Osteology and digital reconstruction of the skull of the early tetrapod *Whatcheeria deltae*

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ABSTRACT—The Early Carboniferous stem tetrapod *Whatcheeria deltae* is among the earliest-branching limbed tetrapods represented by multiple near-complete specimens, making it an important taxon in understanding the vertebrate water-to-land transition. However, all preserved skulls of *Whatcheeria* suffer from post-mortem crushing and lateral compression, which has made cranial reconstruction problematic. In this study, computed tomography data of three *Whatcheeria* specimens were segmented using visualization software to digitally separate each individual skull bone from matrix. Digital methods were used to repair and retrodeform the bones and produce the first complete three-dimensional skull reconstruction of *Whatcheeria*. We provide a revised description of the cranial and lower jaw anatomy of *Whatcheeria* based on CT data, focusing on sutural morphology and previously unknown anatomical details. Our findings suggest that *Whatcheeria* had one of the narrowest skulls of any known early tetrapod, a gap between the nasals, and significant overlap of the lacrimal onto the nasal and prefrontal. Sutural morphology is used to infer loading regime in the skull during feeding and suggests the skull of *Whatcheeria* was well-adapted to resist stresses induced by biting large prey with its enlarged anterior fangs.

INTRODUCTION

The evolution of the tetrapod body plan and subsequent colonization of terrestrial environments were key steps in vertebrate evolution (Clack, 2002; Daeschler et al., 2006; Pardo et al., 2017; Beznosov et al., 2019). Viséan deposits near the town of Delta in Iowa have yielded a rich fauna of fishes and tetrapods, including *Whatcheeria deltae* (Lombard and Bolt, 1995), *Sigournea multidentata* (Bolt and Lombard, 2006) and *Deltaherpeton hiemstrae* (Bolt and Lombard, 2010). *Whatcheeria*, which along with *Pederpes finneyae* (Clack, 2002) and possibly *Ossinodus pueri* (Ruta and Bolt, 2006) comprise the Whatcheeriidae (Clack, 2002), is considered a key taxon in tetrapod evolution due to the completeness of its fossils (Lombard and Bolt, 1995) and its basal position in the tetrapod phylogeny (Marjanović and Laurin, 2019). However, it is currently unclear whether the Whatcheeriidae form a distinct clade or merely represent a paraphyletic grade of stem tetrapods (Warren, 2007). The term ‘whatcheeriid-grade’ has been widely applied to numerous isolated or poorly-preserved tetrapod remains (Olive et al., 2016), but this diagnosis remains uncertain in many cases (Otoo et al., 2021). A greater understanding into the anatomy of these animals is therefore important to provide a more precise definition of the whatcheeriid group and how they fit into the story of early tetrapod evolution.

Four descriptive accounts of *Whatcheeria* have been published, focusing on the overall anatomy (Lombard and Bolt, 1995), the lower jaw (Lombard and Bolt, 2006), the palate and braincase (Bolt and Lombard, 2018) and the postcrania (Otoo et al., 2021). These previous works have suggested that the skull of *Whatcheeria* was tall and narrow compared to other early tetrapods (Bolt and Lombard, 2018) but other aspects of the general morphology and anatomy remain unclear. A complete reconstruction of the *Whatcheeria* skull would assist in highlighting the unusual morphology of this taxon and provide data for future cladistic or biomechanical analyses. Digital preparation of fossil material using microcomputed tomography (μCT) scanning and three-dimensional (3D) visualization allows fragile or obscured material to be explored and reconstructed for further analyses. These methods have already been applied to the lower jaw of the tetrapodomorph fish *Eusthenopteron foordi* (Porro et al., 2015a) and the skull of the early tetrapod *Acanthostega gunnari* (Porro et al., 2015b), revealing bones previously obscured by matrix and aiding in more accurate identification of bones and repairing post-mortem distortion. These discoveries have resulted in new reconstructions that have promoted a step-change in our understanding of intricate anatomy of these organisms, though these digital models are still hypotheses based on specimen availability, scan resolution and personal interpretation. In this study, multiple specimens of *Whatcheeria* were segmented from µCT scans in order to explore skull anatomy, augment existing descriptions and produce the first 3D digital reconstruction of the skull of this early tetrapod taxon.

Institutional Abbreviations—**FM,** Field Museum of Natural History, Chicago, IL, U.S.A.

Anatomical Abbreviations—**ad**, adsymphysial; **af**, adductor fossa; **an**, angular; **ar**, articular region of Meckelian ossification; **bo**, basioccipital; **bs**, basiparasphenoid; **ch**, choana; **co1**, anterior coronoid; **co2**, middle coronoid; **co3**, posterior coronoid; **d**, dentary; **ect**, ectopterygoid; **endofen**, endomeckelian fenestra(e); **f**, frontal; **in**, intertemporal; **j**, jugal; **l**, lacrimal; **me**, Meckelian ossification; **mx**, maxilla; **n**, nasal; **o**, orbit; **p**, parietal; **pa**, prearticular; **pf**, prefrontal; **pl**, palatine; **pmx**, premaxilla; **po**, postorbital; **poc**, preopercular; **psp**, postsplenial; **pt**, pterygoid; **ptf**, postfrontal; **ptp**, postparietal; **q**, quadrate; **qj**, quadratojugal; **sa**, surangular; **sp**, splenial; **sq**, squamosal; **st**, supratemporal; **tab**, tabular; **v**, vomer.

MATERIALS AND METHODS

The three *Whatcheeria* specimens µCT-scanned in this study – FM PR 1634, FM PR 1665 and FM PR 1814 – were collected from the disused Hiemstra Quarry in SE Iowa in 1986 and 1988 (Lombard and Bolt, 1995). FM PR 1634 (Figs. 1A and lB) is a laterally compressed but largely complete skull (161mm from anterior premaxilla to posterior quadratojugal, as preserved) with an intact skull roof, snout and left cheek, along with both lower jaws and additional post-cranial material not examined in this study. FM PR 1814 (Figs. 1C and 1D) is an incomplete skull (170mm in length from anterior premaxilla to posterior quadratojugal, as preserved) including a partial skull roof, left cheek and a complete left lower jaw. FM PR 1665 (Figs. 1E and 1F) is a complete left lower jaw (194 mm in length) completely freed of matrix.

All specimens were scanned in 2017 in the Department of Organismal Biology and Anatomy at the University of Chicago on a dual tube X-ray µCT system (General Electric, Fairfield, Connecticut, U.S.A.) at 200µA using a 0.5 mm copper filter; FM PR 1634 was scanned at 200 kV, FM PR 1665 was scanned at 180 kV, and FM PR 1814 was scanned at 210 kV. Reconstructions of both FM PR 1634 and FM PR 1814 produced 2022 transverse TIFF slices composed of isometric voxels with a resolution of 0.122 mm/voxel. FM PR 1665 produced 2022 transverse TIFF slices composed of isometric voxels with a resolution of 0.099 mm/voxel. Scans were processed using the 3D visualization software Avizo 8.0 (Thermo Fisher Scientific, Waltham, Massachusetts, U.S.A.). Density thresholding was used to distinguish boundaries between fossils and surrounding matrix, empty space and artificial infilling. Scans were then segmented slice-by-slice, interpolating across no more than 5 slices at a time, to separate individual bones, teeth and sutures (Figs. 2 and 3). Sutures were identified as low-density gaps between bones that persisted through all relevant slices. Information from photographs of original specimens and previous descriptions were used to distinguish sutures from post-mortem damage. For example, bones at abutting sutures tend to have more rounded margins than those produced by cracks, and cracks often persist across multiple bones. Individual bones were isolated and converted to 3D surface models (Figs. 2 and 3) that could be digitally manipulated, allowing the following anatomical description.

It should be noted that specimens underwent some post-mortem damage and deformation. In FM PR 1634, the left cheek, left snout and skull roof are well-preserved (Fig.

1A), with the right cheek, part of the right snout and palate crushed underneath. The left jugal and maxilla appear to have been subjected to minor deformation posterior to the 11th preserved tooth (Fig. 2). The left lower jaw of FM PR 1634 is missing the anterior tip and is split into two undamaged sections. The right lower jaw is mostly complete, though the posterior half is obscured by the left cheek. The anterior portion of the braincase of FM PR 1634 is partially preserved, with a mostly intact parasphenoid and partial basisphenoid (Fig. 2). FM PR 1814 preserves a complete snout with little deformation, and partial left and right cheeks (Fig. 1C). Some sections of the skull roof are also clearly visible, though less so than in FM PR 1634. The anterior section of the palate in FM PR 1814 is very well-preserved, though the posterior section of the pterygoid is slightly deformed. Scans reveal that the right lower jaw is preserved intact within the matrix underneath the exposed left lower jaw. A partial parasphenoid is also preserved. FM PR 1665 (Fig. 1E) is very well-preserved, with the only visible damage being a small amount of bone missing from the dorsal surface of the prearticular and surangular, and the posterior-most section of the dentary.

Digital retrodeformation of disarticulated skulls is an increasingly reliable method for reconstructing the anatomy of fossil taxa (Arbour and Currie, 2012; Lautenschlager et al., 2014; Cuff and Rayfield 2015; Lautenschlager, 2016; Lautenschlager, 2017), including early tetrapods (Porro et al., 2015a; Porro et al., 2015b). These reconstructions have provided new insights into early tetrapod skull morphology as well as necessary data for further morphometric and biomechanical studies. Our 3D reconstruction of *Whatcheeria* is largely based on FM PR 1634, as this specimen preserves a complete skull roof, left snout and left cheek with little damage (Fig. 2). The left postorbital, squamosal, and quadratojugal of FM PR 1634 are fractured; individual pieces were segmented separately, moved into place and repaired using interpolation. Additional steps were taken to address the deformation of the maxilla and jugal of FM PR 1634. The deformed portion of the maxilla was split into four sections which were then translated to create a mediolaterally straight profile, as is seen in the undeformed maxilla of FM PR 1814. To address the deformation in the medial section of the jugal of FM PR 1634, the bone was constructed using the undeformed anterior and posterior sections from FM PR 1634, and the undeformed middle section from FM PR 1814. The premaxilla shelf, vomer, palatine, pterygoid and ectopterygoid from the left side of FM PR 1814 (Figs. 3A and 3B) were used to reconstruct the palate. The pterygoid of FM PR 1814 was segmented into three separate pieces (anterior, middle and posterior) to address the dorsally convex profile caused by post-mortem deformation. The jugal and palatal bones from FM PR 1814 were scaled to the size of FM PR 1634 by a factor of 0.899, as determined by comparing the length of the dentary, the length of the lacrimal and the height of the maxilla between specimens. The lower jaw was segmented from FM PR 1665 and scaled to the size of FM PR 1634 by a factor of 0.795 using measurements of the dentary. The missing portions of the prearticular and surangular immediately posterior to the tooth row were reconstructed using interpolation to match other described specimens (Lombard and Bolt, 2006) which preserved this region intact. The prearticular, surangular and Meckelian ossification were segmented as multiple pieces to reconstruct the mandibular adductor chamber, which experienced mediolateral crushing.

The well-preserved skull roof was used as the starting point for the reconstruction. The left side of the skull was reconstructed by fitting the snout and cheek bones together along sutural contacts and checked using the course of lateral line canals. The initial reconstruction used a skull length to width (L:W) ratio of 2.2, as described in Bolt and Lombard (2018), a model that assumed that the pterygoids were orientated horizontally, with no dorsal vaulting along the midline. The palatal bones were then added to the reconstruction, allowing us to adjust the L:W accordingly. The model was also tested using a vaulted palate, as suggested in the recent 3D reconstruction of *Acanthostega* (Porro et al., 2015b). The right side of the skull was created by mirroring the left side, as many of the right bones in FM PR 1634 were deformed during fossilization (Fig. 2). The palate was used as a test for the model; the pterygoids must articulate with one another anteriorly while leaving space for the parasphenoid to fit between them posteriorly (Bolt and Lombard, 2018), as well as articulate correctly with the marginal palatal bones (vomer, palatine, ectopterygoid). Transformation matrices for all skull bones from the original data set to the final, 3D reconstruction are available as a matrix (Supplementary Data 1) and a 3D model of the reconstructed skull is available for inspection (Supplementary Data 2). The raw CT scan data for all three specimens and an STL file of the final 3D model is available on Morphosource (https://www.morphosource.org/projects/000344379).

OSTEOLOGICAL DESCRIPTION

Here we do not provide a detailed description of the skull of *Whatcheeria*, as this work is currently being undertaken elsewhere (Coates and Lombard, pers. comm.). Instead, we focus on describing new anatomical details visible in µCT scans, which allows access to morphological features not visible in physical specimens. In particular, we focus on 3D sutural morphology within the skull that can be visualized in scan data but cannot be easily observed in fossils.

Skull Roof

Nasal—When viewed in transverse section, the nasal is dorsally arched posteriorly and becomes flatter anteriorly. It is dorsoventrally thickest near the midline and thins laterally. The posterior half of the medial margin of the nasal overlaps the frontal along a slightly interdigitated contact. The nasals meet anteriorly at the midline in a simple butt joint, but our 3D model (Fig. 4) produced a midline gap which widens posteriorly. The contact between the premaxilla and nasal is interdigitated, with µCT scans revealing that the nasal also underlaps the premaxilla. As described by Lombard and Bolt (1995:8), the nasal forms the majority of the dorsal margin of the external naris, where it is marked by a “fimbriate” morphology and a shallow depression that extends onto the lacrimal (Fig. 2), a feature also seen in *Pederpes* (Clack and Finney, 2005). This morphology may indicate the presence of a missing anterior tectal (Lombard and Bolt, 1995), though none has yet been recovered in either taxon. Retrodeformation of the cranium (Fig. 4) indicates that the ventral surface of the nasal is strongly overlapped by the lacrimal. The posterior margin of the nasal shallowly overlaps the prefrontal. 3D manipulation indicates that the anteroventral margin of the nasal has a short contact with the maxilla, which it meets at a simple butt joint (Fig. 4A). The supraorbital lateral line extends along the length of the nasal as an open sulcus from the premaxilla anteriorly to the prefrontal posteriorly. This sulcus is briefly roofed at the midpoint of the nasal to form an enclosed canal, being only externally visible as a single pore halfway between the two openings, though µCT scans reveals a straight internal course.

Frontal—In FM PR 1634, the right frontal slightly overlaps the left frontal; this is most likely due to deformation, as the medial margins of both frontals are smooth when viewed in isolation. This indicates that the midline contact was most likely a butt joint. The interfrontal contact surface thickens dorsoventrally posterior to the midpoint of the bone. The posterolateral margin of the frontals dorsally overlap the medial edges of the postfrontals, with the degree of overlap increasing anteriorly. The posterior margins of the frontals meet the parietals at a highly interdigitated contact; scan data reveals that the frontals also slightly underlap the parietals. The supraorbital lateral line extends onto the lateral surface of the frontal from the nasal as an open canal, terminating anterior to the frontal-postfrontal contact.

Parietal—The contact between the parietals in FM PR 1634 is weakly interdigitated anterior to the parietal foramen but forms a butt joint posterior to the foramen, a pattern also seen in *Acanthostega* (Porro et al., 2015b). The parietal-postparietal contact extends perpendicular to the midline and is weakly interdigitated. Scans of FM PR 1634 reveal that the left postparietal overlaps the left parietal for the lateral portion of the contact. The posterolateral corner of the parietal overlaps the supratemporal, with minor interdigitations at the surface. The posterior half of the lateral margin of the parietal forms a tight, interdigitated suture with the intertemporal. Anteriorly, the lateral surface of the parietal is incised by the postfrontal, which the parietal overlaps dorsally. As mentioned in the original description, the parietal foramen is surrounded by a tall roughened, ridge that becomes smoother and tapers anteriorly, and broadens posteriorly (Lombard and Bolt, 1995). Laterally, this ridge transitions into a broad, smooth depression posterior to the parietal foramen (Fig. 4B). Similar features have been reported in several early tetrapods such as the seymouriamorph *Utegenia shpinari* (Klembara and Ruta, 2003), the anthracosaur *Proterogyrinus scheelei* (Holmes, 1984) and an isolated posterior skull table from the Upper Carboniferous of Northumberland (Boyd, 1985). Given that the parietal of *Pederpes* has not been recovered (Clack, 2002) it is unclear whether this feature was present in other whatcheeriids, though it is absent in *Ossinodus* (Warren, 2007). This feature may perhaps be indicative of an unknown soft tissue structure, though this is purely conjectural and should be examined in additional specimens. The supraorbital lateral line canal crosses the anterior portion of the parietal foramen and continues laterally across the parietal surface as an open sulcus before crossing onto the postfrontal.

Postparietal—The midline suture between the postparietals is strongly interdigitated. The lateral surface of the postparietal contacts the supratemporal in a highly interdigitated suture that becomes more gently undulating deeper ventrally into the bone. Although the suture is difficult to distinguish in some slices, μCT scans of FM PR 1634 reveal a tongue and groove contact between the postparietal and tabular, with the tabular overlapping dorsally and underlapping ventrally. The postparietals possess similar, albeit smaller, depressions to the parietals towards their anterior margins (Fig. 4B).

Postfrontal—The anterior portion of the postfrontal is characterized by depressions marking overlap surfaces for the prefrontal and frontal. Posteriorly, scans reveal that the postfrontal strongly overlaps the intertemporal, with the degree of overlap increasing ventrally. The posteroventral section of the postfrontal forms a short, interdigitated contact with the postorbital. The supraorbital lateral line crosses the posterior region of the postfrontal from the parietal to the postorbital.

Intertemporal—The posterior margin of the intertemporal is perpendicular to the midline and meets the supratemporal along a highly interdigitated suture. The lateral margin mostly contacts the postorbital, with the posterolateral corner meeting the squamosal. Both contacts are interdigitated. The dorsal surface bears several very small, shallow depressions, at least eight in the left intertemporal of FM PR 1634, but is otherwise devoid of ornamentation.

Supratemporal—Best preserved on the left side of FM PR 1634 (Fig. 2A), the supratemporal curves ventrally where it meets the cheek region. The anterior margin tapers towards the midline and contacts the intertemporal and parietal. The posterior margin contacts the tabular at an interdigitated suture. As in *Acanthostega* (Porro et al., 2015b), the supratemporal has a posterolaterally tapering process between the squamosal and tabular

(Fig. 4A), though the process seen in *Whatcheeria* is less pronounced. The lateral surface of the supratemporal forms a tight interdigitated contact with the squamosal, as noted by Lombard and Bolt (1995).

Tabular—The lateral margin of the tabular curves ventrally along with the supratemporal, though there is no contact with the squamosal. The dorsal surface of the left tabular of FM PR 1634 possesses three small shallow pits similar in morphology to those found on the intertemporal, but otherwise has no ornamentation. The posterolateral corner of the tabular forms a posteriorly projecting process referred to as the "tabular horn" in the initial description by Lombard and Bolt (1995:7). A rimmed pit is present on the posterior surface of the process. The stubby appearance of this structure reflects the original morphology and is not the result of post-mortem damage.

Cheek

Premaxilla—The midline contact between the premaxillae is a simple butt joint. The premaxilla forms the anterior border of the narial opening (Fig. 4A), as well as a portion of the ventral margin of the narial opening where it meets the maxilla at a butt joint. The posteriorly projecting palatal shelf of the premaxilla (Fig. 4C) contacts both the vomer and the pterygoid. µCT scans confirm the presence of a scarf joint morphology at the anterior end of the vomer, strongly implying that the vomer dorsally overlaps the palatal shelf of the premaxilla, as well as being interdigitated. The pterygoid-premaxilla contact in FM PR 1814 is slightly disarticulated but is likely a simple butt joint. µCT scans reveal the course of the lateral line within the premaxilla, which is largely encased in bone. The infraorbital canal enters the premaxilla through a small foramen on the anterior portion of the narial opening dorsal to the palatal shelf. This canal continues anteriorly within the bone before branching off into many thin anteriorly directed canals that exit the anterior surface of the premaxilla as small pits (Fig. 4A), confirming that these are sensory openings to the lateral line as suggested in (Bolt and Lombard, 2018). The course of the main canal then curves posteriorly and exits onto the external dorsal surface of the premaxilla as the supraorbital lateral line before continuing posteriorly onto the nasal.

Maxilla—Externally, the dorsal surface of the maxilla is straight and forms a simple butt joint with the lacrimal and jugal. The medial surface of the maxilla also contacts the lateral edges of the palatine and ectopterygoid (the lateral edge of the vomer is excluded from the maxilla by the choana) (Fig. 4C). In FM PR 1814, µCT scans reveal that the maxilla-palatine contact is mostly a smooth-edged butt joint, as described in Bolt and Lombard (2018), but shows signs of weak interdigitation at the anterior-most portion of the dorsal surface. Bolt and Lombard (2018:6) noted that the maxilla and palatine of larger specimens of *Whatcheeria* such as FM PR 2891 possess an interdigitated or “rugose” surface for the entire maxilla-palatine contact. Evidence of the beginnings of such a contact in FM PR 1814 indicates that this suture became more tightly interdigitated in larger individuals. Conversely, the maxilla-ectopterygoid contact observed in FM PR 1814 is a simple butt joint with no signs of interdigitation. µCT scans also show that the anteroventral sulcus on the internal surface of the maxilla is indeed a lateral line canal that branches from the infraorbital canal on the adjacent lacrimal, where it is encased in bone.

Lacrimal—The posterior edge of the lacrimal is characterized by a deep, wide triangular incision that tapers to a point where it contacts the anterior portion of the jugal. The long posterior process of the lacrimal that forms the ventral rim of incision is highly unusual and may be a diagnostic feature of *Whatcheeria*. The lacrimal of *Parmastega aelidae* (Beznosov et al., 2019) also bears a posteroventral process, but it is dorsoventrally wider and lacks the straight lateral profile seen in *Whatcheeria*. The left lacrimal in FM PR 1634 indicates that this bone slightly underlaps the jugal, though no signs of interdigitation, such as are seen in *Acanthostega* (Porro et al., 2015b), are present. The infraorbital canal is enclosed along most its course within the lacrimal, opening only at a large foramen near the middle of the bone and as an open canal at the anterior most edge. This lateral line likely crosses the narial opening (possibly through a missing anterior tectal) and joins a foramen seen on the posterior surface of the premaxilla (Bolt and Lombard, 2018). The lateral line system is much clearer in *Whatcheeria* than in *Pederpes,* which only displays hints of possible lateral line on the lacrimal and jugal (Clack and Finney, 2005).

Prefrontal—In transverse section, the prefrontal is thickened dorsally where it contacts the nasal and very thin ventrally where it contacts the lacrimal. The dorsal margin of the prefrontal, best preserved on the left side of FM PR 1634 (Fig. 2), overlaps both the frontal and postfrontal, with the degree of overlap increasing over the postfrontal. Retrodeformation of the cranium (Fig. 4) suggests that the prefrontal underlapped the lacrimal and the dorsal portion of the jugal. The anterodorsal area of the prefrontal contains the supraorbital lateral line that continues from the adjacent nasal as an open canal. The most distinct feature of the prefrontal of *Whatcheeria* is the prominent ridge or ‘eyebrow’ (Lombard and Bolt, 1995) anterior to the orbit (Fig. 4A). This feature is seen on the postfrontal of *Panderichthys rhombolepis* and *Elpistostege watsoni* (Schultze and Arsenault, 1985; Vorobyeva and Schultze, 1991) as well as the prefrontal of *Parmastega aelidae* (Beznosov et al., 2019) but is not seen in *Pederpes* (Clack and Finney, 2005). The prefrontal of *Ossinodus* has not yet been recovered (Warren, 2007). µCT scans of the foramina present on the underside of the prefrontal ridge reveal small spaces within the prefrontal that exit onto the anterior margin of the orbit.

Jugal—The description of the jugal of *Whatcheeria* is based on the left sides of both FM PR 1634 and FM PR 1814. Having identified the contact between the jugal and quadratojugal from µCT scans, we can confirm that the jugal is completely excluded from the ventral surface of the cranium by the maxilla (Fig. 4A). In transverse section, the jugal is dorsoventrally straight with little lateral curvature, indicating a near vertical cheek. The ventral surface of the jugal is mediolaterally thickened where it contacts the maxilla. The posterior section of the jugal contacts the squamosal and quadratojugal at overlapping, interdigitated sutures, with a narrow process that extends dorsally to contact the postorbital at an interdigitated joint. The infraorbital lateral line continues onto the jugal from the adjacent portion of the lacrimal as an open sulcus and extends posteriorly parallel to the ventral margin of the orbit, represented by a series of openings. Posterior to the orbit, the lateral line curves upwards and diverges into two paths visible as open sulci and openings. The dorsal path continues onto the postorbital; the ventral path continues posterodorsally onto the squamosal.

Postorbital—The postorbital of *Whatcheeria* is greatly reduced, far more so than in *Pederpes* (Clack and Finney, 2005) and *Ossinodus* (Warren, 2007). The left postorbital of FM PR 1634 (Fig. 2) is broken into two pieces but remains complete. The postorbital tapers ventrally from the dorsal contacts with the postfrontal and intertemporal to the ventral contact with squamosal, which is interdigitated. The postorbital bears an open sulcus running dorsoventrally along its length (Fig. 4A) that connects the infraorbital lateral line in the adjacent portion of the jugal to the lateral line on the postfrontal.

Squamosal—As noted by Lombard and Bolt (1995), the squamosal joins the skull roof via the intertemporal and supratemporal in a highly interdigitated suture that is also visible in *Pederpes* (Clack and Finney, 2005), though the contact in *Ossinodus* is a butt joint (Warren, 2007). There is no squamosal-tabular contact; the posterodorsal edge of the squamosal forms the ventral rim of the otic notch and is separated from the tabular by the supratemporal (Fig. 4A). The preopercular-squamosal contact is very tight but appears to be a smooth butt joint. The ventral surface of the squamosal, which meets the quadratojugal at a closely fitted butt joint, is slightly dorsally concave. A short open sulcus crossing the jugal-squamosal contact at the anterior margin of the squamosal of FM PR 1634 marks the ventral branch of the infraorbital lateral line. The canal continues as an open sulcus on the posterior section of the squamosal, which curves ventrally and crosses onto the preopercular.

Quadratojugal—The posterodorsal margin of the quadratojugal underlaps the preopercular for its entire length. Unlike *Acanthostega*, there does appear to be a contact between the quadratojugal and the quadrate, though the exact position of the suture was difficult to discern in our specimens. This joint is a simple butt joint between the medial surface of the quadratojugal and the lateral surface of the quadrate.

Preopercular—The contacts of the preopercular of *Whatcheeria* are often difficult to distinguish in physical specimens and are usually inferred from a change in surface lineation (Lombard and Bolt, 1995). This contact is more clearly visible in the µCT scans, particularly on the left side of FM PR 1634. The dorsal margin of the preopercular is rounded and curves smoothly to form the posterior margin of the cranium, which is straight except for two shallow embayments located just above and below the dorsoventral midline of the preopercular. The ventral edge, which contacts the quadratojugal, is more mediolaterally flattened and extends slightly anteriorly. The lateral line seen on the squamosal continues onto the preopercular as an open sulcus angled posteroventrally.

Quadrate—It should be noted that the quadrate is not complete in any of the observed specimens, with only the lateral portion that contacts the quadratojugal being preserved. This result was not surprising, given that previous descriptions have noted the absence of a complete quadrate in other *Whatcheeria* specimens (Bolt and Lombard, 2018). The lateral surface of the partial left quadrate of FM PR 1634 (Fig. 2B) contacts the quadratojugal at a simple butt joint; it was difficult to ascertain the course of the suture in places. The contact between the quadrate and the quadrate ramus of the pterygoid could not be discerned in any of our specimens.

Palate

The components that make up the palate of *Whatcheeria* (vomer, palatine, ectopterygoid and pterygoid) have been previously described in Bolt and Lombard (2018), and our study largely corroborates their morphological descriptions. Here we add information pertaining to the sutural contacts between the bones.

Pterygoid—The pterygoid (Fig. 4C) is by far the largest palatal bone and is the only one to bear denticles, a derived feature that separates *Whatcheeria* from its sister taxon *Pederpes* (Bolt and Lombard, 2018). The pterygoid in FM PR 1814, as with most specimens of *Whatcheeria*, is crushed into a two-dimensional plane, leaving any vertical component absent from our reconstruction. The anterior portion of the pterygoids contact one another at a butt joint to form the midline suture. The lateral margin of the pterygoid contacts the entire medial margins of the vomer, palatine and ectopterygoid. Bolt and Lombard (2018) used evidence from FM PR 1792 to suggest that the three lateral bones contact the dorsal surface of the pterygoid, though deformation and matrix made it impossible to confirm this in other specimens. µCT scans of FM PR 1814 revealed these contacts in detail and confirm that the vomer, palatine and ectopterygoid dorsally overlap the pterygoid, producing a thin scarf joint. The long quadrate ramus extends posteriorly to form the medial border of the adductor fossa (Fig. 4C), though no quadrate is visible in articulation in FM PR 1814.

Vomer—The vomer contacts the palatal shelf of the premaxilla anteriorly, the pterygoid medially and the palatine posteriorly. The vomer-palatine contact is a close-fitting, finely interdigitated suture, with µCT scans indicating that the palatine slightly dorsally overlaps the vomer.

Palatine—The palatine, which is approximately similar in size to the vomer contributes to the posterior border of the choana (Fig. 4C). The posterior contact with the ectopterygoid exhibits minor scarf joint morphology, with the ectopterygoid slightly dorsally overlapping the palatine.

Ectopterygoid—The ectopterygoid of FM PR 1814 is obscured by in matrix, but additional ectopterygoid material was visible in the µCT scans. The ectopterygoid, which is longer than the vomer and palatine, extends posteriorly to form the anterior margin of the adductor fossa.

Braincase

The braincase of *Whatcheeria* is comprehensively described in (Bolt and Lombard, 2018), and our findings corroborate their results. The parasphenoid and the basisphenoid (Fig. 4C) are entirely fused; no sign of a suture between these bones could be detected in µCT scans. The basipterygoid joint surface is also visible, particularly in FM PR 1814 where the left pterygoid and the basisphenoid appear to be in articulation. The ventral surface of the anterior process of the parasphenoid of FM PR 1634 (Fig. 2B) preserves a contact surface which would presumably meet the dorsal surface of the pterygoids at a butt joint, though deformation and fragmentation makes this conclusion uncertain. The rest of the braincase was not preserved in our specimens and has likely been crushed under the posterior skull roof. Some fragments of the otic capsules and exoccipitals may be visible in the µCT scans of FM PR 1634 but were not complete enough to yield any useful anatomical information.

Lower Jaw

Broadly speaking, the lower jaw of *Whatcheeria* bears strong similarity to many Devonian stem tetrapods, including a dorsally opening adductor fossa and the lack of an elevated surangular crest. The lower jaw has been described in detail by (Lombard and Bolt, 2006), so a full description will not be included here. The use of µCT scans allowed us to identify several features that could not be observed in the physical specimens, including the nature of sutural contacts.

Adsymphysial—The lateral and medioventral edges of the adsymphysial dorsally overlap the dentary and splenial respectively, whereas the posterior edge contacts the anterior coronoid at an interdigitated suture. Our digital manipulation of the 3D model (Fig. 5) confirms that the adsymphysial contributes to the lower jaw symphysis where it meets its counterpart at the midline at an interdigitated, rugose contact.

Coronoid Series—The anterior coronoid is strongly interdigitated with the dentary whereas the middle and posterior coronoids contact the dentary at a simple butt joint. Additionally, µCT scans reveal that each coronoid exhibits a laterally projecting shelf on its ventral surface that inserts into the medial shelf of the dentary to form a tongue-and-groove joint, a feature previously undescribed in *Whatcheeria*. This shelf doubles the width of the coronoids in places but can only be observed in physical specimens as a short posterolateral process on the posterior coronoid (Lombard and Bolt, 2006). This process overlaps the dorsal margin of the surangular and partially forms the anterior boundary of the mandibular adductor fossa (Fig. 5C), although part of this contact is missing in FM PR 1665. µCT scans of FM PR 1665 clearly show the contact between the coronoid bones and the splenial/prearticular, which is often obscured in physical specimens (Lombard and Bolt, 2006). The anterior coronoid-splenial contact has no interdigitation and meets at a simple butt joint. The contacts between the coronoids and the prearticular have a small number of deeply incised interdigitations but are otherwise smooth with no overlap. The contacts between the coronoids are interdigitated, with the middle and posterior coronoids each possessing an anterolateral process that overlaps the coronoid anterior to it.

Dentary—Posteriorly, the dentary overlaps the surangular for the entire length of the contact, including along the narrowly tapering post dental process that we observed in FM PR 1634 (Fig. 2A). At the moderately interdigitated dentary-angular contact, the lateral profile of the dentary angles sharply ventrally (Fig. 5A), a feature which Lombard and Bolt (2006) notes is only seen elsewhere to a lesser degree in *Crassigyrinus scoticus* (Clack, 1997), though *Greererpeton burkemorani* has a similar morphology in the dentary-surangular contact (Bolt and Lombard, 2001). The dentary overlaps both the postsplenial and splenial apart from at the anterior portion of the dentary-splenial contact, which is interdigitated. A rugose surface on the medial portion of the anterior tip marks the symphysial area, which joins its counterpart at an interdigitated suture. This area also features a broad channel running posteroventrally through the rugose surface (Fig. 5B), first described by Lombard and Bolt (2006). µCT scans do not reveal any novel internal anatomy in this area, leaving the function of the channel unknown. Furthermore, µCT scans were able to confirm that the mandibular lateral line, which can be seen as several sulci on the lateral surface of the surangular, does not cross on to the dentary internally.

Angular—The ventral margin of the angular overlaps the postsplenial in lateral view, save for the posterior-most process of the postsplenial, which laterally overlaps the angular, a feature visible through the fourth endomeckelian fenestrae (Fig. 5B) (see description of Meckelian ossification below) in FM PR 1665. A short anterior process of the angular, not visible at the surface, is completely laterally overlapped by the postsplenial ventrally and the dentary dorsally. Dorsally, the surangular narrowly overlaps the angular, with the degree of overlap increasing at the anterior-most end of the contact. The ventral portion of the angular-surangular contact has no overlap and, along with the ventral-most region of the angular-postsplenial contact, has a zig-zag morphology (Figs. 5A and 5D) (Lombard and Bolt, 2006), though this suture was hard to discern in our scans. The section of the angular that forms the ventral surface of the lower jaw contacts the Meckelian ossification at a simple butt joint. The angular also bears a section of the mandibular lateral line, as shown by a continuous series of foramina and several short sulci. This lateral line crosses anteriorly from the ventral part of the postsplenial and crosses posteriorly onto the surangular as an open sulcus.

Surangular—Ventrally, the surangular forms a butt joint with the Meckelian ossification along the posteroventral margin of the lower jaw. The lateral surface of the surangular also bears the mandibular lateral line, which is expressed as a series of open sulci. The oral lateral line also branches from the mandibular canal roughly dorsoventrally in line with the anterior of the articular surface and terminates just before the contact with the dentary.

Articular and Meckelian Ossification—Complete ossification of the Meckelian cartilage and continuous medial exposure of this ossification from the articular to the anterior of the single, elongate “exomeckelian” fenestra (following Bolt and Lombard (2006:8)) in *Whatcheeria* is unique among post-Devonian tetrapods, including other whatcheeriids, though it is present in *Panderichthys* and several Devonian tetrapods (Lombard and Bolt, 2006). Certain aïstopods possess some ossification of the Meckelian, but these elements have far less medial exposure than in *Whatcheeria* and, in the case of *Coloraderpeton brilli*, are fused to the prearticular (Pardo and Mann, 2018). The Meckelian ossification covers the exomeckelian fenestra and features a variable number of arches, the endomeckelian fenestrae (following Bolt and Lombard (2006)), on its ventromedial surface (Fig. 5B). The anterior extent of the Meckelian ossification in medial view terminates as a thin, tapering strip of bone separating the prearticular from ventral margin of the jaw (Fig. 5B), but µCT scans reveal that the Meckelian ossification continues anteriorly to the anterior margin of the exomeckelian fenestra, where it is overlapped by the splenial. The Meckelian ossification extends dorsally far above the ventral margin of the prearticular, which it underlaps, forming a scarf joint that extends up to halfway up the dorsoventral height of the prearticular. The contact between the Meckelian ossification and the splenial/postsplenial has proven obscure due to damage to the ventral surfaces of the endomeckelian fenestrae in all specimens (Lombard and Bolt, 2006), which may indicate that this contact had little structural strength. A very small portion of a possible Meckelian-postsplenial suture can be been in FM PR 1665 and µCT scans suggest this was a simple butt joint, but a lack of preserved contact elsewhere makes this conclusion far from unequivocal.

Prearticular—. Though the prearticular of FM PR 1665 is slightly mediolaterally deformed, it clearly exhibits the longitudinal "crest" separating dorsal and ventral faces described by Lombard and Bolt (2006:21). µCT scans reveal that the ventral margin of the prearticular extends anteriorly and strongly underlaps the dorsal portion of the splenial, a feature also present in *Acanthostega* (Porro et al., 2015b). Ventrally, the prearticular strongly overlaps the Meckelian bone (see above) and forms the dorsal surface of the anterior-most endomeckelian fenestra. The posterior end of the prearticular bears a foramen on the medial surface that connects to a foramen on the Meckelian bone by a shallow groove. The position of these foramina varies between specimens (Lombard and Bolt, 2006). µCT scans show that this foramen also pierces the underlapping Meckelian bone.

Splenial—In transverse section, the splenial is laterally convex and is mediolaterally thickest in its middle section. The posterior section of the splenial forms a scarf joint with the postsplenial; the postsplenial laterally overlaps the entire dorsal process and all but the most ventral part of the ventral process. The splenial contributes slightly to the ventral portion of the mandibular symphysis, where it meets its counterpart at an interdigitated suture, as indicated by a rugose surface. The lateral surface of the splenial bears the anterior extent of the mandibular lateral line, which crosses from the posterior margin of the postsplenial. Externally, the lateral line is visible as a series of small foramina that make its anterior extent difficult to trace. µCT scans of this area indicate that the lateral line extends to almost halfway towards the anterior of the splenial.

Postsplenial—The postsplenial is slightly laterally convex in transverse section, though less so than the splenial. The course of the mandibular lateral line can be traced along the external surface of the postsplenial as a series of foramina which cross from the ventral portion of the angular posteriorly onto the ventral portion of the splenial anteriorly.

SKULL RECONSTRUCTION

The initial description of *Whatcheeria* suggested that the skull was tall and narrow, had a very long postoccipital cheek region (21% of skull length) and a bluntly pointed snout (Lombard and Bolt, 1995). Reconstructions of the lower jaw of *Whatcheeria* (Lombard and Bolt, 2006) indicates that it conforms to the primitive morphology commonly observed in Devonian stem tetrapods: it is curved in overall shape, there is no elevated surangular crest, and the adductor fossa opens dorsally. A recent reconstruction of the skull in ventral view using the palatal bones as constraints (Bolt and Lombard, 2018) suggested that *Whatcheeria* had a skull L:W ratio of 2.2, assuming a horizontal palate, and up to 2.5 if the pterygoid is vaulted. This would mean *Whatcheeria* had the narrowest skull of any tetrapod on the stem lineage, followed by *Crassygyrinus* at 1.9 (Bolt and Lombard, 2018). With less certainty, Bolt and Lombard (2018) also estimated that the skull H:L ratio as 0.38, which is unusually high for an early tetrapod.

Our 3D digital reconstruction is congruent with previous evidence that *Whatcheeria* possesses an unusually high and narrow skull (Fig. 6). Our model has a L:W ratio of 2.25 when measured in palatal view and the pterygoids slope ventrally away from the midline at 21° to the horizontal. The vaulted palate results in a narrower skull than the horizontal palate reconstruction of Bolt and Lombard (2018) (L:W ratio of 2.2) but falls short of their narrower reconstruction (L:W ratio of 2.5) in which the palate is angled more sharply from the midline. In palatal view (Fig. 4C), the skull largely resembles the long U-shape of the previous palatal reconstruction except the anterior snout, where the premaxillae form a more rounded profile than the flattened anterior edge reconstructed by Bolt and Lombard (2018). The cheek is near vertical and meets the skull roof almost perpendicularly (Fig. 4B), resulting in a tall skull with a H:L ratio of 0.37. This measurement is very slightly smaller than previous estimates and indicates that *Whatcheeria* had the same H:L ratio as *Crassigyrinus* (Clack, 1997) and *Pholiderpeton scutigerum* (Clack, 1987). Maximum orbital length is approximately 21% of total skull length and the center of the orbit lies at 63% along the horizontal distance from the tip of the snout to the posterior edge of the skull roof, slightly more posterior than previous estimate (60%) (Lombard and Bolt, 1995). The postorbital region of *Whatcheeria* is approximately 33% of total skull length. Our measurement of postoccipital cheek length (13%) is significantly smaller than previously suggested (21%) (Lombard and Bolt, 1995). This is likely caused by the bones of the cheek being shifted anteriorly in our 3D model, given that digital manipulation of these bones was otherwise unable to produce a reconstruction in which anterior edge of the maxilla met the posterior edge of the premaxilla (Fig. 4A). This shift also results in a large lateral overlap of the lacrimal over the prefrontal and nasal. The absence of the posterior braincase prevents us from fully reconstructing the occipital region, making the posterior profile of the skull, including its effect on H:L ratio, likely the largest area of uncertainty in our 3D model. It should also be noted that the specimens in our study, like most of the recovered *Whatcheeria* material, likely represent immature animals (Otoo et al., 2021). Fragmentary material suggests that some individuals reached approximately twice the size of the largest specimen examined here (Otoo et al., 2021), and whether fully mature individuals would differ in morphology from our reconstruction is currently unknown.

The lower jaw corresponded very closely with previous reconstructions due to the good preservation of FM PR 1665; little retrodeformation was needed to restore its original shape (Fig. 5). The angular, surangular and dentary dominate in lateral view, with the lateral profile of the dentary narrowing sharply where it meets the angular. The splenial has slightly less exposure in lateral view than in the previous reconstruction (Lombard and Bolt, 2006), with the dentary forming a larger proportion of the anterior ventral surface of the jaw (Fig. 5A). The Meckelian ossification has a shorter anterior exposure than the previous reconstruction, only just reaching the anterior point of the exomeckelian fenestra, though this may be due to variation between individuals documented by Lombard and Bolt (2006).

DISCUSSION

Skull Shape and Wider Implications for Tetrapod Morphology

Studies during the last three decades have demonstrated that early tetrapods showed considerable morphological diversity, both cranially and postcranially, indicating that they were able to occupy a range of aquatic and terrestrial ecological niches (Ruta and Wills 2016; Pardo et al., 2017; Ruta et al., 2019). Aside from *Whatcheeria*, tetrapods outside the crown group currently known to possess narrow skulls include *Crassigyrinus*, *Greererpeton* and possibly *Pederpes* (following Bolt and Lombard (2018)) as well as *Lethiscus* (Pardo et al., 2017), with the anthracosaurs *Proterogyrinus* and *Pholiderpeton* showing similar morphology early in the crown group. *Spathicephalus mirus*, a stem tetrapod from the Namurian of Scotland and Nova Scotia, has another distinct morphology; an anteriorly flattened, almost square skull and small, chisel-shaped teeth that may have been adapted to filter-feed on soft invertebrates (Beaumont and Smithson, 1998; Smithson et al., 2017). *Acherontiscus*, a small limbless tetrapod from the Early Carboniferous, possessed heterodont dentition and was likely durophagous, feeding on hard aquatic invertebrates (Clack et al., 2019). Additionally, a recent phylogenetic analysis recovered aïstopods, an order of legless tetrapods with highly derived, snake-like skulls, as nested deeply within the stem tetrapod lineage, further highlighting the early evolution of unusual body plans in tetrapod history (Pardo et al. [2017] though see Marjanović and Laurin [2019] for an alternative interpretation).

Skull Loading Patterns Predicted by Suture Morphology

Sutures between bones in the skull likely perform a functional role by absorbing strain during mechanically demanding behavior such as feeding (Herring and Mucci, 1991; Rafferty and Herring, 1999; Ross et al., 2011; Moazen et al., 2009). Butt joints likely mark points of increased tension or bending whereas interdigitated sutures are better adapted to resist compression (Herring and Mucci, 1991; Rafferty and Herring, 1999). Scarf joints may have a more complicated function to withstand between multiple stress regimes (Markey et al., 2006) or may be adapted to cope with increased torsion (Bolt, 1974; Busbey, 1995; McHenry et al., 2006). Additionally, tongue-and-groove joints are associated with tension (Herring and

Mucci, 1991). Patterns of suture morphology can therefore be used to infer loading regimes in the skulls of extinct organisms and therefore predict feeding behavior. This has proven particularly useful in understanding the terrestrialization of tetrapods and the transition from aquatic suction feeding to terrestrial biting (Porro et al., 2015a; Porro et al., 2015b; Markey and Marshall, 2007). The ecology and feeding habits of *Whatcheeria* remain somewhat unclear: large and robust limbs suggest a reliance on appendicular locomotion but a well-developed lateral line system, poorly ossified wrists and ankles and the presence of numerous articulated specimens in freshwater deposits indicate a largely aquatic lifestyle (Bolt and Lombard, 2000), possibly utilising an aquatic walking gait in cluttered environments (Otoo et al., 2021). A long neck may have allowed greater head mobility in *Whatcheeria* compared to other early tetrapods (Otoo et al., 2021), but no other hypotheses regarding feeding mode have been published.

Anteriorly, the cranial suture pattern of *Whatcheeria* generally resembles that of *Acanthostega* (Porro et al., 2015b) and the temnospondyls *Archegosaurus decheni* and *Cheliderpeton latirostre* (Kathe, 1999), with anterior bones overlapping posterior bones at scarf joints and butt joints at the midline (Fig. 7A). One notable difference is the extensive, interdigitated scarf joint between the premaxilla and nasal, a feature not seen in *Acanthostega* or the high skulled *Crassigyrinus* (Clack, 1997). The posterior skull roof of *Whatcheeria* has increased interdigitation and is strongly connected to the cheek region (Figs. 7A and 7E), even more so than in *Acanthostega* (Porro et al., 2015b). The sutures between the bones of the ventral margin of the skull and those of the cheek, along with the midline of the snout, are the loosest within the cranium, a feature also seen in *Acanthostega* (Porro et al., 2015b). As in *Acanthostega*, many of the palatal contacts are scarf joints (Fig. 6B). The maxilla is loosely sutured to the marginal palatal bones, though the beginnings of interdigitation in FM PR 1814 combined with the observations of Bolt and Lombard (2018) on FM PR 2891 suggest that the morphology of these contacts, specifically the maxilla-palatine contact, may have varied between individuals in connection with size and ontogeny. The lower jaw is characterized by scarf joints with posterior bones overlapping anterior ones in many cases, though a few interdigitated contacts are found anteriorly and between the coronoids (Figs. 7C–D and 7F–G). The zig-zag sutures seen at the postsplenial-angular and angular-surangular contacts are not present in *Acanthostega* but are similar to the deep interdigitations at these contacts in the stereospondyl *Metoposaurus krasiejowensis* (Gruntmejer et al., 2019) and the posteroventral sutures in extant crocodilians (Porro et al., 2011). Another key difference to *Acanthostega* is the structural contribution of the Meckelian bone the medial surface of the lower jaw in *Whatcheeria*, where the Meckelian significantly underlaps the prearticular at a scarf joint.

Based on previously established relationships between suture morphology and loading regime, we predict that the skull table and posterior cheek region of *Whatcheeria* was subject to compression, given the dominance of interdigitated contacts in these areas. The strongly interdigitated contact between the posterior cheek and skull roof would have resisted stress moving from the sides of the skull to the dorsal surface. The higher proportion of interdigitation in this area compared to *Acanthostega* may counter additional loading at these contacts brought about by the high-sided, narrow skull shape of *Whatcheeria*. More efficient generation of vertical bite force associated with a deeper skull may also have contributed to the need for reinforcement in this area, though biomechanical studies are needed to support this. The scarf joints in anterior snout and cheek would have resisted torsion as stress induced by feeding was directed from the tooth row to the skull roof, including unilateral forces generated at the large maxillary fangs. The loose butt joint between the maxilla and the ventral cheek may have resisted vertical stresses induced by bite force and lateral stress produced by struggling prey. As in *Acanthostega*, the nasals and frontals are interdigitated posteriorly, suggesting that these areas were subject to longitudinal compressive stress, though unlike *Acanthostega*, this morphology extends to the premaxilla-nasal contact. This may suggest that *Whatcheeria* was adapted to resist higher stresses in the anterior snout caused by forceful biting, a hypothesis consistent with the large premaxillary teeth present in this taxon that are absent in *Acanthostega* and *Crassigyrinus*. This morphology is replicated somewhat around the large palatal fangs, though the contacts between the maxilla and palatine/ectopterygoid are surprisingly loose. Indeed, they are much more loose than in *Crassigyrinus* (L. Porro, pers. observ.), despite both taxa having large palatal teeth. The increased interdigitation seen here in some specimens may indicate a higher capacity for resisting vertical bite force and torsion in the palates of larger individuals. Contacts between the marginal palatal bones and the lacrimal/jugal could also have assisted in resisting compressive stress, but flattening of the cheek onto the palate in our specimens has obscured any evidence of such contacts during preservation. The scarf and butt joints in the medial palate would have assisted to resist tension and torsion produced in unilateral biting and holding struggling prey.

Extensive scarf jointing in the lower jaw of *Whatcheeria* suggests a complex loading regime adapted to resist torsion, likely induced by a combination of muscle forces bite force application. Jaw shape likely induces further torsion; the dentary tooth row is laterally offset from the midline of the jaw which would twist the dorsal portion outwards during vertical biting. This resembles the condition seen in modern crocodilians, which often feed on large prey using direct biting (Erickson et al., 2003). A higher proportion of strong interdigitated joints surrounding the large anterior dentary fang (dentary, adsymphysial and anterior coronoid) would have resisted compressive stress induced by biting, further suggesting that *Whatcheeria* used its anterior teeth to seize prey.

We found no evidence to suggest the possibility of cranial kinesis in the skull or lower jaws of *Whatcheeria*, in agreement with previous studies (Lombard and Bolt, 2006). The strongly sutured contacts between the cheek and skull table would render intracranial movement in this area impossible, and the scarf and interdigitated morphology of the sutures between the palatal bones would greatly limit any flexibility in this region. Similarly, the sutures at the lower jaw symphysis are strongly connected and our 3D reconstruction does not feature an interdentary gap, indicating a lack of kinesis between the lower jaws.

In summary, sutural morphology in the skull and lower jaws of *Whatcheeria* supports a feeding mode whereby prey was initially seized by biting using enlarged anterior teeth, with vertical forces generated being directed through the anterior snout to the skull roof (and through the adsymphysials and dentaries to the posterior lower jaw). Early tetrapods and their relatives likely utilised a combination of suction-feeding and direct biting, as exemplified by the transitional, gar-like feeding system of *Tiktaalik roseae* (Lemberg et al., 2021). The shift from suction to biting across the water-to-land transition therefore appears to be a gradual one, with taxa falling somewhere along a spectrum rather than as two distinct functional categories. We find that sutural morphology in the skull of *Whatcheeria* is consistent with increased reliance on biting, perhaps to capture large prey, though some degree of incipient suction-feeding would have taken place as it does in extant aquatic tetrapods (Wainwright et al., 2015). However, further biomechanical analyses are needed to support these predictions.

CONCLUSIONS

The results presented here supplement previous descriptions of *Whatcheeria* and provide the first complete cranial reconstruction of this phylogenetically significant taxon. This reconstruction highlights the unusual morphology of *Whatcheeria* and demonstrates the value of digital preparation and retrodeformation in studying distorted and fragmented fossil specimens. Our examination of sutural morphology suggests that *Whatcheeria* was adapted to resist loading generated by direct biting using large anterior teeth, though future biomechanical modelling will be invaluable in testing these hypotheses. The increased use of CT scanning and digital preparation is helping to reveal the morphological diversity of early tetrapods and their relatives, which in turn provides new avenues and valuable data for understanding the evolution and function of the skull across this crucial period of vertebrate history.

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Figure Captions

FIGURE 1. Photographs of original *Whatcheeria deltae* specimens. **A**, lateral view of the left side of FM PR 1634; **B**, line drawing of FM PR 1634 showing position of sutural contacts; **C**, lateral view of FM PR 1814; **D**, line drawing of FM PR 1634 showing position of sutural contacts. Many of the bones on right side the skull were crushed and proved unidentifiable in our scans; **E**, lateral view of FM PR 1665; **F**, line drawing of FM PR 1665 showing position

of sutural contacts. Position of lateral line canals and pores visible on the fossil surface are marked in grey. All scale bars equal 50 mm. [planned for 2/3 page width]

FIGURE 2. Surface model of FM PR 1634 prior to retrodeformation. **A**, lateral view of the left side of the skull and left lower jaw; **B**, medial view of same. Individual bones are shown in various colors. The suture between the splenial and postsplenial was indistinguishable in this specimen. The lower jaws of FM PR 1634 was not used in the final reconstruction. Scale bars equal 50mm. [planned for 2/3 page width]

FIGURE 3. Surface models of FM PR 1814 and FM PR 1665 prior to retrodeformation. **A**, dorsal view of the segmented bones of FM PR 1814; **B**, ventral view of same; **C**, lateral view of FM PR 1665; D, medial view of same; **E**, ventral view of same; **F**, dorsal view of same. Individual bones are shown in various colors. Scale bars for A and B equal 25mm and scale bars for C, D, E and F equal 50mm. [planned for 2/3 page width]

FIGURE 4. 3D reconstruction of the cranium of *Whatcheeria deltae*. **A**, lateral view of cranium; **B**, dorsal view of same; **C**, ventral view of same. Individual bones are shown in various colors and the position of lateral line canals and pores are highlighted. Dotted outlines in C show the approximate outlines of the posterior basiparasphenoid, basioccipital and posterior extremities of pterygoids based on Bolt and Lombard (2018). All scale bars equal 50mm. [planned for page width]

FIGURE 5. 3D reconstruction of the lower jaw of *Whatcheeria deltae*. **A**, left jaw in lateral view; **B**, medial view of same; **C**, dorsal view of same; **D**, ventral view of same. Individual bones are shown in various colors and the position of lateral line canals and pores are highlighted. Dotted outlines in A and C show the approximate outline of the posterior dentary-surangular contact based on our observations of the left jaw of FM PR 1634 and Lombard and Bolt (2006). All scale bars equal 50mm. [planned for page width]

FIGURE 6. 3D reconstruction of the skull of *Whatcheeria deltae*. **A**, articulated skull and lower jaws in frontal view; **B**, oblique left lateral view of same; **C**, Left lateral view of same. Individual bones are shown in various colors. Scale bar for A equals 20mm and scale bar for C equals 50mm. [planned for 2/3 page width]

FIGURE 7. Suture maps of the skull and jaws of *Whatcheeria deltae*. **A**, left half of the cranium in dorsal view; **B**, left half of the cranium in ventral view; **C**, left lower jaw in dorsal view; **D**, left lower jaw in ventral view; **E**, cranium in lateral view; **F**, lower jaw in lateral view; **G**, lower jaw in medial view. Solid lines indicate butt joints; grey shading indicates scarf joints and the direction (but not extent) of underlap; cross hatches indicate interdigitated sutures; dashed lines (C) indicate tongue-and-groove contacts; black shading indicates openings in the skull and jaw. Dotted lines (B, D and G) indicate contacts for which sutural morphology is uncertain. Position of lateral lines are shown in grey. Scale bars shown for A/B, C/D, E and F/G all equal 50mm. [planned for 2/3 page width]