Early Vertebrate Evolution

Feeding structures in the ray-finned fish *Eurynotus crenatus* (Actinopterygii: Eurynotiformes): implications for trophic diversification among Carboniferous actinopterygians

Matt FRIEDMAN[1]*, Stephanie E. PIERCE[2], Michael COATES[3] and Sam GILES[4]

[1] Museum of Paleontology and Department of Earth and Environmental Sciences, University of Michigan, 1105 N University Ave, Ann Arbor, MI 48109, USA. Email: mfriedm@umich.edu

[2] Museum of Comparative Zoology and Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, USA.

[3] Department of Organismal Biology and Anatomy, University of Chicago, 1027 E 57th St, Chicago, IL 60637, USA.

[4] Department of Earth Sciences, University of Oxford, South Parks Road, Oxford, OX1 3AN, UK. Current Address: School of Geography, Earth and Environmental Sciences, University of Birmingham, Edgbaston, B15 2TT, UK.

*Corresponding author

ABSTRACT: The Permo-Carboniferous eurynotiforms show conspicuous modifications to post-cranial and cranial morphology relative to primitive actinopterygian conditions, and represent an important early example of functional experimentation within ray-finned fishes. Although eurynotiforms are represented by abundant articulated fossil material, the internal anatomy of the group is not well known. Microcomputed tomography (μCT) of *Eurynotus crenatus* from the early Carboniferous (Viséan) Wardie Shales Member of the Gullane Formation of Wardie, Scotland provides detailed information on the jaws, palate and dentition. The lower jaw is deep and bears a well-developed convex dental plate on the prearticular/coronoids. The dentary bears a dorsally directed posterior process and lacks any obvious marginal dentition. The prearticular bears a low coronoid process. Apart from the first and second dermopalatines, and a likely accessory vomer, bones of the palate are tightly sutured or fused. The upper dental plate comprises a longitudinal, concave horizontal dental surface that occludes with the convex lower toothplate, and a more vertical region consisting of anastomosing ridges. The parasphenoid has a narrow anterior corpus and a broad posterior stalk that bears a pronounced midline notch. The smooth, irregularly punctated surfaces of the dental plates are formed by closely packed teeth with conjoined crowns, providing clues to the evolution of the more monolithic toothplates of *Amphicentrum* from the peg-like teeth reported in the earliest and most anatomically generalised eurynotiforms. The feeding apparatus shows many qualitative and quantitative features consistent with the processing of hard prey items. *Eurynotus* and its relatives show the first clear example of jaw and dental structures consistent with durophagy among actinopterygians. The origin of the group in the early Carboniferous is suggestive of diversification into newly available ecological roles in the aftermath of the end-Devonian extinction.

KEY WORDS: durophagy, feeding, Viséan, Wardie.

The first half of the Carboniferous record of actinopterygians is marked by two remarkable – and likely interrelated – events: the increase in numerical dominance relative to other groups of fishes, and accompanying substantial anatomical innovation (Sallan 2014; Friedman 2015). Long appreciated by palaeontologists (e.g., Woodward 1895), these complementary patterns have recently been viewed through the lens of evolutionary recovery following the end-Devonian or Hangenberg extinction event (Sallan & Coates 2010; Friedman & Sallan 2012). The early Carboniferous record provides the oldest unambiguous evidence for key functional innovations in feeding (e.g., durophagy) and locomotion (e.g., body elongation) that would become repeated motifs over the subsequent evolutionary history of ray-finned fishes (Bellwood 2003; Claverie & Wainwright 2014).

Although the Carboniferous ray-finned fish record is rich, most available fossil material is heavily flattened, restricting investigations to the limited suite of characters apparent in the external dermal skeleton. However, some deposits from the United States and United Kingdom do yield three-dimensionally preserved actinopterygian specimens that permit more detailed examination of internal structures. Such material has been studied through traditional mechanical preparation and observation (Moodie 1915; Watson 1928; Case 1937;
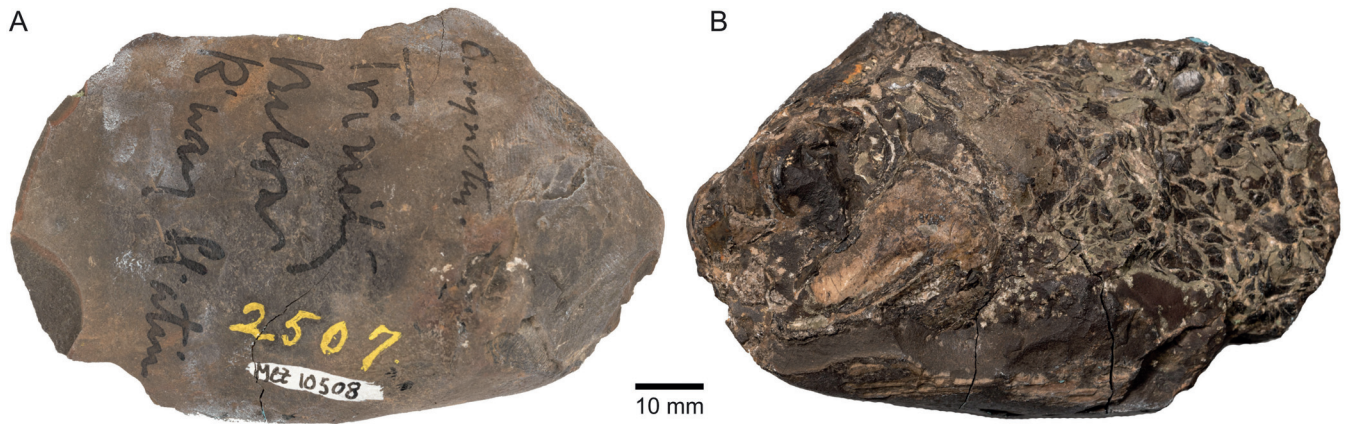
Figure 1 *Eurynotus crenatus*, MCZ 10508, Wardie Shales Member, Gullane Formation, Edinburgh, Scotland. Specimen in (A) right-lateral view; (B) left-lateral view. Images copyright President and Fellows of Harvard College.

Bradley Dyne 1939; Poplin & Véran 1996; Coates 1999), physical tomography (Moodie 1920; Poplin 1974, 1984; Hamel & Poplin 2008), and, more recently, computed tomography (Giles & Friedman 2014; Pradel *et al.* 2016; Coates & Tietjen 2019). Fossils collected from Wardie on the south shore of the Firth of Forth, Scotland, are of particular interest because of their age, preservation and the diversity of fauna represented. Of Viséan age, the Wardie assemblage includes the oldest substantial collection of three-dimensionally preserved Carboniferous actinopterygian remains. It lies stratigraphically above the Tournaisian-earliest Viséan Romer's Gap, an interval variously interpreted as characterised by poor sampling, biotic recovery from extinction or some combination of the two (Ward *et al.* 2006; Smithson *et al.* 2012; Clack *et al.* 2016). Wardie yields roughly a dozen nominal actinopterygian species divided between seven anatomically divergent genera, and many of these are known from almost complete individuals preserved in concretions (Wood 1975; Dineley & Metcalf 1999). These include taxa that differ from most geologically older ray-finned fishes in terms of body size and shape, as well as major modifications to jaw and dental structure. The most recent substantive examination of any of the Wardie ray-fins is over half a century old (Gardiner 1963), and itself represents only an incremental advance on foundational early works (Traquair 1867, 1875, 1877–1914; Watson 1928). The tenacious ironstone matrix that characterises and surrounds Wardie fossils impedes mechanical preparation, although some success has been achieved with chondrichthyan material (Dick 1978, 1981, 1998). Microcomputed tomography (μCT) was first applied to material from Wardie as an alternative more than a decade ago (Anderson *et al.* 2003), and subsequent efforts targeting tetrapods (Pardo *et al.* 2017) and chondrichthyans (Coates & Tietjen 2018) have revealed new anatomical details with important functional and phylogenetic implications.

Here we employ μCT to examine the jaws and dentition of the eurynotiform (*sensu* Sallan & Coates 2013) actinopterygian *Eurynotus* from Wardie. Although available details are incomplete, it is nevertheless clear that the feeding apparatus of *Eurynotus* is substantially modified relative to primitive actinopterygian conditions. This taxon is of particular interest in being among the earliest ray-finned fishes with functional modifications consistent with the processing of hard prey. Egerton (1850, p. 3) first noted 'blunt and rounded teeth' based on correspondence from, and casts provided by, Hugh Miller (Young 1866, p. 314, provides text of Miller's letters). Drawing on several specimens from various Scottish localities, Traquair (1867, 1879) provided more detailed accounts of the palate, parasphenoid, and upper and lower jaws, accompanied

by illustrations of the maxilla, 'pterygoid' and some teeth. Watson (1928) subsequently described and figured a single specimen from Wardie showing bones of the palate and jaws in articulation, but the specimen was badly broken and his figure lacks detail as a consequence. More recently, Coates (1994, fig. 7) described and illustrated a flattened specimen of *Eurynotus* from East Kirkton with a disarticulated head showing some details of the jaws and toothplates. By clarifying the anatomy of the feeding apparatus of *Eurynotus*, we seek to address previous hypotheses of its relationships, provide interpretations of its palaeoecology and determine its implications for patterns of trophic turnover among fishes between the Devonian and Carboniferous.

1. Material and methods

1.1. Specimen and background

Two of us (M.F. and S.E.P.) identified a three-dimensionally preserved specimen (Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA (MCZ) 10508) of *Eurynotus* from Wardie Beach, Edinburgh, Scotland (Fig. 1). Material from Wardie at MCZ represents a personal collection sold by Thomas Stock, and received in two instalments in November 1883 and March 1884; MCZ 10508 arrived as part of the first shipment. This individual comprises much of the skull except for the anterior tip of the snout. The nodule is broken behind the skull, but includes the pectoral girdle. The left side of the skull is exposed, while the opposite face of the specimen is completely buried within the enclosing siderite matrix and was therefore undamaged by splitting of the concretion. Locality information is written on the external surface of the concretion: '*Eurynothus* [sic], Trinity, below Railway Station'.

Agassiz (1835) named two species of *Eurynotus* from the early Carboniferous of Scotland: the type specimen *E. crenatus*, based on several specimens from Burdiehouse (Hopetun Member of the West Lothian Oil-Shale Formation) housed (in part) at the National Museum of Scotland, Edinburgh, UK (NMS 1878.18.11, 1878.18.12, 1878.18.13, 1878.18.14, 1950.38.99, 1950.38.100; Agassiz 1835: pl. 14a, b; Henrichsen 1970) and the referred *E. fimbratus*, based on a portion of trunk from Wardie at the Oxford University Museum, Oxford University Museum of Natural History, Oxford, UK (OUMNH E.03152; Agassiz 1835: pl. 14c, figs 1–3). The genus is a characteristic member of the so-called 'Oil-Shale fish fauna' (Coates 1994) of Scotland, and its abundance has been noted by Traquair (1879: 349–350). Traquair temporarily adopted the convention of identifying material of *Eurynotus* from Wardie as belonging
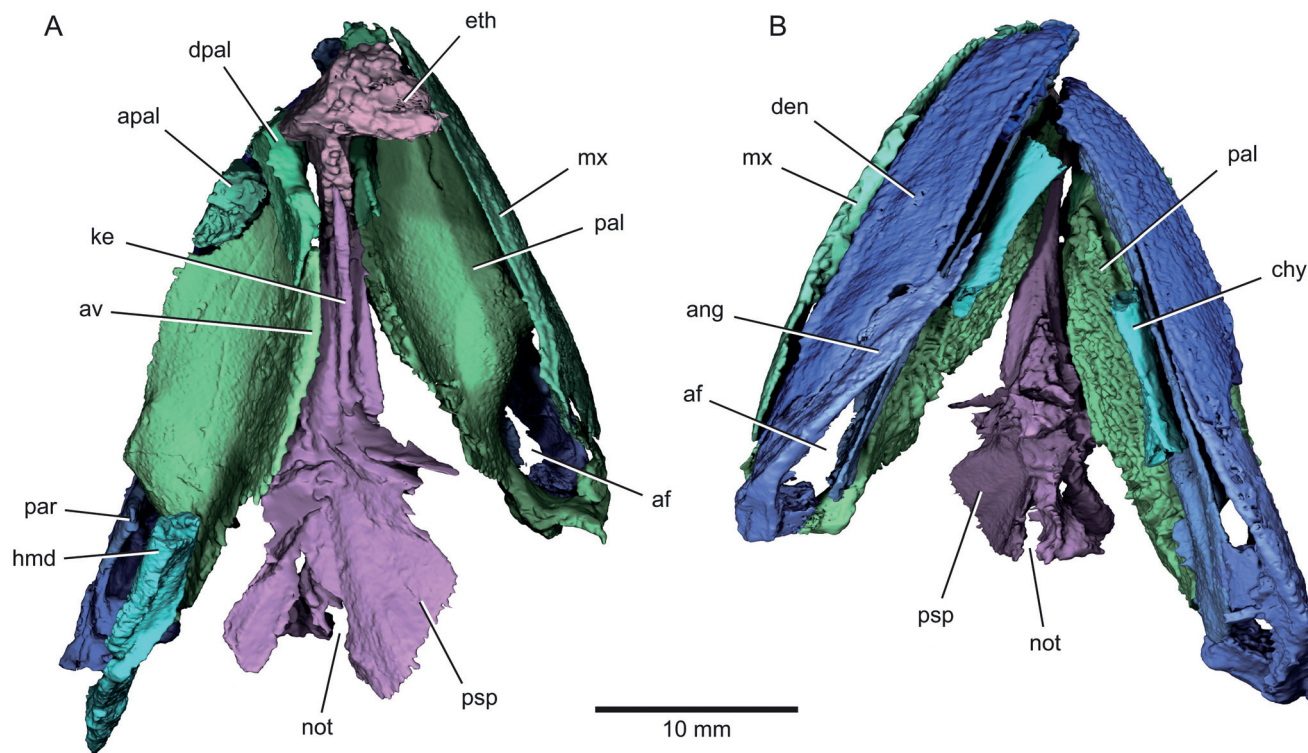
Figure 2 *Eurynotus crenatus*, MCZ 10508, Wardie Shales Member, Gullane Formation, Edinburgh, Scotland. μCT model of jaws, palate, and hyoid arch in (A) dorsal view; (B) ventral view. Abbreviations: af = adductor fossa; ang = angular; apal = autopalatine; av = accessory vomer; chy = ceratohyal; den = dentary; dpal = dermoplalatine; eth = ethmoid; hmd = hyomandibula; ke = dorsal keel of parasphenoid; mx = maxilla; not = aortic notch; pal = palate; par = prearticular; psp = parasphenoid. Colour coding of the skeleton (adopted in subsequent figures): blue = lower jaw complex; green = upper jaw complex; purple = braincase and parasphenoid; turquoise = hyoid arch.

to *E. fimbratus* (e.g., Traquair 1867), but here we follow Woodward (1891) and Traquair (1903) in considering material from Wardie as referable to the type species *E. crenatus*. Taxonomy of other probable examples of *Eurynotus*, including a specifically unassigned example from East Kirkton (Coates 1994; NMS G 1993.6.30) and the Belgian 'Platysomus' insignis (De Koninck 1878; Royal Belgian Institute of Natural Sciences, Brussels, Belgium (RBINS) 10.445; pers. obs. M.F.), is in need of revision, but this is beyond the scope of the current report.

1.2. Geological context

The shales at Wardie have been known for their fossils since the first half of the 19th Century, when materials collected by Lord Greenock were described by Agassiz in his *Recherches* (1835). At present these deposits are recognised as the Wardie Shales Member of the Gullane Formation which, along with the underlying Arthur's Seat Volcanic Formation and overlying Westlothian Oil-Shale Formation, comprise the Strathclyde Group in West Lothian (Chisholm *et al.* 1989; Chisholm & Brand 1994; Waters *et al.* 2011a, fig. 44). Goniatites from the MacGregor Marine Bands above the Wardie Shales Member are assigned to zone B2 of the English succession (Currie 1954; Wilson 1989; Waters *et al.* 2011b), which is contained entirely within the Asbian substage of the Viséan stage of the Mississipian (Waters *et al.* 2011a). The *Lochriea mononodosa* Zone is the oldest conodont zone restricted entirely to the overlying Brigantian substage. The base of the *nodosa* Zone is no less than 333.95 ± 0.39 Ma, the estimated age of the base of the younger *Lochriea ziegleri* Zone (Davydov *et al.* 2012); this defines a youngest age constraint for the Wardie Shales Member. $^{40}Ar/^{39}Ar$ dating of intrusive rocks of the Arthur's Seat Volcanic Formation that are overlain by the Gullane Formation yields an age estimate of 335.1 ± 0.6 Ma

(Monoghan *et al.* 2014), and provides an oldest age constraint. Thus the age of the Wardie Shales Member, and the specimen of *Eurynotus* described here, is restricted to a relatively narrow window of ~333.5–335.5 Ma.

The Wardie Shale Member consists of roughly 325 m of shales, calcareous mudstones and sandstones. The depositional environment is interpreted as deltaic with occasional marine influence (Greensmith 1962). Fossil fishes are best known from outcrops exposed along the Wardie shore between Granton and Newhaven. These include abundant plants indicating proximity to the shore, brachiopods, bivalves, ostracods, chondrichthyans, actinopterygians, sarcopterygian fishes and the tetrapod *Lethiscus* (Traquair 1903; Wood 1975; Dineley & Metcalf 1999). Vertebrates are preserved within siderite nodules found within a series of distinctive fish beds. These show differences in faunal composition and relative abundance, as well as the structure of fossil-bearing nodules (Wood 1975). Sumner (1991) investigated the taphonomy of Wardie nodules, which are rarely barren and most frequently contain coprolites. Wood's (1975) fish beds 2–6 yield *Eurynotus crenatus*. In no case is the species the most common actinopterygian, and instead falls within the middle of the abundance distribution (Wood 1975).

1.3. Computed tomography and segmentation

MCZ 10508 was scanned at the Center for Nanoscale Systems, Harvard University using a HMXST225 X-Tek Micro-CT System. X-rays (220 kV, 110 μA) were filtered with 2 mm of copper, with a resulting scan resolution of 33.965 μm. Tomograms were saved as a TIFF image stack and loaded into the segmentation software Mimics v.19.0 (http://biomedical.materialise.com/mimics). Surface files exported from Mimics were rendered in Blender (blender.org) for figures.
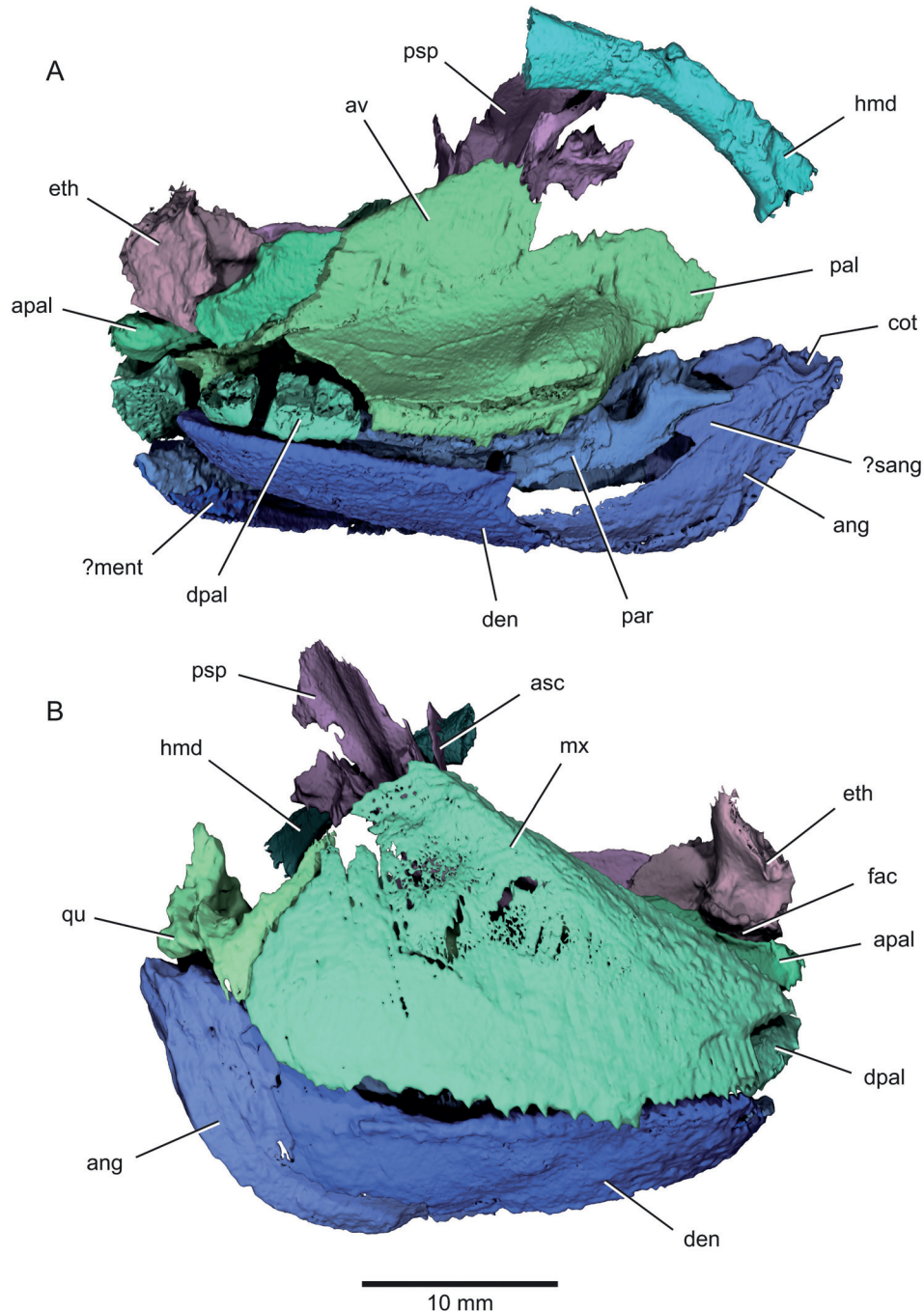
Figure 3 *Eurynotus crenatus*, MCZ 10508, Wardie Shales Member, Gullane Formation, Edinburgh, Scotland. μCT model of jaws, palate, and hyoid arch in (A) left-lateral view; (B) right-lateral view. Abbreviations: ang = angular; apal = autopalatine; asc = ascending process of the parasphenoid; av = accessory vomer; cot = articular cotyle; den = dentary; dpal = dermopalatine; eth = ethmoid; fac = articular facet for autopalatine; hmd = hyomandibula; ?ment = possible mentomeckelian ossification; mx = maxilla; pal = palate; par = prearticular; psp = parasphenoid; qu = quadrate; ?sang = surangular.

2. Description

We restrict our description to components of the skull intimately associated with feeding: the palate, jaws and hyoid arch (Figs 2, 3). Other components visible in tomograms, but not presented here, include fragmentary ceratobranchials and portions of the dermal shoulder girdle.

2.1. Upper jaw
The maxilla (Figs 3, 4) is triangular, with external ornament comprising thin ridges. Two prominent features are found on the inner surface. First, a mesially directed flange (fl, Fig. 4B) extends parallel to, but offset from, the oral margin. Second, a low ridge (ri, Fig. 4B) that traces the oral margin of the bone appears to bear small teeth (dent, Fig. 4b) not visible from the external surface of the maxilla. Both features are restricted to the anterior two-thirds of the maxilla, and together define a broad trough that embraces the ventrolateral margin of the palate anterior to the level of the adductor chamber. The premaxilla is not preserved.

2.2. Palate
Individually ossified palatal bones include an autopalatine and two anterior dermopalatines (Figs 5, 6). An accessory vomer is continuous with the dorsal margin of the palatal toothplate on one side of the specimen, with a clear suture dividing the two
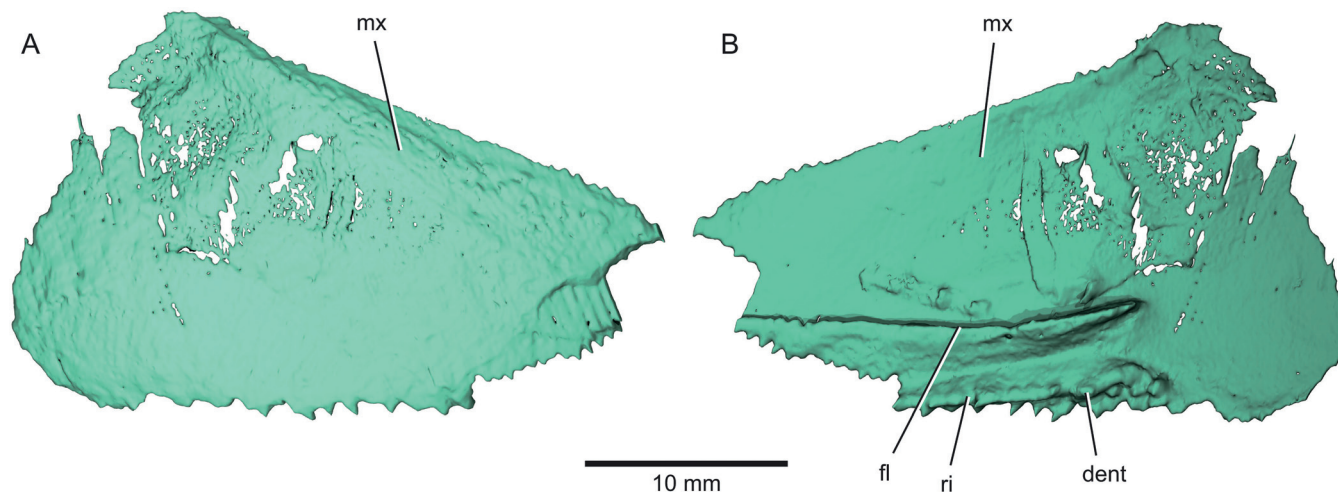
Figure 4 *Eurynotus crenatus*, MCZ 10508, Wardie Shales Member, Gullane Formation, Edinburgh, Scotland. µCT model of right maxilla. (A) Lateral view. (B) Mesial view. Abbreviations: dent = denticles; fl = flange on inner surface of maxilla; mx = maxilla; ri = ridge.
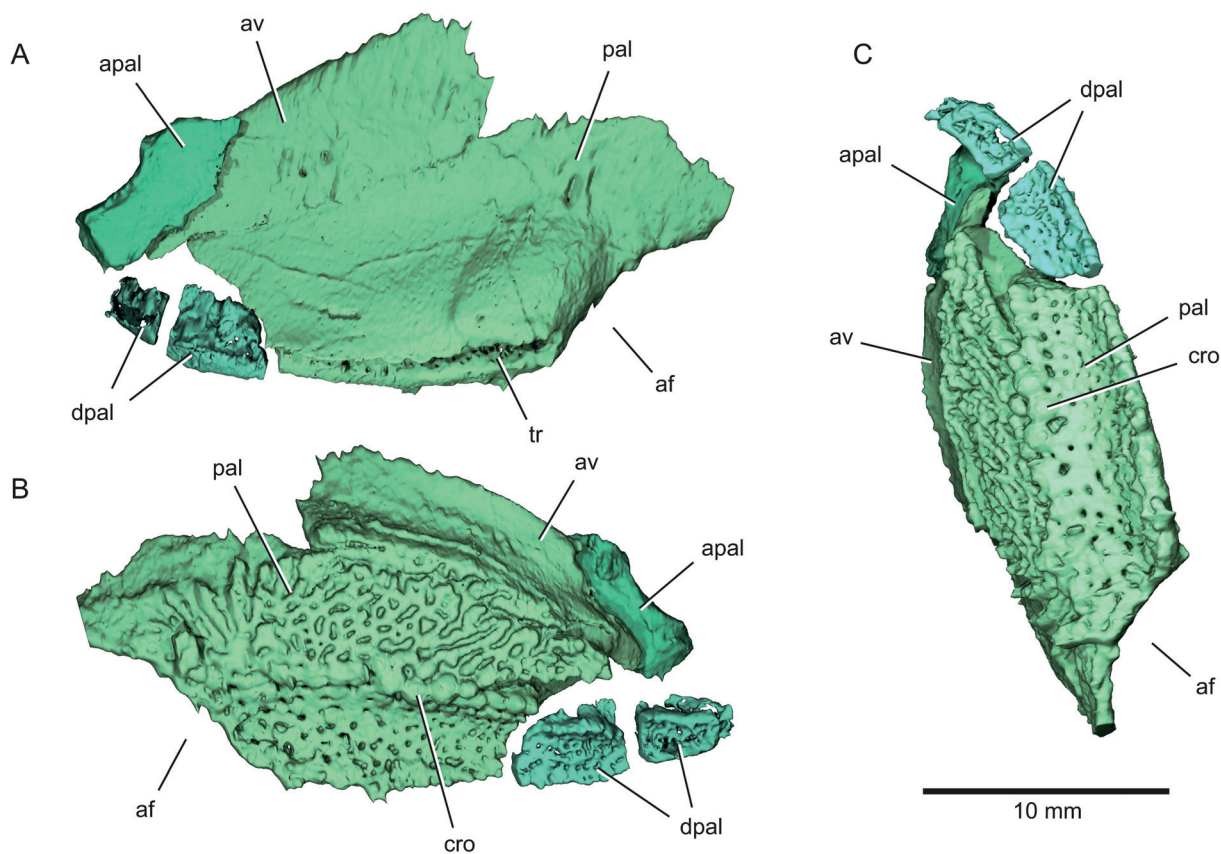
Figure 5 *Eurynotus crenatus*, MCZ 10508, Wardie Shales Member, Gullane Formation, Edinburgh, Scotland. µCT model of left palatoquadrate complex. (A) Dorsolateral view. (B) Ventromesial view. (C) Ventral view. Abbreviations: af = adductor fossa; apal = autopalatine; av = accessory vomer; cro = crown; dpal = dermopalatine; pal = palate; tr = trough marking articulation with maxilla.

structures. All remaining bones – including the quadrate, entopterygoid, ectopterygoid and any additional dermal ossifications – are either co-ossified or too tightly sutured to be distinguished from one another. No independent vomers are apparent, although the tip of the snout is missing. Posteriorly, each half of the palate is widely separated from its antimere. However, only a narrow gap separates them anteriorly, and this appears to broadly reflect life position of the jaws (Fig. 2).

The gently curved autopalatine is free from the dermal palate (apal, Figs 2, 3, 5, 6). Its posteroventral margin appears unfinished, and much of its dorsal margin consists of a long, slightly concave surface that articulates with the ethmoid region of the braincase. The two free dermopalatines are the most anterior preserved portions of the dermal palate (dpal, Figs 2, 3, 5, 6). The first dermopalatine is convex medially, and articulates posteriorly with the trapezoidal second dermopalatine. Coalesced teeth cover the buccal surfaces of both dermopalatines, with gaps between them resulting in an irregular pattern of large perforations in an otherwise smooth dental surface. Bones and teeth show homogeneous greyscale values
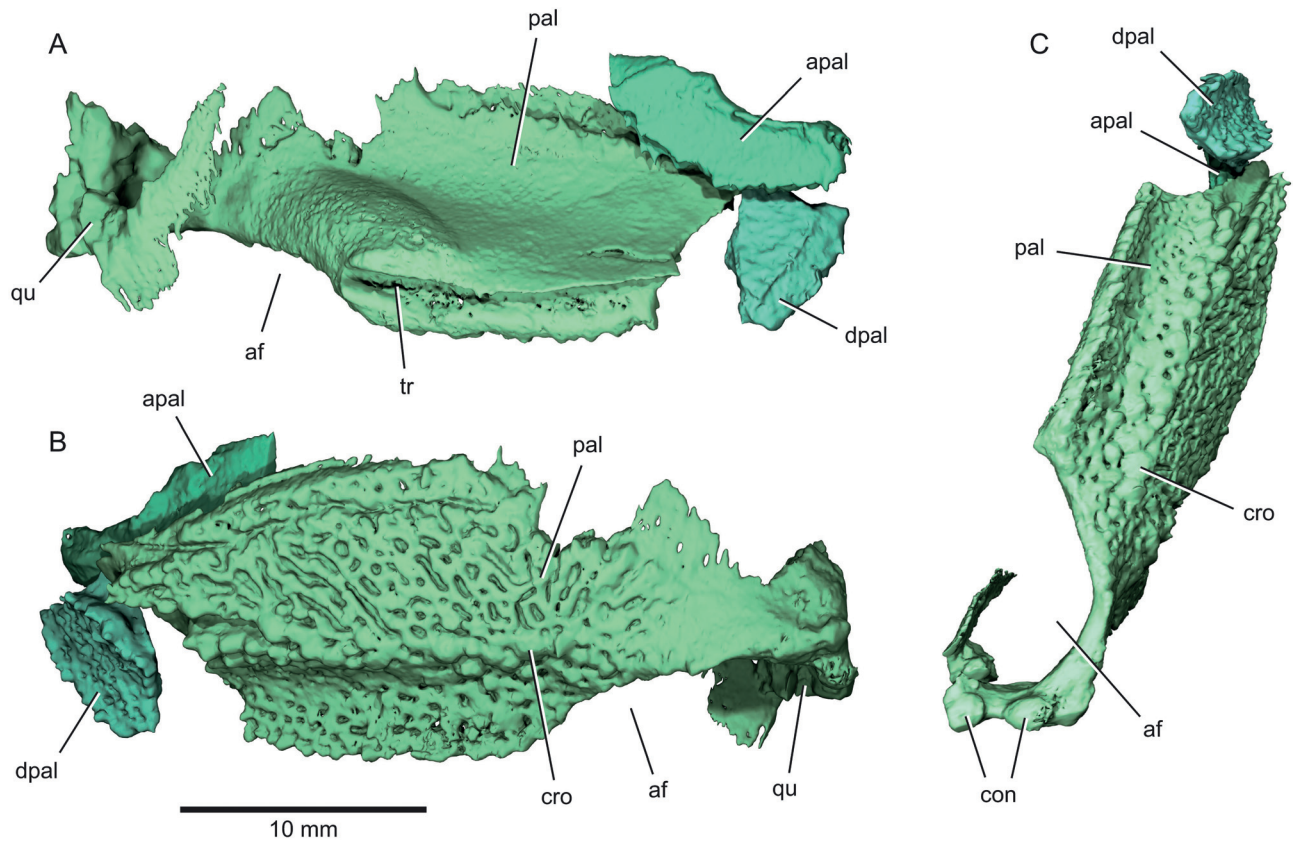
Figure 6 *Eurynotus crenatus*, MCZ 10508, Wardie Shales Member, Gullane Formation, Edinburgh, Scotland. μCT model of right palatoquadrate complex. (A) Lateral view. (B) Mesial view. (C) Ventral view. Abbreviations: af = adductor fossa; apal = autopalatine; con = quadrate condyle; cro = crown; dpal = dermopalatine; pal = palate; qu = quadrate; tr = trough marking articulation with maxilla.

in tomograms of the specimen, and we can detect no obvious internal structure of any palatal bones beyond their cross section. However, it appears that all the structures are formed from a single generation of teeth because there is no obvious trace of superimposed dentition. Low dental ridges mark the lateral and mesial edges of the bones, and are particularly well developed on the second dermopalatine. The ventral surface of the dermopalatine series is interrupted by a concave trough bounded by these marginal ridges. Both the trough and ridges align with similar features on more posterior portions of the palate, and mark the region of occlusion with the convex toothplate of the lower jaw.

Posterior to the dermopalatines, the buccal surface of the palatal toothplate (pal, Figs 2, 3, 5, 6) consists of two regions: a horizontal surface continuous with that of the dermopalatines, and a vertical lamina corresponding to the expected position of the entopterygoid (Figs 2, 5, 6). We are unable to detect any divisions within this plate, which occupies the region of several distinct ossifications in many early actinopterygians (Watson 1928; Gardiner 1984). The horizontal portion of the upper toothplate occludes directly with the mandibular toothplate. It forms a shallow, anteroposteriorly oriented gutter that conforms to the convex dorsal surface of the lower dentition. As on the dermopalatines, teeth are coalesced, with no indication in tomograms of underlying tooth generations.

Raised dental ridges define either side of the longitudinal trough of the upper toothplate, and bear separate crowns (cro, Figs 5, 6) as noted by Traquair (1867, 1879). Anteriorly, each ridge appears to comprise two or more radiating rows of teeth. Dentition on the vertically oriented region of the toothplate shows a contrasting arrangement to that of the trough-like occlusal area. Individual teeth are coalesced, but

they form an anastomosing series of ridges separated by irregular gaps rather than a smooth sheet punctated by subcircular pits. Ridges define a radiating pattern in the area of the toothplate immediately anterior to the adductor chamber. A plate-like accessory vomer is sutured to the dorsal margin of the toothplate (av, Figs 2, 3, 5). Apart from an apparent dental ridge extending along its ventral margin, the buccal surface of the accessory vomer is devoid of any obvious teeth.

The external surface of the toothplate-bearing bone is smooth, and bears a broad swelling immediately anterior to the excavation for the jaw adductor muscles. A well-defined trough extends along the thick lateral face of the toothplate (tr, Figs 5, 6). This trough clasps the complementary flange on the inner surface of the maxilla. Neither side of the skull appears to preserve the posterior of the palate in its entirety. The right quadrate is present (qu, Figs 3, 6), and is connected to the remainder of the palate by a bowed sheet of bone that forms the mesial wall of the adductor chamber. Two convex facets (con, Fig. 6), the mesial offset anteriorly relative to the lateral, mark the jaw joint on the ventral surface of the quadrate, matching paired depressions (cot, Fig. 7) on the articular of the mandible.

2.3. Mandible

The mandible (Figs 2, 3, 7) is stout, with a maximum depth equivalent to one-third of overall jaw length. External dermal bones of the lower jaw comprise a dentary, angular and possible surangular. The dentary (den, Figs 2, 3, 7) is 'L'-shaped, with a long horizontal arm forming the principal ramus of the jaw, and a short dorsally directed process at its posterior end. Anterior to this dorsal process, the oral margin of the dentary is thickened. This appears as a low band laterally
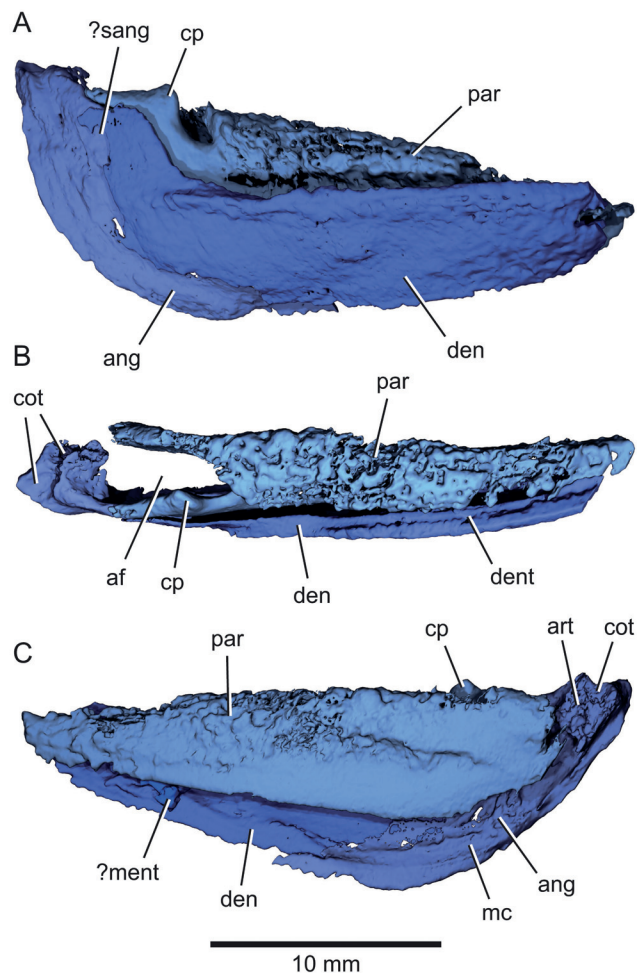
Figure 7 *Eurynotus crenatus*, MCZ 10508, Wardie Shales Member, Gullane Formation, Edinburgh, Scotland. μCT model of right mandible. (A) Lateral view. (B) Dorsal view. (C) Mesial view. Abbreviations: af = adductor fossa; ang = angular; art = articular; cot = articular cotyle; cp = coronoid process; den = dentary; dent = denticles; mc = mandibular canal; ?ment = possible mentomeckelian ossification; par = prearticular = ?sang = possible surangular.

Figure 8 *Eurynotus crenatus*, MCZ 10508, Wardie Shales Member, Gullane Formation, Edinburgh, Scotland. μCT model of parasphenoid and ethmoid ossification. (A) Dorsal view. (B) Ventral view. (C) Lateral view. Abbreviations: asc = ascending process of the parasphenoid; dent = denticles; eth = ethmoid ossification; fac = articular facet for autopalatine; ke = keel; not = aortic notch; psp = parasphenoid.

and a short shelf mesially. Externally, there is no obvious dentition visible along the dorsal edge of the jaw, but roughness on the inner surface appears to represent a band of denticles (dent, Fig. 7). A low ridge extending along the inner surface of the dentary close to its ventral margin marks the course of the mandibular sensory canal (mc, Fig. 7). The posterior margin of the dentary overlaps the crescentic angular (ang, Figs 2, 3, 7), the mesial surface of which also bears a raised ridge corresponding to the mandibular canal. A possible surangular (?sang, Figs 3, 7) occupies the space between the angular and the dorsal process of the dentary. It is lenticular, extends beyond the adjacent anterior margin of the angular, and terminates anteriorly in a pointed tip. This region of the possible surangular is concealed by the dentary in lateral view.

Divisions between mesial dermal bones of the lower jaw are not apparent. Although it is not clear whether multiple ossifications were present, we refer to the entire complex as the prearticular (par, Figs 2, 3, 7). The most conspicuous feature is a well-developed dental surface, which comprises a series of closely packed to partially coalesced bluntly rounded teeth forming a toothplate that extends far above the dorsal margin of the dentary in lateral view. The fusion of adjacent teeth results in a pattern of large pits distributed across the occlusal surface of the tooth plate. Ventral and mesial to this
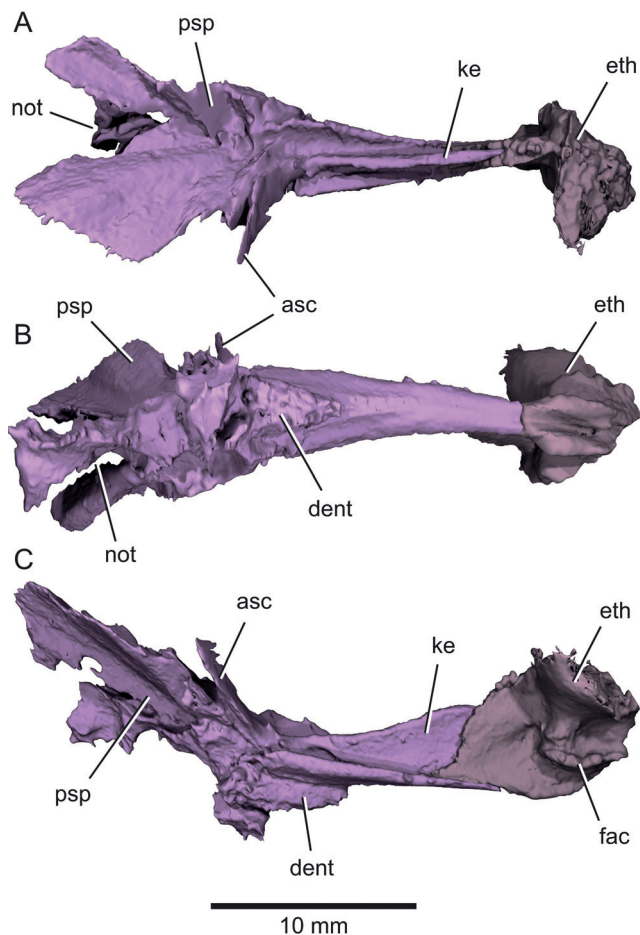
toothplate, the prearticular consists of a smooth, vertical lamina of bone. There is a broad gap between the lower margin of the prearticular and that of the dentary and infradentaries. This lamina defines the mesial wall of the adductor fossa, and joins the articular at its posterior end. The lateral wall is defined by an additional posterior projection of the prearticular that sutures with the surangular. This posterior process bears a 'U'-shaped notch in lateral view that separates the toothplate from a low, rounded coronoid process (cp, Fig. 7). An excavation on the posterior margin of the prearticular represents the contact with the infradentary bones.

The articular defines the posterior wall of the adductor fossa, and bears two large, dorsally directed cotyles, one lateral and one mesial (cot, Fig. 7). The level of the articular cotyles is offset dorsally relative to the occlusal surface of the toothplates (Figs 3, 7A). There is limited ossification of the mesial surface of Meckel's cartilage ventral to the prearticular on one jaw. Poorly preserved structures, restricted to the anterior quarter of each mandible and almost completely concealed by the prearticular and dentary, might represent mentomeckelian ossifications (ment, Figs 3, 7).

2.4. Parasphenoid and braincase
The parasphenoid (Fig. 8) consists of a narrow anterior corpus and a wider posterior stalk. The posterior stalk is deeply notched (not, Figs 2, 8), with dorsolaterally extensive wings
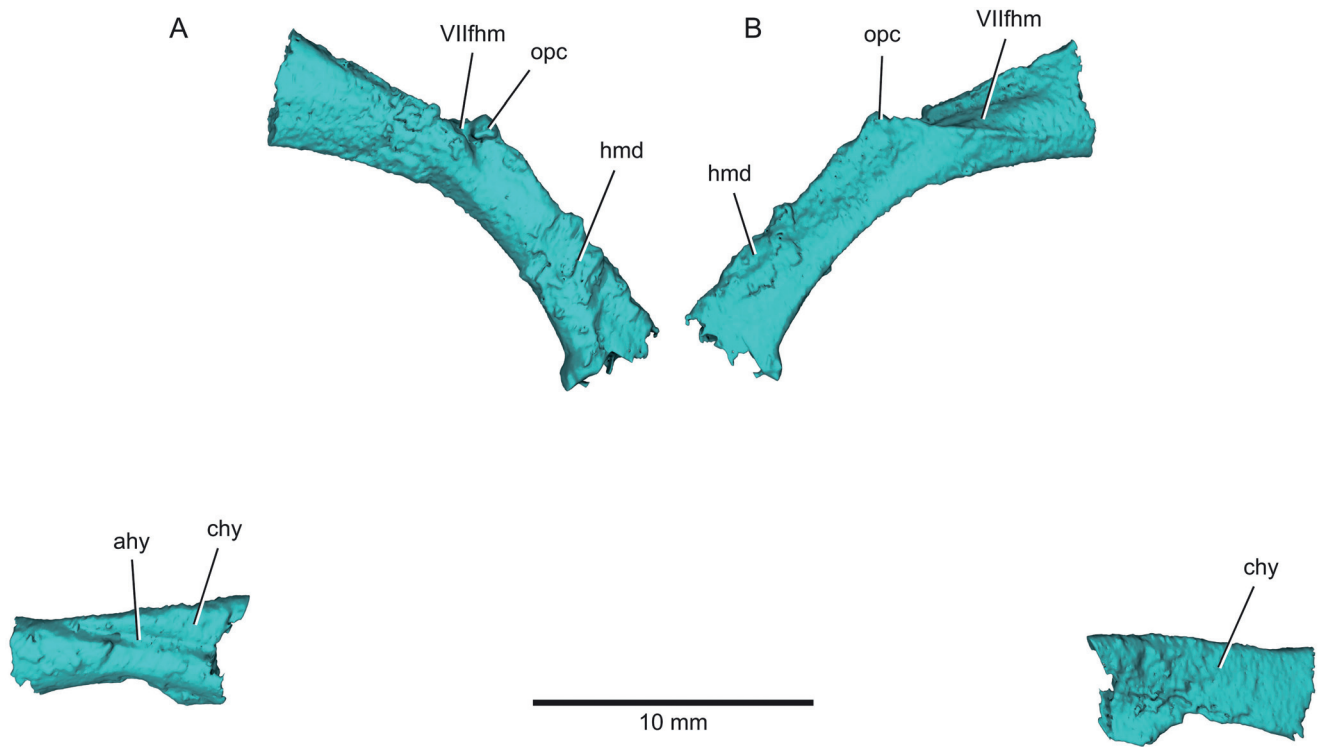
Figure 9 *Eurynotus crenatus*, MCZ 10508, Wardie Shales Member, Gullane Formation, Edinburgh, Scotland. μCT model of left hyoid arch. (A) Lateral view. (B) Mesial view. Abbreviations: ahy = groove for afferent hyoid artery; chy = ceratohyal; hmd = hyomandibula; opc = opercular process; VIIfhm = groove for hyomandibular branch of the facial nerve.

that would have embraced much of the otic sidewall of the neurocranium in life. A slender ascending process (asc, Fig. 8), preserved only on one side, lies at the junction between these two regions. Anterior to the ascending process, the ventral surface of the parasphenoid bears a greatly thickened teardrop-shaped platform with its pointed tip directed anteriorly. Irregular pits mark the buccal surface of this plinth, which appears to be a hypertrophied denticle field (dent, Fig. 8). The ventral surface of the parasphenoid is gently convex in axial section anterior to this dentition, with no conspicuous features. Passage of the buccohypophyseal canal through the parasphenoid is not apparent, and there is no indication of a foramen on either the dorsal or ventral surface. A longitudinal trough extends along the dorsal surface of the parasphenoid corpus. A high keel emerges dorsally from the midline of this trough. In lateral view, the dorsal margin of the keel rises from its origin anterior to the ascending process, reaching its greatest height at the intersection between the parasphenoid and the ethmoid (ke, Fig. 8). Curiously, there are no indications of a basipterygoid process or alternative means of articulation between the posterior portion of the palate and basicranium.

The ethmoid (eth, Figs 2, 8) is the only region of the braincase that is clearly preserved. A vertical sheet of bone that embraces the dorsal keel of the parasphenoid forms the posterior half of the ethmoid. The anterior half of the ethmoid is massive, and has a 'T'-shaped profile in axial section. A large, curved facet (fac, Fig. 8) for the autopalatine dominates the ventral half of the lateral face of the ethmoid in this anterior region.

2.5. Hyoid arch
Preserved components of the hyoid arch are limited to the hyomandibula and ceratohyal (Fig. 9). The anteroventral margin of the hyomandibula is gently curved. By contrast, the posterodorsal margin of the hyomandibula appears more angular, with distinct dorsal and ventral arms that join the

apex of a modest opercular crest (opc, Fig. 9). The lateral surface of the hyomandibula is smooth, with no obvious features, but the inner face of the dorsal limb bears a low ridge that extends from the opercular process to near the ventral edge of the proximal facet of the bone. The hyomandibula is somewhat flattened mediolaterally, with an elliptical cross section. No foramina pierce the bone, although a deep groove likely housed the hyomandibular trunk of the facial nerve (VIIfhm) and there is no fusion with the dermohyal.

The ceratohyal has a convex external surface and a concave inner face. A deep groove extends longitudinally along the external surface of the bone and blends into its dorsal rim (ahy, Fig. 9). A straight dorsal margin and convex ventral margin give the ceratohyal a boot-like shape in lateral view.

3. Discussion

3.1. Comparison with past accounts
The handful of accounts of the jaw anatomy in *Eurynotus* draw on either disarticulated (Traquair 1867, 1879; Coates 1994) or badly broken (Watson 1928) material, and only the maxilla and palate have been illustrated beyond schematic reconstructions (Traquair 1867, pl. 45, fig. 13; Traquair 1879, pl. 3, figs 10–15; Watson 1928, fig. 12).

Although our μCT models add considerable information on the upper jaw and palate, there is little in the accounts of Traquair (1867, 1879) that requires substantial revision. Our specimen shows a greater coalescence of individual teeth on the horizontal component of the palatal toothplate than his disarticulated example of an undetermined species of *Eurynotus* from the younger Queensferry beds. Similarly, where our specimen preserves a smooth mesial surface adjacent to the oral margin of the maxilla, in material from Queensferry, Loanhead and Burdiehouse, Traquair (1879) illustrates a distinct strip of large denticles.

Watson (1928) illustrated a more complete palate from a specimen of *E. crenatus* from Wardie that indicates divisions between individual ossifications. Although the position of these sutures is plausible based on conditions in other early actinopterygians, we cannot detect these divisions in our fossil. The tongue-and-groove connection between the palate and maxilla is accurately described by Watson (1928, p. 63), with the articular flange on the inner surface of the maxilla clearly figured – but not discussed – by Traquair (1879).

Our specimen substantially improves understanding of the lower jaw, which is only superficially described in previous accounts. Traquair (1867, 1879) reconstructed the mandible of *Eurynotus*, whereas Watson (1928) and Coates (1994) provided specimen illustrations. Traquair's figure shows a series of individual cusps rather than a coalesced plate, while both Watson's text and illustration are ambiguous.

The parasphenoid and braincase of *Eurynotus* have only previously been described by Watson (1928). In terms of overall shape of the parasphenoid, our models confirm his illustration, and we can confirm the presence of an ascending process. Watson's broken specimen shows only the base of the keel on the upper face of the parasphenoid, and he did not appreciate the dorsal extent of this structure. We have not detected clearly defined pits or capsules for the olfactory bulbs in our scans, but otherwise Watson's account of the ethmoid appears accurate given the limitations of his material.

3.2. Systematic implications

Deep-bodied actinopterygians first appear in the fossil record during the early Carboniferous. The relationships of these taxa to one another, to more 'generalised' contemporary species, and to deep-bodied taxa from younger deposits has long been confused (see summary in Sallan & Coates 2013). Traquair (1879) rejected earlier associations of deep-bodied Palaeozoic taxa with Mesozoic groups like pycnodonts and dapediids, and restricted Platysomidae to those forms appearing in the early Carboniferous. Evidence for anatomical diversity among platysomids presented by Traquair and others led Moy-Thomas (1939) to elevate the group to subordinal status and include within it two separate families: Platysomidae (e.g., *Platysomus*) and Amphicentridae (e.g., *Amphicentrum*). Notably, the hypothesised close relationship between these platysomoid lineages persists, recurring in cladistic surveys (Gardiner & Schaeffer 1989, although queried by Coates 1993) and results of formal phylogenetic analysis (Wilson *et al.* 2018). However, Sallan & Coates (2013) argued for multiple, distinct origins of deep-bodied Carboniferous actinopterygians, with parallel acquisition of this geometry in the two 'platysomoid' divisions recognised by past workers (see also Zidek 1992, who anticipated this arrangement by placing platysomids and amphicentrids in separate orders). Their thesis rests on the interpretation of the styracopterids *Fouldenia* (late Tournaisian) and *Styracopterus* (early Viséan) as a fusiform sister group of Amphicentridae (used here in a manner corresponding roughly to the concept of the group outlined by Moy-Thomas 1939) to the exclusion of Platysomidae. Sallan & Coates (2013) recognise the clade comprising styracopterids and amphicentrids as Eurynotiformes, and present a list of derived features – including many of the jaws and dentition – supporting the monophyly of the group. This argumentation is verbal, but the proposed systematic arrangement has been corroborated by recent analyses (Giles *et al.* 2017; Wilson *et al.* 2018), which we use as a broad framework within which to assess possible patterns of character evolution within amphicentrids (here taken to include *Amphicentrum*, *Benedenius*, *Cheirodopsis*, *Eurynotus*, *Mesolepis*, *Proteurynotus* and *Wardichthys*).

Most amphicentrids are known almost exclusively from external anatomy. Detailed knowledge of internal structure is limited to *Eurynotus* and *Amphicentrum*, with fewer, as yet unreported, details of the palatal toothplate preserved in *Cheirodopsis* (pers. obs. M.I.C.). Relative to primitive actinopterygian conditions (e.g., *Mimipiscis*; Gardiner 1984), *Eurynotus* and *Amphicentrum* share conspicuous derived features, including a posterior stalk of the parasphenoid formed of broad, winglike processes; a slender anterior corpus of the parasphenoid; a prominent dorsal keel of the parasphenoid (NMS SPW 2273); a well-developed ethmoid ossification; and narrowly separated and anteroposteriorly elongate autopalatine facets (NMS SPW 2273). Unfortunately, none of these features can be assessed for other eurynotiforms, and their implications for interrelationships within the group remain ambiguous pending new data. However, dental specialisations of *Eurynotus* and *Amphicentrum* suggest broader patterns of relationships. All eurynotiforms in which such conditions can be assessed appear to bear rows of blunt dentition on the palate and inner dermal bones of the lower jaw. However, individual crowns appear to remain separate from one another in styracopterids (Sallan & Coates 2013, fig. 14) and the amphicentrids *Benedenius* (Boulenger 1902) and *Mesolepis* (Traquair 1879, pl. 4, figs 6–8). Outgroup comparison indicates this is a primitive arrangement. By contrast, individual teeth are placed so closely in *Eurynotus* that their crowns are mostly fused in both the upper and lower toothplates. The resultant smooth surface appears formed from only a single generation of teeth, as we have not detected buried crowns. In this way, amphicentrid toothplate construction probably differs from the 'phyllodont' (i.e., comprising multiple superimposed sets of replacement teeth) upper and lower toothplates present in *Platysomus* and bobasatraniids (Zidek 1992; Böttcher 2014).

We suggest the condition in *Amphicentrum* is an exaggeration of the arrangement seen in *Eurynotus*, to the degree that gaps are no longer present at the occlusal surface of the toothplate, and individual cusps can only be recognised in dental ridges. The shared presence of extensive dental coalescence implies that *Amphicentrum* and *Eurynotus* form a group to the exclusion of at least some amphicentrids. Furthermore, we suggest that dental structure in *Eurynotus* provides a model for understanding the evolution of fully consolidated dental plates of *Amphicentrum*, with tomographic or histological study of dentition in the latter genus representing a critical test of this dental coalescence hypothesis.

One of the more clearly defined groups of early actinopterygians, eurynotiforms are geologically long-lived, ranging in age from the early Mississippian (late Tournaisian) to the late Pennsylvanian (Kasimovian), a span of nearly 50 million years. Generic diversity is highest early in the history of the group, with only *Amphicentrum* reported from the Pennsylvanian; whether this reflects either a genuine biological pattern or neglect of stratigraphically younger material is not certain. In any case, it is clear that eurynotiforms represented important components of a range of aquatic settings in the Carboniferous. Although *Eurynotus* is restricted to freshwater or brackish units (Coates 1994: 325), other eurynotiforms are known from sites with a stronger marine influence. In the Mississippian, these include the Tournaisian of Foulden, Scotland (*Fouldenia*; Clarkson 1985; Sallan & Coates 2013), the Viséan of Glencartholm, Scotland (*Styracopterus*, *Proteurynotus*, *Cheirodopsis*; Moy-Thomas & Bradley Dyne 1938; Schram 1983), and Denée, Belgium (*Benedenius*; Mottequin *et al.* 2015), and the Serpukhovian of Bearsden, Scotland (*Amphicentrum*; Wood 1982; Coates 1993). *Amphicentrum* is known from both marine and freshwater deposits in North

America and Europe during the Pennsylvanian (Zidek 1992; Bardack 1997). Eurynotiforms have only rarely been included within formal phylogenetic analyses, and their position within the actinopterygian tree is unclear. Gardiner & Schaeffer (1989, fig. 12) placed their '*Platysomus* Group' (comprising platysomids and eurynotiforms as recognised here) within the actinopterygian crown, as part of a large clade of fossil forms representing the sister lineage of crown Actinopteri. By contrast, Giles *et al.* (2017) do not resolve eurynotiforms and platysomids as sister lineages (cf. Sallan & Coates 2013), placing the former just outside crown Actinopterygii and the latter within the actinopteran crown. Subsequently, Wilson *et al.* (2018) recovered platysomids and eurynotiforms as successive stem members of the Chondrostei. Most recently, Latimer & Giles (2018) resolve eurynotiforms as stem actinopterygians and platysomids as sister to a clade comprising cladistians and chondrosteans (although the implausibility of this latter clade is noted in the text). Additional study of well-preserved eurynotiform material, including the use of µCT, will be vital in providing further anatomical data that might be helpful in constraining the phylogenetic position of the clade.

3.3. Functional considerations

Beginning with Agassiz's (1835) initial description, authors have emphasised the distinctive jaw geometry and dentition of *Eurynotus*, with many drawing explicit functional inferences from these structures (Traquair 1879, p. 361; Watson 1928, p. 63; Coates 1994, p. 325). Here we build on these accounts by examining the anatomy of *Eurynotus* in terms of both qualitative comparisons with other groups showing similar structural modifications and examination of explicit quantitative metrics.

Eurynotus and other eurynotiforms show modifications seen elsewhere among early lungfishes and holocephalans, most notable of which is an elaboration of the palatal dentition. All three groups show a decrease in the midline gap between the two halves of the palate, with lungfishes and holocephalans exhibiting midline contact between dental surfaces associated with the right and left sides of the palate. The geometry in lungfishes and holocephalans is achieved by fusion between the palatoquadrate and neurocranium, whereas the palate remains separate from the braincase in *Eurynotus* and other eurynotiforms in which the condition can be assessed (Bradley Dyne 1939; Sallan & Coates 2013). As in those other groups, eurynotiform toothplates appear to be derived from the union or coalescence of non-shedding teeth on the palate and lower jaw. While the mechanisms of toothplate growth in lungfishes (Ahlberg *et al.* 2006) and holocephalans (Stahl 1999) are reasonably well understood, additional study of eurynotiform dentitions – particularly *Amphicentrum* – is necessary. It seems likely that µCT study of well-preserved material could yield important information, with studies of fossil tetraodontiform dentitions providing proof-of-concept for this approach (Close *et al.* 2016; Bemis *et al.* 2017). In addition to bearing surfaces that are flat or gently curved, the toothplates of *Eurynotus*, *Amphicentrum* and many early lungfishes bear low cusps, often crowned by acute tips, and are arranged in rows. In shape, these correspond broadly to tooth geometries that are most effective at fracturing hard prey under experimental conditions (Crofts & Summers 2014). Lungfishes, holocephalans and eurynotiforms also share a rearrangement of the suspensorium that permits more perpendicular – rather than oblique – insertion of adductor muscles on the mandible, more effectively transmitting force for jaw closing (see below).

Similarities are not restricted to coeval durophages, and *Eurynotus* anticipates features arising independently in later groups of ray-finned fishes either interpreted or confirmed as hard-prey specialists. Broad dental surfaces on the lower jaw and palate are found in numerous groups, including the Mesozoic semionotiforms (López-Arbarello & Sferco 2011), dapediids (Thies & Herzog 1999; Smithwick 2015), pycnodonts (Nursall 1999) and several modern lineages including gymnodont tetraodontiforms (Tyler 1980). The independent histories of these groups is apparent in specific arrangements of an otherwise similar feeding system, including contrasting composition of upper (vomer in pycnodonts; dermopalatines and possibly more internal bones of the palate in dapediids and some semionotiforms; premaxilla in gymnodonts) and lower (coronoids or prearticular in pycnodonts, dapediids, and some semionotiforms; dentary in gymnodonts) dental plates (Tyler 1980; Nursall 1999; Thies & Herzog 1999; López-Arbarello & Sferco 2011; Smithwick 2015). In addition to the obvious convergent specialisation of palatal bites mediated by closely packed, molariform teeth or continuous dental surfaces, some of these groups share other specialisations with eurynotiforms including beak-like oral jaws or modified anterior teeth for prey manipulation (gymnodonts, pycnodonts) and deeply keeled parasphenoids that might confer additional rigidity to the skull in compression (dapediids, gymnodonts; Tyler 1980; Nursall 1999; Latimer & Giles 2018).

Qualitative comparisons of anatomy are suggestive of durophagy in *Eurynotus* and its relatives, but quantification of specific, biomechanically relevant attributes permit more explicit comparison. Overall geometry of the mandibles also carries functional consequences, and these can be quantified using simple metrics. Here we compare such measures for *Eurynotus* with those presented for other early jawed vertebrates by Anderson *et al.* (2011). We draw on their sample of Devonian actinopterygians ($n = 13$) as being representative of primitive jaw mechanics for ray-finned fishes and toothplate-bearing Devonian lungfishes ($n = 20$) as a roughly contemporaneous osteichthyan group with dental modifications similar to – but derived independently of – those in *Eurynotus* (Fig. 10).

Jaw-closing mechanical advantage (Barel 1983) has been applied to a variety of extant and fossil fishes to investigate contrasts in feeding mode (Bellwood 2003; Westneat 2004). This metric models the mandible as a simple third-order lever, and incorporates the distance between the jaw joint and a designated point along the dentition (outlever) as well as the site of muscle attachment (inlever) and the angle of that muscle attachment. Here we consider outlever measurements to both the most anterior and posterior points of the dentition. The ratio of the outlever to the inlever yields the unitless jaw-closing mechanical advantage (MA) of the mandible, with higher values indicating greater force transmission from jaw closing muscles to the dentition and, in turn, prey item. The simple approximation of MA provided by Anderson *et al.* (2011) treats the angle of adductor insertion as being perpendicular to the inlever because of uncertainties in many fossil taxa (cf. Bellwood 2003). Anterior jaw-closing MA for *Eurynotus* (0.22) narrowly exceeds that reported for Devonian actinopterygians (maximum MA = 0.19; mean MA = 0.15), but falls well below the minimum (0.3) value recorded for toothplate-bearing Devonian lungfishes (Fig. 10A). With toothplates that extend posterior to the midpoint of the adductor fossa, *Eurynotus* has a posterior jaw-closing MA (0.83) substantially larger than that of Devonian actinopterygians (maximum MA = 0.68; mean MA = 0.50) but within the
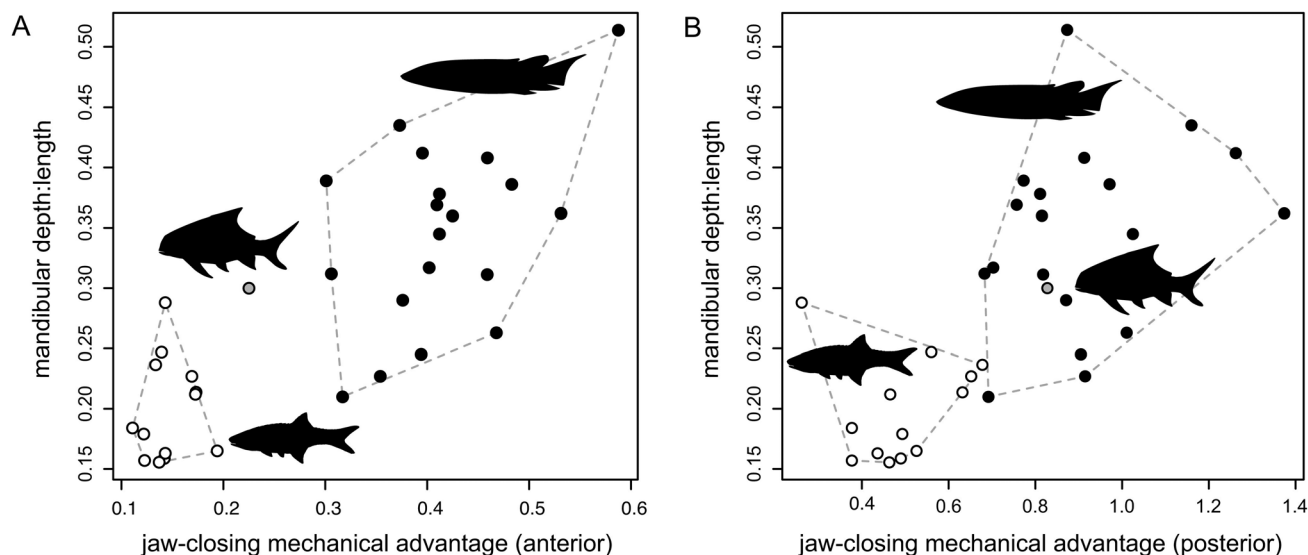
Figure 10 Functionally relevant measures of the mandible of *Eurynotus* (grey-filled circle) in comparison with Devonian actinopterygians (open circles) and lungfishes (black-filled circles). The ratio of mandibular depth to length plotted against: (A) jaw-closing mechanical advantage (anterior); (B) jaw-closing mechanical advantage (posterior). Measurements for taxa apart from *Eurynotus* taken from Anderson *et al.* (2011). Silhouettes adapted from Traquair (1879; *Eurynotus*), Ahlberg & Trewin (1995; *Dipterus*), Choo (2012; *Mimipiscis*).

range of Devonian lungfishes (0.69–1.37). A major caveat accompanies these observations. The assumption of uniform angles of muscle insertion across taxa is likely to lead to an overestimate in MA is some cases. This overestimation is most probable for Devonian actinopterygians due to the oblique orientation of the suspensorium – and presumably adductor musculature (Schaeffer & Rosen 1961) – in these taxa relative to the more vertical arrangement characteristic of *Eurynotus* and lungfishes that permits an approximately perpendicular orientation of jaw-closing muscles relative to the input lever.

In addition to a relatively high MA compared to Devonian actinopterygians, the mandible of *Eurynotus* also shows a ratio of maximum jaw depth to maximum jaw length that deviates from more general conditions. Given simplifying assumptions about aspects including jaw thickness and material properties, this value is taken as a proxy for flexural stiffness of the mandible when loads are applied vertically, as during biting (Anderson *et al.* 2011 and references therein). The value of 0.3 for *Eurynotus* exceeds that of any Devonian actinopterygian (mean = 0.2), and falls within the lower half of the range of toothplate-bearing Devonian lungfishes (mean = 0.34). Thus, the shift in jaw depth in *Eurynotus* relative to earlier actinopterygians might represent an adaptation for accommodating the increased loads associated with the consumption of hard prey.

3.4. A review of durophagy in Devonian–Carboniferous fishes and possible impacts of the Hangenberg event

Apparent specialisations for durophagy appear early in the history of jawed vertebrates (Anderson *et al.* 2011), and are most clearly manifest in broad dental plates and changes to mandibular geometry. In our discussion below, we principally consider those taxa with anatomical structures consistent with the consumption of hard-shelled prey rather than simply the processing of animals with a stiff (but possibly weakly mineralised) carapace or exoskeleton. As such, our definition of durophagy is more restrictive than the broadest sense of the term.

The Lochkovian *Diabolepis* provides the earliest unambiguous evidence for this feeding mode in the form of a palatal bite, upper and lower toothplates, and changes in jaw proportions relative to more generalised sarcopterygians (Chang 1995). The *incertae sedis* osteichthyan *Megamastax* has recently been advanced as an even older specialist on hard prey, based on the presence of low, rounded prominences in the position of the coronoids (Choo *et al.* 2014), although the slender morphology of the mandible in this taxon conflicts with this interpretation. In any case, lungfishes, including *Diabolepis*, were the dominant group of durophagous osteichthyans during the Devonian, obtaining considerable taxonomic and morphological diversity, and inhabiting environments ranging from lakes to reefs (Campbell & Barwick 1990; Ahlberg *et al.* 2006; Lloyd *et al.* 2012).

Several lineages of durophagous placoderms appeared during the Devonian. The most diverse of these, the ratfish-like ptyctodonts, never achieved levels of richness or disparity similar to their lungfish contemporaries. Lockhovian remains attributed to ptyctodonts consist of thoracic plates (Mark-Kurik 1977), with the distinctive dental plates of the group appearing later (Denison 1978, 1985). Isolated dental plates represent the most common remains of ptyctodonts, which have greatly reduced cranial and thoracic armour relative to other placoderms. It is possible that reduction of the skeleton might, in part, be responsible for the low sampled diversity of ptyctodonts, which only number roughly a dozen genera during the entirety of the Devonian (Trinajstic & Long 2009). Ptyctodonts are joined by two or possibly three genera of mylostomatids, durophagous arthrodires of uncertain relationships. Apart from rare Givetian material (Case 1931), myostomatids are restricted to the Late Devonian and achieved larger sizes than most ptyctodonts (Denison 1978). Their dentition comprises broad tritors on the supragnathals opposed to a similar surface on the infragnathals. Unlike ptyctodonts, some of which are known from lacustrine settings, mylostomatids appear to have been exclusively marine (Denison 1978; Dineley & Metcalf 1999). Mylostomids are the most diverse group of durophagous arthrodires, but Hlavin & Boreske (1973, p. 9) argued for similar feeding ecologies in other arthrodire lineages, including the selenosteid *Paramylostoma*

and the bungartiid *Bungartius*, both of which are known from the latest Devonian Cleveland Member of the Ohio Shale.

Holocephalans are the last group of durophagous fishes to appear in the Devonian, where they are known exclusively from toothplates. Reliable examples appear restricted to the Late Devonian (especially Famennian; Stahl 1999), but Darras *et al.* (2008) report a questionable specimen of Givetian age. These Middle Devonian fossils substantially predate the oldest holocephalan body fossils that bear crushing dentition (Viséan; Finarelli & Coates 2012), as well as the earliest skeletal remains attributed to the total group (Famennian; Coates & Sequeira 2001; Coates *et al.* 2017). By the time the earliest complete skeletons of durophagous holocephalans appear in the fossil record in the early Carboniferous, the group had already undergone substantial anatomical change relative to generalised chondrichthyan conditions, including major modifications to the skull (e.g., autostyly) and evidence of substantial experimentation in postcranial anatomy that anticipates the considerable postcranial diversity of later Permo-Carboniferous holocephalans (Stahl 1999; Finarelli & Coates 2012).

The early Carboniferous is marked by proliferation of holocephalans and ray-finned fishes, including the first appearance of durophagous lineages in the latter, and follows the complete extinction of placoderms and the apparent environmental marginalisation of lungfishes. This pattern has long been appreciated (Woodward 1891; Romer 1966; Signor & Brett 1984), but it is only recently that this substantial taxonomic turnover within the durophagous fish guild has been viewed as a consequence of recovery from the end-Devonian extinction or Hangenberg event (Sallan & Coates 2010, 2013; Sallan *et al.* 2011; Friedman & Sallan 2012; Sallan & Friedman 2012; Richards *et al.* 2018). It is clear that the extinction did not result in a complete taxonomic shift, as members of the dominant Devonian and Carboniferous durophagous fish groups overlapped to varying degrees in the Late Devonian and early Carboniferous (Sallan *et al.* 2011). The only groups not present both before and after the Devonian–Carboniferous boundary are durophagous placoderms, which persist to the latest Famennian (Denison 1978), and durophagous actinopterygians, which first appear in the late Tournaisian, roughly 10 million years after the Devonian–Carboniferous boundary (Sallan & Coates 2013). Significantly, durophagy probably arose multiple times within actinopterygians during the early Carboniferous. This mirrors, to some degree, the proliferation of new durophagous groups in the aftermath of other extinction events: neopterygian fishes and marine reptiles in the Triassic (Tintori 1998; Rieppel 2002; Lombardo & Tintori 2005; Latimer & Giles 2018), and the many groups of modern teleost durophages like sparids, wrasses and tetraodontiforms in the early Palaeogene (Bellwood 2003).

Precise patterns of turnover among durophagous fishes during the Devonian–Carboniferous are obscured by taxonomic neglect. In particular, the diversity of tooth morphologies co-occurring in articulated holocephalans casts doubts on the value of systematic interpretations drawn from isolated dental material (Finarelli & Coates 2012) and, in turn, palaeobiological conclusions drawn from counts of dental form taxa. Further complicating the picture, recent efforts to better sample vertebrate diversity during 'Romer's Gap' have provided evidence – at least on a local scale – for high dental disparity and taxonomic richness among lungfishes during the Tournaisian (Smithson *et al.* 2016). This adds nuance to a longstanding narrative depicting the post-Devonian interval of dipnoan evolution as one of reduced anatomical innovation and increasing environmental restriction (Westoll 1949; Lloyd *et al.* 2012). These Tournaisian lungfishes, and indeed post-Devonian taxa more generally, overwhelmingly bear dentitions with well-developed dental ridges suggesting precise occlusion between upper and lower toothplates. Similar patterns are also found in some earlier lungfishes, and mark a pronounced shift from the broad flattened or gently rounded dental surfaces typical of exclusively Devonian assemblages like 'dipnorhynchids' and 'chirodipterids' (Campbell & Barwick 1990). This ridged geometry foreshadows the condition in modern lepidosirenid lungfishes, where precise occlusion between blade-like dental ridges marks a shift to shearing from the grinding found in *Neoceratodus* and, presumably, many fossil lungfishes (Bemis 1986). By contrast, the relatively flat dental surfaces of *Eurynotus* and some other eurynotiforms are geometrically similar to those of contemporary holocephalans (Stahl 1999; Finarelli & Coates 2012).

Such differences between these groups indicate contrasting feeding modes, a suggestion bolstered by a further outstanding distinction between toothplated actinopterygians and their holocephalan and lungfish contemporaries. Crucially, these early actinopterygians retain cranial kinesis: palatal toothplates are not fused to the basicranium; maxillae and premaxillae remain separate; the mandibular symphysis is never fused. It follows that these persistent articulations allowed movement between left and right sides of the jaws, and mediolateral movement between the grinding surfaces of upper and lower toothplates. Thus, in addition to a refined taxonomic framework, a more detailed appraisal of patterns of turnover and replacement among groups will require more sophisticated analyses of the attributes of 'crushing' dentitions, along with consideration of ecologically relevant attributes like body size and environmental associations, which are readily available (Sallan & Coates 2010; Sallan & Galimberti 2015).

4. Conclusion

μCT of *Eurynotus crenatus* from Wardie reveals considerable new anatomical data on the feeding apparatus of one of the earliest durophagous actinopterygians. *Eurynotus* shares many distinctive specialisations with the stratigraphically younger *Amphicentrum*, the only other eurynotiform in which the internal structure of the skull is described in detail. These traits are specialised in comparison with outgroups, but their implications for eurynotiform intrarelationships will remain ambiguous until anatomy in other members of the group is better known. With the exception of *Wardichthys* and some isolated parts of *Cheirodopsis*, much of the relevant material is compressed (Traquair 1879; Moy-Thomas & Bradley Dyne 1938; Sallan & Coates 2013), but it is possible that μCT of even flattened specimens might yield important details of robust and potentially informative structures like dental plates. Additional information might help resolve the relationships within the structurally diverse and stratigraphically long-ranging eurynotiforms, thereby providing a framework for documenting the assembly of the extreme morphologies of its later occurring – and presumably anatomically derived – members.

It is probable that such data will also prove useful in addressing broader questions of ray-finned fish evolution. Apart from the braincase (Rayner 1952; Poplin 1974; Schaeffer & Dalquest 1978; Coates 1998, 1999; Giles & Friedman 2014; reviewed in Friedman & Giles 2016), internal skeletal structure is largely unknown for Permo-Carboniferous actinopterygians (but see Watson 1925, 1928). Instead, knowledge of character-rich anatomical systems like palates and hyoid and branchial arches in early ray-finned fishes has historically derived from a few Late Devonian examples from Gogo (Gardiner 1984) and structurally disparate – and likely to be phylogenetically derived – taxa from the Early Triassic

of Greenland (Nielsen 1942, 1949). More details have emerged recently for Devonian forms (e.g., Choo 2012; Giles *et al.* 2015), but these are broadly consistent with classical accounts. This anatomical gap for Permo-Carboniferous actinopterygians is associated with considerable phylogenetic instability of those same taxa (Giles *et al.* 2017). Ambiguous patterns of relationships have consequences extending beyond taxonomy and systematics, and represent an obstacle to dissecting the striking patterns of anatomical and taxonomic diversification apparent in the fossil record in a rigorous, comparative framework. Along with the results presented here for *Eurynotus*, emerging μCT results for three-dimensionally preserved Permo-Carboniferous fossils point to unanticipated and phylogenetically informative characters that might help to clarify this important episode in actinopterygian evolution (Pradel *et al.* 2016; Coates & Tietjen, 2019). We anticipate that μCT study of ray-finned fishes from key localities including Wardie will provide critical new insights on the relationships, ecology and evolution of ray-finned fishes during their Carboniferous rise to taxonomic dominance.

5. Acknowledgements

6. References

Agassiz, L. 1835. *Recherches sur les poissons fossiles*. Tome II. Neuchatel: Imprimerie de Petitpierre. xii + 336 pp. + LXXV pls.

Ahlberg, P. E., Smith, M. M. & Johanson, Z. 2006. Developmental plasticity and disparity in early dipnoan (lungfish) dentitions. *Evolution & Development* **8**, 331–49.

Ahlberg, P. E. & Trewin, N. H. 1995. The postcranial skeleton of the Middle Devonian lungfish *Dipterus valenciennesi*. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **85**, 159–75.

Anderson, J. S., Carroll, R. L. & Rowe, T. B. 2003. New information on *Lethiscus stocki* (Tetrapoda: Lepospondyli: Aistopoda) from high-resolution computed tomography and a phylogenetic analysis of Aistopoda. *Canadian Journal of Earth Sciences* **40**, 1071–83.

Anderson, P. S., Friedman, M., Brazeau, M. D. & Rayfield, E. J. 2011. Initial radiation of jaws demonstrated stability despite faunal and environmental change. *Nature* **476**, 206–9.

Bardack, D. 1997. Fishes: 'Agnatha', Acanthodii, and Osteichthyes. *In* Shabica, C. W. & Hay, A. A. (eds) *Richardson's guide to the fossil fauna of Mazon Creek*, 226–43. Chicago: Northeastern Illinois University.

Barel, C. D. N. 1983. Toward a constructional morphology of cichlid fishes (Teleostei, Perciformes). *Netherlands Journal of Zoology* **33**, 357–424.

Bellwood, D. R. 2003. Origins and escalation of herbivory in fishes: a functional perspective. *Paleobiology* **29**, 71–83.

Bemis, K. E., Tyler, J. C., Bemis, W. E., Kumar, K., Rana, R. S. & Smith, T. 2017. A gymnodont fish jaw with molariform teeth from the early Eocene of Gujarat, India (Teleostei, Tetraodontiformes). *Journal of Vertebrate Paleontology* **37**, e1369422.

Bemis, W. E. 1986. Feeding systems of living Dipnoi: anatomy and function. *Journal of Morphology* **190**(Suppl.), 249–75.

Böttcher, R. 2014. Phyllodont tooth plates of *Bobasatrania scutata* (Gervais, 1852) (Actinopterygii, Bobasatraniiformes) from the Middle Triassic (Longobardian) Grenzbonebed of southern Germany and eastern France, with an overview of Triassic and Palaeozoic phyllodont tooth plates. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **274**, 291–311.

Boulenger, G. A. 1902. VIII. – Further remarks on the Carboniferous Ganoid, Benedenius deneensis, Traquair. *Journal of Natural History* **10**, 52–53.

Bradley Dyne, M. 1939. The skull of *Amphicentrum granulosum*. *Proceedings of the Zoological Society of London, Series B* **1939**, 195–210.

Campbell, K. S. W. & Barwick, R. E. 1990. Paleozoic dipnoan phylogeny: functional complexes and evolution without parsimony. *Paleobiology* **16**, 143–69.

Case, E. C. 1931. Arthodiran remains from the Devonian of Michigan. *Contributions from the Museum of Paleontology* **3**, 163–82.

Case, E. C. 1937. The brain and skull of a paleoniscid fish from the Pennsylvanian of western Missouri. *Proceedings of the American Philosophical Society* **78**, 1–10.

Chang, M.-M. 1995. *Diabolepis* and its bearing on the relationships between porolepiforms and dipnoans. *Bulletin du Muséum national d'Histoire naturelle, Paris*, 4ᵉ série, Section C **17**, 235–68.

Chisholm, J. I., McAdam, A. D. & Brand, P. J. 1989. Lithostratigraphical classification of Upper Devonian and Lower Carboniferous rocks in the Lothians. British Geological Survey Technical Report WA/89/26.

Chisholm, J. I. & Brand, P. J. 1994. Revision of the late Dinantian sequence in Edinburgh and West Lothian. *Scottish Journal of Geology* **30**, 97–104.

Choo, B. 2012. Revision of the actinopterygian genus *Mimipiscis* (=*Mimia*) from the Upper Devonian Gogo Formation of Western Australia and the interrelationships of the early Actinopterygii. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **102**, 77–104.

Choo, B., Zhu, M., Zhao, W., Jia, L. & Zhu, Y.-A. 2014. The largest Silurian vertebrate and its palaeoecological implications. *Scientific Reports* **4**, 5242.

Clack, J. A., Bennett, C. E., Carpenter, D. K., Davies, S. J., Fraser, N. C., Kearsey, T. I., Marshall, J. E. A., Millward, D., Otoo, B. K. A., Reeves, E. J., Ross, A. J., Ruta, M., Smithson, K. Z., Smithson, T. R. & Walsh, S. A. 2016. Phylogenetic and environmental context of a Tournaisian tetrapod fauna. *Nature Ecology & Evolution* **1**, 0002.

Clarkson, E. N. K. 1985. Palaeoecology of the Dinantian of Foulden, Berwickshire, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **76**, 97–100.

Claverie, T. & Wainwright, P. C. 2014. A morphospace for reef fishes: elongation is the dominant axis of body shape evolution. *PLoS One* **9**, e112732.

Close, R. A., Johanson, Z., Tyler, J. C., Harrington, R. C. & Friedman, M. 2016. Mosaicism in a new Eocene pufferfish highlights rapid morphological innovation near the origin of crown tetraodontiforms. *Palaeontology* **59**, 499–514.

Coates, M. I. 1993. New actinopterygian fish from the Namurian Manse Burn Formation of Bearsden, Scotland. *Palaeontology* **36**, 123–46.

Coates, M. I. 1994. Actinopterygian and acanthodian fishes from the Viséan of East Kirkton, West Lothian, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **84**, 317–27.

Coates, M. I. 1998. Actinopterygians from the Namurian of Bearsden, Scotland, with comments on early actinopterygian neurocrania. *In* Norman, D.B., Milner, A.R. & Milner, A.C. (eds) *A study of fossil vertebrates*, **122**, 27–59. London: Zoological Journal of the Linnean Society.

Coates, M. I. 1999. Endocranial preservation of a Carboniferous actinopterygian from Lancashire, UK, and the interrelationships of primitive actinopterygians. *Philosophical Transactions of the Royal Society of London, Series B* **354**, 435–62.

Coates, M. I., Gess, R. W., Finarelli, J. A., Criswell, K. E. & Tietjen, K. 2017. A symmoriiform chondrichthyan braincase and the origin of chimaeroid fishes. *Nature* **541**, 208–11.

Coates, M. I. & Sequeira, S. E. K. 2001. A new stethacanthid chondrichthyan from the Lower Carboniferous of Bearsden, Scotland. *Journal of Vertebrate Paleontology* **21**, 438–59.

Coates, M. I. & Tietjen, K. 2018. The neurocranium of the Lower Carboniferous shark *Tristychius arcuatus* (Agassiz, 1837). *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **108**, 19–35.

Coates, M. I. & Tietjen, K. 2019. 'This strange little palaeoniscid': a new early actinopterygian genus, and commentary on pectoral fin conditions and function. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh.* DOI: 10.1017/S1755691018000403.

Crofts, S. B. & Summers, A. P. 2014. How to best smash a snail: the effect of tooth shape on crushing load. *Journal of the Royal Society Interface* **11**, 20131053.

Currie, E. D. 1954. Scottish carboniferous goniatites. *Transactions of the Royal Society of Edinburgh* **62**, 527–602 + IV pls.

Darras, L., Derycke, C., Blieck, A. & Vachard, D. 2008. The oldest holocephalan (Chondrichthyes) from the Middle Devonian of the Boulonnais (Pas-de-Calais, France). *Comptes Rendus Palevol* **7**, 297–304.

Davydov, V. I., Korn, D. & Schmitz, M. D. 2012. The carboniferous period. *In* Gradstein, F. M., Schmitz, M. & Ogg, G. (eds) *The geologic timescale 2012*, **1**, 603–51. Amsterdam: Elsevier.

De Koninck, L. G. 1878. Fauna du Calcaire carbonifère de la Belgique. *Annales du Museé Royal d'Historie Naturelle de Belgique* **2**, 1–152 + 31 pls.

Denison, R. 1978. Placodermi. *In* Schultze, H.-P. (ed.) *Handbook of paleoichthyology*, **2**, 1–128. Suttgart: Gustav Fischer Verlag.

Denison, R. H. 1985. A new ptyctodont placoderm, Ptyctodopsis, from the Middle Devonian of Iowa. *Journal of Paleontology* **59**, 511–22.

Dick, J. R. F. 1978. On the carboniferous shark *Tristychius arcuatus* Agassiz from Scotland. *Transactions of the Royal Society of Edinburgh* **70**, 63–109.

Dick, J. R. F. 1981. *Diplodoselache woodi*, gen. et sp. nov. an early carboniferous shark from the Midland Valley of Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **72**, 99–113.

Dick, J. R. F. 1998. *Sphenacanthus*, a Palaeozoic freshwater shark. *Zoological Journal of the Linnean Society* **122**, 9–25.

Dineley, D. L. & Metcalf, S. J. 1999. *Fossil fishes of Great Britain*. Peterborough: Joint Nature Conservation Committee.

Egerton, P. D. G. 1850. Palichthyologic notes. No. 3. – on the Ganoidei Heterocerci. *Quarterly Journal of the Geological Society of London* **6**, 1–10 + II pls.

Finarelli, J. A. & Coates, M. I. 2012. First tooth-set outside the jaws in a vertebrate. *Proceedings of the Royal Society B* **279**, 775–9.

Friedman, M. 2015. The early evolution of ray-finned fishes. *Palaeontology* **58**, 213–28.

Friedman, M. & Giles, S. 2016. Actinopterygians: the ray-finned fishes – an explosion of diversity. *In* Clack, J. A., Fay, R. & Popper, A. (eds) *Evolution of the vertebrate ear.* Springer Handbook of Auditory Research, **59**, 17–49. Berlin: Springer Verlag.

Friedman, M. & Sallan, L. C. 2012. Five hundred million years of extinction and recovery: a Phanerozoic survey of large-scale diversity patterns in fishes. *Palaeontology* **55**, 707–42.

Gardiner, B. G. 1963. Certain palaeoniscoid fishes and the evolution of the snout in actinopterygians. *Bulletin of the British Museum (Natural History): Geology* **8**, 255–325 + II pls.

Gardiner, B. G. 1984. The relationships of the palaeoniscid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from the Upper Devonian of Western Australia. *Bulletin of the British Museum (Natural History): Geology* **37**, 173–428.

Gardiner, B. G. & Schaeffer, B. 1989. Interrelationships of lower actinopterygian fishes. *Zoological Journal of the Linnean Society* **97**, 135–87.

Giles, S., Darras, L., Clément, G., Blieck, A. & Friedman, M. 2015. An exceptionally preserved Late Devonian actinopterygian provides a new model for primitive cranial anatomy in ray-finned fishes. *Proceedings of the Royal Society B* **282**, 20151485.

Giles, S., Xu, G.-H., Near, T. J. & Friedman, M. 2017. Early members of 'living fossil' lineage imply later origin of modern ray-finned fishes. *Nature* **549**, 265–68.

Giles, S. & Friedman, M. 2014. Virtual reconstruction of endocast anatomy in early ray-finned fishes (Osteichthyes, Actinopterygii). *Journal of Paleontology* **88**, 636–51.

Greensmith, J. T. 1962. Rhythmic deposition in the Carboniferous Oil-Shale Group of Scotland. *The Journal of Geology* **70**, 355–64.

Hamel, M. H. & Poplin, C. 2008. The braincase anatomy of *Lawrenciella schaefferi*, actinopterygian from the Upper Carboniferous of Kansas (USA). *Journal of Vertebrate Paleontology* **28**, 989–1006.

Henrichsen, I. G. C. 1970. A catalogue of fossil vertebrates in the Royal Scottish Museum, Edinburgh. Part One/Actinopterygii. *Royal Scottish Museum, Information Series, Geology* **1**, ix + 1–102.

Hlavin, W. J. & Boreske, J. R., Jr. 1973. *Mylostoma variabile* Newberry, an Upper Devonian durophagous brachythoracid arthrodire, with notes on related taxa. *Berviora* **412**, 1–12.

Latimer, A. E. & Giles, S. 2018. A giant dapediid from the Late Triassic of Switzerland and insights into neopterygian phylogeny. *Royal Society Open Science* **5**, 180497.

Lloyd, G. T., Wang, S. C. & Brusatte, S. L. 2012. Identifying heterogeneity in rates of morphological evolution: discrete character change in the evolution of lungfish (Sarcopterygii; Dipnoi). *Evolution* **66**, 330–48.

Lombardo, C. & Tintori, A. 2005. Feeding specializations in Late Triassic fishes. *Annali dell'Università degli Studi di Ferrara, Museologia Scientifica e Naturalistica, Volume Speciale* **2005**, 25–32.

López-Arbarello, A. & Sferco, E. 2011. New semionotiform (Actinopterygii: Neopterygii) from the Late Jurassic of southern Germany. *Journal of Systematic Palaeontology* **9**, 197–215.

Mark-Kurik, E. 1977. The structure of the shoulder girdle in early ptyctodontids. *In* Menner, V. V. (ed.) *Ocherki po filogenii i sistemaike iskopaemykh myb i beschelyustryck* [*Sketches in phylogenesis and taxonomy of fossil fishes and Agnatha*], 61–70. Moscow: Nauk.

Monoghan, A. A., Browne, M. A. E. & Barford, D. N. 2014. An improved chronology for the Arthur's Seat volcano and Carboniferous magmatism of the Midland Valley of Scotland. *Scottish Journal of Geology* **50**, 165–72.

Moodie, R. L. 1915. A new fish brain from the coal measures of Kansas with a review of other fossil brains. *Journal of Comparative Neurology* **25**, 135–81.

Moodie, R. L. 1920. Microscopic examination of a fossil fish brain. *Journal of Comparative Neurology* **32**, 329–33.

Mottequin, B., Pouty, E. & Prestianni, C. 2015. Catalogue of types and illustrated specimens recovered from the 'black marble' of Denée, a marine conservation-Lagerstätte from the Mississippian of southern Belgium. *Geologica Belgica* **18**, 1–14.

Moy-Thomas, J. A. 1939. *Palaeozoic fishes*. London: Methuen.

Moy-Thomas, J. A. & Bradley Dyne, M. 1938. Actinopterygian fishes from the Lower Carboniferous of Glencartholm, Eksdale, Dumfriesshire. *Transactions of the Royal Society of Edinburgh* **59**, 437–80.

Nielsen, E. 1942. Studies on Triassic fishes from East Greenland. I. *Glaucolepis* and *Boreosomus*. *Meddelelser om Grønland* **138**, 1–403 + 30 pls.

Nielsen, E. 1949. Studies on Triassic Fishes. II. *Australosomus* and *Birgeria*. *Meddelelser om Grønland* **146**, 1–309 + 20 pls.

Nursall, J. R. 1999. The family †Mesturidae and the skull of pycnodont fishes. *In* Arratia, G. & Schultze, H.-P. (eds) *Mesozoic fishes 2 – systematics and fossil record*, 153–82. Munich: Verlag Dr Friedrich Pfeil.

Pardo, J. D., Szostakiwskyj, M., Ahlberg, P. E. & Anderson, J. S. 2017. Hidden morphological diversity among early tetrapods. *Nature* **546**, 642–5.

Poplin, C. M. 1974. *Étude de quelques paléoniscidés pennsylvaniens du Kansas*. Cahiers de Paléontologie, Paris: Éditions du CNRS. 151 pp. + XL pls.

Poplin, C. M. 1984. *Lawrenciella schaefferi* n.g., n.sp. (Pisces: Actinopterygii) and the use of endocranial characters in the classification of the Palaeonisciformes. *Journal of Vertebrate Paleontology* **4**, 413–21.

Poplin, C. M. & Véran, M. 1996. A revision of the actinopterygian fish *Coccocephalichthys wildi* from the Upper Carboniferous of Lancashire. *In* Milner, A.R. (ed.) *Studies on Carboniferous and Permian vertebrates*. Special Papers in Palaeontology, **52**, 7–29. London: Palaeontological Association.

Pradel, A., Maisey, J. G., Mapes, R. H. & Kruta, I. 2016. First evidence of an intercalar bone in the braincase of "palaeonisciform" actinopterygians, with a virtual reconstruction of a new braincase of *Lawrenciella poplin*, 1984 from the Carboniferous of Oklahoma. *Geodiversitas* **38**, 489–504.

Rayner, D. H. 1952. On the cranial structure of an early palæoniscid, *Kentuckia*, gen. nov. *Transactions of the Royal Society of Edinburgh* **62**, 53–83.

Richards, K. R., Sherwin, J. E., Smithson, T. R., Bennion, R. F., Davies, S. J., Marshall, J. E. A. & Clack, J. A. 2018. Diverse and durophagous: early Carboniferous chondrichthyans from the Scottish Borders. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **108**, 67–87.

Rieppel, O. 2002. Feeding mechanics in Triassic stem-group sauropterygians: the anatomy of a successful invasion of Mesozoic seas. *Zoological Journal of the Linnean Society* **135**, 33–63.

Romer, A. S. 1966. *Vertebrate paleontology*, 3rd edn. Chicago: University of Chicago Press.

Sallan, L. C. 2014. Major issues in the origins of ray-finned fish (Actinopterygii) biodiversity. *Biological Reviews* **89**, 950–71.

Sallan, L. C., Kammer, T. W., Ausich, W. I. & Cook, L. A. 2011. Persistent predator–prey dynamics revealed by mass extinction. *Proceedings of the National Academy of Sciences of the USA* **108**, 8335–8.

Sallan, L. C. & Coates, M. I. 2010. End-Devonian extinction and a bottleneck in the early evolution of modern jawed vertebrates. *Proceedings of the National Academy of Sciences of the USA* **107**, 10131–35.

Sallan, L. C. & Coates, M. I. 2013. Styracopterid (Actinopterygii) ontogeny and the multiple origins of post-Hangenberg deep-bodied fishes. *Zoological Journal of the Linnean Society* **169**, 156–99.

Sallan, L. C. & Friedman, M. 2012. Heads or tails: staged diversification in vertebrate evolutionary radiations. *Proceedings of the Royal Society of London B* **279**, 2025–32.

Sallan, L. C. & Galimberti, A. K. 2015. Body-size reduction in vertebrates following the end-Devonian mass extinction. *Science* **350**, 812–5.

Schaeffer, B. & Dalquest, W. W. 1978. A palaeonisciform braincase from the Permian of Texas, with comments on cranial fissures and the posterior myodome. *American Museum Novitates* **2658**, 1–15.

Schaeffer, B. & Rosen, D. E. 1961. Major adaptive levels in the evolution of the actinopterygian feeding mechanism. *American Zoologist* **1**, 187–204.

Schram, F. R. 1983. Lower Carboniferous biota of Glencartholm, Eksdale, Dumfriesshire. *Scottish Journal of Geology* **19**, 1–15.

Signor, P. W., III & Brett, C. E. 1984. The mid-Paleozoic precursor to the Mesozoic marine revolution. *Paleobiology* **10**, 229–45.

Smithson, T. R., Wood, S. P., Marshall, J. E. & Clack, J. A. 2012. Earliest Carboniferous tetrapod and arthropod faunas from Scotland populate Romer's Gap. *Proceedings of the National Academy of Sciences of the USA* **109**, 4532–7.

Smithson, T. R., Richards, K. R. & Clack, J. A. 2016. Lungfish diversity in Romer's Gap: reaction to the end-Devonian extinction. *Palaeontology* **59**, 29–44.

Smithwick, F. M. 2015. Feeding ecology of the deep-bodied fish *Dapedium* (actinopterygii, Neopterygii) from the Sinemurian of Dorset, England. *Palaeontology* **58**, 293–311.

Stahl, B. 1999. Chondrichthyes III, Holocephali. *In* Schultze, H.-P. (ed.) *Handbook of paleoichthyology*, **4**, 1–164. Munich: Verlag Dr. Friedrich Pfeil.

Sumner, D. 1991. *Palaeobiology, taphonomy and diagenesis of a Lower Carboniferous fish fauna*. Unpublished PhD thesis, University of St Andrews, UK. 336 pp.

Thies, D. & Herzog, A. 1999. New information on Dapedium LEACH 1822 (Actinopterygii, Seminotiformes). In Arratia, G. & Schultze, H.-P. (eds), *Mesozoic Fishes 2 – Systematics and Fossil Record*, 143–52. Munich: Verlag Dr Friedrich Pfeil.

Tintori, A. 1998. Fish biodiversity in the marine Norian (Late Triassic) of northern Italy: the first neopterygian radiation. *Italian Journal of Zoology* **65**(Suppl.), 193–8.

Traquair, R. H. 1867. Description of *Pygopterus greenockii*, with notes one the structural relations of the genera *Pygopterus*, *Amblypterus* and *Eurynotus*. *Transactions of the Royal Society of Edinburgh* **24**, 701–713 + I pl.

Traquair, R. H. 1875. On some fossil fishes from the neighbourhood of Edinburgh. *Journal of Natural History* **15**, 258–268 + I pl.

Traquair, R. H. 1877–1914. *The Ganoid fishes of the British Carboniferous Formations. Part I. Palæoniscidae*. London: Palaeontographical Society.

Traquair, R. H. 1879. On the structure and affinities of the Playtsomidae. *Transactions of the Royal Society of Edinburgh* **29**, 343–391 + IV pls.

Traquair, R. H. 1903. On the distribution of fossil fish-remains in the Carboniferous rocks of the Edinburgh district. *Transactions of the Royal Society of Edinburgh* **40**, 687–707.

Trinajstic, K. & Long, J. A. 2009. A new genus and species of ptyctodont (Placodermi) from the Late Devonian Gneudna Formation, Western Australia, and an analysis of ptyctodont phylogeny. *Geological Magazine* **146**, 743–60.

Tyler, J. C. 1980. Osteology, phylogeny, and higher classification of the fishes of the order Plectognathi (Tetraodontiformes). *NOAA Technical Report NMFS Circular* **434**, 1–422.

Ward, P., Labandeira, C., Laurin, M. & Berner, R. A. 2006. Confirmation of Romer's Gap as a low oxygen interval constraining the timing of initial arthropod and vertebrate terrestrialization. *Proceedings of the National Academy of Sciences of the USA* **103**, 16818–22.

Waters, C. N., Browne, M. A. E., Jones, N. S. & Somerville, I. D. 2011a. Midland valley of Scotland. *In* Waters, C.N. (ed.) *A revised correlation of Carboniferous rocks in the British Isles*. Special Report Number 26, 96–102. London: The Geological Society.

Waters, C. N., Somerville, I. D., Stephenson, M. H., Cleal, C. J. & Long, S. L. 2011b. Biostratigraphy. *In* Waters, C. N. (ed.) *A revised correlation of Carboniferous rocks in the British Isles*. Special Report Number 26, 11–22. London: The Geological Society.

Watson, D. M. S. 1925. On the structure of certain palæoniscids and the relationships of that group with other bony fish. *Proceedings of the Zoological Society of London* **1925**, 815–870 + II pls.

Watson, D. M. S. 1928. On some points in the structure of palæoniscid and allied fish. *Proceedings of the Zoological Society of London* **1928**, 49–70.

Westneat, M. W. 2004. Evolution of levers and linkages in the feeding mechanisms of fishes. *Integrative and Comparative Biology* **44**, 378–89.

Westoll, T. S. 1949. On the evolution of the Dipnoi. *In* Jepsen, G. L., Simpson, G. G. & Mayr, E. (eds) *Genetics paleontology and evolution*, 121–84. Princeton: Princeton University Press.

Wilson, C. D., Pardo, J. D. & Anderson, J. S. 2018. A primitive actinopterygian braincase from the Tournaisian of Nova Scotia. *Royal Society Open Science* **5**, 171727.

Wilson, R. B. 1989. A study of the Dinantian marine microfossils of central Scotland. *Transactions of the Royal Society of Edinburgh* **80**, 91–126.

Wood, S. P. 1975. Recent discoveries of Carboniferous fishes in Edinburgh. *Scottish Journal of Geology* **11**, 251–8.

Wood, S. P. 1982. New basal Namurian (Upper Carboniferous) fishes and crustaceans found near Glasgow. *Nature* **297**, 574–7.

Woodward, A. S. 1891. *Catalogue of fossil fishes in the British Museum (Natural History). Part II. Containing the Elasmobranchii (Acanthodii), Holocephali, Ichthyodorulites, Ostracodermi, Dipnoi, and Teleostomi (Crossopterygii and Chondrostean Actinopterygii)*. London: Trustees of the British Museum (Natural History).

Woodward, A. S. 1895. *Catalogue of fossil fishes in the British Museum (Natural History). Part III. Containing the Actinopterygian Teleostomi of the Orders Chondrostei (Concluded), Protospondyli, Aethospondyli, and Isospondyli (in Part)*. London: Trustees of the British Museum (Natural History).

Young, J. 1866. On the affinities of *Platysomus* and allied genera. *Quarterly Journal of the Geological Society of London* **22**, 301–317 + II pls.

Zidek, J. 1992. Late Pennsylvanian Chondrichthyes, Acanthodii, and deep-bodied Actinopterygii from the Kinney Quarry, Manzanita Mountains, New Mexico. *In* Zidek, J. (ed.) *Geology and paleontology of the Kinney Brick Quarry, Late Pennsylvanian, Central New Mexico*, **138**, 145–82. Socorro, NM: New Mexico Bureau of Mines & Mineral Resources Bulletin.