d–e**, “intermediate” mesotarsal ankle interpretation. **f–g**, crurotarsal

427 ankle interpretation. Note the different interpretation and position of the astragalus,

428 calcaneum and tarsals (i–iii). The grey ‘?’ in panel **a** represents our recommended scoring

429 strategy: ‘unscored ankle’. Scale bars equal 5 mm in b–g. See main text for abbreviations.

430 Silhouettes by Scott Hartman from [www.phylopic.org](http://www.phylopic.org), covered by

431 <https://creativecommons.org/licenses/by/3.0/>, used with permission.

432

433 **Figure 4. Digital 3D life reconstruction of *Scleromochlus taylori*. a**, Digital 3D model,

434 created by Matt Humpage based on  $\mu$ CT data. **b**, life reconstruction by Gabriel Ugueto. Scale

435 bar equals 50 mm. [1.5 column-width]

436 **Methods**

437 **Anatomical abbreviations:** **aeg**, anterior extensor groove; **aof**, antorbital fossa; **ar**, articular;  
438 **as**, astragalus; **asf**, astragalar facet; **ast**, tubercle on astragalus; **c**, carpal; **ca**, calcaneum; **cat**,  
439 calcaneal tuber; **c**, carpal; **ctf**, crista tibiofibularis; **emf**, external mandibular fenestra; **en**,  
440 external naris; **fe**, femur; **hy**, hyoid; **il**, ilium; **lco**, lateral condyle; **le**, lateral emargination; **mc**  
441 **I-V**, metatarsals I to IV; **mco**, medial condyle; **mt**, metatarsal; **mx**, maxilla; **ph**, phalanx;  
442 **pmx**, premaxilla; **poz**, postzygapophysis; **prz**, prezygapophysis; **q**, quadrate; **qj**,  
443 quadratojugal; **ra**, radius; **rap**, retroarticular process; **sc**, scapula; **sk**, skull fragment; **t**, tarsal;  
444 **ti**, tibia; **ul**, ulna.

445

446 **Institutional abbreviations:** **BNM**, Bündner Naturmuseum, Chur (Switzerland); **GR**, Ghost  
447 Ranch Ruth Hall Museum of Paleontology, Abiquiú, NM (USA); **NHMUK**, Natural History  
448 Museum, London (United Kingdom); **PVL**, Paleontología de Vertebrados, Fundación-  
449 Instituto Miguel Lillo, Universidad Nacional de Tucumán, San Miguel de Tucumán,  
450 Tucumán (Argentina); **TMM**, Vertebrate Paleontology Laboratory, Texas Natural Science  
451 Center, Austin, TX (USA); **ULBRA**, Universidade Luterana do Brasil, Coleção de  
452 Paleovertebrados, Canoas, Rio Grande do Sul (Brazil).

453

454 **Micro-computed tomography acquisition and image processing**

455 This work is based on seven individuals (the holotype NHMUK PV R3556, the two  
456 individuals in NHMUK RV R3146, NHMUK PV R3914, NHMUK PV R4823/4, NHMUK  
457 PV R5589) referred to *Scleromochlus taylori*. All of them were subjected to  $\mu$ CT scanning.  
458 Because each specimen is embedded in broken sandstone blocks consisting of multiple parts,  
459 these blocks were first re-assembled and held together with rubber bands before  $\mu$ CT  
460 scanning started. This additional step was necessary to: capture the specimens in their entirety

461 in a single scan; to minimise the risk of misidentification of individual elements that have  
462 been broken into separate sections and preserved in different parts of the original articulated  
463 blocks (e.g. the humerus in NUMUK PV R3556); and to improve measurement accuracy<sup>14</sup>.  
464 Five specimens (NHMUK PV R3556, NHMUK RV R3146, NHMUK PV R3914, NHMUK  
465 PV R4823/4, NHMUK PV R5589) were scanned at the Imaging and Analysis Centre of the  
466 NHMUK, using the Nikon XT H 225 by Dr Vincent Fernandez with the assistance of PMB.  
467 NHMUK PV R3557 was scanned at the Palaeobiology Lab of the University of Bristol by Dr  
468 Tom G. Davis with the assistance of Dr Elizabeth G. Martin-Silverstone using a Nikon XT H  
469 225. The  $\mu$ CT scans and their parameters are freely available in MorphoSource alongside  
470 videos of the complete digital models (see Data availability), following community  
471 recommendations for the availability of digital data<sup>46</sup>.

472 The  $\mu$ CT data were processed and segmented using Mimics Research v22.0<sup>47</sup>. We  
473 additionally checked and, where possible confirmed, our observations on multiple  
474 generations of casts and moulds of the same specimens. DF and PMB worked with the peels  
475 in the collections of NHMUK, while SJN worked on additional peels made by Kevin Padian  
476 in the 1980s and then cast in epoxy by Marilyn Fox (YPM); this set of casts is currently  
477 located with SJN at Virginia Tech.

478

### 479 **Phylogenetic analyses**

480 Using our new anatomical data, *Scleromochlus taylori* was scored for ~40–42% of the  
481 character states in the phylogenetic data matrix of Ezcurra *et al.*<sup>7</sup>. This more than doubles the  
482 information available for this taxon in the previous version of the dataset, and makes  
483 *Scleromochlus* one of the most completely scored Triassic avemetatarsalians. We used this  
484 dataset<sup>7</sup>, which is an expanded version of the matrix in reference<sup>19</sup>, because it contains the  
485 most comprehensive sample of Permian–Triassic archosauromorphs available and includes

486 the most relevant character states and taxa to appropriately test all of the historical hypotheses  
487 concerning the relationships of *Scleromochlus*.

488 The final dataset includes 822 characters and 158 terminal taxa. Following previous  
489 works, 36 undiagnostic and/or problematic operational taxonomic units (OTUs), and some  
490 that were scored solely for the purpose of disparity analyses, were excluded *a priori*  
491 (references<sup>7,48–50</sup> for further justifications regarding these exclusions) (i.e. *Dinocephalosaurus*  
492 *orientalis*, *Fuyansaurus acutirostris*, *Pectodens zhenyuensis*, *Protanystropheus antiquus*,  
493 *Trachelosaurus fischeri*, *Tanystropheus haasi*, *Malerisaurus robinsonae*, *Arctosaurus*  
494 *osborni*, *Eorasaurus olsoni*, *Prolacertoides jimusarensis*, *Archosaurus rossicus* (complete),  
495 Panchet proterosuchid, *Vonhuenia fredericki*, *Chasmatosuchus rossicus* (combined),  
496 *Chasmatosuchus magnus* (combined), *Chasmatosuchus vjushkovi*, *Koilamasuchus*  
497 *gonzalezdiazi*, *Kalisuchus rewanensis* (holotype), NMQR 3570, *Shansisuchus kuyeheensis*,  
498 *Uralosaurus* (combined), *Osmolskina czatkoviensis*, *Osmolskina* (complete), *Triopticus*  
499 *primus*, *Angistorhinus talanti*, Otter Sandstone Formation Archosaur, *Dagasuchus*  
500 *santacruzensis*, *Hypselorhachis mirabilis*, *Waldhaus poposauroid*, *Vytshgedosuchus*  
501 *zbeshtartensis*, *Bystrowisuchus flerovi*, *Bromsgroveia walkeri*, Moenkopi Formation  
502 poposauroid, *Lutungutali sitwensis*, *Nyasaosaurus parringtoni*). *Petrolacosaurus kansensis*  
503 was selected as the outgroup. The following characters were treated as additive: 1, 2, 7, 10,  
504 17, 19–21, 28, 29, 36, 40, 42, 46, 50, 54, 66, 71, 74–76, 122, 127, 146, 153, 156, 157, 171,  
505 176, 177, 187, 202, 221, 227, 263, 266, 278, 279, 283, 324, 327, 331, 337, 345, 351, 352,  
506 354, 361, 365, 370, 377, 379, 386, 387, 398, 410, 414, 424, 430, 435, 446, 448, 454, 455,  
507 458, 460, 463, 470, 472, 478, 482, 483, 485, 489, 490, 502, 504, 510, 516, 521, 529, 537,  
508 546, 552, 556, 557, 567, 569, 571, 574, 581, 582, 588, 636, 648, 652, 662, 701, 731, 735,  
509 737, 738, 743, 749, 766, 784 and 816 (taxon-character matrix).

510 Three different ankle interpretations were scored in different *Scleromochlus taylori*  
511 OTUs, plus an additional one where all ambiguous ankle characters were left unscored. To  
512 explicitly test how the ankle interpretation affects the position of *Scleromochlus* in the  
513 phylogeny we ran a different phylogenetic analysis for each of these. In each analysis only a  
514 single *Scleromochlus* OTU was kept active.

515 **Maximum parsimony.** Maximum parsimony analyses were performed in TNT 1.5<sup>51–</sup>  
516 <sup>52</sup> using equally weighted parsimony. A tree space was generated and searches for the most  
517 parsimonious trees (MPTs) were conducted using a similar protocol to that in ref.<sup>7</sup>: the tree-  
518 search algorithm Wagner trees, tree bisection and reconnection (TBR) branch swapping, and  
519 New Technology search (Sectorial Search, Ratchet, Drift and Tree fusing) until 100 optimal  
520 hits were reached. This was followed by a final round of tree bisection reconnection (TBR)  
521 branch swapping, with a 50% collapsing rule. Consistency Index (CI) and Retention Index  
522 (RI) were calculated using the script statsB.run<sup>51</sup>, which, unlike stats.run<sup>52–53</sup>, does not  
523 include deactivated terminals when calculating CI and RI<sup>51</sup>. Branch support was calculated  
524 using bootstrap resampling analyses, with 1,000 technical pseudo-replicates for both absolute  
525 and group present/contradicted (GC) frequencies, and Bremer support.

526 **Bayesian inference analysis.** We conducted Bayesian tip-dating analysis using  
527 MrBayes (3.2.7)<sup>54</sup> and repeated it for all the interpretations of *Scleromochlus* ankle anatomy.  
528 Our analysis was run with the same settings as the unconstrained version of ref.<sup>7</sup>. We ran a  
529 Markov k-state variable substitution using the same set of characters as in the maximum  
530 parsimony analysis. No topological constraint was applied to the tree, only some time  
531 constraints to specific nodes: uniform age priors and gamma-rate relaxed clock models were  
532 modelled on First and Last Appearance Dates (FAD and LAD) for all tips of the tree; the  
533 oldest split of the tree was set a 304.4–318 Mya and was based on the age of earliest  
534 occurrence of crown-amniotes in the Joggings Formation<sup>55</sup>, and the estimated age of

535 *Petrolacosaurus kansensis*; the node age calibration of Archosauria was set with a uniform  
536 prior at 249.2–257.4 Mya, respectively, based on the oldest archosaur in the fossil record, and  
537 the age estimate of the archosaur–squamate lines split (see<sup>49,56</sup>). All tips were specified to be  
538 fossils, in a fossilised birth–death process under standard parametrization. All analyses ran  
539 Metropolis-coupling Markov chain Monte Carlo algorithm, two runs of four chains each with  
540 a heat coefficient of 0.05 and three swap attempts per generation.

541

## 542 **Systematic Palaeontology**

543 **Archosauria** Cope, 1869

544 **Avemetatarsalia** Benton, 1999

545 **Ornithodira** Gauthier, 1986

546 **Pterosauroomorpha** Padian, 1997

547 *Scleromochlus taylori* Woodward, 1907

548

549 **Holotype.** NHMUK PV R3556, an almost complete impression of a skeleton in  
550 sandstone split into four blocks. Some additional elements (pedal phalanges, ribs and caudal  
551 vertebrae) are only visible in the  $\mu$ CT scans because they are still completely embedded in  
552 the sandstone matrix.

553 **Referred material.** NHMUK PV R3557; NHMUK PV R3146 (two individuals);  
554 NHMUK PV R3914; NHMUK PV R4823/4; NHMUK PV R5589 all of which are partial to  
555 complete impressions of skeletons preserved in sandstone similarly to the type specimen, and  
556 with variable numbers of elements still embedded in the sandstone matrix.

557 **Locality and horizon.** All specimens were collected from the Lossiemouth East  
558 Quarry in Lossiemouth near Elgin (Moray, Scotland, United Kingdom), except NHMUK PV  
559 R5589, which was recovered from the West Quarry of the same location. All of the

560 specimens come from the aeolian sandstone deposits of the Lossiemouth Sandstone  
561 Formation (Late Triassic: ~late Carnian/early Norian) (see<sup>5,13,56</sup> and refer to<sup>7,48–49, 56–58</sup> for  
562 comments on the biostratigraphic correlations of the Lossiemouth Sandstone Formation with  
563 other Late Triassic formations).

564         **Diagnosis.** *Scleromochlus taylori* is a small-bodied, gracile pterosauromorph  
565 avemetatarsalian with the following unique combination of character states (autapomorphies  
566 denoted by an asterisk): \* retroarticular process of the mandible moderately expanded  
567 posteriorly, with a distal end that is weakly expanded dorsolaterally-to-ventromedially; \*  
568 parietal with a transverse posterolateral process; anterior cervical with transversely convex  
569 ventral surface; \* middle and posterior dorsal vertebrae with an elongated centrum  
570 (height/length ratio > 2.5); straight (i.e. not sigmoidal) humerus; gracile humerus (present in  
571 some trees) with a maximum proximal transverse width /total length ratio ~0.16 to 0.2; \*  
572 short deltopectoral crest, reaching only 15–18% of the humeral length; short pubis, <30% of  
573 the total length of the femur; narrow femur distal transverse width, ~11% of the total length;  
574 short metacarpal, <10% of the length for the humerus and only ~18% the length than the  
575 longest metatarsals; metatarsals I–IV equal in length (shared with pterosaurs but not  
576 lagerpetids).

577

#### 578 **Data availability**

579 The taxon/character data matrices for the phylogenetic analyses for TNT and MrBayes are  
580 available in Nexus and TNT formats in the SI and in MorphoBank at  
581 [https://morphobank.org/index.php/Projects/ProjectOverview/project\\_id/4327](https://morphobank.org/index.php/Projects/ProjectOverview/project_id/4327). The  $\mu$ CT  
582 datasets and videos of the six specimens of *Scleromochlus taylori* are available in  
583 MorphoSource <https://www.morphosource.org/projects/000414456/?locale=en> (the videos  
584 are also available as SI files).



585

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629

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643

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645 P.M.B.; S.L.B. and S.J.N.; D.F. processed the  $\mu$ CT data and described the material; D.F.,  
646 with the assistance of S.J.N. and P.M.B., scored the phylogenetic matrices and conducted  
647 the phylogenetic analyses; D.F. wrote the bulk of the manuscript and made the figures;  
648 P.M.B. conducted sedimentological tests on the specimens. All authors contributed to the  
649 writing, discussions and conclusions.

650

651 **Competing interests.** The authors declare no competing interests.

652

### 653 **Additional Information**

654 **Supplementary Information** is available for this paper at [to be completed]

655 **Correspondence and requests for materials** should be addressed to D.F.

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659 **Reprints and permissions information** is available at <http://www.nature.com/reprints>.

660

661 **Extended Data**

662 **Extended Data Figure 1. Life reconstruction of *Scleromochlus taylori*.** Artwork by

663 Gabriel Ugueto (high-resolution version).

664

665 **Extended Data Figure 2. Digital rendering of *Scleromochlus taylori* specimens from  $\mu$ CT**

666 **scans.** Holotype NHMUK PV R3556, dorsal view (top left); NHMUK PV R3557, ventral

667 view (right); NHMUK PV R3914, ventral view (bottom left). Red shading highlights the

668 skeleton traces on the digital peels, while solid red rendering indicates previously unknown

669 body parts.

670

671 **Extended Data Figure 3. Strict consensus phylogenetic tree of analysis including**

672 **indeterminate ankle scores.** Absolute and present/contradicted group bootstrap frequencies

673 (respectively left and right above the branches) and Bremer support values (below the

674 branches). Note that in ~95% of the most parsimonious trees *Scleromochlus* is found as the

675 earliest-diverging lagerpetid (it is alternatively found as the earliest-diverging member of a

676 lagerpetid clade also composed of *Ixalerpeton*, *Kongonaphon* and *Lagerpeton*).

677

678 **Extended Data Figure 4. Strict consensus phylogenetic tree of analysis using scores for**

679 **an advanced fused mesotarsal ankle.** Absolute and present/contradicted group bootstrap

680 frequencies (respectively left and right above the branches) and Bremer support values

681 (below the branches). Note that in ~95% of the most parsimonious trees *Scleromochlus* is

682 found as the earliest-diverging lagerpetid (it is alternatively found as the earliest-diverging

683 member of a lagerpetid clade also composed of *Ixalerpeton*, *Kongonaphon* and *Lagerpeton*).

684

685 **Extended Data Figure 5. Strict consensus phylogenetic tree of analysis using scores for**  
686 **an “intermediate” mesotarsal ankle.** Absolute and present/contradicted group bootstrap  
687 frequencies (respectively left and right above the branches) and Bremer support values  
688 (below the branches).

689

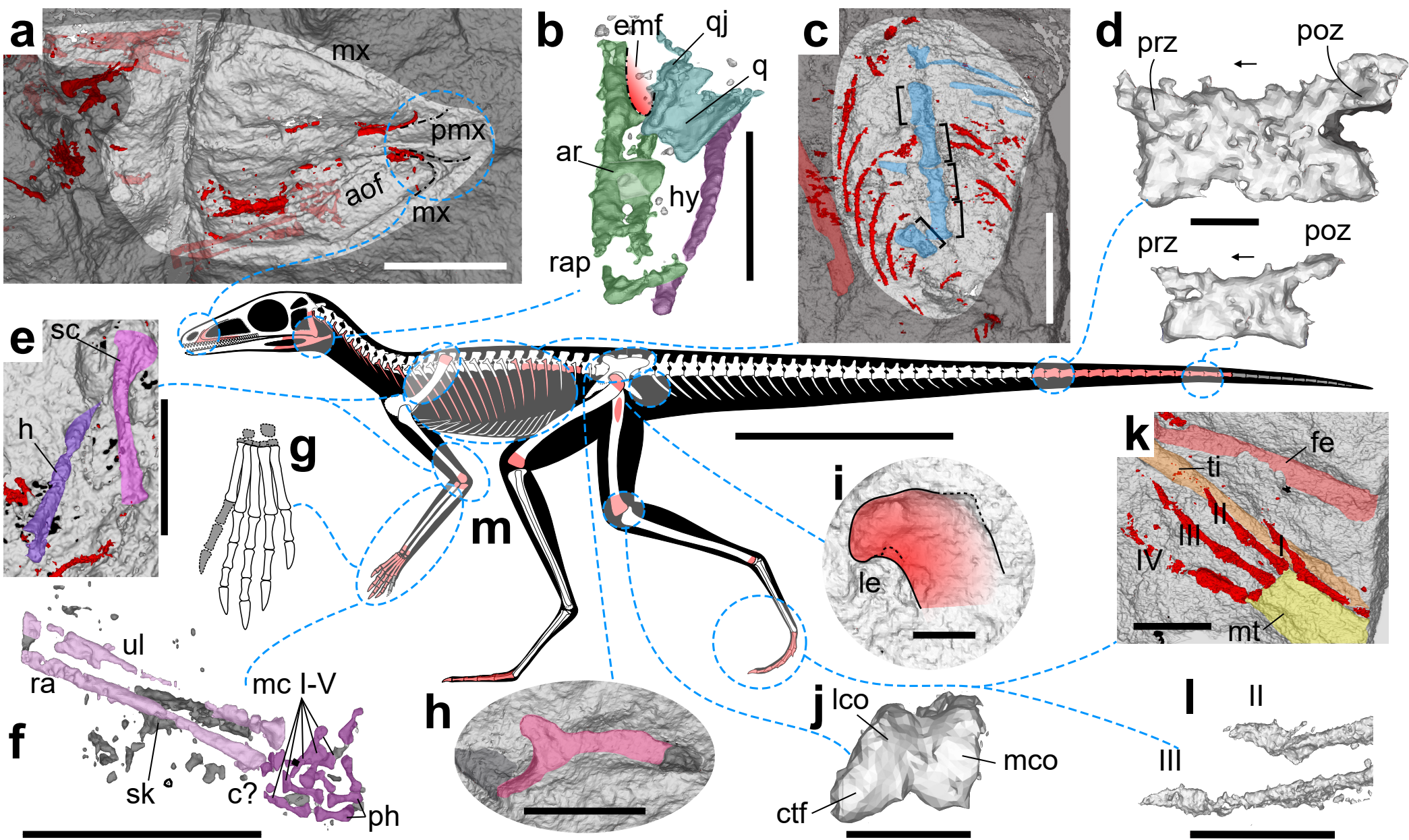
690 **Extended Data Figure 6. Strict consensus phylogenetic tree of analysis based on scores**  
691 **for a crurotarsal ankle.** Absolute and present/contradicted group bootstrap frequencies  
692 (respectively left and right above the branches) and Bremer support values (below the  
693 branches).

694

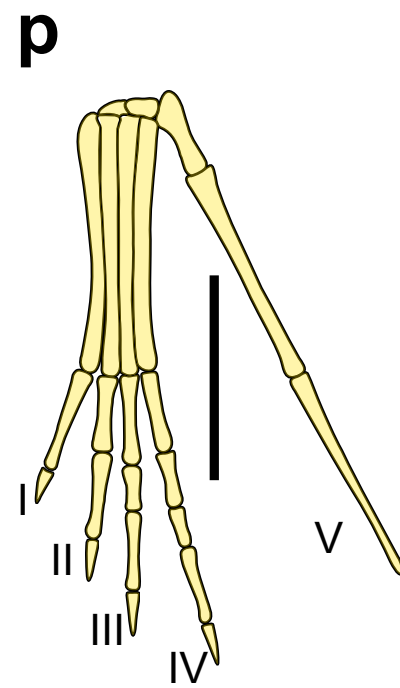
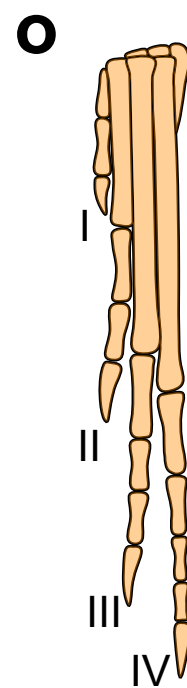
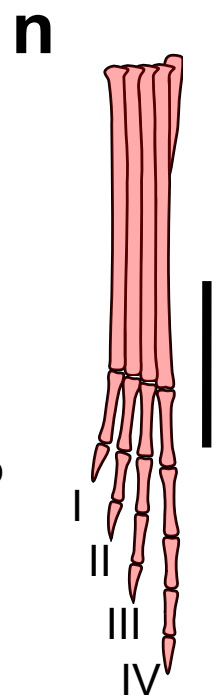
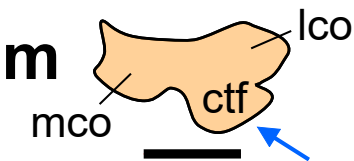
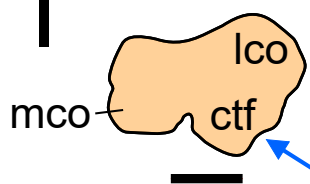
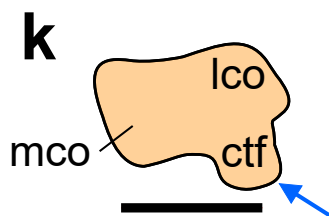
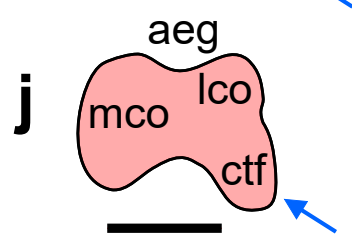
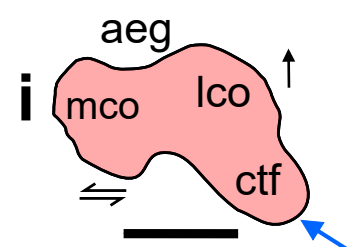
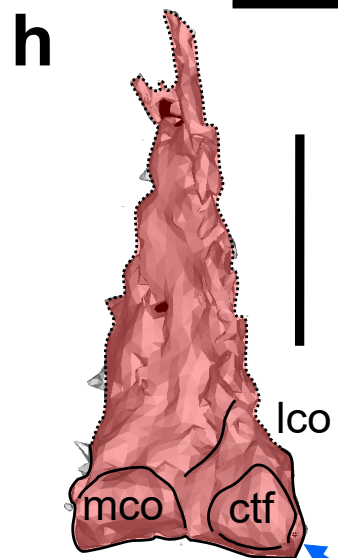
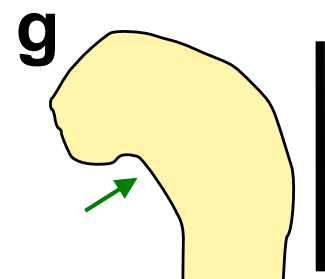
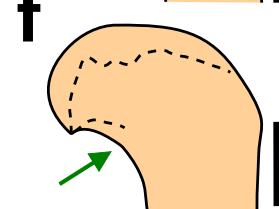
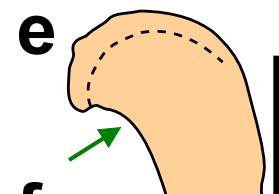
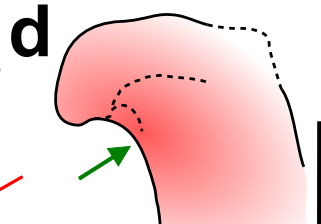
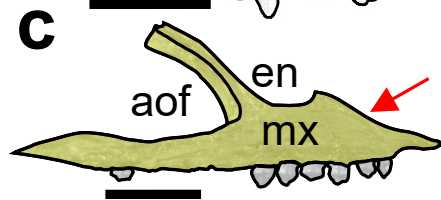
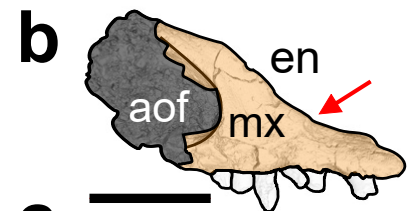
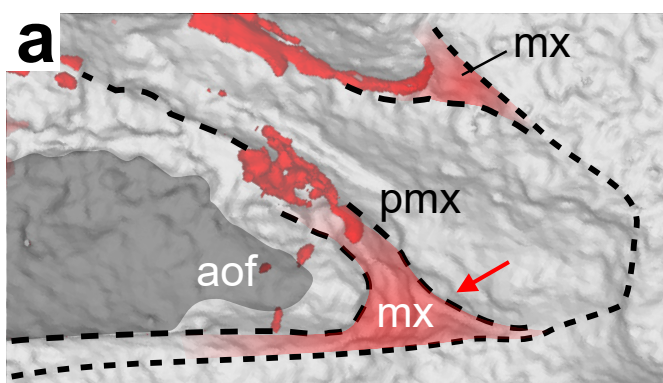
695 **Extended Data Figure 7. Bayesian inference convergence topology trees.** The position of  
696 *Scleromochlus taylori* remains the same regardless of the scoring strategy of the ankle. The  
697 alternative topology within Pterosauria is found only when using the ‘crurotarsal ankle’  
698 settings.

699

700 **Extended Data Table 1. Table of measurements.** Measurements (maximum length in mm)  
701 of *Scleromochlus taylori* individuals. i, incomplete; e, estimated; ---, not available.







 *Scleromochlus taylori*

 Lagerpetidae

 Pterosauria

