

A *Crassigyrinus*-like jaw from the Tournaisian (Early Mississippian) of Scotland.

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Running head: Tournaisian *Crassigyrinus*-like jaw

ABSTRACT: The early tetrapod *Crassigyrinus scoticus* was a large aquatic predator from the mid Carboniferous (late Viséan or early Serpukovian) of Scotland, around 330 MY in age. There are five main specimens with cranial remains: an articulated skeleton; two incomplete skulls; and two lower jaws. *Crassigyrinus* retains several apparently primitive features of the palatal dentition and lower jaw, and its phylogenetic position is disputed. A partial lower jaw resembling that of *Crassigyrinus* was discovered at Burnmouth in the Borders Region of Scotland. The horizon in which it was found is dated as late Tournaisian, CM palynozone, around 350 MY in age. Though it lacks dentition, the jaw preserves much of the postsplenial, angular and surangular, whose appearance externally and internally is almost identical to that of *C. scoticus*. Internally the jaw shows a similarly limited extent of the suturing between the splenial series and the prearticular, a primitive condition. Externally, the type and distribution of dermal ornamentation closely matches that of *C. scoticus*, as does the deeply excavated and marginally positioned lateral line groove. As well as external and internal features, all specimens of *C. scoticus* are of similar skull size, though the Burnmouth jaw is somewhat smaller. If correctly attributable to *Crassigyrinus*, this specimen extends the existence of the genus by approximately 20 million years towards the base of the Carboniferous.

KEY WORDS, Burnmouth; Borders Region; tetrapod; TW:eed project; Romer's Gap

Hitherto, the earliest Carboniferous deposits of the Tournaisian stage have been considered depauperate as a result of a poor fossil record of vertebrates and arthropods. A mass extinction event at the end of the Devonian saw the demise of many ancient fish groups such as placoderms, acanthodians, and the majority of sarcopterygians that had flourished in the Devonian ‘Age of Fishes’ (Sallan & Coates 2010). Tetrapods of the Devonian, notable for fish-like primitive characters and multidigitated limbs, were apparently wiped out (but see Anderson *et al.* 2015). The poor fossil record following the end-Devonian was taken to be a long-lasting result of this extinction event. Tetrapods from the Tournaisian were virtually unknown, the record consisting only of a range of isolated limb and girdle bones from Nova Scotia (Clack & Carroll 2000, Anderson *et al.* 2015), and a single articulated tetrapod from western Scotland (Clack 2002, Clack & Finney 2005).

Recent excavations in the Borders Region of Scotland by members of the TW:eed project (Tetrapod World, early evolution and diversification) have shown that the hiatus is to a large extent an artefact of collection failure. A multitude of specimens including new taxa of tetrapods, as well as other vertebrate groups such as chondrichthyans and lungfishes, plus arthropods and plants are coming to light (Smithson *et al.* 2012). Here, we describe a partial lower jaw similar to the mid-Carboniferous genus *Crassigyrinus*, from the Tournaisian of Scotland. The specimen was previously mentioned and figured in Smithson *et al.* (2012 figure 2C,D).

Crassigyrinus scoticus is known from five main specimens, all from Scotland, dated, with some margin for error, as ‘Upper Viséan’ or ‘Lower Namurian E1’, and in more recent terminology, uppermost Viséan to lowest Serpukovian, in the Brigantian to Pendleian European substages (Gradstein *et al.* 2012). The holotype specimen consists of the right snout, cheek and suspensorial region of a skull (NMS

G.1859.33.104) from the Gilmerton Ironstone near Edinburgh and first described by Watson (1929). Other specimens include NHMUK R310, a partial lower jaw exposed in external view, GSE 4722, an almost complete lower jaw exposed in internal view, and NHMUK 30532, a partial cranium, all from Gilmerton near Edinburgh, and probably all from the Gilmerton Ironstone. Specimen NHMUK R10000, an articulated individual including a skull and much of the postcranium. Additionally, NMS G.1975.40.50/51 consists of matching articular and quadrate from the Dora Bone bed, in the Limestone Coal Formation, near Cowdenbeath. These were described and/or listed by Panchen (1973, 1985), Clack (1996, 1998) and Ahlberg and Clack (1998).

The new specimen described here is about 20 million years older than any of these specimens, potentially extending the geological range of the genus much further down towards the base of the Carboniferous, and about 10 million years after the end of the Devonian. When first collected, its identity, obscured by the coarse matrix in which it was preserved, was eventually recognized to be part of a lower jaw. It was still largely in the matrix when Stanley Wood first identified it as belonging to *Crassigyrinus*, an intuitive observation that is probably correct.

Figure 1 about here

1. Materials and Methods

The new specimen, University Museum of Zoology, Cambridge (UMZC) 2011.9.1, from the locality of Burnmouth, in the Borders Region of Scotland, comes from deposits dated as within the CM (claviger-macra) palynozone, although the palynozonation of the Tournaisian stage in Scotland is being reviewed as a result of work undertaken as part of the TW:eed project. The sequence at Burnmouth covers much of the Tournaisian stage, somewhat condensed, but extending from slightly

below the Devonian-Carboniferous boundary, through to the base of the Visean Fell Sandstone.

The specimen was collected from a 200 mm thick localised conglomerate lag that occurs at the base of a 4 m thick fluvial sandstone channel deposit, about 383 m above the base of the Ballagan Formation at Burnmouth. The conglomerate lies between sandstones 4 & 5 of Scrutton & Turner (1995) and is weakly bedded, poorly sorted, matrix-supported and cemented with dolomite, which makes preparation extremely difficult in places. Centimetre-sized clasts (average size 30 mm) are composed of red and grey siltstone and bioclasts, within a coarse sandstone matrix. The clasts and matrix are likely derived from lakes (grey silt) and palaeosols (red silt) on the floodplain, which were eroded and incorporated into the lag during river flow and subsequent sediment deposition. Bioclasts are more concentrated towards the base of the unit and include numerous isolated bones, including some very large examples, of lungfishes, rhizodonts, gyracanth spines and girdle elements, actinopterygians, a few teeth of the stem chondrichthyan *Ageleodus*, and occasional tetrapod elements. The bed also contains charcoalfied plant stems, charcoal fragments and wood fragments. However, the more fragile ostracod and bivalve fossils that are a common element of floodplain sediments are absent. The jaw described here is one of the larger finds from this bed.

Collection from this bed presents difficulties as it is almost vertically orientated like all other beds at Burnmouth, and is set between the overlying massive sandstone and a cementstone, close to the cliff face. There is a high risk of losing fragments into the gap between these two harder beds left by erosion of the relatively soft conglomerate.

The jaw was prepared mechanically by JAC, mainly with a mounted needle under binocular microscope, and occasional judicious use of a dental mallet. The specimen was set into a series of silastomer jackets as each face was prepared in turn. The bone was extremely fragile and required careful consolidation with the resin Paraloid B72. Matrix has been left on parts of the lingual surface, where the bone is too delicate to support itself.

For comparison with existing *Crassigyrinus* specimens, Natural History Museum UK (NHMUK) R10000 and R310, and British Geological Survey Edinburgh (GSE) 4722 were scanned using micro-computed tomography (μ CT) at the Imaging and Analysis Centre of the Natural History Museum (London, UK) on an X-Tek HMX-ST μ CT 225 scanner (Nikon Metrology, Tring, UK). Scans of NHMUK R10000 produced two separate data sets consisting of 1958 DICOM slices of the anterior half of the specimen and 1953 DICOM slices of the posterior half of the specimen with a resolution of 0.1083 mm/voxel. GSE 4722 is preserved in three large pieces, each of which was scanned separately. The anterior portion of this specimen produced 1995 DICOM slices with a resolution of 0.1271 mm/voxel. The central-posterior portion was scanned to produce 1995 slices with a resolution of 0.1099 mm/voxel. The posterior portion of GSE 4722 was scanned to produce 1687 DICOM slices with a resolution of 0.1099 mm/voxel. NHMUK R310 was scanned in two parts: the anterior half produced 1956 DICOM slices at a resolution of 0.1034 mm/voxel while the posterior half produced 1939 DICOM slices at a resolution of 0.1034 mm/voxel. Scans were segmented to remove matrix from bone and separate individual bones from each other, then rendered into three-dimensional models using Avizo 7.1.1 (FEI Visualization Sciences Group, Mérignac Cedex, France). An isolated articular, National Museum of Scotland (NMS) 1975.48.50 was also studied,

and part of UMZC 2011.9.1 was μ CT- scanned at the Cambridge Biotomography Centre (Zoology Department) at the University of Cambridge on an X-Tek H 225 μ CT scanner (Nikon Metrology, Tring, UK). This produced a data set of 1866 16bit TIFF images with a resolution of 0.0465mm/voxel. These 16bit TIFFs were converted to 8bit TIFF using imageJ and the resulting dataset loaded into Mimics (Materialise NV – Technologielaan 15, 3001 Leuven, Belgium).

2. Systematic Palaeontology

Osteichthyes Huxley, 1880

Sarcopterygii Romer, 1955

Tetrapodomorpha Ahlberg 1991

Family Crassigyrinidae Huene, 1948

Genus cf. *Crassigyrinus* Watson, 1929

Type species, *Crassigyrinus scoticus*

Specimen UMZC 2011.9.1. cf. *Crassigyrinus*

3. Description

3.1 Comparative anatomy of the Burnmouth jaw

The preserved part of the specimen measures 250 mm and includes the angular, postsplenial and parts of the splenial, dentary and surangular of the lower jaw. It lacks the symphyseal region, prearticular, articular and all the dentigerous bones (Fig. 1).

The lateral line is a deep open groove approximately following the ventral margin, although approaching it more closely near the mid-point of the angular. It

continues to the rearmost point of the surangular. Ornamentation ventral to the lateral line takes the form of long, fairly regular grooves and ridges, less marked on the angular, which instead bears a few elongate, individual pits. Dorsal to the lateral line, the ornamentation consists of sparsely distributed individual pits, very shallow on the angular, deeper on the postsplenial and surangular, and shallow radiating grooves. The fragment of dentary, parts of the angular and the surangular also bear fine striations. There is no indication of the extent or orientation of the adductor fossa, nor whether or not there was a surangular crest, and there is no evidence of a postsplenial pit line.

By comparison with the isolated articular NMS 1975.48.50, it appears that the articular in UMZC 2011.9.1 is missing. The smooth excavated surface at the rear of the jaw is more likely to have been contributed by the surangular, as seen in the NMS articular. A series of grooves and ridges at the extreme posterior end of the jaw could indicate a suture to the articular. From that point, the ventral margin of the jaw is smooth until approximately the midpoint of the angular, suggesting no sutural contact between either the angular or the surangular and the prearticular until that point. Sutures between the angular and surangular are difficult to determine on the internal surface in part because of breakages and adhering matrix.

From the section of jaw exposed in a break, a circular feature indicated the existence of a canal running through the lower part of the jaw (Figs 1F, 2). Micro-CT scanning has revealed the shape and course of the canal and confirmed that it does not appear connected to the lateral line, except possibly at the extreme posterior end, where matrix in the lateral line may obscure a foramen (Figs 1B, 2). It takes a medial course through the angular (Fig. 2B, arrows) and is distinct from the groove of the lateral line canal. At least some of the branches off the canal appear to be genuine

features, although some may be artefacts as a result of breakages. The canal could be the course of a blood vessel or nerve, but it appears to end blindly rather than exiting via a foramen. No such canal has been identified in any of the other specimens, but most of them are too fragmented to be certain. On the lingual surface near the articulation, two foramina appear to be linked by what may be a branch of this canal (Fig. 2A arrows). The status of this feature as an apomorphy is unknown: it could be at individual or specific level rather than generic.

Figure 2 about here

A series of robust ridges and crests marks the ventral edge and inner face of what is probably the angular, suggesting a sutural contact between it and the prearticular along a length of about 50 mm (Fig. 1). This may constitute a very limited mesial lamina of the angular as noted by Ahlberg & Clack (1998) in specimen GSE 4722 (Fig. 3) and NHMUK R10000 of *Crassigyrinus scoticus*. Thereafter, the lower margin of the Burnmouth jaw is smooth except for a small protuberance near the posterior end of the postsplenial. This may represent a point of attachment for a pillar defining a Meckelian fenestra. There is no other contact surface for the prearticular along the length of the jaw. Only the posteriormost part of the splenial is preserved including its contact with the postsplenial, but the region where the mesial lamina would normally be situated is missing. Figure 4 shows the three *C. scoticus* jaw specimens compared with the Burnmouth jaw and to the same scale.

Figures 3 and 4 about here

3.1 Micro-CT data from *C. scoticus* jaws

The inner face of the jaw of *C. scoticus* is most clearly exposed in specimen GSE 4722 (Fig. 3), most recently described and reinterpreted by Ahlberg & Clack (1998), but the external surface of this specimen is inaccessible by conventional means. The

specimen is broken into three parts, all of which are exposed in medial view and which we scanned. The middle portion (Fig 5 E) preserves parts of the prearticular, angular and the posterior portion of the postsplenial. The mesial lamina of the angular is present but incomplete on the central portion of GSE 4722. Strong deformation and breakage may have reduced the lamina in this specimen to a pronounced ridge. Although damaged, visual inspection and μ CT-scanning demonstrate that this ridge medially overlaps the thickened ventral margin of the prearticular in this specimen. Nonetheless, there are significant regions along the ventral edge where it is clear that no sutural contact existed between the angular and prearticular. The extent of the sutural area on the angular for the prearticular in GSE 4722 can be estimated as about 100 mm long, and is thus more extensive than that in the Burnmouth jaw.

Figure 5 about here

The lateral surface of the Burnmouth jaw shows the ornament to be consistent with that of other specimens of *C. scoticus*, although the finer striations are beyond the resolution of the scan data (Fig 5E). The lateral line expression is similarly deep and continuous, but more dorsally placed than in *C. scoticus*.

Specimen NHMUK R310 (Fig. 5 A-C) preserves the portion of the jaw from the symphysis to the posterior end of the postsplenial. The ornament pattern on the postsplenial is in many ways similar to that of the Burnmouth jaw, with elongate ridges and grooves ventral to the lateral line, but more numerous and shorter pits and grooves dorsal to it. The dentary and a preserved fragment of the surangular are marked by fine almost parallel striations. The lateral line itself is similarly expressed as a deep groove and positioned parallel to the ventral edge. Segmentation of μ CT scan data reveals the medial surface of the specimen for the first time (Fig. 5 A-C). The mesial lamina of the splenial can be visualized and internally overlaps the

adsymphysial and the anterior process of the prearticular. Posterior to the mesial lamina, the splenial and prearticular separate and the ventral margin of the prearticular approaches but does not firmly contact the postsplenial. The angular weakly contacts the prearticular, although the mesial lamina of the angular is not preserved in this specimen.

Specimen NHMUK R10000 is the most complete skull known for *C. scoticus*; unlike GSE 4722 and NHMUK R310, NHMUK R10000 experienced dorsoventral (as opposed to mediolateral) compression. The anterior portion of the right jaw is illustrated in Figure 4A. The labial surfaces of both antimeres have similar ridge and groove ornament to that of the Burnmouth jaw, if more marked. The lateral line is likewise an open groove parallel to the ventral margin. Much of the internal face including the prearticular is damaged and broken, but μ CT scans have clarified the morphology and sutural contacts of the medial aspect of the lower jaw. Both sides preserve the prearticular, articular, and infradentaries, as well as all the dentigerous bones. Posterior to the mesial lamina of the splenial, the prearticular intermittently makes point and lapping contacts with the splenial and postsplenial, but these are almost certainly due to the deformation undergone by the specimen and are artifacts. The ventral margin of the prearticular thickens at the level of the angular (as in GSE 4722) and passes lateral (internal) to the mesial lamina of the angular on both sides of NHMUK R10000. The prearticular does not contact the surangular on either side of this specimen and terminates by ventrally and medially lapping the articular. The surangular wraps around the articular, broadly overlapping it both laterally and posteriorly. No fine interdigitations are visible in μ CT scans between the surangular and articular, however, larger-scale ridging is present between these two bones. This arrangement leaves only a small area of the articular externally exposed

posteromedially in addition to the jaw joint surface. Scans and the resulting three-dimensional models (Fig. 5D) of NHMUK R10000 confirm the presence of a substantial mesial lamina of the angular. This is broken and folded dorsally in the right ramus, but is better visualized than on the left ramus. It overlaps the ventral margin of the prearticular medially (Fig. 5D). These observations all accord with the condition seen in the Burnmouth jaw. Altogether, the morphology of the medial aspect of the lower jaw in NHMUK R10000 is very similar to that of the Burnmouth jaw.

4. Discussion

The new Burnmouth lower jaw specimen UMZC 2011.9.1 requires comparison with other known early Carboniferous tetrapod jaws, as well as those of Late Devonian ones, to establish its identity and to examine its combination of features both primitive and derived. Among early Carboniferous forms, those of *Pederpes* (Clack & Finney 2005) *Sigournea* (Bolt & Lombard 2006), *Whatcheeria* (Lombard & Bolt 2006), *Greererpeton* (Smithson 1982, Bolt & Lombard 2001) and a lower jaw from Parrsborough, Nova Scotia (Sookias *et al.* 2014) are the most appropriate comparators. Of these, only *Pederpes* is Tournaisian in age with all the others being late Viséan or early Serpukhovian. The Parrsboro jaw preserves mainly the dentigerous bones, but has a narrow denticulated prearticular dorsally bounding a large Meckelian space. There are few points of comparison between this and the Burnmouth jaw. Sookias *et al.* (2014) found the Parrsborough jaw to nest within a polytomy of mainly later Carboniferous forms. In that analysis *Sigournea*, *Whatcheeria* and *Greererpeton* were all found to be basal to *Crassigyrinus*. Clack *et al.* (2012) did not include *Sigournea*, but their analysis also placed *Whatcheeria* and

Greererpeton basal to *Crassigyrinus*. This is in contrast to the analysis of Ahlberg & Clack (1998), in which *Greererpeton* sat crownward of *Crassigyrinus*. *Pederpes* and *Whatcheeria* sometimes emerge as basal to *Crassigyrinus* (Warren 2007) and sometimes immediately crownward (Ruta & Clack 2006). *Crassigyrinus* has also appeared in a more basal position among embolomeres and *Eoherpeton* (Klembara et al. 2014), or with baphetids (Laurin 2004).

Sigournea, which has so far been included in only one phylogenetic analysis (Sookias et al. 2014), resembles the Burnmouth jaw in the position and expression of the lateral line canal, but differs in having a mesial lamina of the angular that appears to suture with the prearticular to a more posterior extent. The postsplenial shows evidence of several separate Meckelian fenestrae along its ventromedial margin. Larger specimens of the jaw of *Whatcheeria* preserve ossified Meckelian bone between the angular, postsplenial and the prearticular, though in smaller specimens it is absent or unossified, and there is no angular-prearticular or postsplenial-prearticular contact. There is very little ornamentation on the external face of the jaw, and the lateral line is expressed as a series of pores, some of which are elongated. The lower jaw of *Pederpes* is not well enough preserved for comparison. *Greererpeton* possesses well-marked radiating pit and ridge ornament on the external face of the lower jaw, and the lateral line, though mainly open, is interrupted in places and posteriorly is seen as pores. There is a strong sutural contact between the surangular and prearticular and the angular and prearticular, although there is a large single Meckelian fenestra in which the prearticular does not contact the postsplenial. These combinations of characters appear to rule out the Burnmouth specimen from all three of these genera.

Ahlberg & Clack (1998) showed a progressively increasing degree of sutural contact between the prearticular and the infradentary bones through the evolution of early tetrapods, namely the postsplenial and angular. Although there is a contact between the angular and prearticular in some Devonian taxa such as *Ventastega* and *Ichthyostega*, it does not appear to be strongly sutured, and there is no such contact in *Acanthostega*, *Metaxygnathus*, or *Ymeria* (Clack et al. 2012). In *Whatcheeria*, the condition is variable depending on size, with either no contact or an intervening Meckelian ossification, but no mesial lamina of the angular. Such ontogenetic effects are interesting and could be more widespread than we currently appreciate. Both *Greererpeton* and *Crassigyrinus* may represent early stages of the development of contacts between the prearticular and the infradentary series. In *Greererpeton*, the prearticular has a smooth and excavated margin defining a large single Meckelian fenestra, an apparently more specialized condition compared to the ragged and poorly defined ventral margin in *Crassigyrinus*, as seen in GSE 4722.

Figure 6 about here

When compared with the known specimens of *C. scoticus* the new jaw shows similarities such as the overall shallow and curved shape of the jaw and the condition of the dermal ornament. More general early tetrapod characters include the open lateral line sulcus and the degree of contact between the prearticular with the angular and postsplenial. The position of the lateral line is further dorsally placed for most of its length than in *C. scoticus*. There are also differences in proportion between the infradentary bones between the Burnmouth jaw and *C. scoticus*, as seen in Figure 6. However, such differences could be expected in taxa 20 million years apart, and could simply indicate specific rather than generic distinctions. In summary, the Burnmouth

jaw shows most resemblance to that of *C. scoticus* among early Carboniferous tetrapod lower jaws, and in fact also later ones such as baphetids.

From the articular to the point of inception of the splenial, all *C. scoticus* jaws are similar in size. In GSE 4722, the total length is about 320 mm, and the specimen shows a greater degree of curvature than the Burnmouth jaw. Differential crushing and distortion could account for that, in that the bone of GSE 4722 is thicker and much more robust than that of the Burnmouth jaw, and so is less liable to distortion.

The holotype specimen of *C. scoticus*, NMS G.1859.33.104, consists of the right side of a skull from the tip of the snout to the quadrate. It is about 336-340 mm long. Assuming that the lower jaw would be slightly shorter, it is possible to estimate its length at about 325-330 mm. The 'Dora Bone Bed' specimen, NHMUK R.10000, has a lower jaw length of 328 mm, and a restoration of NHMUK R310 (Fig 4), based on the reconstruction by Panchen (1985) measures 320 mm. A feature of *C. scoticus* is that all specimens are of almost identical size. This could be considered a coincidence, but it could also imply that the genus reached, if not a determinate size, at least one in which growth slowed considerably after a certain ontogenetic age.

Attribution of the Burnmouth jaw to a genus only known from much later in time might be problematic. However, the genus *Neoceratodus*, the modern Australian lungfish is known from the Early Cretaceous (Kemp & Molnar 1981), although Cavin et al. (2007) suggested that it might extend back to the Early Triassic. Such longevity for a genus is thus not unprecedented.

On the other hand, there is a precedent for animals with similar skull morphology to have very different postcranial characteristics and be placed in different genera. The Viséan tetrapod *Whatcheeria*, while having a similar skull shape and dermal bone anatomy to that of the Tournaisian *Pedepes*, has a humerus that

differs radically from that of *Pederpes*. There has been doubt expressed as to the validity of the family *Whatcheeriidae* (Warren 2007): in addition to the differences between *Pederpes* and *Whatcheeria*, *Ossinodus* lacks many of the features characteristic of the other members. Such a wide disparity between constituent members of a family might suggest caution in placing them together. Without further evidence, a similarly cautious argument could be used against attributing such a small fragment of a lower jaw to a genus with a highly specialized postcranium.

The Burnmouth jaw is less robust than the later specimens of *Crassigyrinus*, and the degree of prearticular – angular contact less extensive. However, given the similarities in size, ornamentation, lateral line expression and overall construction, attribution to the genus *Crassigyrinus* may be justified, but only further evidence from Tournaisian specimens could corroborate this attribution.

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Figure legends

1. Cf. *Crassigyrinus* UMZC 2011.9.1. (A) Specimen photograph in lateral view. Asterisk indicates the break at which the photograph in (F) was taken. (B) Interpretive drawing of specimen in external view. (C) Interpretive drawing of specimen in medial view. (D) Photograph of specimen in medial view. Double-ended arrow shows portion scanned in Figure 2. (E) Enlargement of area showing main articulation point

for prearticular. (F) Section at level of asterisk in (A), arrow shows the section through the canal in Figure 2. Scale bars = 10 mm. Grey fill indicates matrix, diagonal hatch indicates broken bone.

2. Cf. *Crassigyrinus* UMZC 2011.9.1. (A) Micro-CT of the posterior region showing the course of the canal (see double arrow in Figure 1(D)). Vertical line shows the position of the view in (B). Paired arrows show the possible canal that crosses the surangular to emerge on the internal surface. (B) View from the posterior side of the section shown in (A), looking anteriorly along the jaw. At this point only the tip of the canal can be seen (left arrow): other traces (right arrow) are breaks.

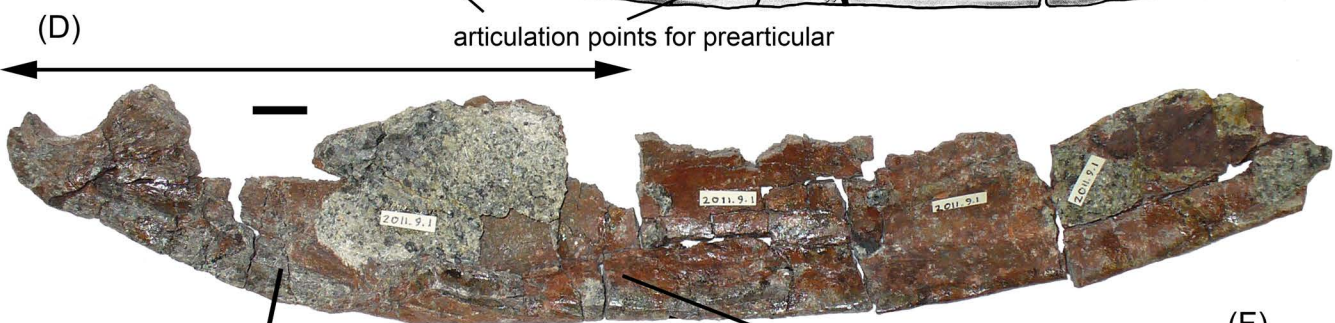
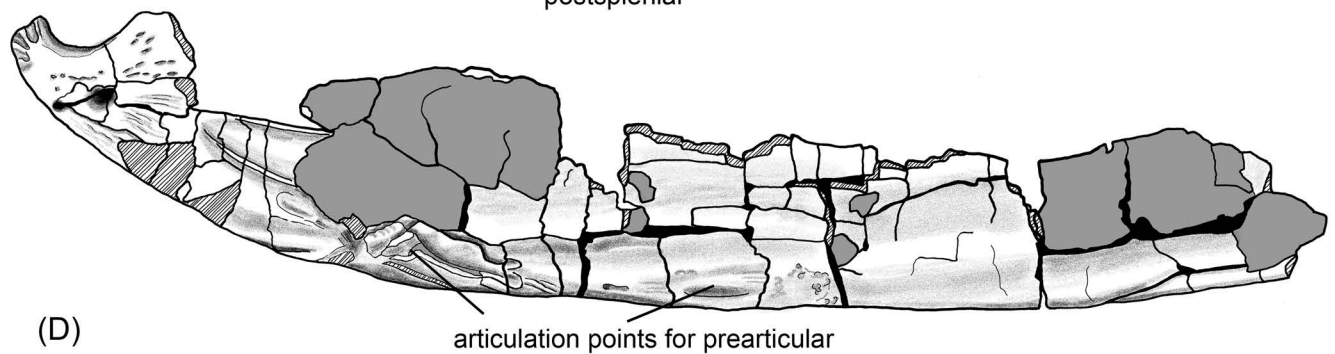
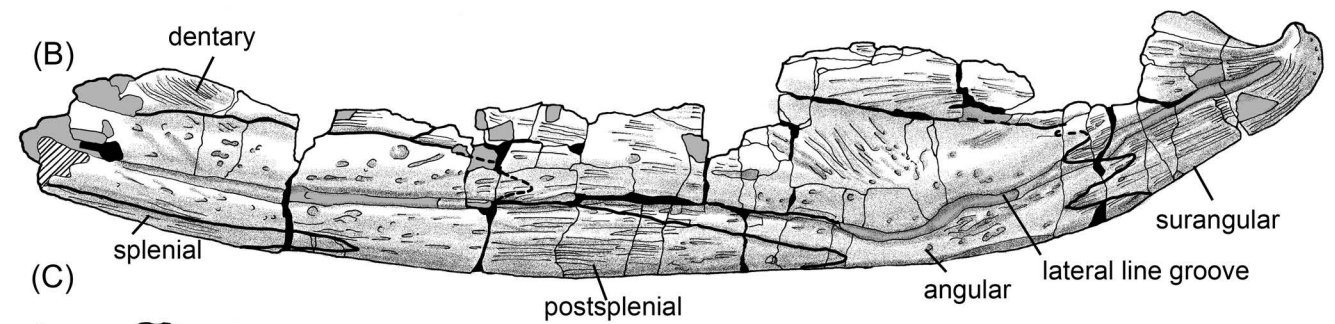
3. *Crassigyrinus scoticus*, GSE 4722. (A) Complete specimen, exposed in medial view. (B) Enlargement of middle section showing the lower margin and articulation points for the prearticular. Note that areas to the right and left of the main articulation point has been abraded away. (C) Interpretive drawing of specimen from Ahlberg and Clack (1998) with sutures shown in red. Scale bar = 10mm.

4. *Crassigyrinus* lower jaws. (A) *C. scoticus* Part of NHMUK R10000, placed on the reconstruction of the jaw by Panchen (1985). (B) Cf. *Crassigyrinus* UMZC 2011.9.1. lateral view. (C) *C. scoticus* NHMUK R310. (D) *C. scoticus* GSE 4722. Photographs all to the same scale. Scale bars = 10mm.

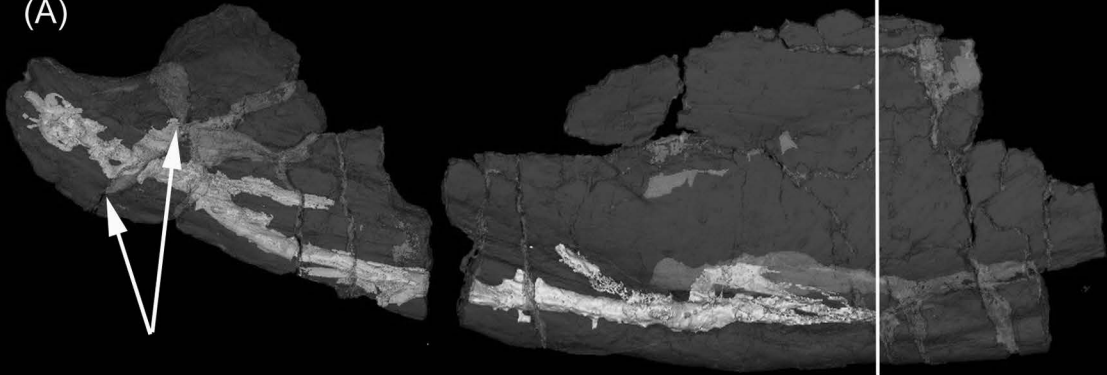
5. *Crassigyrinus scoticus*. Micro-CT renders of lower jaws. (A)-(C) Posterior portion (isolated angular, postsplenial and splenial) of NHMUK R310 in (A) ventral view, (B) ventro-medial view, and (C) medial view – i.e., the specimen is rotated about its

long axis in (A) – (C). (D) Posterior portion (isolated angular and postsplenial) of right lower jaw ramus of NHMUK R10000. (E) Middle portion (isolated surangular, angular and postsplenial) of GSE 4722 in lateral view, showing lateral line and dermal ornament.

6. *C. scoticus* lower jaw reconstruction from Panchen (1985) with UMZC 2011.9.1 superimposed. Panchen's sutures shown in green. (A) with UMZC 2011.9.1 to the same scale. (B) with UMZC 2011.9.1 to approximately the same size.



(A)



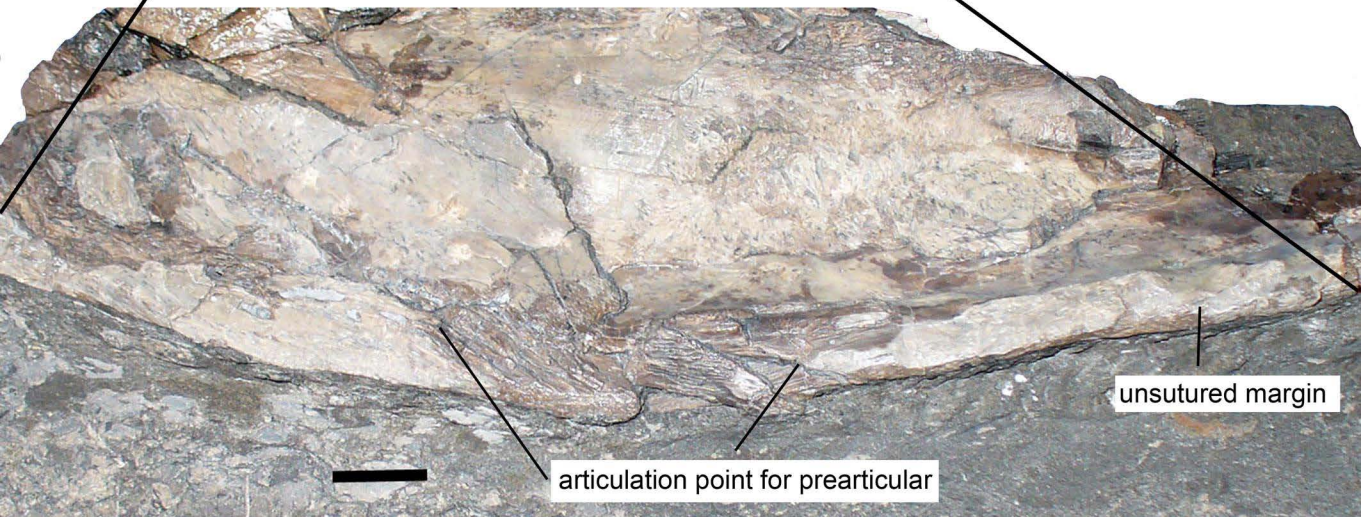
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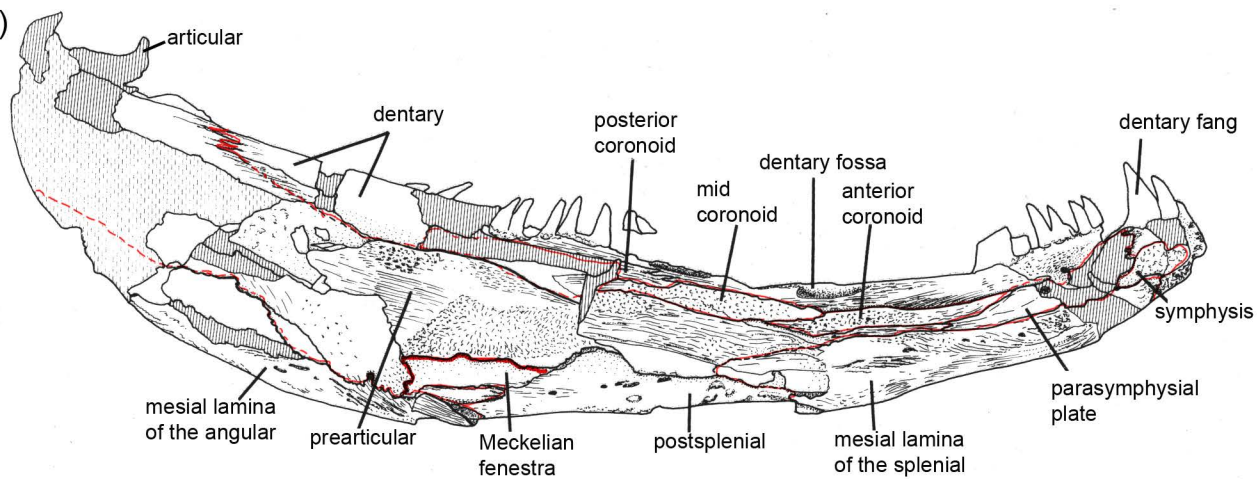
(A)

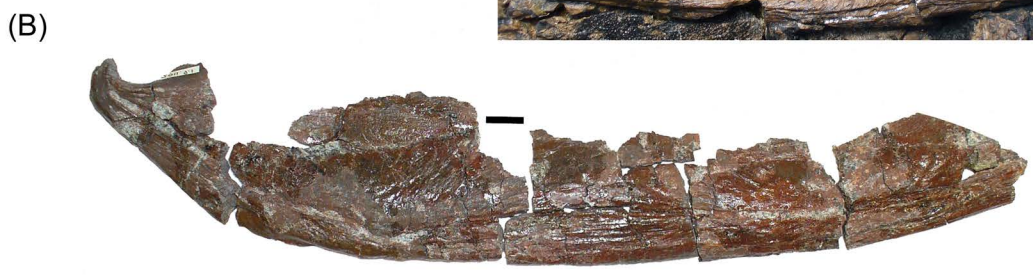
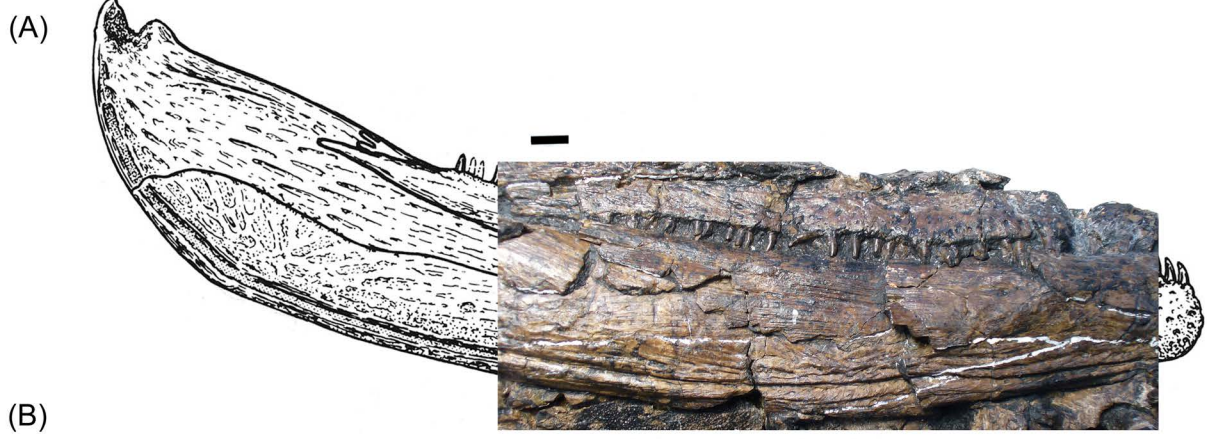


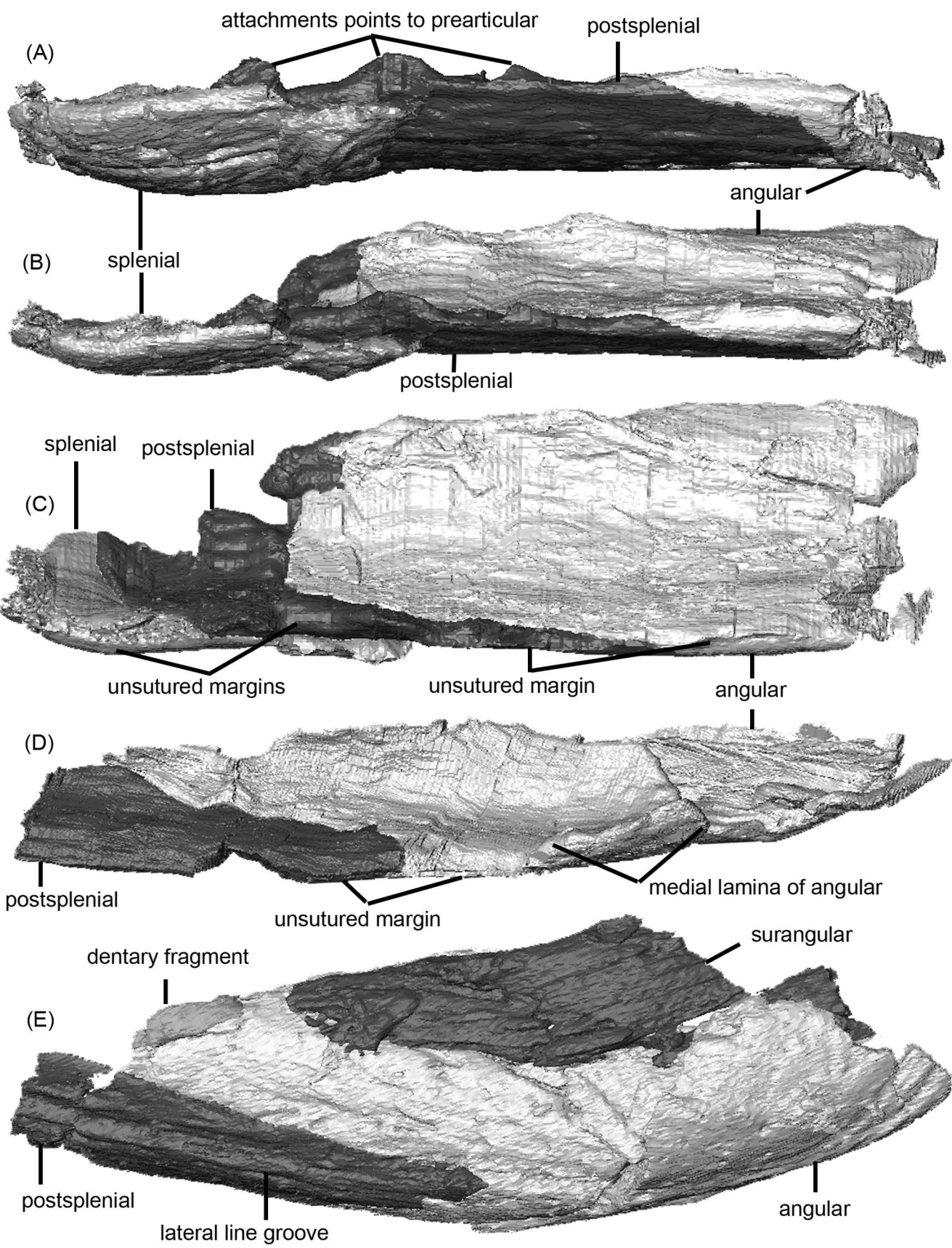
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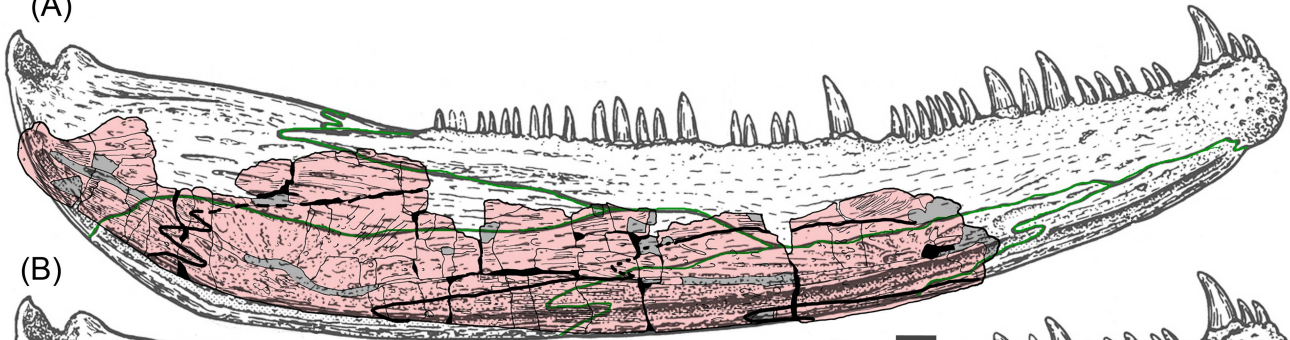
(C)







(A)



(B)

