Early Vertebrate Evolution

Traquair's lungfish from Loanhead: dipnoan diversity and tooth plate growth in the late Mississippian

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ABSTRACT: Ramsay Heatley Traquair, the eminent Victorian Scottish palaeoichthyologist and museum curator, procured an extensive collection of Palaeozoic fishes from across Scotland with the help of local miners and quarrymen. One very productive locality near Edinburgh was Loanhead. Traquair described numerous fossil fish from this Serpukhovian site, including four lungfish taxa: *Ctenodus interruptus*, *Sagenodus quinquecostatus*, *Uronemus splendens* and *Ctenodus angustulus*. The first three are now quite well known, but the fourth was only briefly described and never figured. It is based entirely on tooth plates, which are unusual both in their very small size and the arrangement of the tooth ridges. They lack the diagnostic characters of *Ctenodus* tooth plates and are here renamed *Clackodus angustulus*. A further taxon, *Conchopoma* sp., has recently been identified. Represented by a spade-shaped parasphenoid and denticulated jaw elements, it is the earliest known occurrence of the genus, extending its range into the Mississippian. A sixth taxon may be represented by an isolated parasphenoid bearing an anterior process, previously only seen in Devonian lungfish. The presence of up to six lungfish taxa at a single locality is unprecedented in the Carboniferous and indicates that the high level of lungfish diversity encountered in the Tournaisian of the Scottish Borders continued throughout the Mississippian, adding to the growing evidence that post-Devonian lungfish evolution was not as limited as previously proposed. This may have been due to changes in tooth plate growth, enabling greater variation in dentition and diet. In most Devonian taxa, tooth plate growth can be explained by comparison with that in extant forms, but analysis of Carboniferous tooth plates suggest growth was different in many taxa, possibly based on more than one pioneer tooth, allowing for novel patterns of tooth ridges and different types of teeth to develop on the same plate.

KEY WORDS: Carboniferous, Dipnoi, diversity, Scotland, Serpukhovian.

Westoll's (1949) classic study on the evolution of the Dipnoi concluded that diversity among lungfish was at its greatest in the Devonian, following the origin of the group, and then declined sharply after establishing a body form that was then little changed to the present day. These ideas gained support and influence with the subsequent description of new lungfish from the Devonian of Greenland (Lehman 1959) and North America (Thomson & Campbell 1971), and discoveries in Australia (Miles 1977) and China (Chang & Yu 1982). Little was published on later Palaeozoic lungfish in the years following Westoll's study, especially in the UK. Thompson (1965) named and described neglected material from the Lower Carboniferous of Scotland collected in the 19th Century and Smith *et al*. (1987) redescribed the dentition of *Uronemus*, but it was not until Jenny Clack supervised a PhD project on British Carboniferous lungfish undertaken by Esther Sharp (Sharp 2007; Clack *et al*. 2011; Sharp & Clack 2012, 2013), that interest was revived. Around the same time, new analyses on the rates of evolution began to question some of the assumptions in Westoll's study, in particular what the impact of mass extinction events had on the trajectory of evolution (e.g., Jablonski 2001). A re-examination of lungfish evolution by Lloyd *et al*. (2011) using a higher level of resolution and shorter time bins, found that morphological evolution among

lungfish may not have slowed significantly until the Cretaceous (see also Kemp *et al*. 2017). The subsequent discovery of a diverse lungfish fauna in the early Mississippian of Scotland (Smithson *et al*. 2016) is consistent with this analysis. Our recent examination of lungfish material from the Serpukhovian of the Scottish Midland Valley in the Natural History Museum (NHM), London, that formed part of a collection purchased from the Traquair estate in 1914, has revealed that the high level of morphological diversity found in the Tournaisian may have continued throughout the Mississippian.

During his time as the Keeper of Natural History at the Museum of Science and Arts in Edinburgh (now National Museums Scotland (NMS)), Ramsay Heatley Traquair cemented his reputation as an eminent Victorian palaeoichthyologist through the procurement of an extensive collection of Palaeozoic fishes from across Scotland. His efforts were aided by local quarrymen and miners, in particular from one very productive locality at Loanhead, near Edinburgh. In a series of papers that began in 1873, Traquair described numerous fossil fish from this Serpukhovian site, including four lungfish taxa: *Ctenodus interruptus*, *Sagenodus quinquecostatus*, *Uronemus splendens* and *Ctenodus angustulus* (Traquair 1873, 1881, 1882, 1890a, 1890b, 1903). All but *C. angustulus* are now well known, but *C. angustulus* did not receive the same attention

and was only described briefly and never figured. Here we redescribe this neglected material, together with that of new lungfish specimens from the same locality. The specimens reveal a greater diversity of lungfish than previously recognised and add to the growing evidence of heterodonty among Mississippian taxa.

1. Geological setting

All the material described below was collected in the 1880s from the Blackband Ironstone exposed in the mine workings at Loanhead, Midlothian, Scotland (Fig. 1a). Most specimens were probably recovered at the Burghlee (formerly Borough Lee) colliery, but some may have originated at the Ramsay colliery (Smithson 1985). Following a drafting error in the geological section published by Traquair (1903), the Blackband Ironstone from Burghlee (Borough Lee Ironstone of Traquair 1881, 1882, 1890a) was, for a long time, erroneously thought to be equivalent to the Loanhead Ironstone No 2. This was shown to be incorrect by Smithson (1985), who demonstrated that it was instead equivalent to the Rumbles Ironstone or Loanhead Ironstone No 3. This was later verified and confirmed by Andrews and Brand (in Andrews & Carroll 1991). The Rumbles Ironstone lies above the Great Seam (Tulloch & Walton 1958), near the top of the Limestone Coal Formation in the E1a ammonoid zone of the Pendleian substage of the Namurian in Scotland (Browne *et al*. 1999), in the upper part of the Serpukhovian, in the upper Mississippian (Fig. 1b).

Loanhead is one of four lungfish localities in the Serpukhovian of Scotland; the others are as follows: the Dora opencast site near Cowdenbeath, Fife, lungfish fauna *Sagenodus quinquecostatus* and *Uronemus splendens* (Smith *et al*. 1987); Niddrie near Edinburgh, lungfish fauna *Ctenodus interruptus* and *Sagenodus quinquecostatus* (Henrichsen 1972), on the eastern side of the Midland Valley (Fig. 1a); and Powgree Burn near Longbar, Glengarnock, in Ayrshire, lungfish fauna *Ctenodus interruptus* (Sharp & Clack 2013), on the western side of Scotland.

2. Material and methods

The material described below is housed in the collections of the NHM, London, and NMS, Edinburgh. It is from a single horizon, the Blackband Ironstone of Traquair (1881), equivalent to the Rumbles Ironstone that was worked extensively during the 1880s, at collieries in the Loanhead area (see Section 1). All the material in the NMS has register numbers beginning 1885 or 1886. The material in the NHM forms part of a collection made by Ward, dated 1894, a collection made by Plant acquired in 1896 or the collection purchased from the Traquair estate in 1914 following Traquair's death in 1912. All the specimens in the NHM labelled '*Ctenodus*' *angustulus* are correctly identified. In contrast, only one of the specimens at the NMS is identified correctly. Furthermore, '*C.*' *angustulus* is not listed in their published catalogue (Henrichsen 1972). This suggests that the five specimens available when Traquair first described '*C.*' *angustulus* (Traquair 1881) formed part of the NHM collection purchased from the Traquair estate. In view of this possibility, one of these specimens is identified as the type of the new genus erected in Section 3.

None of the specimens were prepared prior to study because of their small size and delicacy. The terms used by Smithson *et al*. (2016) to describe lungfish tooth plates are used here. Photographs were taken with a Sony Cyber-shot DSC W-180 camera or a Dino-lite AM1331T. Specimens were microcomputed tomography (CT) scanned using the University Museum of Zoology, Cambridge, X-Tek micro-Ct scanner with the following parameters: X ray power 120–200 kv at 120–220 µm; number of slices *c*.1900; at resolutions of between 11.9 and 36.3 µm. The scan data were processed using Mimics V19 and segmented using multiple slice threshold editing techniques. Three-dimensional PDFs were created by exporting stereo lithography (STL) files from Mimics segmentation software. All figures were prepared using Adobe Photoshop. Abbreviations used in this study for institutions housing material are as follows: GSL, British Geological Survey, Keyworth; NHMUK, Natural History Museum, London; NMS, National Museums Scotland, Edinburgh; UMZC, University Museum of Zoology, Cambridge.

3. Systematic palaeontology

Osteichthyes Huxley, 1880
Sarcopterygii Romer, 1955
Dipnomorpha Ahlberg, 1991
Dipnoi Müller, 1845
Family undesignated
Genus *Clackodus* nov.

LSID urn:lsid:zoobank.org:pub:EFFB7007-BE67-495D-B086-5A58AE284B8E

Type species. *Clackodus angustulus* (Traquair, 1881).

Clackodus angustulus (Traquair, 1881)
(Fig. 2)

Derivation of name. In honour of Professor Jennifer Clack for leading the recent revival of interest in British Carboniferous lungfish and from the Greek '*odous*', meaning tooth.

Type specimen. NHMUK PVP 11503e.

Type locality and horizon. Rumbles Ironstone (see Section 1) at Burghlee Colliery, Loanhead, Midlothian, Scotland, in the Limestone Coal Formation of the Clackmannan Group, ammonoid zone E1a of the Pendelian substage, Serpukhovian, Mississippian (Browne *et al*. 1999)

Diagnosis. Small, triangular-shaped tooth plates, maximum length 3.5 mm, securely attached to surrounding jaw bones. Length-to-width ratio *c*.2:1. Four radiating tooth ridges. Tooth ridge angle *c*.35°. Elongate tooth ridge 1 extends both in front and behind tooth ridge 2 and bears up to ten small, laterally compressed teeth. Other tooth ridges much shorter with fewer, larger conical teeth. The youngest, labial tooth on each ridge is pointed and gently recurved.

Referred specimens. NHMUK PVP 8246, NHMUK PVP 8530, NHMUK PVP 11502a–f, NHMUK PVP 11503a–d, NMS G 1885.38.6, NMS G 1885.51.12, NMS G 1886.84.12, NMS G 1886.85.35.2, NMS G 1886.86.14.1, NMS G 1886.86.14.2, NMS G 1886.87.16.1, NMS G 1886.87.16.2, NMS G 1886.87.16.3, NMS G 1886.87.16.4.

Description.

Pterygoid. With the exception of one prearticular (NMS G 1886.87.16.4), all the available specimens are pterygoids. They are preserved in palatal view. All have suffered damage during collection. The most complete is the type specimen (Fig. 2a–c), a right pterygoid, 4.5 mm long and 3.5 mm at its widest point. This specimen was micro-CT scanned and details of the dorsal surface are based on the scan (Fig. 2c).

The mesial edge of the pterygoid forms the midline suture. It extends posteriorly to a point level with the widest part of the palate, approximately two thirds the length of the pterygoid. The edge continues posterolaterally to the most posterior point of the pterygoid, which is approximately midway between
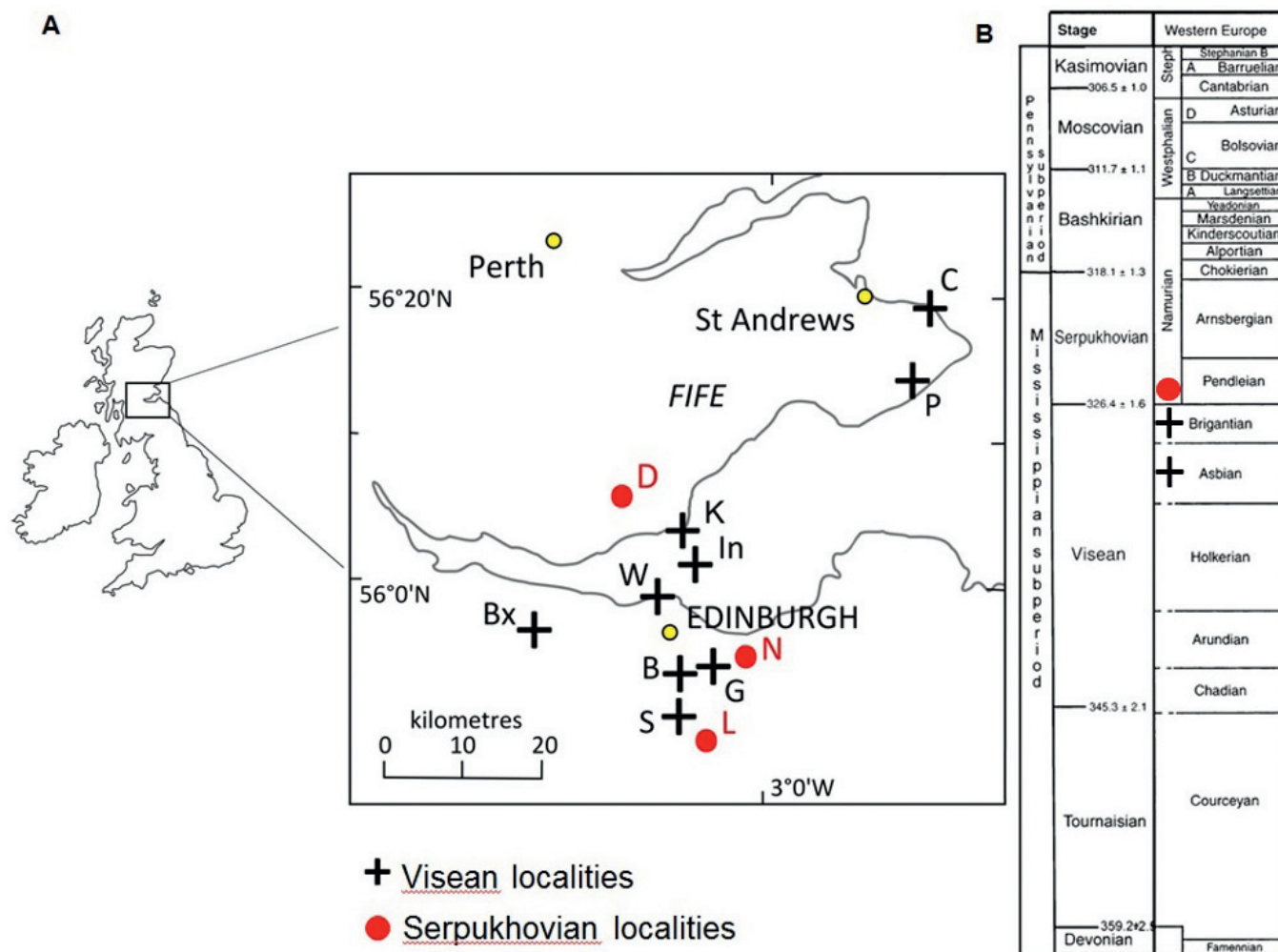
A

B

Figure 1 Carboniferous geology and late Mississippian lungfish sites in eastern Scotland. (A) Late Mississippian lungfish sites in the Lothians and Fife after Smithson *et al.* (2017). (B) Carboniferous geology after Smithson *et al.* (2012). Abbreviations: B = Burdiehouse, Edinburgh; Bx = Broxburn; C = new site in E Fife (see Smithson *et al.* 2017); D = Dora, near Cowdenbeath, Fife; G = Gilmerton, Edinburgh; I = Inchkeith; K = Kinghorn, Fife; L = Loanhead, Edinburgh; N = Niddrie, Edinburgh; P = Pitcorthie, Fife; S = Straiton, Edinburgh; W = Wardie, Edinburgh.

the lateral and mesial margins. This edge forms the suture with the parasphenoid such that the parasphenoid separates the pterygoids for approximately one third of their total length. The dorsal surface in this area is slightly excavated and probably represents a sutural overlap. The edge of the pterygoid then turns anterolaterally towards the lateral corner. This margin is concave, apart from the most lateral part, which is straight and extends more strongly anteriorly. At this widest part of the pterygoid, the thickened edge of the bone turns anteromesially towards the labial edge of the tooth plate. The ventral surface of the posterolateral part of the pterygoid is slightly concave and pitted. More centrally, the surface is raised. On the dorsal surface, extending posteriorly from near the labial margin of the tooth plate, is a low ridge. Anteriorly, it lies above tooth ridge 3 and runs almost parallel with the mesial edge.

Unlike the tooth plates of *Ctenodus interruptus* and *Sagenodus quinquecostatus* from Loanhead, which are typically discrete and separate from the jaw bones, the pterygoid tooth plate of *Clackodus* is securely attached to the bone, and the junction between the two is not obvious. On the type specimen, the tooth plate is *c*.2.5 mm long and bears four radiating tooth ridges. The tooth ridge angle is *c*.35° and the length-to-width ratio is *c*.2:1. Tooth ridge 1 has up to ten small, laterally compressed teeth. All the teeth have worn flattened tips, apart from the most labial teeth which are sharply pointed and recurved.

The tooth ridge extends slightly posterolaterally, beyond the end of tooth ridge 2, and makes an angle of *c*.10° with the midline suture. The teeth on the remaining tooth ridges are cone-shaped and larger than those on tooth ridge 1. They too have flattened tips, apart from those at the labial end of the ridge, which are pointed and recurved. Tooth ridges 2–4 are damaged lingually and only the bases are preserved. The tooth formula on the type specimen is 9, 6, 5, 3, with two teeth on tooth ridge 1 lying in front of tooth ridge 2 and one tooth lying behind. In NHMUK PVP 11502a, the tooth formula is 8, 5, 5, 3, and in NHMUK PVP 11502b, the formula is 7, 7, 6, 5.

Prearticular. NMS G 1886.87.16.4, an incomplete right prearticular (Fig. 2d–f), is the only available specimen. It is *c*.4.0 mm long and 1.2 mm wide. The specimen is partially concealed by the matrix and was micro-CT scanned to reveal its morphology (Fig. 2e, f).

The prearticular is a roughly chevron-shaped bone. Its mesial edge is straight and makes up half the length of the bone. At a point just beyond the posterior end of tooth ridge 1, it extends posterolaterally to form the internal edge of the narrow, flat and almost parallel-sided jaw ramus. The posterolateral end is gently curved and from it the lateral edge extends anteromesially towards the labial edge of the tooth plate. The ventral surface is largely flat, apart from a short, low ridge, beneath the lateral edge of the tooth plate.
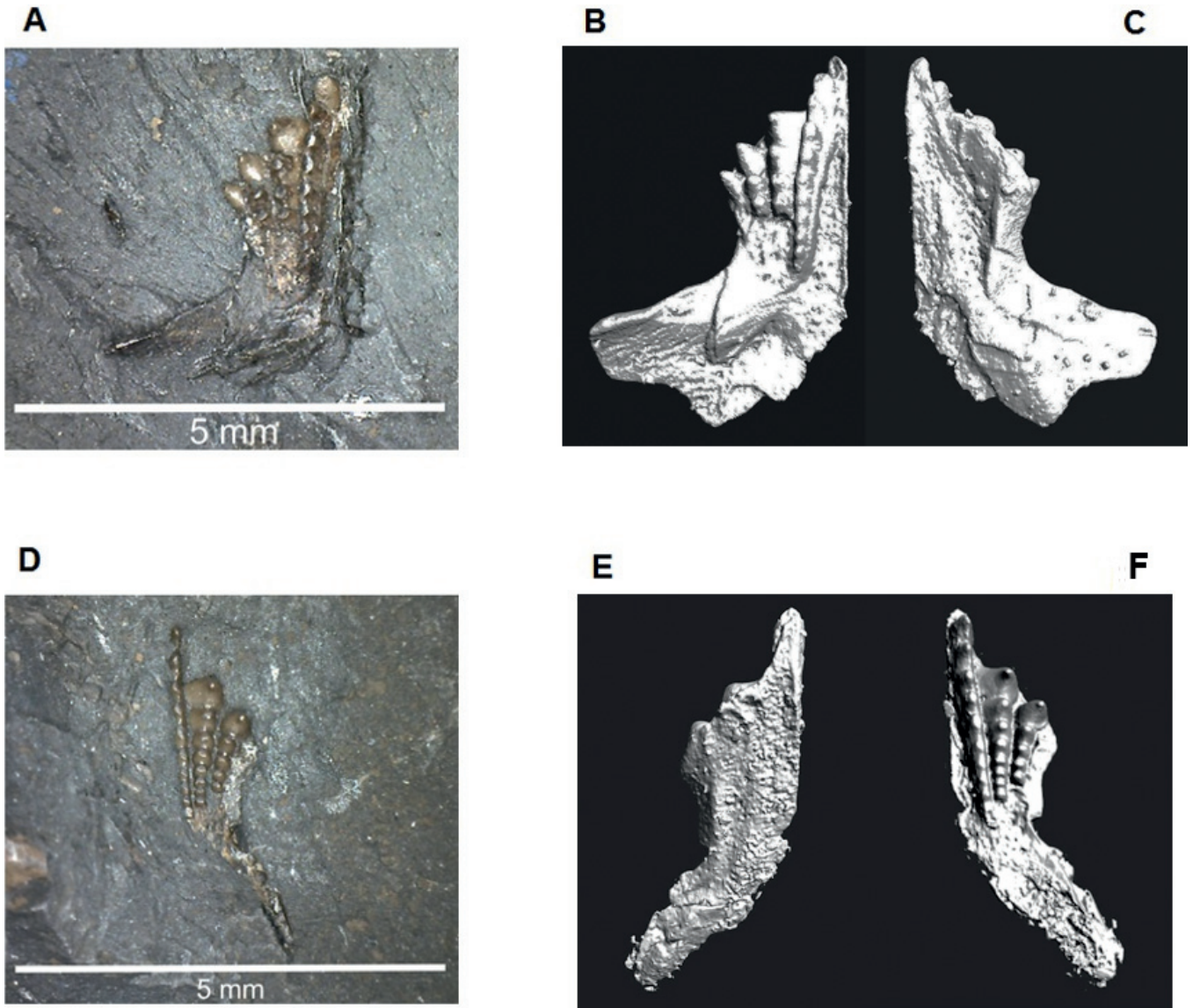
Figure 2 *Clackodus angustulus* (Traquair, 1881) from Loanhead. (A–C) Right pterygoid NHMUK PVP 11503e. (A) Ventral view. (B, C) Micro-CT scans. (B) Ventral view. (C) Dorsal view. (D–F) Left prearticular NMS G 1886.87.16.4. (D) Dorsal view. (E, F) Micro-CT scans. (E) Ventral view. (F) Dorsal view. Scale bars = 5 mm.

The prearticular tooth plate is also securely attached to the bone. It is *c*.2 mm long and bears four radiating tooth ridges. Ridges 1–3 are intact, but tooth ridge 4 is damaged and only parts of the tooth bases are preserved. The tooth ridge angle is *c*.35° and the length-to-width ratio is 2:1. The tooth formula is 10, 8, 5, 3, with two teeth on tooth ridge 1 lying in front of tooth ridge 2 and one behind. The shape of the teeth is like those on the pterygoid tooth plate, with small, laterally compressed teeth on tooth ridge 1 and larger conical teeth on the other ridges. Apart from the labial teeth, all the teeth have worn, flattened tips.

Remarks. An emended diagnosis of *Ctenodus*, based on tooth plates, was recently presented by Smithson *et al*. (2016, p. 31): 'irregular or elliptical in form. 6–23 approximately parallel tooth ridges. Tooth ridge angle less than 40°. Pterygoid tooth plate concave, prearticular tooth plate convex.' Apart from the low tooth ridge angle, the tooth plates of *Clackodus angustulus* lack all the diagnostic characters of *Ctenodus*. Instead, they are superficially most like the tooth plates of juvenile *Andreyevichthys* (Krupina & Reisz 1999; Smith & Krupina 2001). This late Devonian lungfish from Russia is represented

by hundreds of tooth plates of different sizes and growth stages. The smallest are 2 mm long, the largest at least 50 mm long. They have up to seven tooth ridges, with a maximum tooth ridge angle of *c*.50°. However, unlike *Clackodus*, all the teeth on the *Andreyevichthys* tooth plates are the same shape. *Clackodus* has heterodont tooth plates, with the teeth on tooth ridge 1 smaller, and more laterally compressed than those on the other three tooth ridges. This has not been observed previously in late Mississippian taxa, but is not uncommon in lungfish from the early Mississippian (Smithson *et al*. 2016; see Section 4.2). Despite their small size, there is nothing to suggest that the tooth plates of *Clackodus* are juvenile. The tooth plates are firmly attached to the surrounding jaw bones and the teeth show extensive wear.

Family undesignated
Genus *Conchopoma* Kner, 1868

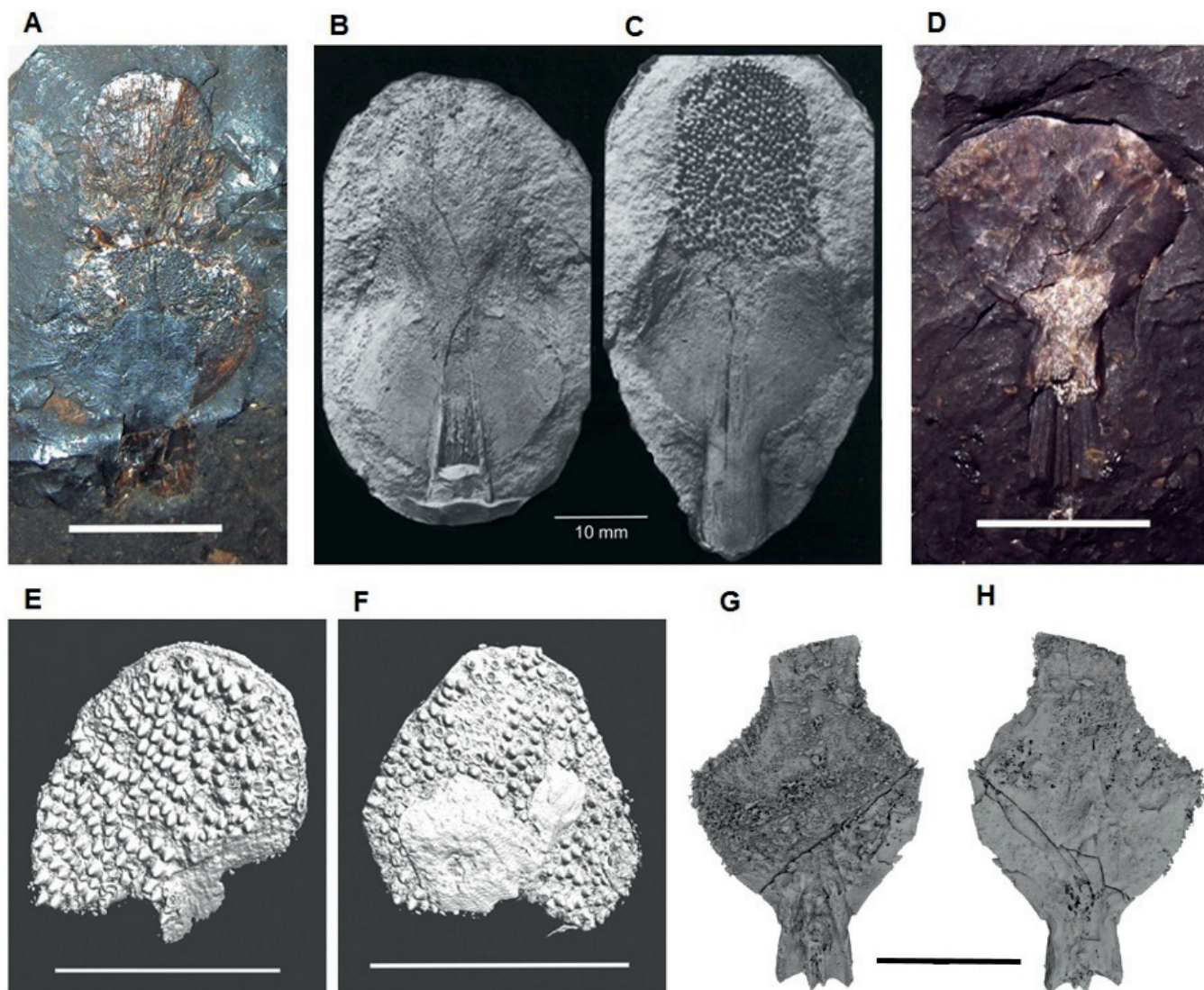**Type species.** *Conchopoma gadiforme* Kner, 1868.

Conchopoma sp.

Figure 3 *Conchopoma* from Loanhead and Braidwood, Illinois, USA, and new lungfish parasphenoid from Loanhead. (A) *Conchopoma* sp. from Loanhead, parasphenoid, NHMUK PVP 11516, dorsal view. (B, C) *Conchopoma edesi* from Braidwood (reproduced from Schultze 1975, pl. 2 with permission). (B) Dorsal view. (C) Ventral view. (D) Unnamed parasphenoid from Loanhead, NMS G 1885.50.18, ventral view. (E, F) *Conchopoma* sp. from Loanhead, micro-CT scans, basihyal plates in dorsal view. (E) NMS G 1885.50.50.2. (F) NMS G 1885.50.50.4. (G, H) Unnamed parasphenoid from Loanhead, NMS G 1885.50.18, micro-CT scans. (G) Dorsal view. (H) Ventral view. Scale bars = 10 mm (A–D, G, H); 5 mm (E, F).

Material. NHMUK PVP 11516, NMS G 1885.50.50.1, NMS G 1885.50.50.2, NMS G 1885.50.50.4, NMS G 1886.89.49.

Description.

Parasphenoid. An isolated parasphenoid in the collection purchased from the Traquair estate, NHMUK PVP 11516 (Fig. 3a), is very similar to that of *Conchopoma edesi* (Fig. 3b, c). Preserved in dorsal view, it is *c*.26 mm long and has a maximum width of *c*.12 mm (compared with *C. edesi*, which is 53 mm long and 24 mm wide). The posterior left side is damaged and preserved as impression.

The paraspenoid is spade-shaped with a large, broad corpus. This has a gently rounded anterior margin, almost parallel sides and gently rounded posterior border where it curves to join a short (or incomplete) posterior process. The corpus is relatively much larger than the typical diamond-shaped body of other Carboniferous lungfish, e.g., *Ctenodus* and *Sagenodus* (Watson & Gill 1923, figs 10, 25), as it extends forward into the territory normally occupied by the pterygoids. A scan of NHMUK PVP 11516 revealed a shagreen of small

denticles on the palatal (ventral) surface. These are smaller than those on the parasphenoid of *Conchopoma edesi* (Fig. 3c) and on the basihyal plates from Loanhead (see Fig. 3e, f). Impressions of tiny denticles are also preserved where the posterior left side is missing. The preserved portion of the posterior stem is relatively much shorter than those of other Carboniferous taxa, accounting for less than 18 % of the total length of the parasphenoid. This compares with *c*.60 % in *Sagenodus* (Schultze & Chorn 1997, fig. 22) and *c*.50 % in *Ctenodus* (Sharp & Clack 2013, fig. 16).

Pterygoid. A partially exposed denticulated element NMS G 1886.50.50.1 was micro-CT scanned. This revealed a long, narrow plate, broken into two parts, approximately 8 mm long. One surface is partially covered with a band of denticles similar in size to those on the basihyal plates. Unlike the denticles on the pterygoid of *Conchopoma gadiforme* (Heidtke 1986, fig. 3), those on NMS G 1886.50.50.1 vary in size. The largest, lateral denticles, have a diameter up to four times that of the smallest, on the medial side. Extending from the area of the medial denticles is a broad shelf, which probably formed

an overlap area with the parasphenoid. Extending forward from the denticulated area is a second shelf, which probably formed an overlap area with the vomer. The lateral edge of the bone is gently rounded, marking the lateral extent of the palate.

Vomer. The partially exposed denticulated element NMS G 1886.89.49 was also micro-CT scanned. This revealed an irregular-shaped plate, approximately 3 mm long, with broken edges bearing a patch of denticles similar in size to those on the basihyal plate (see description below, Fig. 3e, f). The denticles do not cover the entire surface but are concentrated nearer to one of the longer edges. It is most similar to the vomer of *Conchopoma gadiforme* figured by Schultze (1975, fig. 5) and Heidtke (1986, fig. 3).

Basihyal Plate. Two denticulated elements, NMS G 1885.50.50.2 and NMS G 1885.50.50.4, were micro-CT scanned. This revealed that each is a thin, subcircular plate (Fig. 3e, f), approximately 6 mm (maximum) in diameter. The dorsal surface is covered in denticles of an almost uniform size, approximately twice that of the denticles on the parasphenoid. The plates are very similar to the denticulated, basihyal plates of *Conchopoma gadiforme* (Heidtke 1986, fig. 3).

Remarks. The material from Loanhead shares with *Conchopoma* the characteristic of having denticulated pterygoids, vomers, parasphenoid and basihyal. The denticles were described by Schultze (1975) as small, conical single teeth, but their histology has not been studied and it is not known if they contain petrodentine, like the teeth on lungfish tooth plates. There is nothing unusual or diagnostic about the new material and it cannot be assigned to any of the known species. Thus, it will be left in open nomenclature until more diagnostic specimens have been found.

<div align="center">

Family undesignated
Genus undesignated

</div>

Material. NMS G 1885.50.19.
Description.
Parasphenoid. The parasphenoid NMS G 1885.50.19 (Fig. 3d, g, h) is the only known specimen of this new lungfish. It had been recognised as a different genus during an earlier survey of the collection: a typed label attached to the specimen by an unknown curator reads 'Parasphenoid (not of *Ctenodus* or *Sagenodus*)'. The specimen is preserved in ventral view. It is partially concealed by the matrix anteriorly, and much of the posterior process is missing and is represented by an impression of its dorsal surface. The specimen was micro-CT scanned to reveal details of the dorsal surface and anterior end. This showed that it is incomplete anteriorly.

The parasphenoid was, originally, at least 28 mm long, with a maximum width of 15 mm. The posterior process was 10 mm long and 4.5 mm wide, and the anterior process was at least 3 mm long and 6 mm wide. The corpus is essentially diamond-shaped with gently concave edges anteriorly where it met the pterygoids, and gently convex edges posteriorly. The corpus extends anteriorly as a distinct cultriform process with slightly diverging margins. It forms an angle with the corpus of 130°. Posteriorly, it extends to form a relatively short posterior process forming an angle with the corpus of 137°. The posterior process represents around 30 % of the total length of the parasphenoid. The ventral surface of the corpus is essentially smooth apart from some slight pitting. Denticles are absent. Towards the centre are two raised tubercles that are probably homologous with the midline ridge in *Ctenodus cristatus* (Sharp & Clack 2013, fig. 16B). Posteriorly, part of the ventral surface of the corpus and the incomplete end of the posterior process are damaged. The dorsal surface has a granular appearance in the scan (Fig. 3g), but this is probably an artefact. The left antero-lateral edge is slightly furrowed and probably represents an area of sutural overlap with the left pterygoid. This area is less well defined on the right. On the dorsal surface, the edges of the anterior process continue posteriorly as low ridges that form the anterolateral edge of the suture with the pterygoid. The lateral edges of the posterior process are bevelled and diverge slightly. The dorsal surface of the process supports a distinct midline ridge which, judging from the impression, extends along its length. This ridge has a midline groove along its most posterior part. The lateral edges continue forward as low ridges, mirroring the arrangement on the anterior process.

Remarks. A parasphenoid with an anterior process has not previously been described in Carboniferous lungfish. It does not belong to the well-known taxa from Loanhead, *Ctenodus*, *Sagenodus* or *Uronemus*, and as well as being much too large to be the parasphenoid of *Clackodus*, differences in the shape of the areas of sutural contact on the pterygoids of *Clackodus* and the parasphenoid indicate they do not belong together. An anterior process is present in a number of distantly related Devonian taxa, including *Jarvikia*, *Orlovichthys*, *Rhinodipterus stolbovi* and *Stomiahykus* (Friedman 2007), but its phylogenetic significance is unclear.

NMS G 1885.50.19 exhibits several derived characters that indicate it probably originates from a taxon occupying a crownward position in the Devonian–Carboniferous dipnoan tree. These include: a closed buccohypophyseal foramen; parasphenoid overlapping the palate; a rounded lateral angle of the parasphenoid; the presence of a separate, diamond-shaped corpus; the absence of dental material on the ventral surface; and the presence of a furrow on the dorsal surface.

4. Discussion

4.1. Dipnoan diversity in the late Mississippian

Five lungfish taxa have now been recognised at Loanhead: *Ctenodus interruptus*, *Sagenodus quinquecostatus*, *Uronemus splendens*, *Clackodus angustulus* and *Conchopoma* sp. A sixth is represented by an unnamed parasphenoid. Where known, the dentition is notably different in each (Fig. 4). *Ctenodus* (Fig. 4a) has multiple, almost parallel, tooth ridges with blunt cone-like teeth. *Sagenodus* (Fig. 4e) has up to six radiating tooth ridges with sharp, laterally compressed teeth, attached to bony ridges, producing a tooth plate with deep furrows between the tooth ridges similar to those of extant lungfish. *Uronemus* (Fig. 4c) has modified tooth plates with a very long tooth ridge 1 and short lateral ridges – an arrangement that produces a marginal dentition with an accessory segment of denticles on the lingual edge of tooth ridge 1. *Clackodus* (Fig. 4b) has narrow radiating tooth plates with a heterodont arrangement of teeth on four tooth ridges, and *Conchopoma* (Fig. 4d) lacks tooth plates and, instead, has a large number of denticles on the bones forming the roof and floor of the mouth. A similar level of morphological disparity is also seen in the body size of the lungfish. The largest, *Ctenodus*, had an estimated adult length of 40 cm, while the smallest, *Clackodus*, had an estimated adult length of 5 cm.

This level of lungfish diversity at a single locality is unprecedented in the Carboniferous, and only Gogo in the late Devonian of Australia (Long & Trinajstic 2010, and references therein; Clement 2012) and Celsius Bjerg in the late Famennian, Upper Devonian, of East Greenland (Lehman 1959; Clack *et al*. 2018) can match it. A diverse lungfish fauna has recently been described from sites in the early Carboniferous of the Scottish Midland Valley and Borders
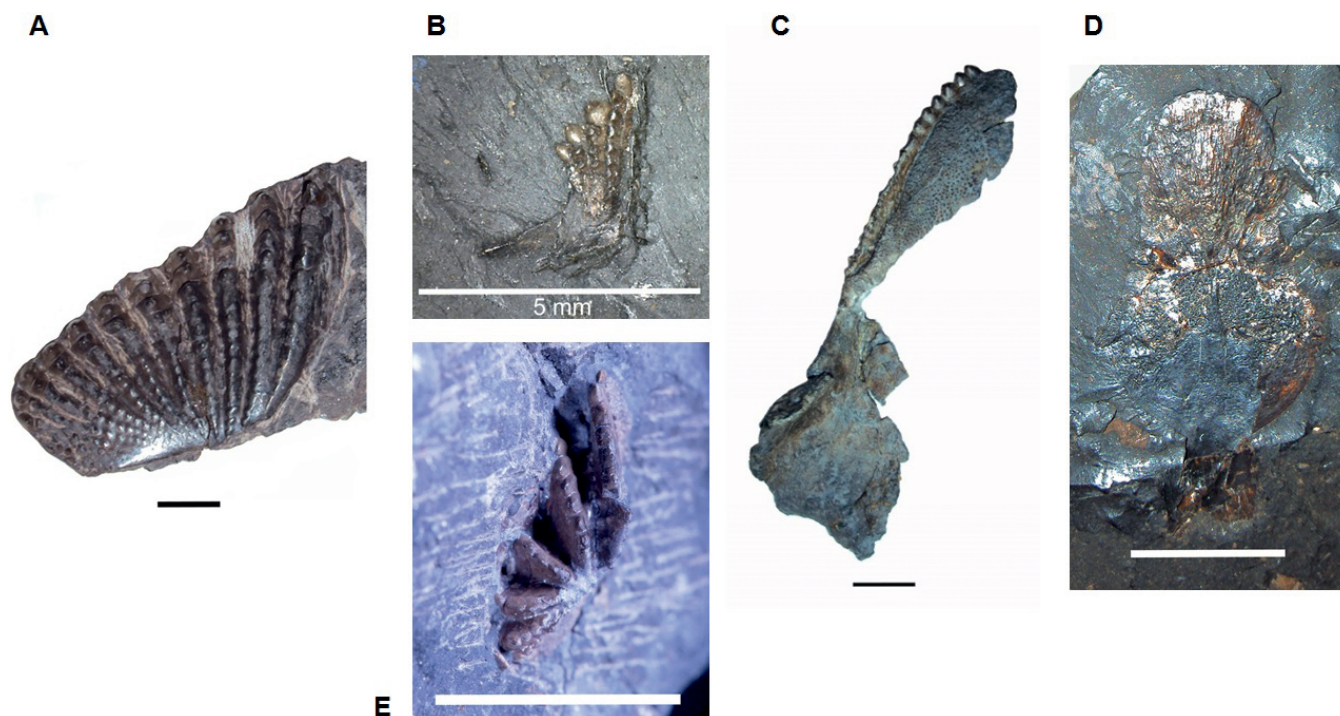
Figure 4 Palatal elements from Loanhead lungfish. (A) *Ctenodus interruptus* right pterygoid tooth plate, NHMUK PVP 11485. (B) *Clackodus angustulus* right pterygoid and tooth plate, NHMUK PVP 11503e. (C) *Uronemus splendens* right pterygoid and tooth plate, NMS G 1976.19.3. (D) *Conchopoma* sp. parasphenoid, NHMUK PVP 11516. (E) *Sagenodus quinquecostatus* right pterygoid tooth plate, NMS G 1993.56.118. Scale bars = 10 mm (A, C–E); 5 mm (B).
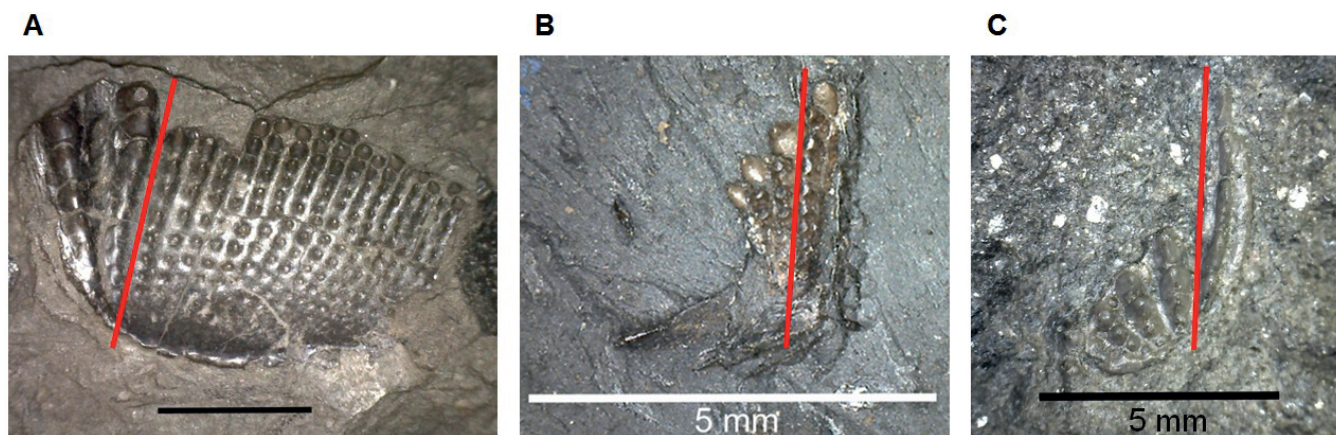

Figure 5 Heterodont tooth plates. (A) *Ctenodus williei* GLS 1312. (B) *Clackodus angustulus* NHMUK PVP 11503e. (C) Unnamed specimen from Burnmouth UMZC 2018.10.9. Red line separates different types of teeth.

(Carpenter *et al.* 2014; Smithson *et al.* 2016). Eight species have so far been identified, with others awaiting description (Challands *et al.* 2015, in press). It has the same size range of fish and a similar variety of tooth plated-forms. Although *Conchopoma* has not been identified, small, denticulated plates have been found at Burnmouth and Cove that may belong to a similar lungfish (Smithson, pers. obs. 2017). However, no more than two taxa have ever been found in the same horizon at any of these Tournaisian sites. This is typical of Carboniferous localities in the UK. *Ctenodus* and *Sagenodus* are commonly found together in the Pennsylvanian (Sharp 2007; Sharp & Clack 2013), and at the other two Serpukhovian sites in eastern Scotland, Dora and Niddrie, only two lungfish taxa have been described (Sharp 2007). Loanhead is very unusual in having at least five.

The large number of lungfish taxa found throughout the Mississippian of Scotland provides further evidence of a

previously unrecorded radiation following the end-Devonian extinction event. Smithson *et al.* (2016) suggested that this may have been in response to gaps in ecospace and the development of new food sources following the extinction event. Little is known about the diet of Palaeozoic lungfish, but the durophagus dentition is usually taken to indicate that food sources were protected by shells, carapaces or scales (e.g., Johanson & Ahlberg 2013). Extant adult lungfish are largely carnivorous, with a varied diet of vertebrate and invertebrate prey; there is some evidence that they may also ingest plant material (Kemp 1987). The tooth plates of *Sagenodus* are most like those of extant lungfish, with blade-like tooth ridges separated by deep furrows; the teeth show little wear. This suggests a diet of relatively soft food items that may have been chewed into smaller pieces before ingestion. In contrast, *Clackodus*, *Ctenodus* and *Uronemus* have tooth plates showing tooth wear. In *Clackodus*, all but the most labial teeth are worn flat, suggesting that

'armoured' food items like ostracods or other crustaceans were processed in the mouth before being swallowed. In *Ctenodus*, the teeth are blunt but not flattened, and there are often pits in the furrows between the tooth ridges, presumably caused during tooth plate occlusion. This suggests a powerful bite that may have been required to deal with the thick carapace or scales protecting their prey. In *Uronemus*, toothed vomers and dentaries are retained. The long first tooth ridge on the pterygoid plate shows wear on the labial side of the posterior teeth. This is matched by similar wear on the lingual side of the first ridge on the prearticular plate, suggesting a sectorial bite, as in the carnassial teeth of carnivorous mammals, for shearing through flesh. *Uronemus* was probably an active predator, with the anterior marginal teeth used to capture prey and the posterior teeth used for chewing. *Conchopoma* lacks teeth and tooth plates. Instead, the roof and floor of the mouth is covered in a shagreen of denticles, which may have helped to hold slippery prey in the mouth before it was swallowed. These different dentitions and feeding strategies hint at a diverse, but unpreserved, invertebrate fauna at Loanhead that matches the rich vertebrate fauna.

A further possibility is that this radiation of lungfish during the early Carboniferous was a response to a move from an essentially marine environment in the Devonian to a coastal floodplain habitat of freshwater and brackish lakes in the Mississippian. Or it may have been due to changes in tooth plate growth, enabling greater variation in dentition (see Section 4.2) and, by extension, diet. Whatever the reason, this shows that lungfish evolution did not slow down significantly among the tooth plated-forms at the end of the Devonian but, *contra* Westoll (1949), continued at a steady rate throughout the Mississippian.

4.2. Tooth plate growth in Carboniferous lungfish
The development and growth of tooth plates in the extant lungfish *Neoceratodus* was described in detail by Kemp (1977). A description of their growth in *Lepidosiren* was given by Bemis (1984) and observations on *Protopterus* were added by Smith (1985). In an elegant study on the dentitions of early lungfish, tooth plate formation in living forms was summarised by Ahlberg *et al.* (2006, pp. 333-34): 'each of the tooth plates starts from a single pioneer tooth on each bone.... After initiation from a pioneer tooth, each of these dentate regions is regulated autonomously as in a modular type of development. However, the pattern of addition and replacement is quite different from that seen in other osteichthyans. The teeth are not cyclically shed through site-specific dentine resorption: they become permanently incorporated into the tooth plate, although the older teeth may eventually be worn away or lost through resorptive remodelling of the mesial margin of the plate. Furthermore, new teeth are not added lingually as in other osteichthyans but always immediately lateral to existing teeth, causing the plate to develop as a set of tooth rows that give it its characteristic shape.' The pattern of teeth on the tooth plates of most lungfish from the Devonian and many from the Carboniferous can readily be explained by comparison with the way tooth plates grow in extant forms, but some, notably from the Mississippian of Scotland, do not appear to have conformed to this pattern.

In a number of Scottish Mississippian lungfish, the teeth on tooth ridge 1, and in one case on both tooth ridge 1 and 2, differ from those on the rest of the tooth plate. In *Ctenodus williei*, a species found at three sites in the Tournaisian of the Scottish Borders (Smithson *et al.* 2016), tooth ridges 1 and 2 of the pterygoid (Fig. 6a) and tooth ridge 1 of the prearticular has up to eight large, labially curved teeth, whilst all the other ridges – 17 on GSL 1312 (Fig. 5a) – have at least 12 small,
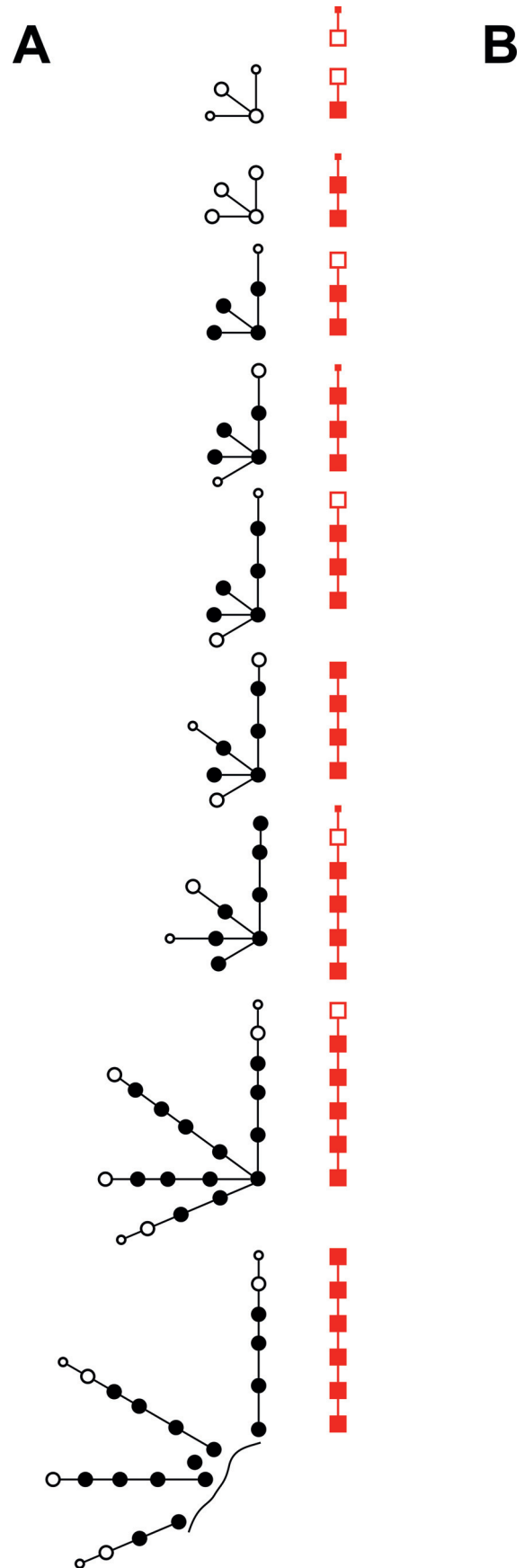

Figure 6 Plan of heterodont tooth plate development assuming the presence of two pioneer teeth. (A) Pattern of development based on a pioneer tooth of the type present in *Neoceratodus* (after Kemp 1977, fig. 5). Small circle, pioneer tooth or new tooth; large circle, newly functional tooth; large solid circle, functional tooth fused to the tooth ridges. (B) Pattern of development based on the second pioneer tooth. Small square, pioneer tooth; large square, newly functional tooth; large solid square, functional tooth fused to the tooth ridge.

cone-shaped teeth with labially curved tips where they were unworn. In *Xylognathus macrustenus*, a species found at two sites in the Scottish Borders (Smithson *et al*. 2016, fig. 5), tooth ridge 1 has up to six large, laterally compressed triangular-shaped teeth in lateral view, with much smaller, cone-shaped teeth on the other three ridges. The younger *Clackodus angustulus* has up to ten small, laterally compressed, recurved teeth when unworn, on tooth ridge 1 and fewer larger, cone-shaped, recurved teeth when unworn, on the other three tooth ridges (Fig. 5b). A further example is seen in an undescribed tooth plate (UMZC 2018.10.9) from the earliest Carboniferous in the Scottish Borders (Fig. 5c). It was collected from a sandy siltstone *c*.30 m above the Devonian/Carboniferous boundary at Burnmouth (Clack *et al*. 2016). This small specimen has extremely laterally compressed teeth on tooth ridge 1 and cone-shaped teeth on the other four ridges. A variation of the heterodonty described above is found in *Uronemus splendens* (Smith *et al*. 1987). Here, all the teeth on the modified tooth plate are similar, but it has an additional segment of denticles on the lingual side of tooth ridge 1 (Fig. 4c; see Smith *et al*. 1987, fig. 20). *Uronemus* is the only known Carboniferous lungfish with a dentition consisting of a mix of tooth plates and denticles. This arrangement is not uncommon among Devonian taxa (Ahlberg *et al*. 2006), but in none are the denticles organised into a discrete area on the pterygoid.

These different heterodont patterns cannot be explained by the manner of tooth plate formation described in *Neoceratodus* (Kemp 1977), nor by presently recognised developmental anomalies in both fossil and living lungfish (Kemp 2003). These anomalies include the division of tooth ridges, fusion of tooth ridges, growth of medial cusps, loss of growth pattern (typically seen in the Carboniferous form *Ctenodus interruptus*) and shortened ridges. None of these processes are manifest in the tooth pattern observed in *Clackodus* or the other heterodont tooth plates from the Tournaisian. The shortening of ridges indicates cessation of growth rather than delayed growth relative to other tooth plates, and in tooth plates where loss of pattern occurs, cusps are still formed but in an irregular way. The cusps in tooth rows 2–4 of *Clackodus* still maintain the typical fan-shape from the point of their origin, indicating that form loss has not occurred.

Instead, the simplest explanation is that the growth was based around two pioneer teeth on each plate. One pioneer tooth initiated the development and growth of tooth ridge 1 (and tooth ridge 2 on the pterygoid of taxa like *Ctenodus williei*), whilst the second pioneer tooth initiated the development and growth of the rest of the tooth plate (Fig. 6). In this model, the second pioneer tooth is probably equivalent to the single pioneer tooth in *Neoceratodus*, producing a number of tooth ridges bearing similar teeth (Fig. 6a): the pioneer tooth initiating the development of tooth ridge 1 is new (Fig. 6b). These examples also suggest that the rate of growth of tooth ridge 1 is independent of that on the other ridges. In *Clackodus*, growth rate appears to have been quicker on tooth ridge 1, producing a longer row of smaller teeth. In *C. williei*, the growth rate on the first rows was slower, producing a smaller number of larger teeth. In the undescribed specimen from Burnmouth (UMZC 2018.10.9), the rate of growth appears to have been similar in tooth ridges 1 and 2, producing the same number of teeth on each ridge.

Though still not completely understood, the genetic and molecular mechanism behind dipnoan tooth plate formation has been demonstrated to be homologous with other osteichthyans (Smith *et al*. 2009) with the initial development of a single tooth primordium (pioneer tooth of Ahlberg *et al*. 2006). Smith *et al*. (2009) demonstrated that tooth induction (i.e., the development of the pioneer tooth) in *Neoceratodus* was controlled by the timing and location of expression of the

Sonic hedgehog (*Shh*) and *pitx* genes, as it is in other bony fish. In the trout *Oncorhynchus mykiss*, the *pitx2* gene was previously found to be responsible for commissioning tooth sites before actual induction of the tooth germ occurred (Fraser *et al*. 2006). In *Neoceratodus*, the expression of *pitx2* is coincident with the regions involved in the earliest stages of tooth induction. In these regions, *Shh* was shown to be expressed at loci of individual tooth induction. The sequential addition model of Smith (2003) proposes reiterative initiation of the original single tooth primordium in each jaw quadrant to produce the typical left–right pattern from the original medial tooth germ. Under this model, with the presence of two pioneer teeth, the resultant tooth pattern would be anticipated to be two separate regions of radial tooth growth on one individual tooth plate. Clearly this is not the case in *Clackodus*. However, whereas the pterygoid and prearticular tooth rows grow in a radial pattern, vomerine teeth are restricted to forming just one row (Smith 2003; Smith & Johanson 2010). Therefore, it seems likely that under this model, the first tooth row in *Clackodus* grows by a mechanism typical of the marginal dentitions, whereas the second–fourth rows follow the typical dipnoan pattern. Superficially, the first tooth row of *Clackodus* does indeed resemble the vomerine tooth plates of, for example, *Andreyevichthys* (Smith & Krupina 2001).

An alternative explanation may be provided by comparison with a condition seen in some mice. Zhang *et al*. (2009) showed that a mutant variant of the transcription factor odd-skipped related (*Osr2*) produced an expanded ontogenetic field that resulted in additional tooth rows. Smith & Johanson (2010) speculated that a molecular mechanism involving the regular expression of *Osr2*, as seen in the single-row dentitions of mammals, may have been responsible for the single-row marginal dentitions found in lungfishes. As such, the appearance of a second independent single-tooth row from a second tooth primordium, as in *Clackodus*, could possibly be a manifestation of such a mutant transcription factor similar to that used by Zhang *et al*. (2009), expanding the ontogenetic field and then moderating tooth growth.

5. Conclusions

The late Mississippian lungfish fauna of Scotland was diverse, with at least five different taxa represented in the Burghlee or Rumbles Ironstone at Loanhead. This discovery is consistent with recent analysis, which has shown that the evolution of lungfish did not slow down significantly among tooth plated-forms at the end of the Devonian but, *contra* Westoll (1949), continued at a steady rate throughout the Mississippian. This may, in part, have been due to the development of heterodonty in some lungfish, enabling teeth of different shapes and sizes to develop on the same tooth plate. This heterodonty may have become possible following the 'duplication' of part of the developmental mechanism, with two pioneer teeth or tooth primordia present on each tooth plate.

6. Acknowledgements

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