

Early Vertebrate Evolution

New insights into the morphology of the Carboniferous tetrapod *Crassigyrinus scoticus* from computed tomography

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ABSTRACT: The Carboniferous tetrapod *Crassigyrinus scoticus* is an enigmatic animal in terms of its morphology and its phylogenetic position. *Crassigyrinus* had extremely reduced forelimbs, and was aquatic, perhaps secondarily. Recent phylogenetic analyses tentatively place *Crassigyrinus* close to the whatcheeriids. Many Carboniferous tetrapods exhibit several characteristics associated with terrestrial locomotion, and much research has focused on how this novel locomotor mode evolved. However, to estimate the selective pressures and constraints during this important time in vertebrate evolution, it is also important to study early tetrapods like *Crassigyrinus* that either remained aquatic or secondarily became aquatic. We used computed tomographic scanning to search for more data about the skeletal morphology of *Crassigyrinus* and discovered several elements previously hidden by the matrix. These elements include more ribs, another neural arch, potential evidence of an ossified pubis and maybe of pleurocentra. We also discovered several additional metatarsals with interesting asymmetrical morphology that may have functional implications. Finally, we reclassify what was previously thought to be a left sacral rib as a left fibula and show previously unknown aspects of the morphology of the radius. These discoveries are examined in functional and phylogenetic contexts.



KEY WORDS: evolution, palaeontology, phylogeny, water-to-land transition.

Crassigyrinus scoticus was a large stem tetrapod from the coal swamps of the Carboniferous of Scotland. Based on its long body, reduced limbs, large size and large orbits, *Crassigyrinus* seems to have been fully aquatic (Panchen 1985). This contrasts with many other Carboniferous (and even late Devonian) tetrapods, which show changes in bone morphology that indicate shifts toward more weight-bearing limb functions and probably at least some modest degree of terrestrial locomotor abilities (Daeschler *et al.* 1994; Coates *et al.* 2002, 2008; Clack 2012; Pierce *et al.* 2012; Smithson *et al.* 2012). It has been suggested that *Crassigyrinus* either represents an ancestrally more aquatic side branch in early tetrapod evolution that remained aquatic or that *Crassigyrinus* became secondarily aquatic. It is difficult to test these hypotheses with the available *Crassigyrinus* material because of its aberrant mix of ancestral and derived features (see page 2), and the uncertainty of its phylogenetic position.

Whilst the aquatic locomotion of *Crassigyrinus* may have been retained from aquatic ancestors, the reduced forelimbs are not a plesiomorphic feature but rather an autapomorphy. The limbless aïstopods are another example of secondary limb reduction in early tetrapods. A recent phylogenetic analysis placed them deep on the tetrapod stem, suggesting that stem tetrapods exhibited a wider range of appendicular morphologies than was previously thought (Pardo *et al.* 2017). It is worth noting that the aïstopods share many features with *Crassigyrinus*,

such as the long body, reduced limbs and large orbits (Anderson *et al.* 2003), all of which have been used to support the hypothesis that *Crassigyrinus* was aquatic. However, unlike *Crassigyrinus*, the aïstopods are thought to have been terrestrial (Germain 2008). Their smaller body size relative to *Crassigyrinus* might have enabled them to move on land despite having reduced limbs. It has become clear that early tetrapods were a morphologically, functionally and ecologically disparate group of organisms. Here, we sought to gain insight into the morphology of *Crassigyrinus* in this context of disparity among stem tetrapods.

Skeletal material of *Crassigyrinus scoticus* has been found in late Viséan (~330-million-year-old) and early Namurian (~326-million-year-old) deposits of Gilmerton and Cowdenbeath, Scotland, although a new *Crassigyrinus*-like partial jaw UMZC (University Museum of Zoology, Cambridge) 2011.9.1 from Burnmouth, Scotland, might extend the temporal range of *Crassigyrinus* back into the Tournasian (Smithson *et al.* 2012; Clack *et al.* 2018). Table 1 provides an overview of *Crassigyrinus* specimens and institutional abbreviations. The Gilmerton Ironstone specimens are all cranial material and *Crassigyrinus* was the most common tetrapod collected at this site. Godfrey (1988) also tentatively attributed a ribcage and ventral scales (CMNH (Cleveland Museum of Natural History) 11230) from the Viséan of Greer, West Virginia, to *Crassigyrinus*, but we think this identification is unlikely because the scales from Greer (Godfrey 1988, fig. 7) are much more rounded at one

Table 1 Specimens attributed to *Crassigyrinus*. Abbreviations: CMNH = Cleveland Museum of Natural History; GSE = British Geological Survey, Edinburgh; NEWHM = Newcastle Hancock Museum, Newcastle upon Tyne; NHMUK VP = Natural History Museum, Department of Vertebrate Palaeontology, London (formerly the British Museum); NMS G = National Museums of Scotland, Department of Geology, Edinburgh (formerly the Royal Scottish Museum); UMZC = University Museum of Zoology, Cambridge.

Specimen	Locality and age	Elements	Reference
NHMUK VP R310 (holotype)	Upper Viséan, Gilmerton	Right jaw ramus	Lydekker (1890) (named ' <i>Macromerium</i> ' <i>scoticum</i> , later attributed to <i>Crassigyrinus</i>), Watson (1929), Panchen (1970, 1973, 1985), Clack <i>et al.</i> (2018)
NMS G 1859.33.104 (previously the holotype before NHMUK VP R310 was attributed to <i>Crassigyrinus</i>)	Upper Viséan, Gilmerton	Right side of skull	Watson (1929), Panchen (1973), Panchen (1985), Clack (1998), Clack <i>et al.</i> (2018)
GSE 4722	Upper Viséan, Gilmerton	Left jaw ramus	Panchen (1985), Ahlberg & Clack (1998), Clack <i>et al.</i> (2018)
GSE unregistered	Probably Upper Viséan, Gilmerton	Anterior right jaw ramus	Panchen (1985)
NHMUK VP R30532	Upper Viséan, Gilmerton	Partial skull	Panchen (1985), Clack (1998), Clack <i>et al.</i> (2018)
NMS G 1975.48.50	Early Namurian of Cowdenbeath, Scotland	Posterior left jaw ramus	Panchen (1985)
NMS G 1975.48.51	Early Namurian of Cowdenbeath, Scotland	Fragment including left quadrate condyle	Panchen (1985)
NEWHM 1978.3.15*	Early Namurian of Cowdenbeath, Scotland	Incomplete interclavicle	Panchen (1985)
NHMUK VP R10000	Early Namurian of Cowdenbeath, Scotland	Skull, left and right clavicles, interclavicle, right cleithrum, left humerus, left radius, left ulna, right ischium, vertebral elements, ribs	Panchen (1985), Clack (1998), Ahlberg & Clack (1998), Panchen & Smithson (1990), Clack <i>et al.</i> (2018)
CMNH 11230*	Viséan of Greer, West Virginia	Ribcage and ventral scales	Godfrey (1988)
NMS G 1984.15.1	Early Namurian of Cowdenbeath, Scotland	Left sacral rib, left ilium, left femur	Panchen & Smithson (1990)
NMS G 1984.15.2	Early Namurian of Cowdenbeath, Scotland	Metatarsal or phalanx	Panchen & Smithson (1990)
NMS G 1984.15.3	Early Namurian of Cowdenbeath, Scotland	Left ischium, incomplete right ilium, right tibia, right fibula, metatarsals, phalanges, neural arch, centrum, presacral rib, scutes, unidentified fragments	Panchen & Smithson (1990)
NMS G 1975.5.5	Early Namurian of Cowdenbeath, Scotland	Right ilium and left ischium	Panchen & Smithson (1990)
UMZC 2011.9.1	Tournasian of Burnmouth, Scotland	<i>Crassigyrinus</i> -like partial jaw*	Smithson <i>et al.</i> (2012), Clack <i>et al.</i> (2018)

* Identification as *Crassigyrinus* is doubtful.

end than the narrow scales of *Crassigyrinus*. The first known postcranial material of *Crassigyrinus* is the NHMUK (Natural History Museum, London) VP R10000 specimen, which was discovered in the Dora bonebed from the Namurian of Cowdenbeath, Fife. Further *Crassigyrinus* material (NMS G (National Museums of Scotland, Department of Geology, Edinburgh) 1975.5.5, NMS G 1984.15.1-3), including the only hindlimb bones discovered, was reported from the same site by Panchen & Smithson (1990). The minimum number of individuals is two, because there are two left ischia and two right ilia (duplicate elements in NMS G 1984.15.3 and NMS G 1975.5.5).

In his analysis of the NHMUK VP (Natural History Museum, Department of Vertebrate Palaeontology, London) R10000 *Crassigyrinus* specimen, Panchen (1985) noted the mosaic of plesiomorphic and derived features. Panchen judged the autapomorphies of *Crassigyrinus* to be the large quadrangular orbits, strongly constricted frontals and parietals, deep jugals and lacrimals and the reduced forelimbs (Panchen 1985). The

morphology of the palate shows similarities to tetrapodomorph fish, but the presence of tabular horns and a large intertemporal bone are more characteristic of anthracosaurian tetrapods. The latter was thought by Panchen to be an early tetrapod plesiomorphy retained in anthracosaurs but reduced or lost in most temnospondyls. However, it is now thought that the large intertemporal may have evolved independently in various post-Devonian tetrapod clades, as this trait is absent in earlier tetrapods such as *Ichthyostega* and *Acanthostega* (Clack 1998). Panchen (1985) determined the large supratemporal suture to the postparietal to be an ancestral character for tetrapods, also retained in temnospondyls but differing from the anthracosaur arrangement. After considering these contradicting characters, Panchen (1985) proposed *Crassigyrinus* to be a sister taxon to anthracosaurs, based on four synapomorphies: tooth morphology, dermal ornamentation, tabular horn and lack of post-temporal fossae.

The phylogenetic analysis of Lebedev & Coates (1995), which placed *Crassigyrinus* in a polytomy with *Tulerpeton*,

Table 2 *Crassigyrinus* scan information. Abbreviations: NHMUK VP = Natural History Museum, Department of Vertebrate Palaeontology, London (formerly the British Museum); NMS G = National Museums of Scotland, Department of Geology, Edinburgh (formerly the Royal Scottish Museum); CT = computed tomography.

Specimen	Scanner type	kVp	µA	Resolution (mm/pixel)
NHMUK VP R10000 (cervical slab piece; Fig. 3a–d)	Nikon Metrology HMX ST 225 µCT (Natural History Museum, London)	200	200	0.101
NHMUK VP R10000 prepped pieces (neural arch mass with ‘banana-shaped piece’ and ‘thoracic rib’; Figs 3e, 7b)	Nikon Metrology HMX ST 225 µCT (Natural History Museum, London)	200	200	0.077
NHMUK VP R10000 prepped piece (‘immediately presacral rib’; Fig. 7a)	Nikon Metrology HMX ST 225 µCT (Natural History Museum, London)	200	200	0.077
NHMUK VP R10000 (mid-thoracic slab piece; Figs 2, 3f, 4, 6, 7)	Nikon Metrology HMX ST 225 µCT (Natural History Museum, London)	200	200	0.110
NHMUK VP R10000 skull-section scan (radius and metacarpal; Fig. 12l)	Nikon Metrology HMX ST 225 µCT (Natural History Museum, London)	210	200	0.108
NMS G 1984.15.1 (slab with left fibula, metatarsal; Figs 9a–f, 10c, 11a)	Nikon Metrology XT H 225 ST High Resolution CT Scanner (University of Cambridge)	120	130	0.125
NMS G 1984.15.2 (slab piece with metatarsal; Fig. 11b)	Nikon Metrology XT H 225 ST High Resolution CT Scanner (University of Cambridge)	170	125	0.016
NMS G 1984.15.3 (slab piece with metatarsals section 1; Figs 10a, 11c, d)	Nikon Metrology XT H 225 ST High Resolution CT Scanner (University of Cambridge)	175	180	0.108
NMS G 1984.15.3 (slab piece with metatarsals section 2; Figs 10b, 11e, f)	Nikon Metrology XT H 225 ST High Resolution CT Scanner (University of Cambridge)	180	175	0.078
NMS G 1984.15.3 prepped piece (right fibula; Fig. 9a–f)	Nikon Metrology XT H 225 ST High Resolution CT Scanner (University of Cambridge)	110	145	0.065
NMS G 1975.5.5 (right ilium and left ischium)	Nikon Metrology XT H 225 ST High Resolution CT Scanner (University of Cambridge)	115	140	0.0901

The morphology of the Dora specimens (NHMUK R10000, NMS G 1975.5.5 and NMS G 1984.15.1–3) remains incompletely studied, because the specimens are buried in slabs of rock, and not all bones have been prepared out. In NHMUK VP R10000, extensive scales and other bones on the surface cover the rest of the skeleton, so manual preparation would destroy the depositional context of the fossil and risk damaging it. Here, we used computed tomographic (CT) scanning as a non-destructive method to further examine the postcranial morphology of *Crassigyrinus scoticus*. CT scans have revealed previously hidden bones in early tetrapods. For example, an ulna and possible sternbrae were discovered in *Ichthyostega* (Pierce *et al.* 2012, 2013), an atlas–axis complex was discovered in the stem amniote *Orobates pabsti* (Nyakatura *et al.* 2015) and an entirely new tetrapod species, *Aytonerpeton microps*, was discovered by chance from micro-CT scans of a lungfish specimen (Clack *et al.* 2016). New material could provide more (or refined) characters for phylogenetic analysis. Finally, new discoveries can be analysed in a comparative framework to investigate the morphological disparity present in tetrapods during the Carboniferous. Why did some animals remain aquatic, or become secondarily aquatic, while their contemporaries became increasingly terrestrial? The aim of our study is to help fill in the gaps in our understanding of the palaeobiology of the enigmatic tetrapod *Crassigyrinus* by contributing new data on its morphology.

1. Materials and methods

We scanned all available postcranial material of *Crassigyrinus scoticus*, including manually prepared elements and pieces of slab containing fossil material (Table 2). For the NMS G 1984.15.1–3 and NMS G 1975.5.5 specimens, a micro-CT

scanner was used to obtain high-resolution scans. However, of the NHMUK VP R10000 slab, only two small slab pieces and the manually prepared elements could be scanned with a micro-CT scanner. The main slab had to be scanned with a regular medical CT scanner, since it was too large to fit in a micro-CT scanner, but these scans yielded no new information because of their poor resolution. Bones from the micro-CT scans were segmented in Mimics 19.0 (Materialise Inc., Leuven, Belgium) software to remove the matrix and create a three-dimensional (3D) model of each bone (Fig. 2). CT image stacks and final 3D models are available on Figshare (https://figshare.com/projects/Crassigyrinus_stem_tetrapod_fossil_CT_scan_data/38249).

2. Results and discussion

The digital preparation revealed previously undiscovered bones in both the NHMUK VP R10000 and the NMS G 1984.15.1–3 and NMS G 1975.5 specimens (Table 3), as described in more detail in the following sections.

2.1. Axial skeleton

2.1.1. Possible pleurocentra. Small boat- or wedge-shaped elements were found in the NHMUK VP R10000 specimen (Fig. 3). We tentatively identify these elements as pleurocentra, although they might also be fragments of other bones. Panchen (1985) did not note the presence of pleurocentra; however, he did refer to a small ‘banana-shape’ piece of bone (Figs 3e, 4f) that could potentially be a pleurocentrum. Yet, in the absence of any other similar bones, he concluded it was more likely to be a fragment of the apex of an intercentrum, and described *Crassigyrinus* as being monospondylous.

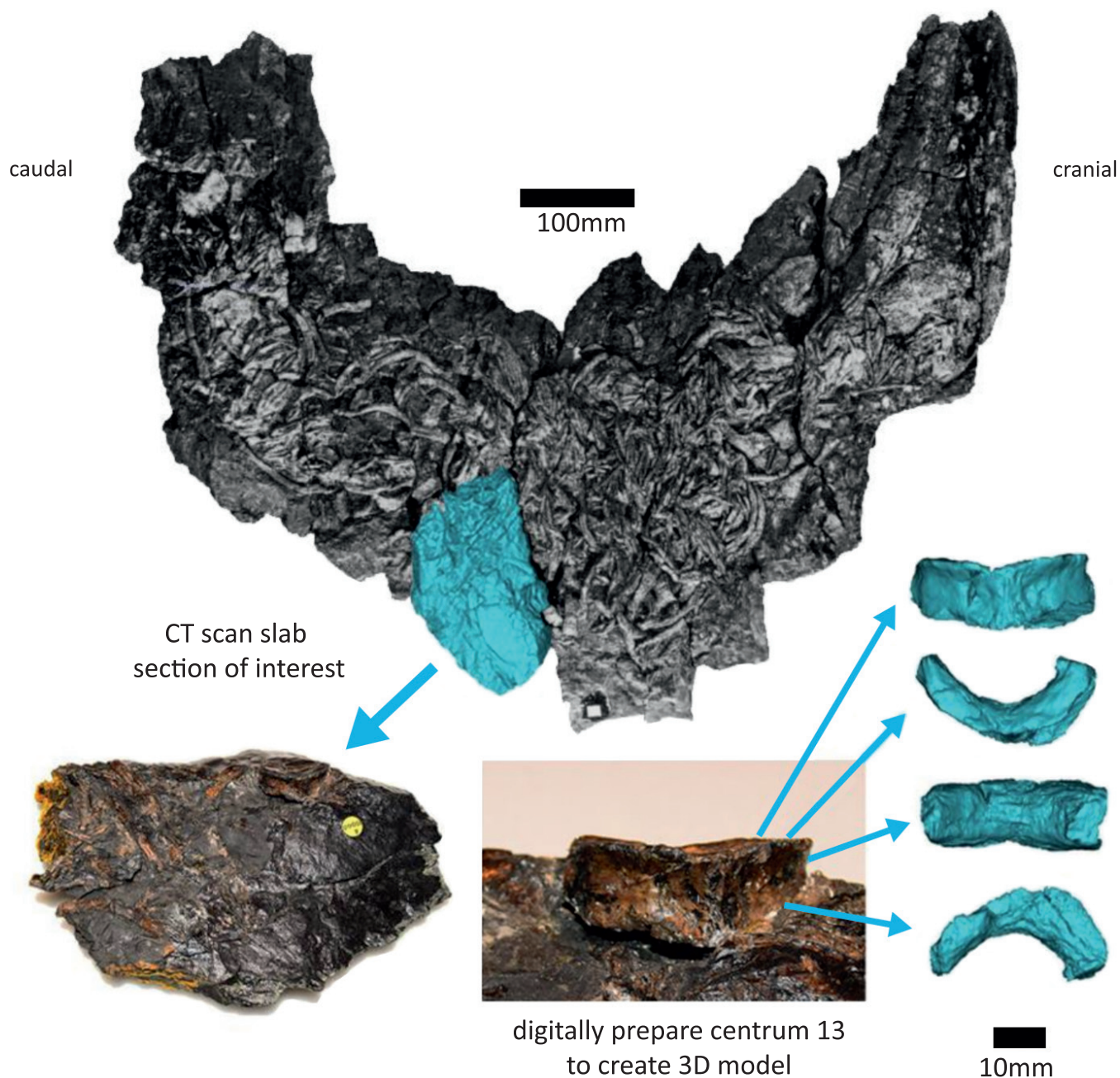


Figure 2 Segmentation process of centrum 13. Model created from segmented CT scans in blue. Full specimen photo from Panchen (1985).

Digital segmentation of the ‘banana-shaped’ piece has clarified its morphology, and we discovered another bone that could potentially be a serial homologue of this element. This element (Figs 3c, 4e) is slightly smaller than Panchen’s (1985) putative pleurocentrum, which is in agreement with its more anterior location along the vertebral column, near the skull (compared to Panchen’s piece, which was found near intercentrum 17). We also discovered two additional elements that, in size and morphology, conceivably are pleurocentrum ossification centres that did not fuse in the midline (Figs 3a, f, 4b, d). The apparent scarcity of these elements may be a preservational artefact, but it is also worth noting that ossified pleurocentra are not necessarily present in every vertebral element. For example, it appears that *Acanthostega* only had pleurocentra from the eighth presacral to around the 22nd caudal vertebra (Coates 1996), and in *Ichthyostega* it appears that the anterior thoracic pleurocentra ossified after the posterior ones (Pierce *et al.* 2013).

If these elements are indeed pleurocentra, it is unclear whether the elements in Figure 3c and 3e are each two ossifications that have fused in the midline, or whether they each represent one ossification centre. Danto *et al.* (2017) provided a valuable overview of pleurocentra and intercentra morphology in early tetrapods, noting that in stem-tetrapods and temnospondyls, the pleurocentra ossify from two dorsal ossification centres which sometimes fuse in the midline. Ontogenetic variation in the degree of ossification of pleurocentra has been reported in *Proterogyrinus* (Holmes 1984) and the seymouriamorph *Discosauriscus* (Klembara & Bartik 1999). In addition to ontogenetic factors, and more relevant to our analysis of the NHMUK VP R10000 specimen, there can also be regional variation in the degree of fusion in a single individual. For example, *Osteolepis* exhibits such change along the vertebral column, with the anterior pleurocentra being a single piece and the mid-trunk pleurocentra being paired (Panchen 1977). Intercentra fuse from two ossification centres, and different stages of fusion can be observed in the growth series of *Greererpeton*

Table 3 New material found through segmentation of CT scans. Abbreviations: NHMUK VP = Natural History Museum, Department of Vertebrate Palaeontology, London (formerly the British Museum); NMS G = National Museums of Scotland, Department of Geology, Edinburgh (formerly the Royal Scottish Museum); CT = computed tomography.

Specimen number	Elements
NHMUK VP R10000	Rib fragments, neural arch, possible pleurocentra, radius, ¹ metacarpal ¹
NMS G 1984.15.1	Metatarsal, left fibula ²
NMS G 1984.15.2	Metatarsal ¹
NMS G 1984.15.3	Metatarsals
NMS G 1975.5.5	Possible ossified pubis

¹ Discovered by Panchen (1985) (bones partially exposed on slab surface) but greater detail revealed by segmentation.

² Bone previously described by Panchen & Smithson (1990), but identified as left sacral rib.

intercentra (Godfrey 1989). The intercentra of *Crassigyrinus* also change in the degree of coossification along the vertebral column – the anterior intercentra have a midline constriction that indicates coossification of bilateral halves, but such a constriction is not visible in the posterior intercentra (Panchen 1985). It is worth noting, however, that the pleurocentra of *Crassigyrinus* do not display a correlation between the degree of fusion and apparent position along the vertebral column. For example, in a slab section near the skull, we found both a bilateral half and a potentially fused pleurocentrum (Fig. 3). This could be due to taphonomic disturbance, as none of the pleurocentra were found in articulation with any other elements. Another explanation is a high degree of plasticity in the amount of fusion of pleurocentra, unrelated to position. The elements we discovered are cautiously interpreted as pleurocentra, but it remains unclear if the two ossification centres fused in the midline in some pleurocentra.

If these additional elements that we discovered are indeed pleurocentra, *Crassigyrinus* was diplospondylous (possessing both intercentra and pleurocentra) instead of monospondylous (having a single repeated centrum down the length of the vertebral column). *Crassigyrinus* could have had rhachitinous vertebrae (Fig. 5c), in which there is an anterior, large horseshoe-shaped intercentrum ventral to the notochord and a pair of smaller pleurocentra dorsal to the notochord and posterior to the intercentrum (shown in *Eryops* in Fig. 5a). A rhachitinous vertebral pattern is present in the whatcheerids *Whatcheeria* and *Pederpes* (Lombard & Bolt 1995; Clack & Finney 2005), to which *Crassigyrinus* has been proposed to be closely related (but see page 3 about the instability of this relationship). In *Whatcheeria*, fusion of the paired pleurocentra was noted in the lumbar region of a specimen (Lombard & Bolt 1995). No such fusion is present in *Pederpes* (Pierce *et al.* 2013). In shape, the intercentra and some putative pleurocentra (Figs 3c, e, 4e, f) of *Crassigyrinus* look similar to those of *Pederpes* (Pierce *et al.* 2013), although the pleurocentrum size, relative to intercentrum size, is smaller in *Crassigyrinus* (Fig. 4). Furthermore, the *Crassigyrinus* intercentrum is a more slender wedge shape in lateral view than the intercentra of *Pederpes*. Note that the left dorsal edge of centrum 13 (Fig. 4a) has been sheared off, so the morphology is distorted. The right side of centrum 13, and centra 14 and 17 (Panchen 1985, fig. 17b, c) show the tapering dorsal edge.

The putative pleurocentra of *Crassigyrinus* differ from those of *Whatcheeria* in that the latter have large anterior facets and small posterior facets for articulation with the neural arches (Lombard & Bolt 1995), a morphology which is also found in *Eryops* (Moulton 1974). No facets are visible in the *Crassigyrinus* pleurocentra, except maybe the slight depression seen in Figure 3f. This piece looks similar to the *Eryops* pleurocentra in overall shape (Moulton 1974, fig. 13d). A rhachitinous pattern in *Crassigyrinus* is conceivable, because in this case the intercentra would hide the pleurocentra if the vertebral column is viewed from the ventral side, which is

the side that is exposed in the NHMUK VP R1000 specimen. We rule out a gastrocentrous vertebral pattern, such as in *Proterogyrinus* (Fig. 5b; Holmes 1984), because in this pattern the pleurocentra are positioned ventrally, and no pleurocentra are visible between the intercentra found in articulation on the exposed surface of the NHMUK VP R1000 slab. In *Ichthyostega*, the ‘reverse’ rhachitinous vertebral pattern was not identified until the material was micro-CT and synchrotron scanned by Pierce *et al.* (2013). The main argument against the identification of the new *Crassigyrinus* elements as pleurocentra became apparent with the discovery of element b in Fig. 3 (c in Fig. 4). We initially interpreted this to be another contender as a pleurocentrum piece, and it even bears a large facet. However, upon comparison with the intercentra, we realised that the facet shape is exactly like the intercentrum facet, and this piece is probably the broken dorsal edge of an intercentrum. We tested an articulation with the broken edge of centrum 13 (Fig. 4a), and while the fit was not exact, it confirmed that element b in Fig. 3 (c in Fig. 4) is likely to be part of an intercentrum. The lack of an obvious fracture line led us to reconsider the other elements. Our identification of them as pleurocentra rested, in part, on the absence of a shear line, so we deemed them complete; but we think it is also possible that they are fractured pieces, hence our caution here. Note that another element in Figure 3, element d (Fig. 3d), was found near element c (Fig. 3c), but is definitely not a pleurocentrum. It could be a distorted neural arch, but looks most like a rib-end fragment.

2.1.2. Discussion of vertebral pattern. Early tetrapods exhibit several different arrangements of centra (Pierce *et al.* 2013; Danto *et al.* 2016, 2017), and the ancestral pattern is unclear. *Eusthenopteron*, *Whatcheeria* and *Acanthostega* were described as having rhachitinous vertebrae (Andrews & Westoll 1970; Lombard & Bolt 1995; Coates 1996). This arrangement was long thought to be the ancestral condition (Romer 1960; Carroll 1988; but see Panchen (1977) for a discussion of alternate hypotheses, and Gardiner (1983) for an overview of hypotheses of vertebral homologies). However, a recent micro-CT analysis of *Ichthyostega* and *Acanthostega* revealed a ‘reverse rhachitinous’ pattern, in which the paired pleurocentra are fused to or articulate with the intercentrum posterior to them (*Ichthyostega* and *Acanthostega*, respectively) (Pierce *et al.* 2013). Such a ‘reverse rhachitinous’ pattern is not unusual in early tetrapods; ‘reverse rhachitinous’ fusion is also found in *Whatcheeria* (Lombard & Bolt 1995) as well as a range of other tetrapods such as *Dvinosaurus*, *Platyops* and *Dendrerpeton* (Shishkin 1989). Even in *Eryops*, which is often used as an example of a typical rhachitinous pattern, the pleurocentra coossified with the intercentrum posterior to them in one specimen (Moulton 1974).

Vertebral arrangement has historically been used as a characteristic to diagnose taxa (van Zittel 1911; Watson 1919; Romer 1960). This is also evident in the names of groups such as Embolomeri, Stereospondyli and Phyllospondyli,

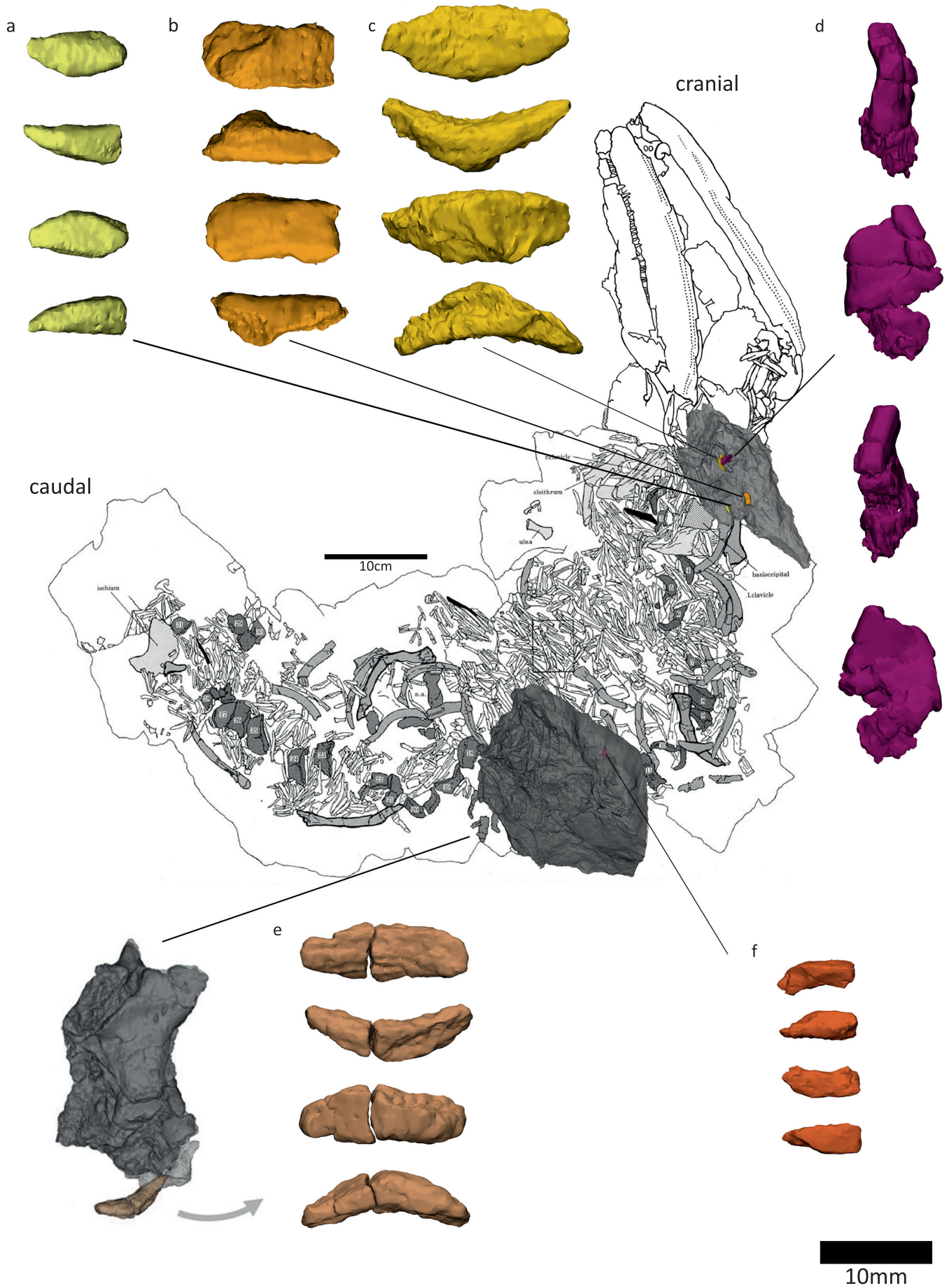


Figure 3 Elements (a–f) discovered from micro-CT scans of two slab sections of the NHMUK VP R10000 specimen, one from the cervical region and the other from the mid-thoracic region. Line drawing from Panchen (1985).

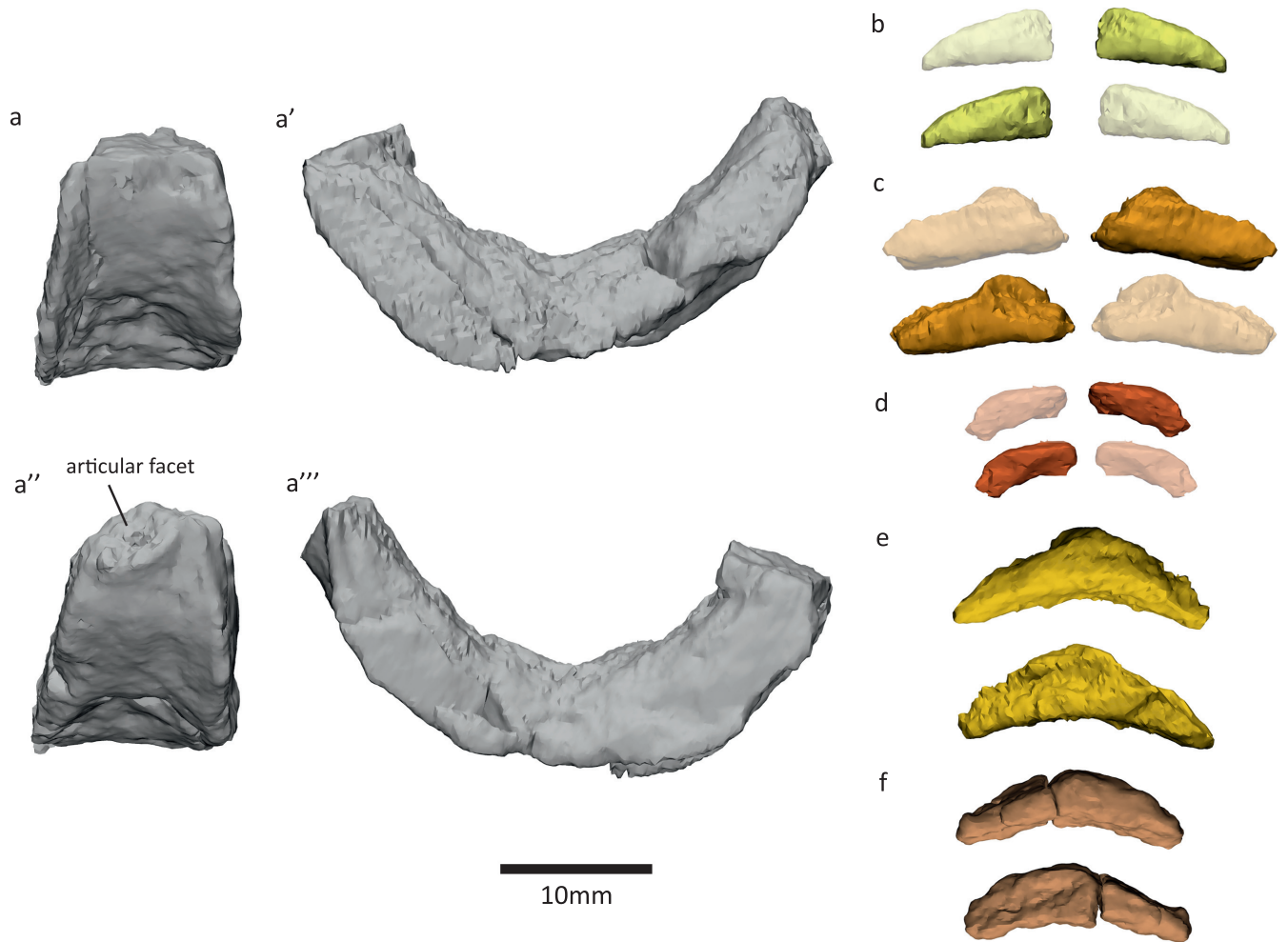


Figure 4 New elements discovered in the NHMUK VP R10000 specimen. (a) Centrum 13 (Panchen 1985). (b, d–f) Possible pleurocentra. (c) Probably an intercentrum fragment.

all of which are based on vertebral pattern (Holmes 1989). Romer approached the question of amphibian relationships by examining vertebral patterns. He divided Amphibia into two main groups: the Lepospondyli (including fossil lepospondyls and the extant lissamphibians Urodela and Apoda) and the Apsidospondyli (including the ‘Labyrinthodontia’ and the amniotes and Anura) (Romer 1960). However, caution is warranted when making phylogenetic inferences based on vertebral element morphology alone. A recent histology study by Danto *et al.* (2016) demonstrated that patterns of vertebral development have a weak phylogenetic signal, and phylogeny is not always a reliable indicator of vertebral pattern. For example, based on phylogenetic position, we would expect the Plagiosauridae to possess a large disc-shaped intercentrum with reduced or absent pleurocentra, like other members of Stereopondyli. Instead, the Plagiosauridae possess a single spool-shaped centrum, and the neural arch is positioned between two centra (Danto *et al.* 2016).

Panchen proposed that in seymouriamorphs, anthracosaurs (except embolomeres), reptiles and microsaur, the pleurocentrum is large relative to the intercentrum because it, and the neural arch it is associated with, supports the vertebral column during weight-bearing (Panchen 1977). Temnospondyls, on the other hand, have a larger intercentrum, the centrum most closely linked with the myoseptum and ribs. This arrangement would be more suited to support lateral movement during swimming (Panchen 1977). Clack (2012) discussed two examples that corroborate Panchen’s idea about vertebral function: the secondarily aquatic embolomeres, such as *Archeria*, increase

the size of the intercentrum, and the more aquatic of the temnospondyls, such as *Mastodonsaurus* (Moser & Schoch 2007), reduce the size of their pleurocentrum – in both cases, the more aquatic environment correlates with a trend to increase the size of the intercentrum, which often becomes a complete disc.

However, Clack (2012) noted that rhachitomous vertebrae do not necessarily imply aquatic locomotion. For example, *Eryops*, interpreted to be capable of at least some degree of terrestrial locomotion, has rhachitomous vertebrae (Clack 2012). Furthermore, not all aquatic organisms are rhachitomous (see discussion of embolomeres and neotridians in Carroll (1988)). There may also be a size effect. Danto *et al.* (2016) discussed the spool-shaped centra in the miniaturised *Microbrachis* and *Dolesempeton*. These two taxa are not closely related and they are thought to be aquatic and terrestrial, respectively. Therefore, because phylogeny and environment are controlled for, Danto *et al.* (2016) concluded that the spool-shaped centra are associated with small body size. Vertebral pattern appears to be a plastic trait influenced by various factors that also include ontogeny.

If the elements we discovered are really pleurocentra, and *Crassigyrinus* is rhachitomous, this does not inform the phylogenetic placement of *Crassigyrinus*, because the rhachitomous pattern is plesiomorphic for tetrapods. Furthermore, the pieces are very small, so they are unlikely to have constricted the notochord much more than the much larger intercentrum and neural arch already did.

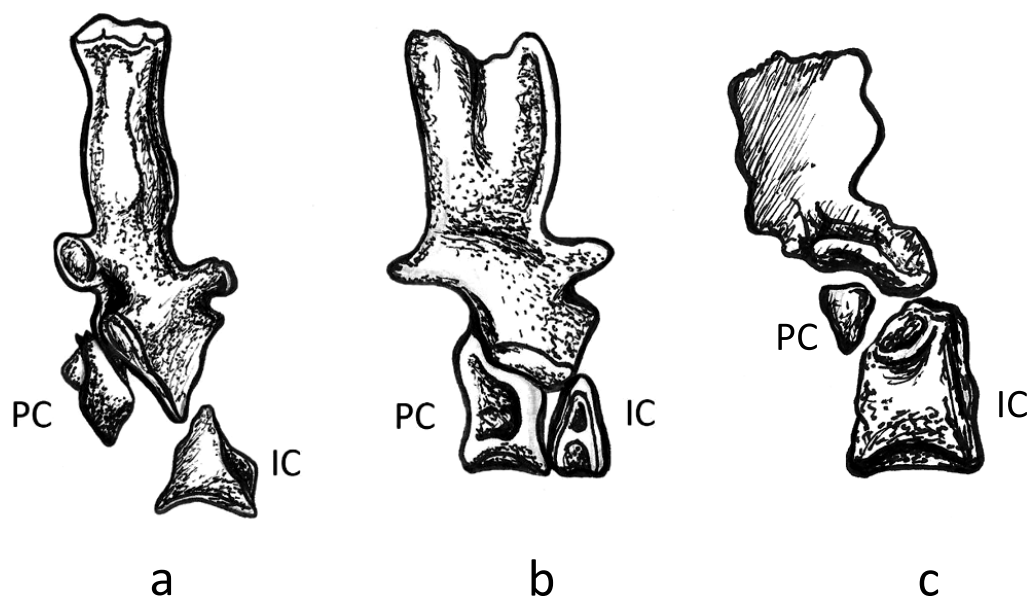


Figure 5 Vertebral patterns. (a) *Eryops* with typical rhachitinous pattern (based on Moulton 1974). (b) *Proterogyrinus* with gastrocentrous pattern (based on Holmes 1984). (c) Inferred rhachitinous pattern for *Crassigyrinus*. Abbreviations: PC = pleurocentrum; IC = intercentrum.

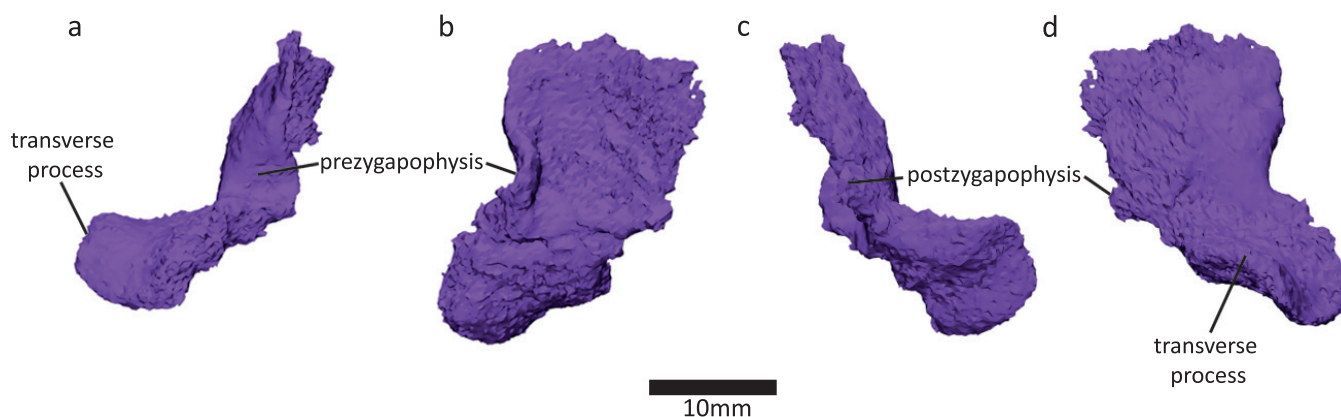


Figure 6 Newly discovered half of neural arch in (a) anterior, (b) medial, (c) posterior and (d) lateral views.

2.1.3. Neural arch. We discovered a neural arch in the slab piece near centrum 13 of the NHMUK VP R10000 specimen (Fig. 6). All neural arches found are bilateral halves, with no midline fusion. This contrasts with *Whatcheeria*, in which all neural arches are fused (Lombard & Bolt 1995). In *Pederpes*, at least some neural arch halves were probably unsutured (Clack & Finney 2005). In *Acanthostega*, only a region of the vertebral column, from the fourth presacral to about the 22nd caudal vertebra, shows fused neural arch pairs (Coates 1996). The neural arches are poorly ossified. Based on the structure of the neural arch and intercentrum, it appears that the notochordal and neural canals were connected, which is also evident in *Acanthostega* (Coates 1996).

The transverse process of the neural arch projects at almost a right angle to the dorsoventral axis of the spine. This also holds true for the most well-preserved neural arch from this specimen (neural arch 14 in Panchen 1985, fig. 17g), so it is unlikely to be a preservational artefact. Neural arch 14 and the new neural arch were found in close proximity to each other, so this morphology seems to be present in the mid-thoracic area of the vertebral column of *Crassigyrinus*. However, there may be regional variation, because the NMS G 1984.15.3 neural arch (Panchen & Smithson 1990, fig. 8f) projects more ventrally.

The transverse process of the new neural arch projects extremely laterally, relative to the more ventrally facing transverse processes in *Acanthostega*, *Ichthyostega* and *Pederpes* (Pierce *et al.* 2013). However, the transverse processes of the posterior thoracic vertebrae of *Ichthyostega* face laterally (Pierce *et al.* 2013), similar to those in *Crassigyrinus*. Smithson (1985) also reported varying orientations for the transverse processes of *Eoherpeton*, pointing either dorsolaterally or ventrolaterally in anterior view. He interpreted the latter to come from a more posterior position, because both *Eryops* (Moulton 1974) and probably also *Eogyrinus* (Panchen 1966) exhibit an anteroposterior shift from lateral to ventrolaterally oriented transverse processes along the vertebral column. Note, this is slightly different from *Ichthyostega* where the transverse processes of the anterior thoracic vertebrae also face ventrally (Pierce *et al.* 2013).

There is a small postzygapophysis and a small prezygapophysis. As in the *Crassigyrinus* neural arch 14 and 17 (Panchen 1985, figs. 17g, 18b), the postzygapophysis is an uneven posterior section of bone (Smithson & Clack 2018).

2.1.4. Ribs. We discovered several ribs in the NHMUK VP R10000 specimen, near centrum 13 (Fig. 7). Only one of these ribs was figured in Panchen's (1985) illustration of the entire specimen, and none were prepared out until now.

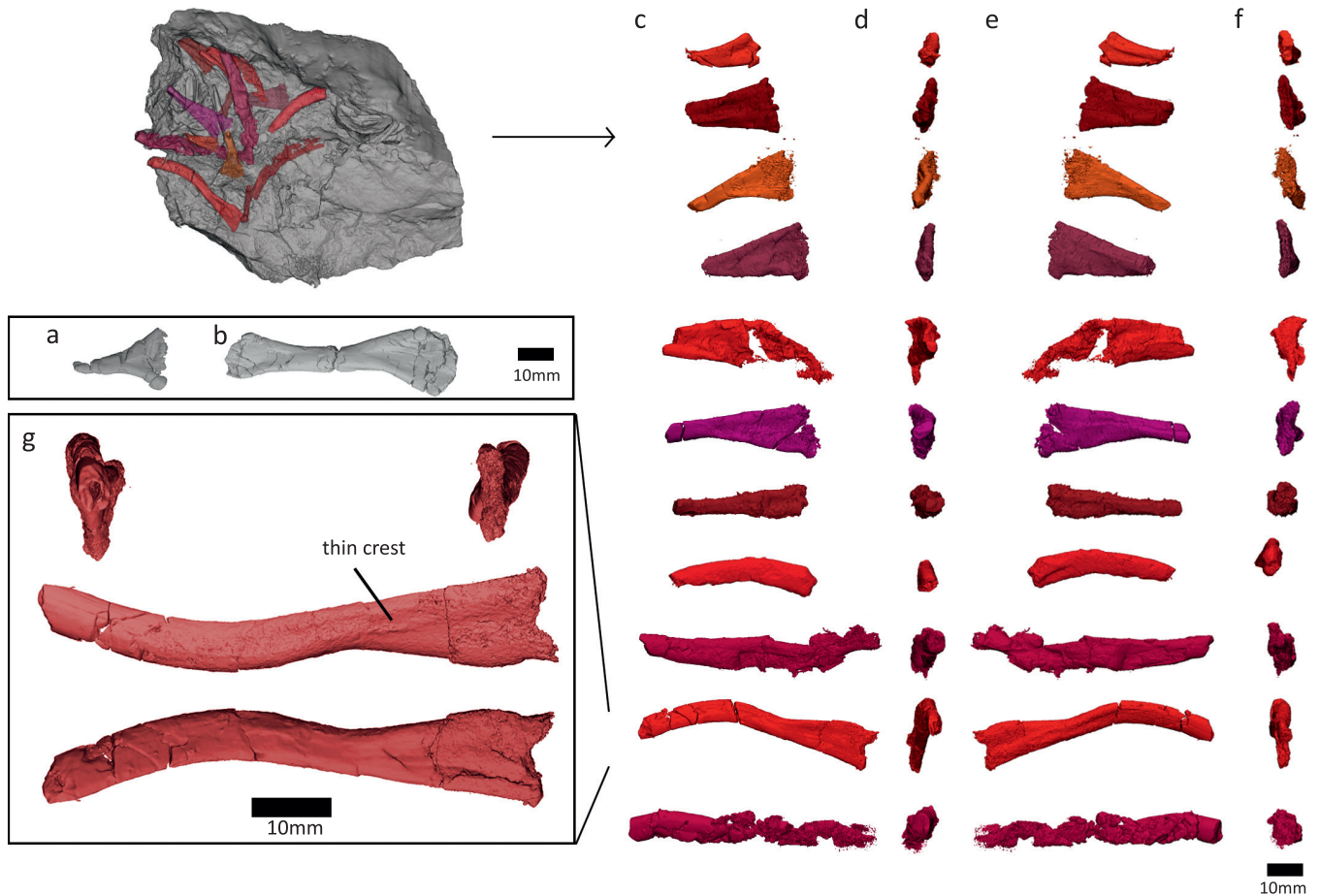


Figure 7 *Crassigyrinus* rib morphology. (a) Panchen's (1985) 'immediately presacral rib'. (b) 'Thoracic rib'. (c–f) New ribs discovered in NHMUK VP R10000. (g) Closeup of the most complete new rib, with breakages mended. Based on comparative material, the views are most likely: (c) anterior; (d) distal; (e) posterior; (f) proximal.

Many of the newly recognised ribs are at the edge of the slab and may be broken. However, the distal shaft ends of several of the ribs (see Fig. 7) look similar and do not appear to be fractured, so it seems that these ribs might be complete (although it is possible that the shaft continued as a cartilaginous extension, as has been proposed for ribs of *Eryops* (Moulton 1974)).

Furthermore, we investigated the fossil as well as the lower-resolution medical CT scans of the rest of the NHMUK VP R10000 specimen, and no ribs have two expanded ends, so they are either all broken, or the ribs are complete and lack a distal expansion. For example, rib g (Fig. 7g) tapers to such a rod-like point, and has only a slight curvature. It is very similar to the posterior thoracic rib of *Ossinodus*. The posterior thoracic rib of *Ossinodus*, which was described as being complete, terminates distally without any flaring (Warren & Turner 2004, fig. 8k–n). Rib ends that are rod-like and do not have a distal expansion are also known from the thoracic region of *Proterogyrinus*, *Colosteus* and *Ossinodus* (Hook 1983; Holmes 1984; Warren & Turner 2004). This shape supports our interpretation that *Crassigyrinus* ribs did not have flared distal ends, except for possibly the 'thoracic rib' described by Panchen (1985), but no other such rib has been found.

All newly recognised ribs have a crest on one side of the proximal end and a concave depression on the other. The crest is also visible in *Ossinodus*, *Proterogyrinus* and *Eoherpeton* (Holmes 1984; Smithson 1985; Warren & Turner 2004). The smaller, more triangular ribs resemble a rib tentatively identified

by Panchen as being an immediately presacral rib (Panchen 1985, fig. 19b; Fig. 7a). These ribs also look similar to the posterior trunk ribs in *Acanthostega* (Coates 1996, fig. 10g, h). In *Crassigyrinus*, these short, almost triangular ribs are preserved near centra 13–16, in the mid-trunk region of the animal, although this location could be due to taphonomic displacement, as no ribs are found in articulation with vertebrae, and several rib morphologies were found in this slab section. Regardless of their location along the vertebral column, there was some amount of variation in the ribs of *Crassigyrinus* (Fig. 7), although the proximal ends all look similar, and only the length of the shaft seems to vary. A greater amount of rib variation along the vertebral column has been described in several early tetrapods, such as *Proterogyrinus*, *Pederpes*, *Acanthostega* and *Ichthyostega* (Holmes 1984; Coates 1996; Jarvik 1996; Clack & Finney 2005).

Coates (1996) noted that regional variation in rib morphology is not only present in early tetrapods but also in the tetrapodomorph *Eusthenopteron*, in which the anterior 3 ribs are much shorter and broader than the more posterior ribs. The ribs of *Tiktaalik* also show regional variation: most ribs have plate-shaped flanges that project caudally, but the flanges become triangular in the posterior ribs (which are also shorter), and the anterior-most ribs have uncinat processes projecting cranially from the shaft (Daeschler *et al.* 2006).

In all discovered ribs, the proximal end is spatulate and does not bear two distinct rib heads. This is similar to the rib-head shapes in many early tetrapods, such as *Acanthostega*, *Pederpes*, *Ichthyostega* and *Ossinodus* (Coates 1996; Jarvik

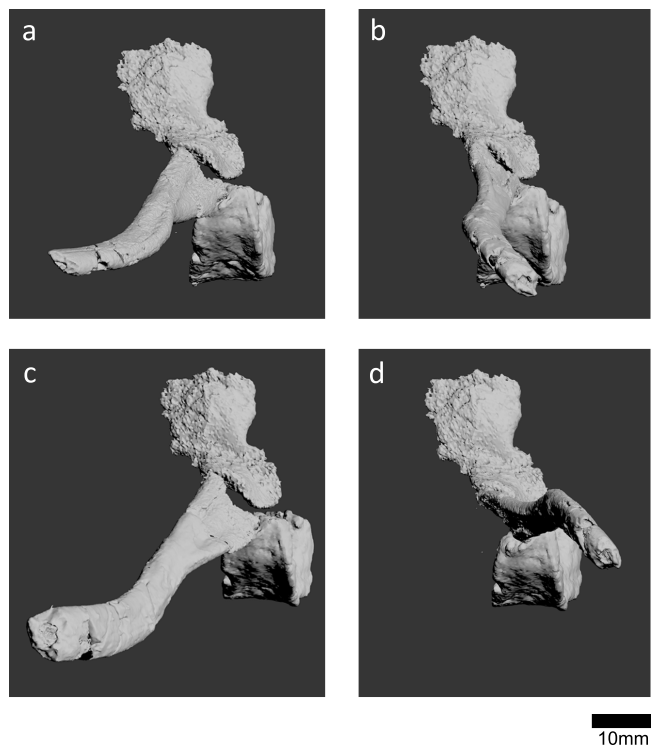


Figure 8 Potential reconstructions of the costal–vertebral articulations of *Crassigyrinus*, based on centrum 13 and a new neural arch and rib found near centrum 13. (a, b) Reconstruction assuming the rib is a right rib. (c, d) Reconstruction assuming the rib is a left rib; rib has been mirrored to reconstruct the right-side articulation.

1996; Warren & Turner 2004; Clack & Finney 2005). The ribs of *Crassigyrinus* also resemble those of *Acanthostega* in the lack of strong ventral curvature or uncinat processes (Coates 1996). Uncinate processes or strongly developed mid-shaft flanges are present on the thoracic ribs of *Whatcheeria* and *Ichthyostega*, and these flanges are located more distally in the posterior ribs (Lombard & Bolt 1995; Ahlberg *et al.* 2005). The only expanded distal end in *Crassigyrinus* is seen in Panchen's 'thoracic' rib, which resembles *Pederpes* ribs 11–13 (Clack & Finney 2005). The anterior thoracic ribs of *Acanthostega* also show this morphology. Our discoveries do not include any ribs with both proximal and distal flared ends as Panchen's 'thoracic' rib does, although this is possibly because many of the longer (presumably mid-thoracic) ribs we discovered are fractured mid-shaft.

2.1.5. Reconstruction of axial articulations. The intercentra of *Crassigyrinus* have small facets on the dorsolateral surface of each side. The facets are present on all intercentra that were manually prepared (centra 1 and 14–17 in Panchen (1985), although on centrum 1 they are not distinct). We also found a facet on centrum 13, but only on one side, because the dorsal apex on the other side is sheared. Panchen interpreted these facets as neural arch facets, and noted that they were positioned on the anterior or posterior sides of the apex (Panchen 1980, 1985).

However, the intercentra (except for the degree of midline fusion) and facets are similar to those of *Ichthyostega*, in which the facets face posterolaterally and are areas of articulation with the ribs rather than with the neural arch (Jarvik 1996). Posteriorly facing rib facets are also present on the intercentra of *Eusthenopteron*, *Greerpeton*, *Whatcheeria*, *Pederpes* and *Ichthyostega* (Andrews & Westoll 1970; Godfrey 1989; Lombard & Bolt 1995, fig. 3; Clack & Finney 2005; Pierce *et al.* 2013). All of these animals had a rhachitomous (or reverse rhachitomous) vertebral pattern, so it appears that

in rhachitomous vertebrae, a posterior facet for rib articulation is usually found near the apex of the horseshoe-shaped intercentrum. Therefore, we conclude that the articular facets on the *Crassigyrinus* intercentra also face posterolaterally and articulate with the ribs rather than the neural arch.

We can use this facet orientation and the structure of the neural arch, specifically the structure of the transverse process, to examine how the ribs may have articulated with the vertebrae in *Crassigyrinus*. Although the rib shape of *Ichthyostega* differs from *Crassigyrinus* in that *Ichthyostega* has very wide, overlapping thoracic ribs (Jarvik 1996), *Ichthyostega* provides the best analogue for constructing the rib-head articulation with the intercentrum and neural arch, because, in the posterior thoracic vertebrae, the transverse processes of the neural arches of *Ichthyostega* project laterally (Pierce *et al.* 2013, fig. 1c). This resembles the transverse processes in *Crassigyrinus* and is unlike the condition in most other early tetrapods (see Section 2.1.3). The intercentrum shape and rib facet position is also similar in *Crassigyrinus* and *Ichthyostega*. Therefore, we hypothesise a similar rib articulation in *Crassigyrinus* as is present in the posterior thoracic vertebrae in *Ichthyostega* (Pierce *et al.* 2013, fig. 1c).

For our reconstruction, we chose to use centrum 13 and a neural arch and rib (Fig. 7g) that we discovered in close proximity to this centrum, to account for variation in size along the vertebral column. We mended the breaks in this rib to reconstruct the morphology. Figure 8 shows four possible arrangements of the costal–vertebral articulation. The rib articulates with the transverse process of the neural arch and the articular facet on the posterolateral surface of the centrum. Because the elements were found disarticulated and we did not know for certain whether the rib was a left or right rib, we tested several different orientations of the rib, as well as its antimeres. Reconstructions b and c (Fig. 8) have the crest of the rib facing posteriorly; a ridge on the posterior surface of the proximal rib has been described for *Eoherpeton* and *Proterogyrinus* (Holmes 1984; Smithson 1985). No early tetrapods show the ribs curving anteriorly, so reconstruction b (Fig. 8) is unlikely. Based on these criteria, reconstruction c (Fig. 8) is the most likely. However, it is worth noting that in *Ossinodus*, the ridge was described to be on the anterior side of the rib (Warren & Turner 2004), although we are not sure how posterior and anterior surfaces were identified for this disarticulated rib. Reconstructions a and d (Fig. 8) were, therefore, included to account for all possible arrangements. Overall, it appears that the ribs of *Crassigyrinus* projected more laterally than ventrally, and that *Crassigyrinus* was, therefore, a fairly flat-bodied animal.

2.2. Appendicular skeleton

2.2.1. Left radius. We also segmented the left radius of the NHMUK VP R10000 specimen. Previously, only the morphology of the proximal articular surface and what was described as the extensor/dorsal surface (Fig. 9a) were known (Panchen 1985, fig. 21). This latter surface is slightly concave, whereas the previously hidden surface (Fig. 9c), which would be the flexor/ventral surface according to Panchen's identification, is convex. The convex surface projects more distally than the exposed surface. In *Archeria*, *Proterogyrinus*, *Acanthostega*, *Ichthyostega*, *Ossinodus* and *Pederpes*, the extensor/dorsal surface is convex and projects more distally than the flexor/ventral surface (Romer 1957; Holmes 1984; Coates 1996; Jarvik 1996; Warren & Ptasznik 2002; Clack & Finney 2005). Therefore, we reinterpret the exposed, concave surface of the *Crassigyrinus* radius (Fig. 9a) as being the flexor/ventral surface, and identify the previously hidden, convex, distally expanding surface

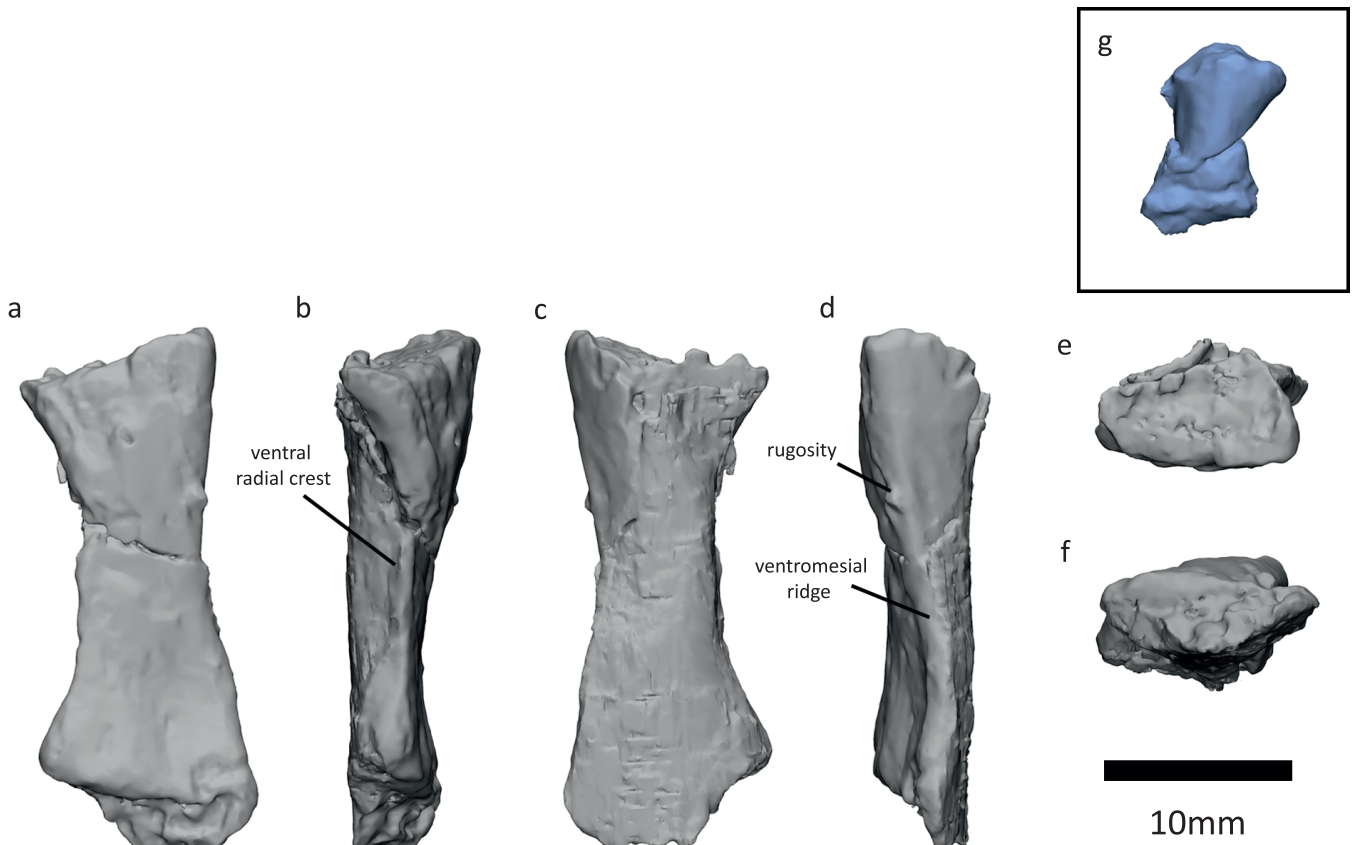


Figure 9 *Crassigyrinus* left radius (a–f) and metacarpal (g), both found near the skull of NHMUK VP R10000 (Panchen 1985, fig. 21). Left radius in (a) flexor/ventral view; (b) lateral view; (c) extensor/dorsal view; (d) medial view; (e) proximal view and (f) distal view; (g) metacarpal in extensor view.

(Fig. 9c) as the extensor/dorsal surface. The radius was associated with the left humerus, and we agree with Panchen's identification of the radius as a left radius. The lateral section of the distal end was in close association with an unknown bone, possibly a branchial element, discussed in Panchen (1985, fig. 21).

Panchen (1985) described a lateral ridge, which probably divided flexor and extensor musculature, and noted that it was similar but not as pronounced as that found in *Archeria* (Romer 1957). With our reinterpretation of dorsal and ventral sides, this ridge (Fig. 9d) is actually on the medial side of the bone, and we interpret it to be homologous to the ventromesial ridge (*sensu* Warren & Ptasznik 2002) found in *Proterogyrinus*, *Acanthostega*, *Baphetes* and *Ossinodus* (Holmes 1984; Coates 1996; Milner & Lindsay 1998; Warren & Ptasznik 2002). This ridge is probably also homologous to the medial ridge in *Archeria* (Romer 1957). Bishop (2014) suggested that the ventromesial ridge is the attachment site for the *brachialis inferior*. On the *Crassigyrinus* radius, there is a small protrusion near the proximal end of the ventromesial ridge (Fig. 9d) – a similar rugosity was interpreted as the insertion of the *humeroradialis* and possibly the *biceps* (if present) in *Archeria* (Romer 1957).

Our segmentation also revealed a sharp ridge on the ventrolateral side of the bone (Fig. 9b), which we interpret to be homologous to the ventral radial crest (*sensu* Coates 1996), and which has been described in several early tetrapods such as *Proterogyrinus*, *Acanthostega*, *Baphetes* and *Ossinodus* (Holmes 1984; Coates 1996; Milner & Lindsay 1998; Warren & Ptasznik 2002). This ridge is probably also homologous to the lateral ridge in *Archeria* (Romer 1957), which is keel-shaped like the ventral radial crest in *Crassigyrinus*. In *Ossinodus*, this crest faces ventrally, whereas in *Crassigyrinus* it faces more

laterally. The ventral radial crest of *Ossinodus* shows no muscle scarring, and might, therefore, not be an area of muscle attachment (Bishop 2014). *Crassigyrinus* lacks the other two ridges – the dorsomesial ridge and the proximoventral ridge (*sensu* Warren & Ptasznik 2002) – that are found in the radii in *Ossinodus*, *Pederpes*, *Acanthostega*, *Greererpeton* and *Baphetes* (Molnar *et al.* 2017).

Overall, the morphology of the radius is very similar to that of *Ossinodus* (Warren & Ptasznik 2002). At the distal end, the lateral surface is more concave than the medial surface, and the dorsomesial surface extends more distally than the ventrolateral surface (Warren & Ptasznik 2002). In both *Crassigyrinus* and *Ossinodus*, the distal surface appears to be abraded (Warren & Turner 2004), and it is likely that both radii were finished in cartilage.

2.2.2. Metacarpal. We segmented a metacarpal found near the radius and humerus of the NHMUK VP R10000 specimen (Fig. 9g). This element was previously figured in outline (Panchen 1985, fig. 21), but here we show greater detail. The metacarpal is ~9 mm long – about half the length of the metatarsals. This is to be expected, because the forelimb is smaller than the hindlimb. There is a break in the metacarpal, and the flexor surface was compressed with the bone beneath, so we were only able to segment the extensor surface. It appears that the metacarpal, like the metatarsals (see Section 2.2.5), was asymmetrical, although taphonomic factors might be responsible for part of this asymmetry.

2.2.3. Potential ossified pubis. In the specimen NMS G 1975.5.5, the ventral/distal end of the right ilium is compacted with an irregular mass of bone (Fig. 10). The irregular mass might be an ossified pubis. One surface of the bone (Fig. 10b) has a layer of dense, laminar bone (see cross section in

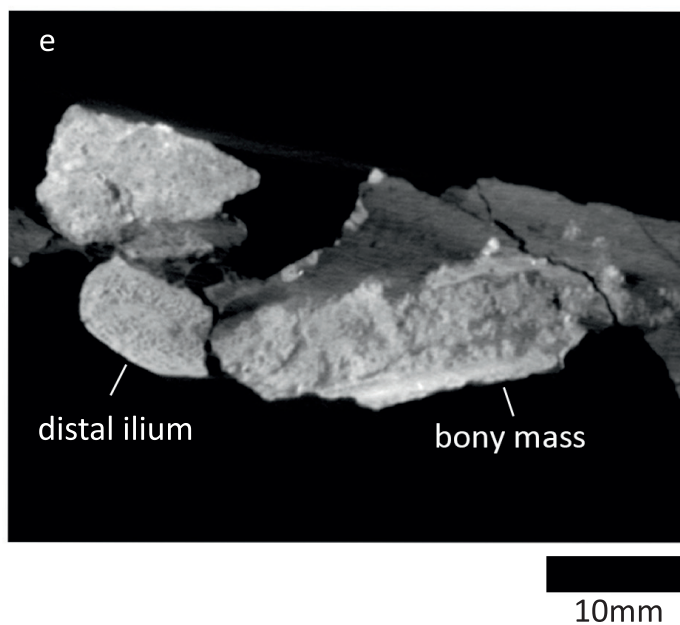
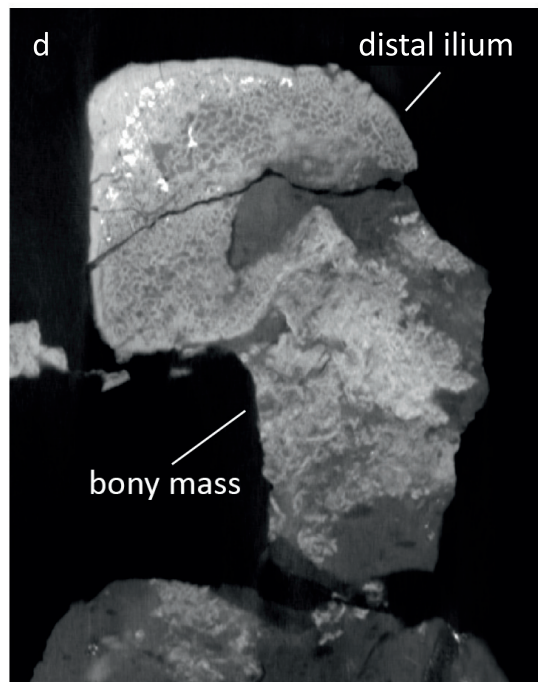
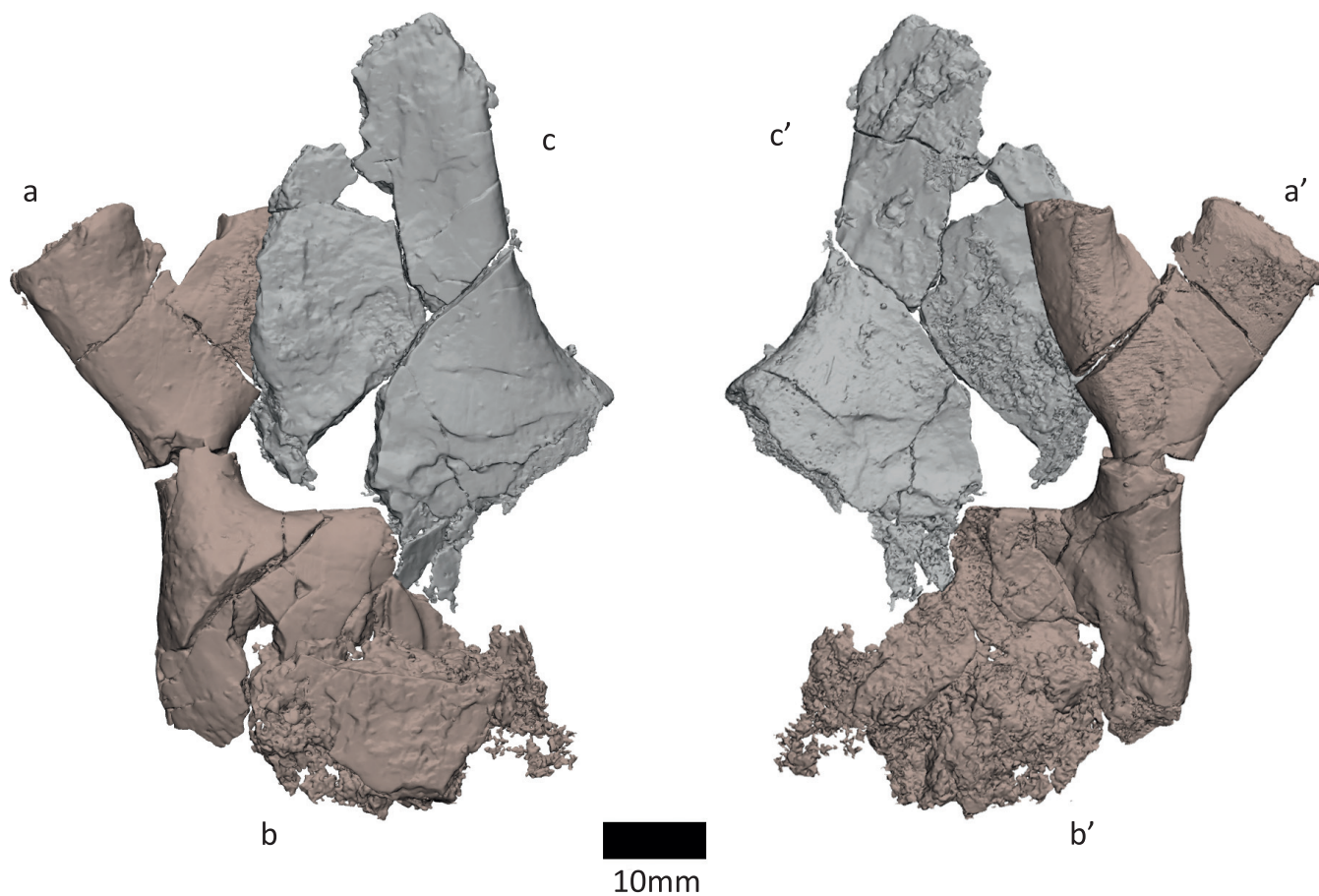


Figure 10 NMS G 1975.5.5 specimen, right ilium in (a) medial and (a') lateral views. (b, b') Mass of bone, potentially an ossified pubis. Left ischium in (c) lateral and (c') medial views. (d) Axial section along distal ilium and bony mass. (e) Transverse section along distal ilium and bony mass.

Fig. 10e), while the other surface is more irregular and less dense (Fig. 10', d). The 'histology' of the laminar layer resembles the shaft of the ilium, whereas the looser layer looks similar to the ischium's bone structure. The NMS G 1984.15.1 ilium does not have this mass of bone on its ventral/distal side.

If this mass of bone is indeed an ossified pubis, it is difficult to determine which side it is from. While it is associated with the right ilium, the finished surface of the pubis, which might even bear some ornamentation (see Fig. 10b), faces the same side as the medial surface of the right ilium. Ornament on the

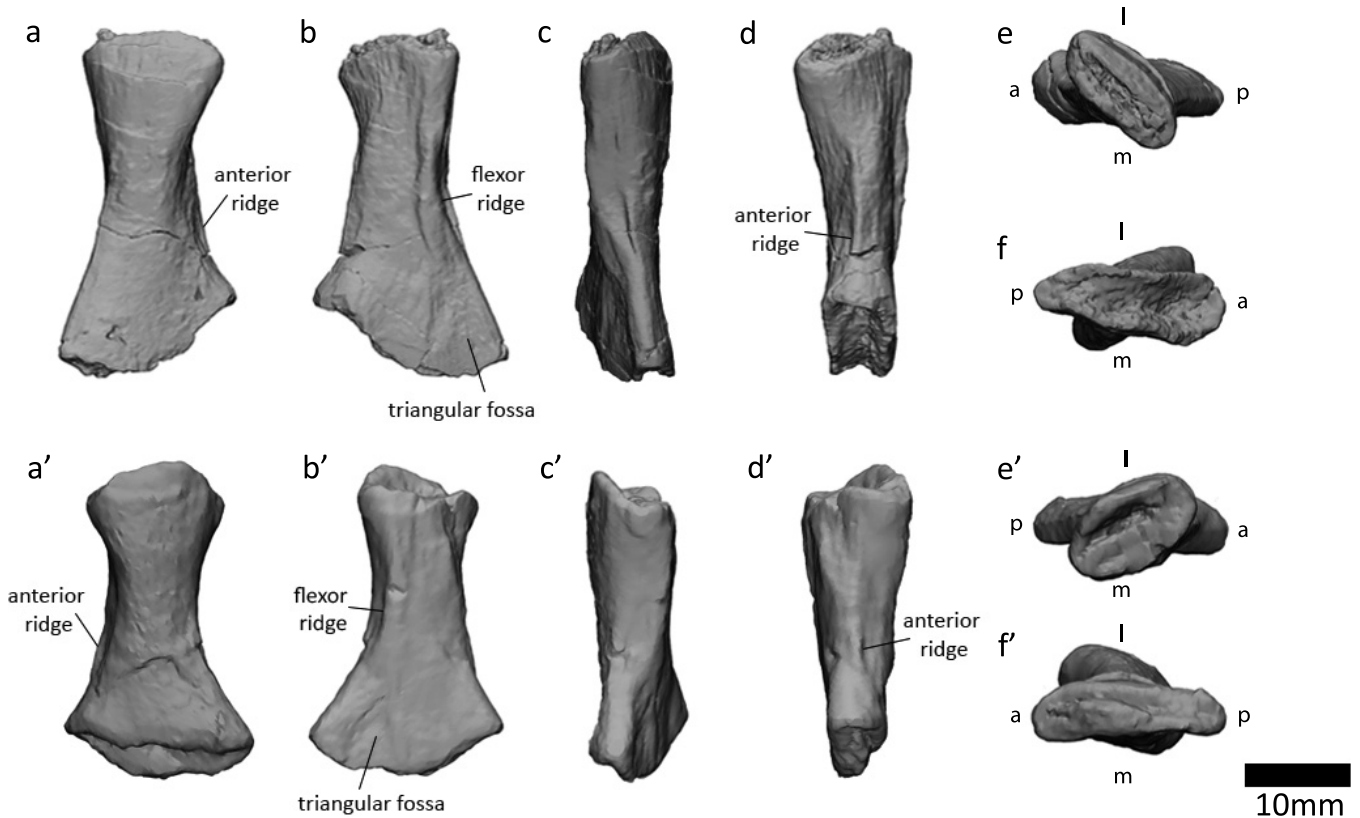


Figure 11 Right fibula at top, left fibula (previously identified as left sacral rib by Panchen & Smithson (1990)) at bottom. (a, a') Lateral (extensor) view. (b, b') Medial (flexor) view. (c, c') Posterior view. (d, d') Anterior view. (e, e') Proximal view. (f, f') Distal view. Abbreviations: l = lateral; m = medial; a = anterior; p = posterior.

medial side would be surprising, based on the lateral location of ornament on the NMS G 1985.15.3 ischium (the ornamentation is less apparent in the 1975.5.5 ischium). If we assume the ornamentation of the pubis to be on the lateral side, this would suggest that the ossified pubis is from the left side and was compacted with the right ilium during taphonomic processes. Taphonomic distortion could also be responsible for the unusual appearance of the bone's structure.

Several Carboniferous tetrapods did not ossify their pubis (Clack 2012). However, the ossified pubis of *Greererpeton* and of NSM005GF045.001 (Nova Scotia Museum, Halifax) from Romer's Gap of Blue Beach (Godfrey 1989; Anderson *et al.* 2015) look very similar to the element we discovered in *Crassigyrinus*.

2.2.4. Left fibula. Examination of the 'left sacral rib' (Panchen & Smithson 1990) in NMS G 1984.15.1 revealed that this bone is actually a left fibula. Indeed, in their description, Panchen & Smithson (1990) noted that this element resembles an epipodial. It shares several key osteological features with the right fibula in NMS G 1984.15.3 (Panchen & Smithson 1990, fig. 11). Both bones have a flexor ridge, an anterior ridge, concave anterior and posterior surfaces and a triangular fossa on the posterodistal medial/flexor surface. The degree of torsion between proximal and distal surfaces is similar (Fig. 11e, e', f, f'). The anterior proximodistal length (measured between the two most anterior points) measures 22 mm in both elements. The main difference between the two bones is that the posterior proximodistal length is greater in the right fibula (29 mm *versus* 23 mm, measured between the two most posterior points). This might be due to variation in the ossification of the ends of the bone, which are unfinished and presumably were covered in cartilage. Variation between bones can be due to variation between individuals (age, sex, idiosyncratic), and can occur between left and right sides of a

single individual. The slabs containing the two elements were found in close proximity, and there are no duplicate elements between the two slabs, so we infer that the two fibulae are from the same individual. The variation between the two bones may also be due to taphonomic distortion.

Reassessment of this element means that no sacral rib has been found for *Crassigyrinus*. Therefore, we do not have direct evidence for the inference that '*Crassigyrinus* had a fully-formed sacrum to transmit the thrust in swimming from the hind limbs to the trunk' (Panchen & Smithson 1990, p. 40). A sacral rib is absent in *Tiktaalik* but present in the Devonian tetrapod *Acanthostega*, and sacral ribs have been found in numerous Carboniferous tetrapods (Clack 2012). It is likely that *Crassigyrinus* had a sacral rib (based on phylogenetic inference from its closest relatives among stem tetrapods), but the morphology and articulation with the pelvis is difficult to infer, because the precise phylogenetic position of *Crassigyrinus* is unclear.

2.2.5. Metatarsals and other pes elements. Panchen & Smithson (1990) tentatively identified three metatarsals (of about 15 mm in length) and four phalanges (of 5–12 mm in length) in specimens NMS G 1984.15.2 and NMS G 1984.15.3. We segmented these (Fig. 12 a1–5, b1, b3), because only a general shape and size have previously been described (Panchen & Smithson 1990). Three of the 'phalanges' (Figs 12a1, a2, b1) could actually be metatarsals: in several early tetrapods, for example *Proterogyrinus*, *Greererpeton*, *Silvanerpeton* and *Pederpes*, the metatarsal of the shortest digit is similar in size and shape to the proximal phalanges of the larger digits (Holmes 1984; Godfrey 1989; Clack 1994, 2002). The fourth potential phalanx (Fig. 12a4) is associated with the distal end of a metatarsal (Fig. 12a5), so it could be the corresponding proximal phalanx. However, it is sheared off at one end, so it could also be another metatarsal.

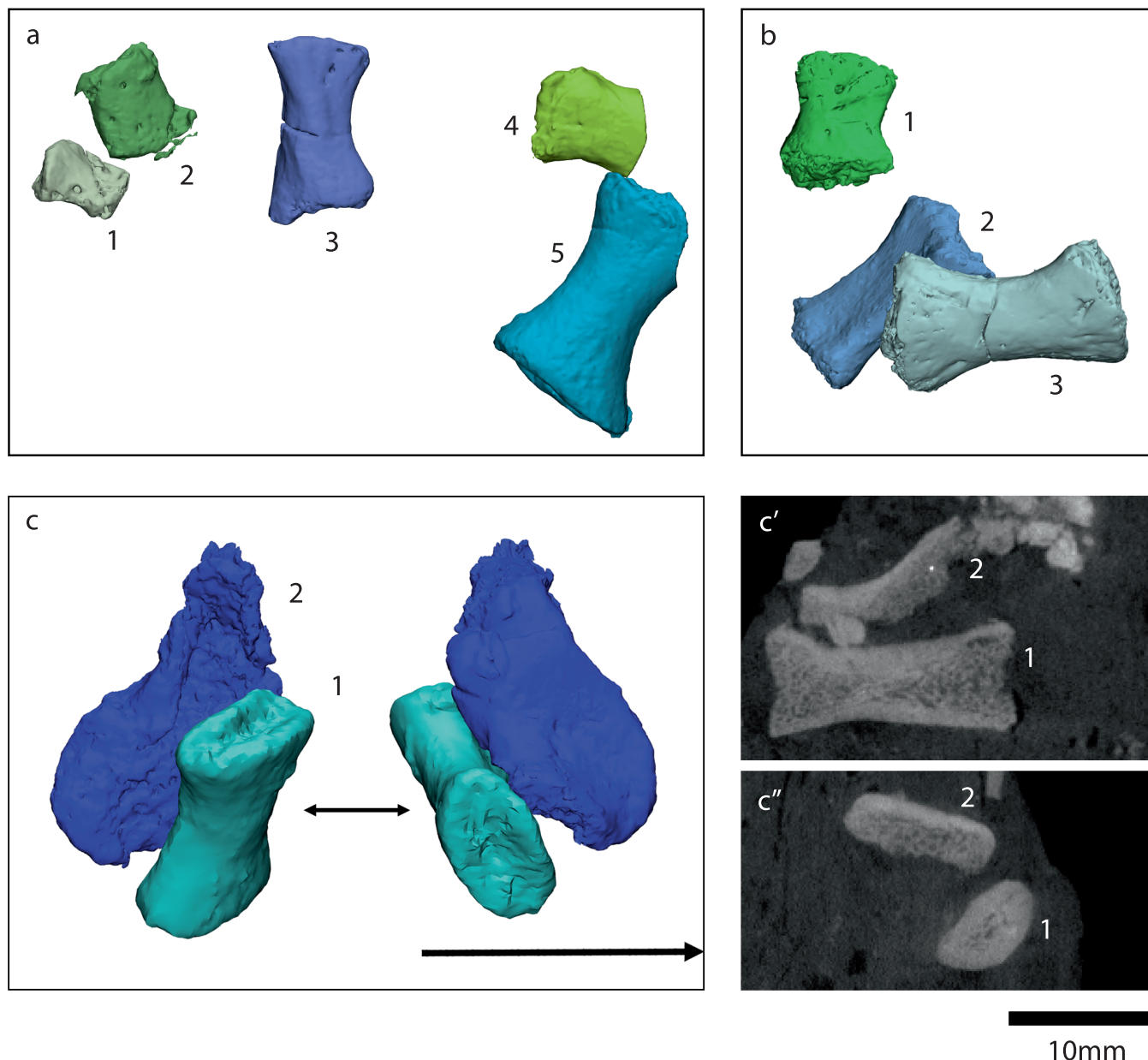


Figure 12 *Crassigyrinus* pes elements. (a, b) NMS G 1984.15.3 (a3, a5, b2, b3: metacarpals; a1, a2, a4, b1: small metatarsals or phalanges). (c) NMS G 1984.15.1 (c1: metatarsal; c2: metatarsal fragment or neural arch fragment). (c') Long-axis cross section view. (c'1, c'1: metatarsal (shown in c1)). (c'') Transverse cross-section view (c'2, c'2: fragment that may be a metatarsal or neural arch (shown in c2)). Note, b2, c1 and c2 are new discoveries.

We identified two additional metatarsals (Figs 12b2, c1, 13a, e) previously hidden in the matrix of the NMS G 1984.15.1 and 1984.15.3 slabs. The greatest proximodistal lengths of these new elements (~17 and ~14 mm, respectively) are similar to the metatarsal length (15 mm) reported by Panchen & Smithson (1990). The shape also agrees with the description in Panchen & Smithson (1990), as follows: the medial and lateral sides of the metatarsal are concave, and the proximal and distal ends are mediolaterally expanded. In the new metatarsals, one end (presumably distal) is slightly less broad than the other (presumably proximal) end. In the NMS G 1984.15.1 metatarsal, the proximal end is ~10 mm wide (measured as the greatest distance along the mediolateral axis), and the distal end is ~12 mm wide. In the NMS G 1984.15.3, the proximal end is ~9 mm wide and the distal end is ~8 mm wide. The flexor surface of the metatarsals is slightly concave, and the extensor surface is convex. The metatarsals are longer than they are wide, like those of

Pederpes, but unlike those of *Whatcheeria* (Clack & Finney 2005). At the proximal end, the flexor surface extends more proximally than the extensor surface (by about 1.5 mm).

The most noteworthy feature of the metatarsals is the presence of bilateral asymmetry (Fig. 13). This asymmetry is also evident in the Carboniferous tetrapods *Pederpes*, *Greererpeton*, *Silvanerpeton*, *Proterogyrinus* and *Ossinodus* (Clack 2002; Warren & Turner 2004; Clack & Finney 2005). It has been proposed that this asymmetry is associated with a more derived pedal orientation better suited for terrestrial locomotion than the lateral foot orientation of earlier animals such as *Acanthostega* and *Ichthyostega*, which have symmetric metatarsals (Clack 2002; Clack & Finney 2005). Therefore, it is unusual that the aquatic *Crassigyrinus* has asymmetric metatarsals. However, if asymmetry is indeed associated with terrestriality, it could support the hypothesis that *Crassigyrinus* is secondarily aquatic. Further comparisons of metatarsal asymmetry in aquatic and terrestrial tetrapods are needed to clarify this, but there is cause

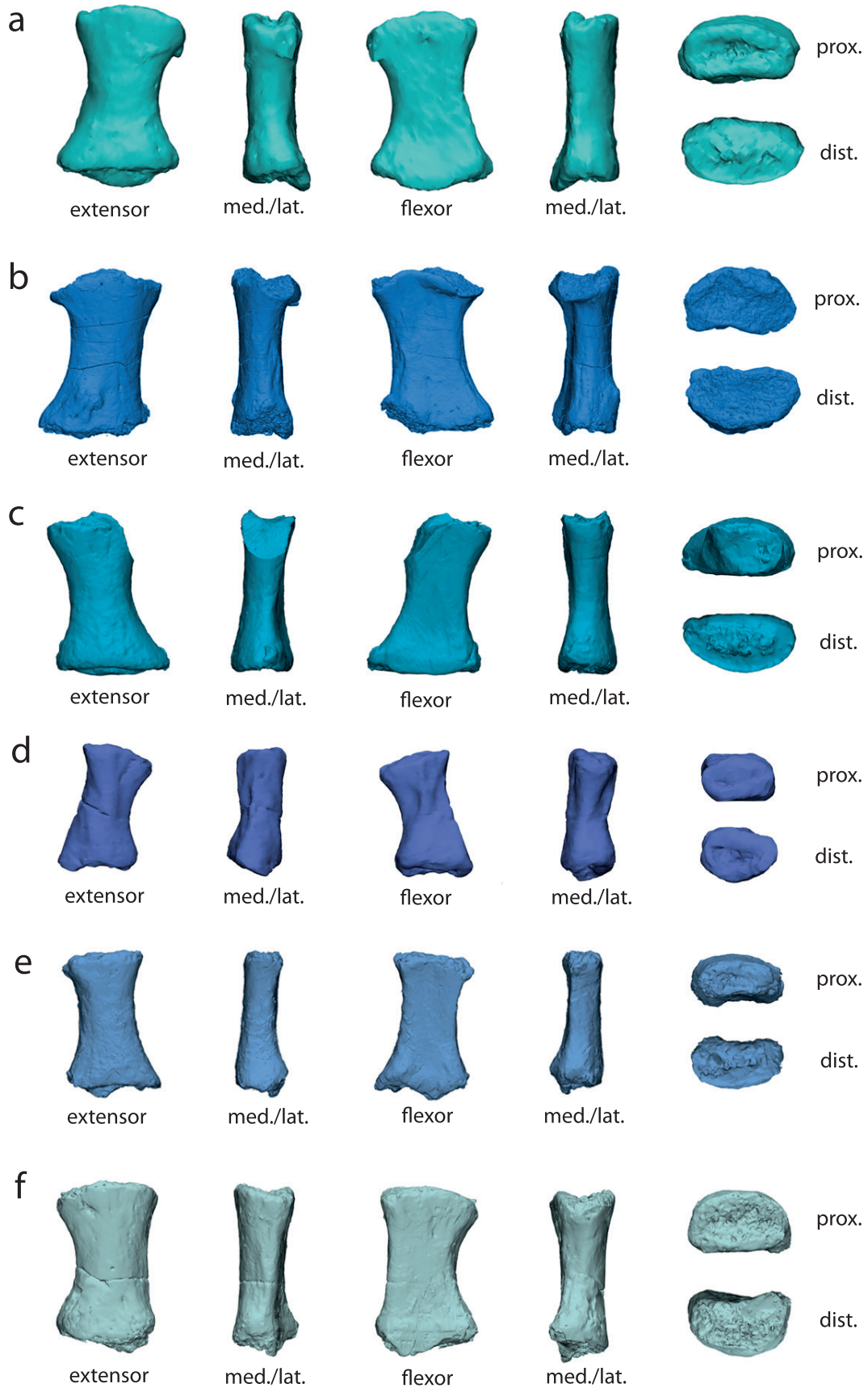


Figure 13 *Crassigyrinus* metatarsals. (a) NMS G 1984.15.1 (new discovery). (b) NMS G 1984.15.2. (c-f) NMS G 1984.15.3 (e is a new discovery). Note that the extreme asymmetry at the distal end of the metatarsal in the third row is due to shearing of the bone, and is a taphonomic artefact. However, note the bilateral symmetry evident in the metatarsals. Abbreviations: med. = medial; lat. = lateral; prox. = proximal; dist. = distal.

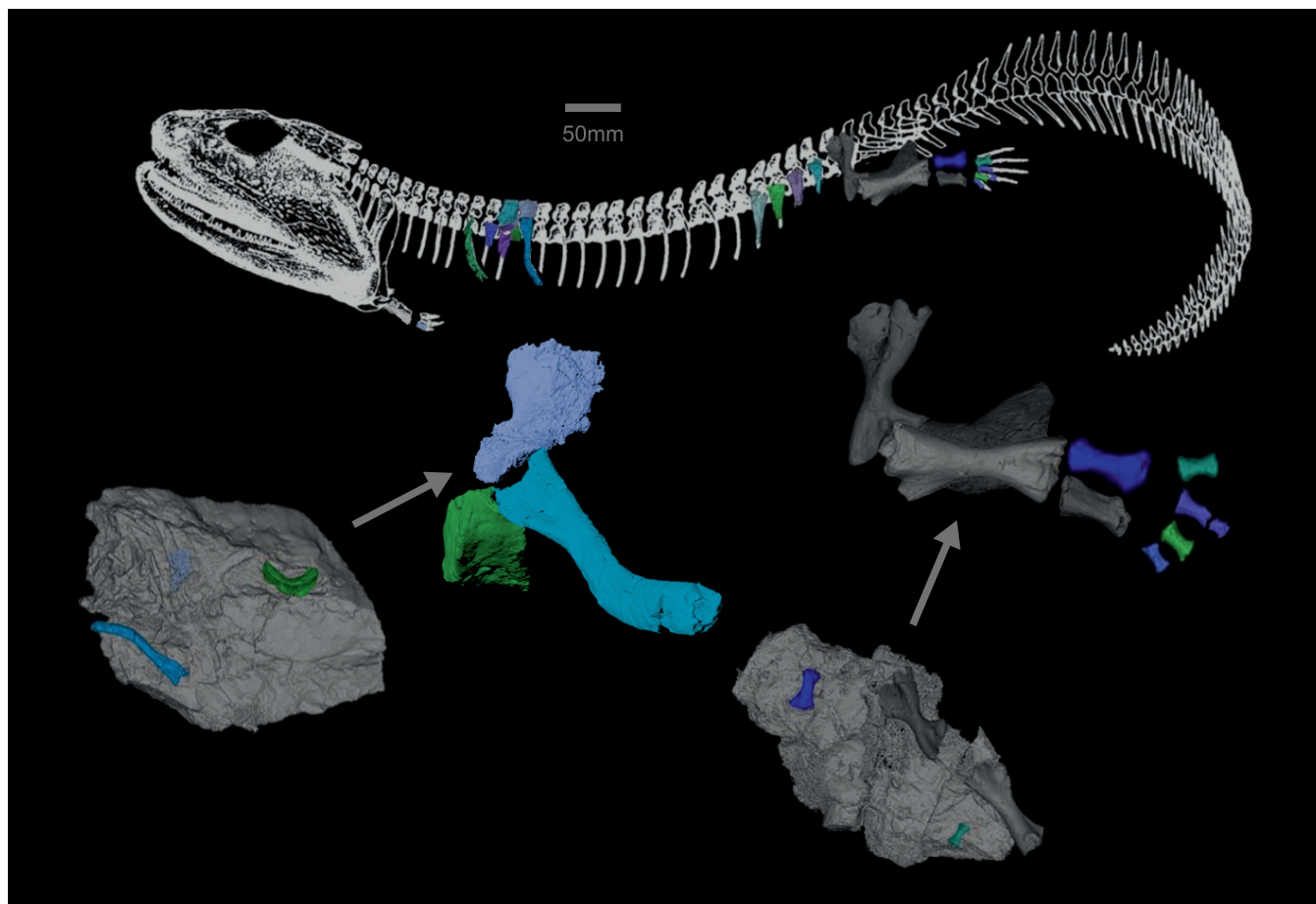


Figure 14 Models of newly discovered or described bones, mapped onto Panchen's (1985) reconstruction of *Crassigyrinus*. Locations of vertebral elements and ribs based on comparative material.

for caution in assuming that metapodial asymmetry indicates (increased) terrestriality.

We also found another fragment next to the newly recognised metatarsal in NMS G 1984.15.3 (Fig. 12c2). This piece is broken, but in cross section, the trabecular and cortical bone is visible (Fig. 12c'2, c''2). The cross section looks similar to the metatarsal's (Fig. 12c'1, c''1), but this piece might also be a neural arch, because a possible transverse process and prezygapophyses are present (see section 2.1.3).

3. Conclusion

CT scanning of the *Crassigyrinus* specimens enabled us to discover several previously unrecognised elements. The presence of pleurocentra is possible, which would make *Crassigyrinus* rhachitinous. Further research and scanning are needed to test the hypotheses that the small elements are pleurocentra. *Crassigyrinus*'s ribs, which seem to be complete in some cases, end in a tapered shaft. The rib and vertebral structures suggest that *Crassigyrinus* had a relatively flat body, although there might have been some variation in the rib orientation along the vertebral column. The metatarsals show asymmetry, which might support the hypothesis of *Crassigyrinus* being secondarily aquatic, but more comparative work is needed to test whether there is a functional relationship between metatarsal asymmetry and locomotor mode. A mass of bone at the distal ilium may be evidence of an ossified pubis, and we show further details of the morphology of the radius. These new discoveries give us a better understanding of the anatomy of this aberrant

animal (Fig. 14) and the morphological variation present in early tetrapods.

4. Acknowledgements

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5. References

- Ahlberg, P. E., Clack, J. A. & Blom, H. 2005. The axial skeleton of the Devonian tetrapod *Ichthyostega*. *Nature* **437**, 137–40.
- Ahlberg, P. E. & Clack, J. A. 1998. Lower jaws, lower tetrapods – a review based on the Devonian genus *Acanthostega*. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **89**, 11–46.
- Anderson, J. S., Carroll, R. L. & Rowe, T. B. 2003. New information on *Lethiscus stocki* (Tetrapoda: Lepospondyli: Aistopoda) from high-resolution computed tomography and a phylogenetic analysis of Aistopoda. *Canadian Journal of Earth Sciences* **40**, 1071–83.

- Anderson, J. S., Smithson, T. R., Mansky, C. F., Meyer, T. & Clack, J. A. 2015. A diverse tetrapod fauna at the base of 'Romer's Gap'. *PLoS ONE* **10**, 1–27.
- Andrews, S. & Westoll, T. 1970. The postcranial skeleton of *Eusthenopteron foordi* Whiteaves. *Transactions of the Royal Society of Edinburgh* **68**, 207–329.
- Bishop, P. J. 2014. The humerus of *Ossinodus pueri*, a stem tetrapod from the Carboniferous of Gondwana, and the early evolution of the tetrapod forelimb. *Alcheringa: An Australasian Journal of Palaeontology* **38**, 209–38.
- Carroll, R. L. 1988. *Vertebrate paleontology and evolution*. New York: W. H. Freeman and Company.
- Clack, J. A. 1994. *Silvanerpeton miripedes*, a new anthracosauroid from the Viséan of East Kirkton, West Lothian, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **84**, 369–76.
- Clack, J. A. 1998. The Scottish Carboniferous tetrapod *Crassigyrinus scoticus* (Lydekker) – cranial anatomy and relationships. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **88**, 127–42.
- Clack, J. A. 2002. An early tetrapod from 'Romer's Gap'. *Nature* **418**, 72–76.
- Clack, J. A. 2012. *Gaining ground: the origin and evolution of tetrapods*. 2nd edn. Bloomington, IN: Indiana University Press.
- Clack, J. A., Bennett, C. E., Carpenter, D. K., Davies, S. J., Fraser, N. C., Kearsey, T. I., Marshall, J. E. A., Millward, D., Otoo, B. K. A., Reeves, E. J., Ross, A. J., Ruta, M., Smithson, K. Z., Smithson, T. R. & Walsh, S. A. 2016. Phylogenetic and environmental context of a Tournaisian tetrapod fauna. *Nature Ecology & Evolution* **1**, 1–11.
- Clack, J. A., Porro, L. B. & Bennett, C. E. 2018. A *Crassigyrinus*-like jaw from the Tournaisian (Early Mississippian) of Scotland. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **108**, 37–46.
- Clack, J. A. & Finney, S. M. 2005. *Pederpes finneyae*, an articulated tetrapod from the Tournaisian of Western Scotland. *Journal of Systematic Palaeontology* **2**, 311–46.
- Coates, M. I. 1996. The Devonian tetrapod *Acanthostega gumari* Jarvik: postcranial anatomy, basal tetrapod interrelationships and patterns of skeletal evolution. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **87**, 363–421.
- Coates, M. I., Jeffery, J. E. & Ruta, M. 2002. Fins to limbs: what the fossils say. *Evolution and Development* **4**, 390–401.
- Coates, M. I., Ruta, M. & Friedman, M. 2008. Ever since Owen: changing perspectives on the early evolution of Tetrapods. *Annual Review of Ecology, Evolution, and Systematics* **39**, 571–92.
- Daeschler, E. B., Shubin, N. H., Thomson, K. S. & Amaral, W. W. 1994. A Devonian Tetrapod from North America. *Science* **265**, 639–42.
- Daeschler, E. B., Shubin, N. H. & Jenkins, F. A. 2006. A Devonian tetrapod-like fish and the evolution of the tetrapod body plan. *Nature* **440**, 757–63.
- Danto, M., Witzmann, F. & Fröbisch, N. B. 2016. Vertebral development in Paleozoic and Mesozoic tetrapods revealed by paleohistological data. *PLoS ONE* **11**, 1–30.
- Danto, M., Witzmann, F., Pierce, S. E. & Fröbisch, N. B. 2017. Intercentrum versus pleurocentrum growth in early tetrapods: a paleohistological approach. *Journal of Morphology* **2017**, 1–22.
- Gardiner, B. G. 1983. Gnathostome vertebrae and the classification of the Amphibia. *Zoological Journal of the Linnean Society* **79**, 1–59.
- Germain, D. 2008. A new phlegethontiid specimen (Lepospondyli, Aistopoda) from the Late Carboniferous of Montceau-Les-Mines (Saône-et-Loire, France). *Geodiversitas* **30**, 669–80.
- Godfrey, S. J. 1988. Isolated tetrapod remains from the Carboniferous of West Virginia. *Kirtlandia* **43**, 27–36.
- Godfrey, S. J. 1989. The postcranial skeletal anatomy of the Carboniferous tetrapod *Greererpeton burkemorani* Romer, 1969. *Philosophical Transactions of the Royal Society of London* **323**, 75–133.
- Holmes, R. 1984. The Carboniferous amphibian *Proterogyrinus scheelei* Romer, and the early evolution of tetrapods. *Philosophical Transactions of the Royal Society B: Biological Sciences* **306**, 431–524.
- Holmes, R. 1989. Functional interpretations of the vertebral structure in paleozoic labyrinthodont amphibians. *Historical Biology: An International Journal of Paleobiology* **2**, 111–24.
- Hook, R. 1983. *Colosteus scutellatus* (Newberry), a primitive temnospondyl amphibian from the Middle Pennsylvanian of Linton, Ohio. *American Museum Novitates* **2770**, 1–41.
- Jarvik, E. 1996. The Devonian tetrapod *Ichthyostega*. *Fossils Strata* **40**, 1–206.
- Klembara, J. & Bartik, I. 1999. The postcranial skeleton of *Discosauriscus kuhn*, a seymouriamorph tetrapod from the Lower Permian of the Boskovic Furrow (Czech Republic). *Transactions of the Royal Society of Edinburgh: Earth Sciences* **90**, 287–316.
- Lebedev, O. A. & Coates, M. I. 1995. The postcranial skeleton of the Devonian tetrapod *Tulerpeton curtum* Lebedev. *Zoological Journal of the Linnean Society* **114**, 307–48.
- Lombard, R. E. & Bolt, J. R. 1995. A new primitive tetrapod, *Whatcheeria deltae*, from the lower Carboniferous of Iowa. *Paleontology* **38**, 471–94.
- Lydekker, R. 1890. On two new species of labyrinthodonts. *Quarterly Journal of the Geological Society London* **46**, 289–94.
- Milner, A. C. & Lindsay, W. 1998. Postcranial remains of Baphetes and their bearing on the relationships of the Baphetidae (=Loxommatidae). *Zoological Journal of the Linnean Society* **122**, 211–35.
- Molnar, J. L., Diogo, R., Hutchinson, J. R. & Pierce, S. E. 2017. Reconstructing pectoral appendicular muscle anatomy in fossil fish and tetrapods over the fins-to-limbs transition. *Biological Reviews* **93**, 1077–107.
- Moser, M. & Schoch, R. 2007. Revision of the type material and nomenclature of *Mastodonsaurus giganteus* (Jaeger) (Temnospondyli) from the Middle Triassic of Germany. *Palaeontology* **50**, 1245–66.
- Moulton, J. 1974. A description of the vertebral column of *Eryops*, based on the notes and drawings of A.S. Romer. *Breviora* **428**, 1–44.
- Nyakatura, J. A., Allen, V. R., Lauströer, J., Andikfar, A., Danczak, M., Ullrich, H. J., Hufenbach, W., Martens, T. & Fischer, M. S. 2015. A three-dimensional skeletal reconstruction of the stem amniote *Orobates pabsti* (Diadectidae): analyses of body mass, centre of mass position, and joint mobility. *PLoS ONE* **10**, 1–20.
- Panchen, A. L. 1966. The axial skeleton of the labyrinthodont *Eogyrinus attheyi*. *Journal of Zoology (London)* **150**, 199–222.
- Panchen, A. L. 1970. *Handbuch der Palaeoherpetologie. Teil 5A. Anthracosauria*. Stuttgart: Fischer.
- Panchen, A. L. 1973. On *Crassigyrinus scoticus* Watson, a primitive amphibian from the Lower Carboniferous of Scotland. *Palaeontology* **16**, 179–93.
- Panchen, A. L. 1977. The origin and early evolution of tetrapod vertebrae. In Andrews, S. M., Miles, R. S. & Walker, A. D. (eds) *Problems in vertebrate evolution*, 289–319. London & New York: Academic Press.
- Panchen, A. L. 1980. The origin and relationships of the anthracosaur amphibians from the late Palaeozoic. In Panchen, A. (ed.) *The terrestrial environment and the origin of land vertebrates*, 319–50. London: Academic Press.
- Panchen, A. L. 1985. On the amphibian *Crassigyrinus scoticus* Watson from the Carboniferous of Scotland. *Philosophical Transactions of the Royal Society of London B* **309**, 505–68.
- Panchen, A. L. & Smithson, T. R. 1990. The pelvic girdle and hind limb of *Crassigyrinus scoticus* (Lydekker) from the Scottish Carboniferous and the origin of the tetrapod pelvic skeleton. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **81**, 31–44.
- Pardo, J. D., Szostakiwskyj, M., Ahlberg, P. E. & Anderson, J. S. 2017. Hidden morphological diversity among early tetrapods. *Nature* **546**, 642–45.
- Pierce, S. E., Clack, J. A. & Hutchinson, J. R. 2012. Three-dimensional limb joint mobility in the early tetrapod *Ichthyostega*. *Nature* **486**, 523–26.
- Pierce, S. E., Ahlberg, P. E., Hutchinson, J. R., Molnar, J. L., Sanchez, S., Tafforeau, P. & Clack, J. A. 2013. Vertebral architecture in the earliest stem tetrapods. *Nature* **494**, 226–29.
- Romer, A. S. 1957. The appendicular skeleton of the Permian embolomeroous amphibian *Archeria*. *Contributions from the Museum of Geology, University of Michigan* **13**, 103–59.
- Romer, A. S. 1960. *Vertebrate paleontology*. 8th edn. Chicago, IL: The University of Chicago Press.
- Ruta, M., Coates, M. I. & Quicke, D. L. J. 2003. Early tetrapod relationships revisited. *Biological Reviews* **78**, 251–345.
- Ruta, M. & Coates, M. I. 2007. Dates, nodes and character conflict: addressing the Lissamphibian origin problem. *Journal of Systematic Palaeontology* **5**, 69–122.
- Shishkin, M. A. 1989. The axial skeleton of the early amphibians and the origin of resegmentation in tetrapod vertebrae. *Fortschritte Der Zoologie* **35**, 180–95.
- Smithson, T. R. 1985. The morphology and relationships of the Carboniferous amphibian *Eoherpeton watsoni* Panchen. *Zoological Journal of the Linnean Society* **85**, 317–410.

- Smithson, T. R., Wood, S. P., Marshall, J. E. A. & Clack, J. A. 2012. Earliest Carboniferous tetrapod and arthropod faunas from Scotland populate Romer's Gap. *PNAS* **109**, 4532–37.
- Smithson, T. R. & Clack, J. A. 2018. A new tetrapod from Romer's Gap reveals an early adaptation for walking. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **108**, 89–97.
- von Zittel, K. A. 1911. *Grundzüge der paläontologie (paläzoologie)*. Muenchen & Berlin: Rudolph Oldenbourg.
- Warren, A. A. & Ptasznik, R. 2002. The earliest fractured tetrapod bone. *Alcheringa: An Australasian Journal of Palaeontology* **26**, 459–63.
- Warren, A. & Turner, S. 2004. The first stem tetrapod from the Lower Carboniferous of Gondwana. *Palaeontology* **47**, 151–84.
- Watson, D. M. S. 1919. The structure, evolution and origin of the amphibia – The 'orders' Rachitomi and Stereospondyli. *Philosophical Transactions of the Royal Society of London (B)* **209**, 1–73.
- Watson, D. M. S. 1929. The Carboniferous amphibia of Scotland. *Palaontologica Hungarica* **1**, 219–52.

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