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LUNGFISH DIVERSITY IN ROMER'S GAP: REACTION TO THE END-DEVONIAN EXTINCTION

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Abstract: Romer's Gap, the interval following the end-Devonian extinction event, has been described as a post-extinction trough for vertebrates. It is a time roughly equivalent to the Tournaisian stage of the early Carboniferous and has been characterized by a lull in diversity of survivors. Lungfish typified this description. One species was known from one locality. Recently, a diverse collection of lungfish tooth plates, representing seven new forms, was recovered from new Tournaisian vertebrate localities in northern Britain. They display a range of previously unknown morphologies, with tooth shape and wear patterns not seen in other post-Devonian forms. A comparison of tooth ridge number and tooth ridge angle in lungfishes from the Famennian, Tournaisian and Visean reveals marked differences between late Devonian and early Carboniferous taxa. The most common tooth plate shape in the Famennian is absent from our sample of Tournaisian taxa. Two completely new shapes have evolved, one with a relatively low tooth ridge angle, no greater than 40°, in which most of the tooth ridges are essentially parallel, and the other with a much higher tooth ridge angle of up to 180° where the tooth ridges are highly divergent. This high level of morphological diversity over a narrow time period suggests that, following the end-Devonian extinction, gaps in eco-space left by the extinction of major groups of fishes were exploited by a previously unrecorded radiation of lungfishes. Whilst taxonomic diversity of lungfishes declined following the end-Devonian extinction, recovery and diversification among tooth-plated forms was rapid, and morphological disparity among these forms subsequently increased. Contrary to previous assumptions, morphological disparity among lungfish did not decline until much later in the Carboniferous.

Key words: Tournaisian, Ballagan Formation, tooth plates, diversity, morphology.

IN the Devonian period, lungfishes were numerous, varied and widely dispersed (Clack *et al.* 2009). Following the Hangenberg event (Sallan and Coates 2010), their numbers and diversity seemingly declined sharply. Becoming restricted to freshwater environments, by the late Carboniferous they had achieved a body form and habit little changed to the present day (Westoll 1949; Lloyd *et al.* 2011). The remarkably varied dentition of Devonian taxa (Ahlberg *et al.* 2006) was largely reduced to one based on tooth plates. Only six genera have been described from the entire early Carboniferous (Mississippian) (Lloyd *et al.* 2011), and by the late Carboniferous, most lungfish species can be placed in one of the two genera: *Ctenodus* with multiple, approximately parallel, rows of teeth or *Sagenodus* with no more than seven, radially arranged, rows of teeth.

Romer's Gap, roughly equivalent to the Tournaisian stage, has been described as a postextinction trough for vertebrates (Sallan and Coates 2010) characterized by a lull in both diversity and abundance of survivors. Accordingly, only four taxa of lungfish have previously been described from the Tournaisian (Thomson 1965; Vorobyeva 1972; Long and Campbell 1985; Carpenter *et al.* 2014). However, of these, only two are securely dated as Tournaisian: *Ctenodus romeri* from the Ballagan Formation near Coldstream, Scotland (Thomson 1965), and *Sagenodus*-like material from the Ballagan Formation on the Isle of Bute, Scotland (Carpenter *et al.* 2014). The lungfish material from East Siberia, Russia, including the genus *Parasagenodus* (Vorobyeva 1972), was dated as undifferentiated 'lower Carboniferous' (Vorobyeva *et al.* 1999). It may be Tournaisian, but the dating of this locality is unconstrained: it could be anything between Famennian and (undifferentiated) lower Carboniferous (O. Lebedev pers. comm.). Similarly, the age of *Delatitia* (Long and Campbell 1985) from Victoria, Australia, is also under review. Until recently, the upper section of the Mansfield Group where it was collected was considered to be Tournaisian in age (Warren *et al.* 2000). However, this cannot be established with certainty and it is more likely to be Visean (J. Long pers. comm.). Thus, only two indisputably Tournaisian taxa remain.

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New forms from localities recently discovered in the Scottish Borders (Smithson *et al.* 2012) reveal previously unrecorded lungfish diversity. Collected mainly from the Tweed Basin, an area of only *c.* 600 km^2, and in a relatively short time interval (see below Materials and Methods), the new materials nevertheless exhibit a variety of novel tooth plate morphologies that we name, diagnose and describe to emphasize their distinctiveness. Their varied patterns of occlusion and wear imply growth patterns, feeding mechanisms and prey items that differed from those exploited by earlier and later forms.

We further suggest some new criteria for diagnosing lungfish tooth plate genera, for potential use in diversity and disparity studies. As a result of our research, the genus *Ctenodus* has been revised.

MATERIAL AND METHODS

All specimens are from the Ballagan Formation: those from Willie's Hole, Burnmouth, Barrow Scar and Coldstream are from the claviger-macra (CM) palynozone, dated as 348–346.6 Ma (Gradstein *et al.* 2004; Scrutton and Turner 2004). The others are from undifferentiated Tournaisian (Fig. 1). The specimens were prepared mechanically with a mounted needle under a binocular microscope. Paraloid B72 was used to repair breaks. The photographs were taken with a Canon EOS 5D Mk2 digital camera fitted with a Canon Macro EF 100-mm lens.

The results presented below are based on the study of 21 tooth plates from eight localities (see Appendix). Of these, 14 are pterygoid tooth plates and seven are prearticular tooth plates. Only four of them have been described previously (Thomson 1965).

The anatomical terminology proposed by Ahlberg *et al.* (2006) to separate different elements of the lungfish dentition is used in the descriptions. A tooth plate consists of a bony plate to which individual teeth attach during ontogeny. These teeth are arranged in rows to form tooth ridges (Fig. 2C), and new teeth are added to the labial end of each ridge (Fig. 2C). No denticles have been observed on any of the specimens from the Ballagan Formation. Two distinct tooth morphologies were recognized by Thomson (1965): laterally compressed teeth with their longest axis along the direction of the tooth ridge and longitudinally compressed teeth with their longest axis at right angles to the direction of the tooth ridge. This terminology is also used in the description of the tooth plates. The tooth ridges are numbered starting from tooth ridge 1, the first and most anterior/lingual tooth ridge. The angle between the first and the last most posterior tooth ridges, here called the tooth ridge angle, was measured from photographs of the tooth plates (Fig. 2A–B). This angle is known to increase during ontogeny as more tooth ridges are added to the growing tooth plate (Kemp 1977). The tooth ridge angle of the pterygoid tooth plates of Famennian and Visean taxa was also measured and compared with those from the Ballagan Formation (see Discussion below).

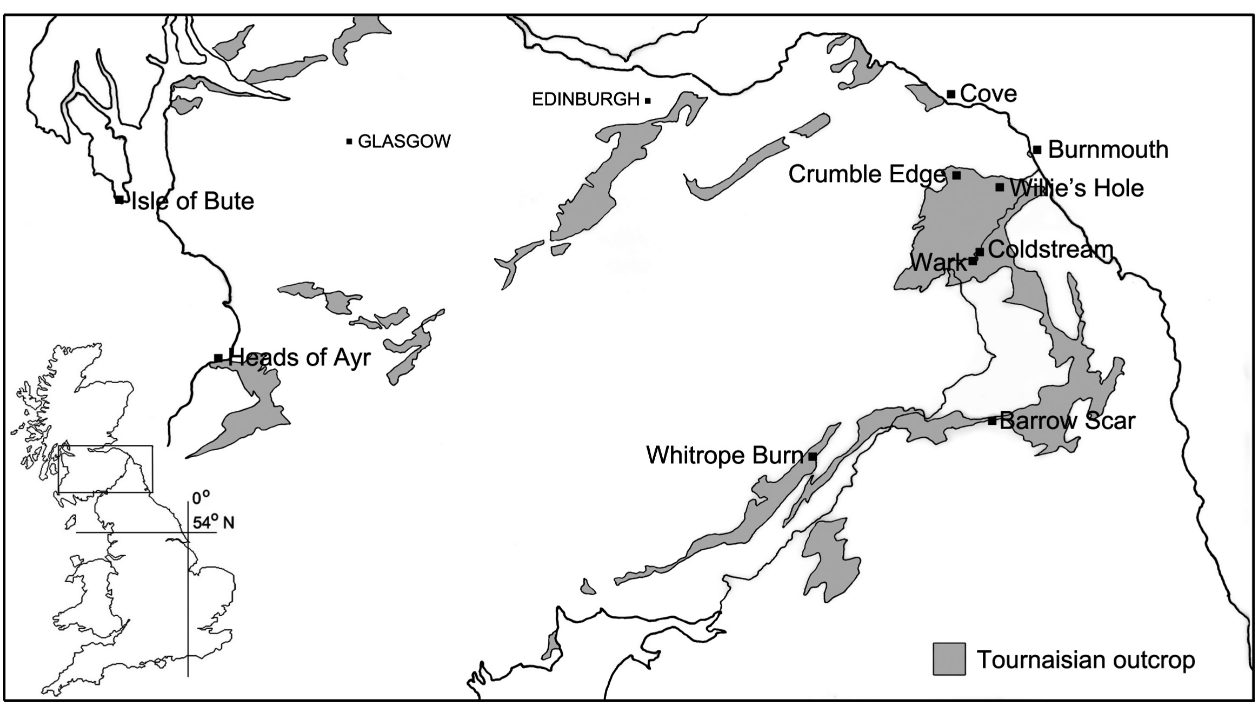

FIG. 1. Map of northern Britain showing Tournaisian lungfish localities.

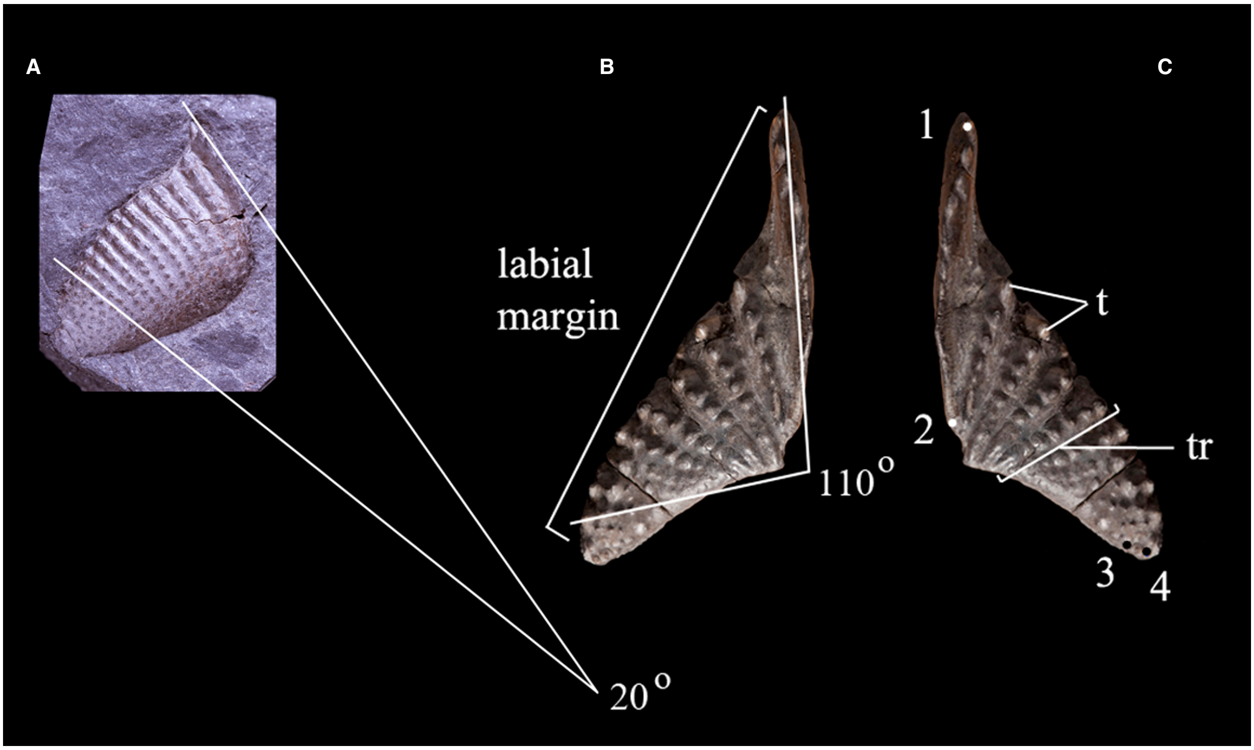

FIG. 2. Key features of lungfish tooth plates. A–B, the tooth ridge angle; A, prearticular tooth plate of *Ctenodus williei* sp. nov. UMZC 2011.7.5; B, prearticular tooth plate of *Occludus romeri* (Thomson, 1965) NMS G 1896.81.43. C, landmarks 1–4 used in the principal component analysis. Position of PCA landmarks on prearticular tooth plate of *Occludus romeri* (Thomson, 1965) NMS G 1896.81.43 reversed. Landmark 1 positioned at last tooth on tooth ridge 1; landmark 2 positioned at first tooth on tooth ridge 1; landmark 3 positioned at first tooth on last tooth ridge; and landmark 4 positioned at last tooth on last tooth row. *Abbreviations*: t, tooth; tr, tooth ridge. Colour online.

Principal component analysis was undertaken on eight tooth plates to analyse the pattern of disparity between them (see Smithson *et al.* 2015 for details). The eight tooth plates were photographed with accompanying scale bars. All tooth plates were positioned similarly so that the occlusal surface was perpendicular to the camera sightline. Some tooth plates were easier to photograph in different orientations due to lighting and matrix constraints, and so the resultant jpeg images were re-orientated in Adobe Photoshop v11.0.2 to a uniform orientation. Four landmarks were chosen (Fig. 2C) that were visible on every specimen and marked onto the jpeg images for repeatability of analysis. All four landmarks were defined by the lingual and labial ends of tooth rows and so were regarded as type 2 landmarks under the classification system of Bookstein (1991). A landmark matrix was built in tpsUtil v1.58 and tpsDig2 v2.17 (http://life.bio.sunysb.edu/morph/). The output.tps file was read into R v3.0.3 (R programming language). (See Smithson *et al.* 2015 for further details.)

Institutional abbreviations. GSL, British Geological Survey; NMS, National Museums of Scotland; UMZC, University Museum of Zoology, Cambridge.

SYSTEMATIC PALAEONTOLOGY

This published work and the nomenclatural act it contains have been registered in Zoobank: http://www.zoobank.org/ED35FA75-3AD9-492F-975F-D1D27D3542DB

OSTEICHTHYES Huxley, 1880
SARCOPTERYGII Romer, 1955
DIPNOMORPHA Ahlberg, 1991
DIPNOI Müller, 1845
Family undesignated

Genus CTENODUS Agassiz, 1838

Type species. *Ctenodus cristatus* Agassiz 1838.

Diagnosis. Emended diagnosis after Sharp and Clack (2013). Tooth plates irregularly ovate or elliptical in form. 6–23 approximately parallel tooth ridges. Tooth ridge angle less than 40°. Pterygoid tooth plate concave, prearticular tooth plate convex.

Stratigraphic range. Tournaisian–Bolsovian (= Westphalian C, Moscovian).

Remarks. Details of the missing holotype and the neotype, and their respective localities and horizons, are given in Sharp and Clack (2013).

Ctenodus williei sp. nov.
Figure 3A–B

LSID. urn:lsid:zoobank.org:act:F2F32CE4-E8C2-4609-8766-D4A471744DA0

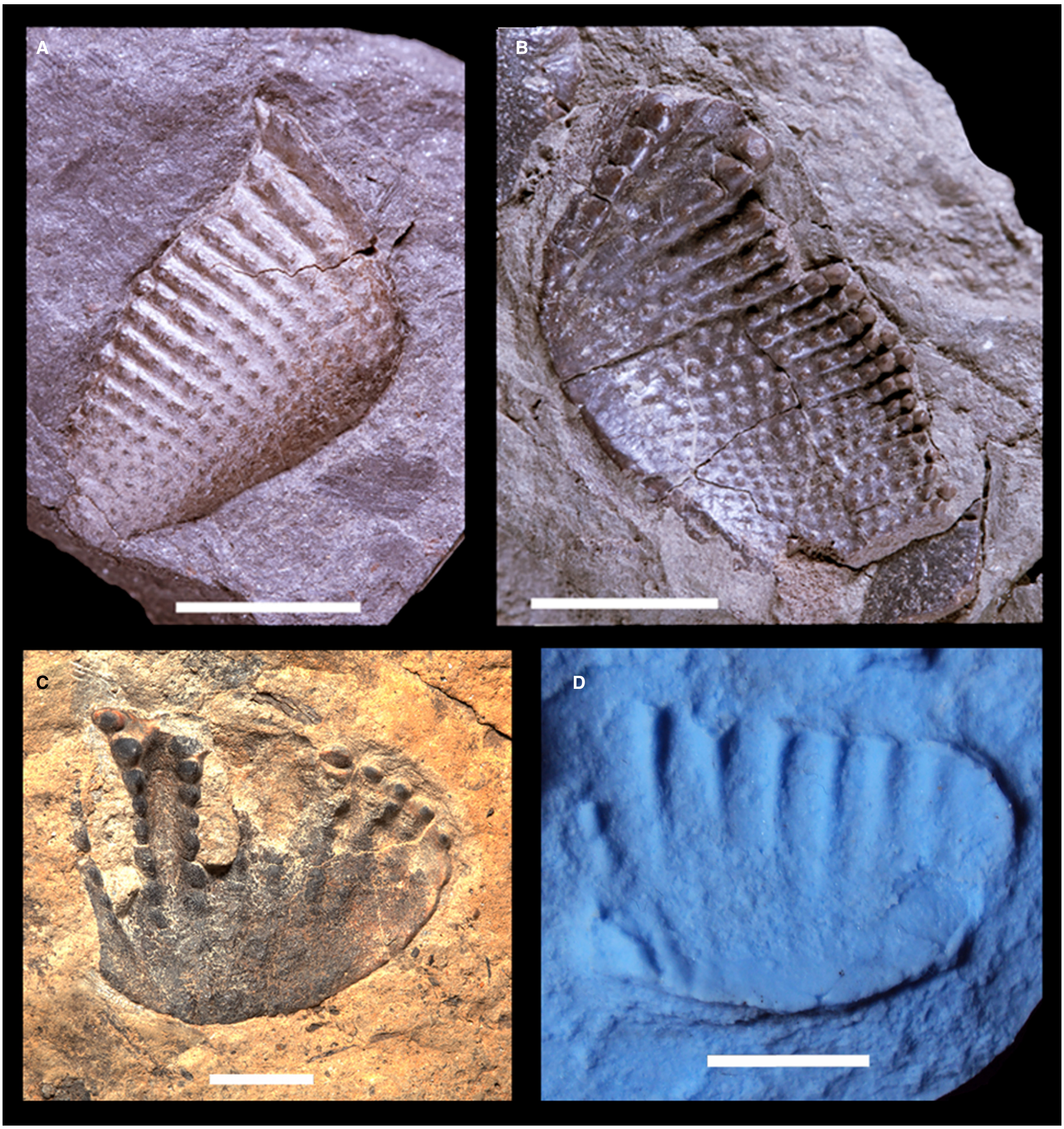

FIG. 3. Lungfish tooth plates from Romer's Gap in occlusal view. A–B, *Ctenodus williei* sp. nov.; A, UMZC 2011.7.5, right prearticular plate from Willie's Hole reversed; B, GSL 1312, right pterygoid plate from Wark. C, *C. whitropei* sp. nov. NMS G 2014.2.1, left pterygoid plate from Whitrope Burn. D, *C. roberti* sp. nov. Silastomer peel of UMZC 2014.10, left pterygoid plate from Heads of Ayr. All scale bars represent 10 mm. Colour online.

Derivation of name. From Willie's Hole, the type locality.

Holotype. UMZC 2011.7.5 right prearticular tooth plate.

Material. UMZC 20011.7.6; UMZC 2104.4.1; GSL 1312.

Type locality and horizon. Bed 2, Willie's Hole, Whiteadder Water, nr Chirnside, Scottish Borders, Scotland; Ordnance Survey grid reference NT 878 547.

Diagnosis. Species of *Ctenodus* with oval tooth plates. Length to width ratio 1.67:1. At least 18 parallel tooth ridges. Pterygoid tooth ridge angle *c.* 40°, prearticular tooth ridge angle *c.* 20°. Pterygoid tooth ridges 1 and 2 and prearticular tooth ridge 1 bear 8 large longitudinally compressed, labially curved teeth. Other tooth ridges bear at least 12 cone-shaped teeth with labially curved tips when unworn.

Description. The tooth plates are approximately oval and up to 25 mm long and 15 mm wide, giving a length to width ratio of approximately 1.67:1 (Fig. 3A–B). They have at least 18 parallel tooth ridges. On the pterygoid plate, the tooth ridge angle is approximately 40°. Most ridges bear at least 12 cone-shaped teeth which have a labially curved tip when unworn. The exceptions are tooth ridges 1 and 2 on the pterygoid and tooth ridge 1 on the prearticular tooth plates which have eight larger teeth. In these anterior tooth ridges, the large, longitudinally compressed teeth also show labial curvature.

All the teeth are worn apart from the newest teeth on the labial edge of each ridge. The labially curved tips of the unworn teeth are most clearly seen in the last tooth on ridges 3 and 13 of the pterygoid plate GSL 1312. On the prearticular plate UMZC 2011.7.5, all the teeth on each ridge are fused. On the pterygoid plates, the teeth in ridge 1 and the three most recent teeth on ridge 2 are unfused. The most recently added teeth on the labial edge of UMZC 2011.7.6 are also unfused. Worn teeth lack enamel and contain petrodentine cores. The area of greatest wear is along the lingual edge of the tooth plates, where the teeth have been completely worn away leaving slight swellings in the dentine. Tooth ridge 2 on the pterygoid plate lies parallel to those behind, but ridge 1 is angled more anteriorly, creating a groove between the two ridges that widens labially. The tooth plates were probably aligned with ridge 1 orientated at 45° to the anterior–posterior axis as in *C. interruptus* (Sharp and Clack 2013, figure 15) (Fig. 4A). During jaw closure, ridge 1 on the prearticular plate slotted into the groove between ridges 1 and 2 on the pterygoid

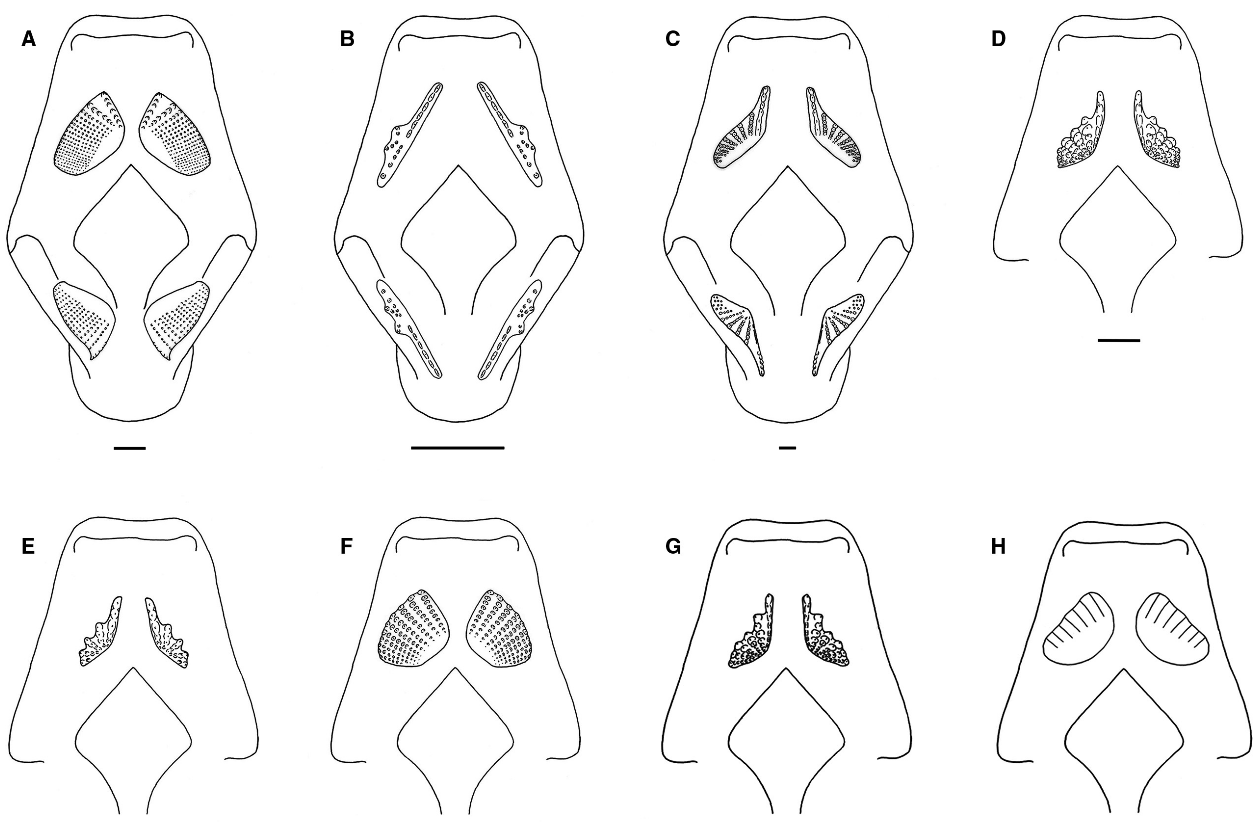

FIG. 4. Reconstructed dentitions of lungfish from Romer's Gap. A–C, pterygoid and prearticular tooth plates in occlusal view. D–H, pterygoid tooth plates in occlusal view. A, *Ctenodus williei* sp. nov. B, *Xylognathus macrustenus* gen. et sp. nov. C, *Occludus romeri* (Thomson, 1965). D, *Ballagadus rossi* gen. et sp. nov. E, *Coccovedus celatus* gen. et sp. nov. F, *Ctenodus whitropei* sp. nov. G, *B. caustrimi* sp. nov. H, *Ctenodus roberti* sp. nov. All scale bars represent 10 mm.

tooth plate as in *Occludus romeri* gen. nov. (see below). However, unlike *O. romeri* there is no evidence that a similar occlusion took place in the rows behind. Wear is on the apex of the teeth rather than laterally and there is no evidence of the wear at the base of the groove between tooth ridges seen in *O. romeri,* apart from in the grooves between tooth ridges 1 and 2: teeth on the remaining ridges may have occluded apically. The pterygoid plate is concave and prearticular plate is convex.

Remarks. *C. williei* has been found at three localities in the Tweed Basin: Willie's Hole and Crumble Edge on Whiteadder Water and Wark on the River Tweed.

Stratigraphical range. Ballagan Formation, Tournaisian.

Ctenodus whitropei sp. nov.
Figure 3C

LSID. urn:lsid:zoobank.org:act:648DDBDC-9E28-4B12-B5B6-2A66A461392F

Derivation of name. From Whitrope Burn, the type locality.

Type material. NMS G 2014.2.1 left pterygoid tooth plate.

Material. The holotype is the only known specimen.

Type locality and horizon. Bed 7, Whitrope Burn, near Hermitage, Liddesdale, Scottish Borders, Scotland; Ordnance Survey grid reference NY 507 965.

Diagnosis. Species of *Ctenodus* with oval tooth plates. Length to width ratio 1.4:1. 10 approximately parallel tooth ridges. Pterygoid tooth ridge angle *c.* 30°. Large, laterally compressed and labially curved teeth.

Description. The concave pterygoid tooth plate is approximately oval-shaped, at least 35 mm long and 25 mm wide, giving a length to width ratio of approximately 1.4:1 (Fig. 3C). It is the largest tooth plate found so far in the Ballagan Formation of northern Britain. It is quite badly worn and many of the teeth are missing, but sufficient remains to enable us to distinguish it from those described above.

Superficially, it resembles the pterygoid tooth plate of *C. interruptus* (Sharp and Clack 2013, fig. 6), although the grooves between the tooth ridges are very much deeper. It has 10 almost parallel tooth ridges. The tooth ridge angle is approximately 30°. Ridge 1 is worn and none of the teeth are preserved, but teeth are present on ridges 2 and 3, and around the labial edge of the tooth plate. They are laterally compressed and appear to have had lingually curved tips when unworn. There were probably at least 10 teeth on ridges 2 and 3. The ridges are separated from each other by a deep groove. This probably received ridge 2 from the prearticular tooth plate, although it bears none of the wear hollows seen in *Coccovedus celarus* and in *Occludus romeri*. The tooth plates were probably aligned as in *C. williei* (Fig. 4F).

Stratigraphical range. Ballagan Formation, Tournaisian.

Ctenodus roberti sp. nov.
Figure 3D

LSID. urn:lsid:zoobank.org:act:9C077249-DE48-4F25-91EF-B9B899E9B69F

Derivation of name. In honour of Robert Clack, the collector of the holotype.

Type material. UMZC 2014.10 left pterygoid tooth plate preserved as a natural mould.

Material. The holotype is the only known specimen.

Type locality and horizon. Loose block from Ballagan Formation, foreshore north of Heads of Ayr, Ayr, Ayrshire, Scotland.

Diagnosis. Species of *Ctenodus* with oval tooth plates. Length to width ratio 1.6:1. Seven parallel tooth ridges. Pterygoid tooth ridge angle *c.* 8°.

Description. The specimen is preserved as a natural mould in fine sandstone, and the description is based on a silicone rubber cast. The concave pterygoid tooth plate is approximately oval-shaped, at least 28 mm long and 18 mm wide, giving a length to width ratio of approximately 1.6:1 (Fig. 3D). Six complete tooth ridges are preserved. A seventh ridge, ridge 1, is incomplete. The tooth ridges are arranged more or less in parallel, and the tooth ridge angle is approximately 8°. None of the tooth ridges bear individual teeth. Instead, each tooth ridge extends labially from the centre of the tooth plate as a gently rounded parallel-sided crest. Each ridge fades out mesially so that the lingual half of the tooth plate appears smooth. It is unclear whether the absence of teeth on the tooth ridges and the smooth appearance of the lingual half of the tooth plate is a preservational artefact or represents the original morphology.

Remarks. Among the Ballagan tooth plates, *C. roberti* most closely resembles *C. whitropei*. It is concave, oval-shaped and with few tooth ridges. However, *C. roberti* has a greater length to width ratio, a much smaller tooth ridge angle and fewer tooth ridges, and teeth are clearly present in *C. whitropei*. In the apparent absence of teeth, *C. roberti* appears to resemble the dentine-plated Upper Devonian taxa, *Chirodipterus australis* (Miles 1977) and *Sunwapta grandiceps* (Thomson 1967), but the lack of preserved material precludes a direct comparison.

Stratigraphical range. Ballagan Formation, Tournaisian.

Family undesignated

Genus XYLOGNATHUS nov.

LSID. urn:lsid:zoobank.org:act:DDFDC0BD-71B6-495A-904A-91EC9126B807

Derivation of name. From the Greek ξύλον *xýlon* wood and γνάθος *gnathus* jaw. In honour and memory of Stanley Wood who discovered the material at Burnmouth and Broom House, near Crumble Edge.

Type species. *Xylognathus macrustenus* sp. nov.

Diagnosis. Narrow, elongate tooth plates, with a length to width ratio of 3.5:1. Four radiating tooth ridges. Tooth ridge 1 with up to 6 large laterally compressed teeth, almost three times larger than teeth on tooth ridges 2–4. The teeth on ridges 2–4 are simple small cones, arranged on successive rows in a pattern of 3, 4 and 5, respectively. Pterygoid tooth ridge angle *c.* 180°, prearticular tooth ridge angle *c.* 165°. The teeth are fused and show little wear. Retained plesiomorphic features: heterocercal tail, separate anal and dorsal fins, and a stalked parasphenoid.

Xylognathus macrustenus sp. nov.
Figure 5

LSID. urn:lsid:zoobank.org:act:0D3B840F-864C-42C6-BD07-AB1C2CEC1043

Derivation of name. From the Greek μακρύς *macrus* long and στενός *stenos* narrow referring to the long and narrow tooth plates.

Type material. UMZC 2014.1.4a, b. Three partial skeletons in part and counterpart.

Material. UMZC 2014.1.3a, b, c, UMZC 2014.1.4a, b, UMZC 2014.1.5, NMS G. 2015.14.1, NMS G. 2015.14.2.

Type locality and horizon. Grey mudstone lens immediately above sandstone 6, Burnmouth, Scottish Borders, Scotland. (See Scrutton and Turner (2004) for horizon details.)

Diagnosis. As for genus.

Description. This taxon is represented by at least 12 incomplete whole body fossils from Burnmouth (Smithson *et al.* 2012) and two tooth plates from Broom House, near Crumble Edge. The skulls are all badly crushed, but four preserve pterygoid and prearticular tooth plates. The plates are up to 13 mm long and 3.5 mm wide, with a length to width ratio of approximately 3.5:1 (Fig. 5). They have four radiating ridges. Tooth ridge 1 has six large teeth, strongly compressed laterally, and almost three times larger than teeth on tooth ridges 2–4. The teeth on ridges 2–4 are simple small cones, arranged in successive rows in a pattern of 3, 4 and 5, respectively. The angle between tooth ridges on the pterygoid plate is almost 180°, and on the prearticular plate, about 165°. On the pterygoid plate, ridge 4 is aligned immediately behind ridge 1. On the prearticular plate, it is offset laterally. The teeth are fused and show little wear. Even the smallest first teeth in each ridge are preserved. In none is petrodentine visible.

Judging by UMZC 2014.1.3a, the tooth plates were probably aligned with ridges 1 and 4 parallel to the jaw margin (see Fig. 4B). During jaw closure, the lingual surface of ridge 1 on the prearticular closed against the labial surface of ridge 1 on the pterygoid. This was repeated for ridge 2. On ridge 3, the opposite occurs and the labial surface of the prearticular ridge 3 closed against the lingual surface of ridge 3 on the pterygoid. Unexpectedly, this pattern of closure is not repeated for tooth ridge 4: because ridge 4 on the prearticular is offset laterally, the lingual surface of this tooth ridge closed against the labial surface of the pterygoid tooth ridge. This arrangement ensures that the two longest ridges 1 and 4 on the prearticular bite outside ridges 1 and 4 on the pterygoid, essentially creating the equivalent of an overbite in mammals. A similar arrangement has been described in the slightly younger lungfish *Uronemus splendens* (Smith *et al.* 1987), which has a much extended tooth ridge 1 but lacks the equivalent of tooth ridge 4 found in *Xylognathus*. All individuals of *Xylognathus* are small (up to about 180 mm snout-to-vent length).

Stratigraphical range. Ballagan Formation, Tournaisian.

Family undesignated

Genus BALLAGADUS nov.

LSID. urn:lsid:zoobank.org:act:F938B038-E206-43B8-86EF-1906731A5394

Derivation of name. From the Ballagan Formation and the Greek ὀδούς *odoús* tooth.

Type species. *Ballagadus rossi* sp. nov.

Diagnosis. Triangular-shaped tooth plates with up to 7 tooth ridges radiating from a point near the posterior end of the lingual edge. Tooth ridge angle between 100° and 120°. Laterally compressed teeth on tooth ridge 1, longitudinally compressed teeth on remaining tooth ridges.

Ballagadus rossi sp. nov.
Figure 6C

LSID. urn:lsid:zoobank.org:act:FD19B7CE-6CAA-4678-9EDE-930D002809DA

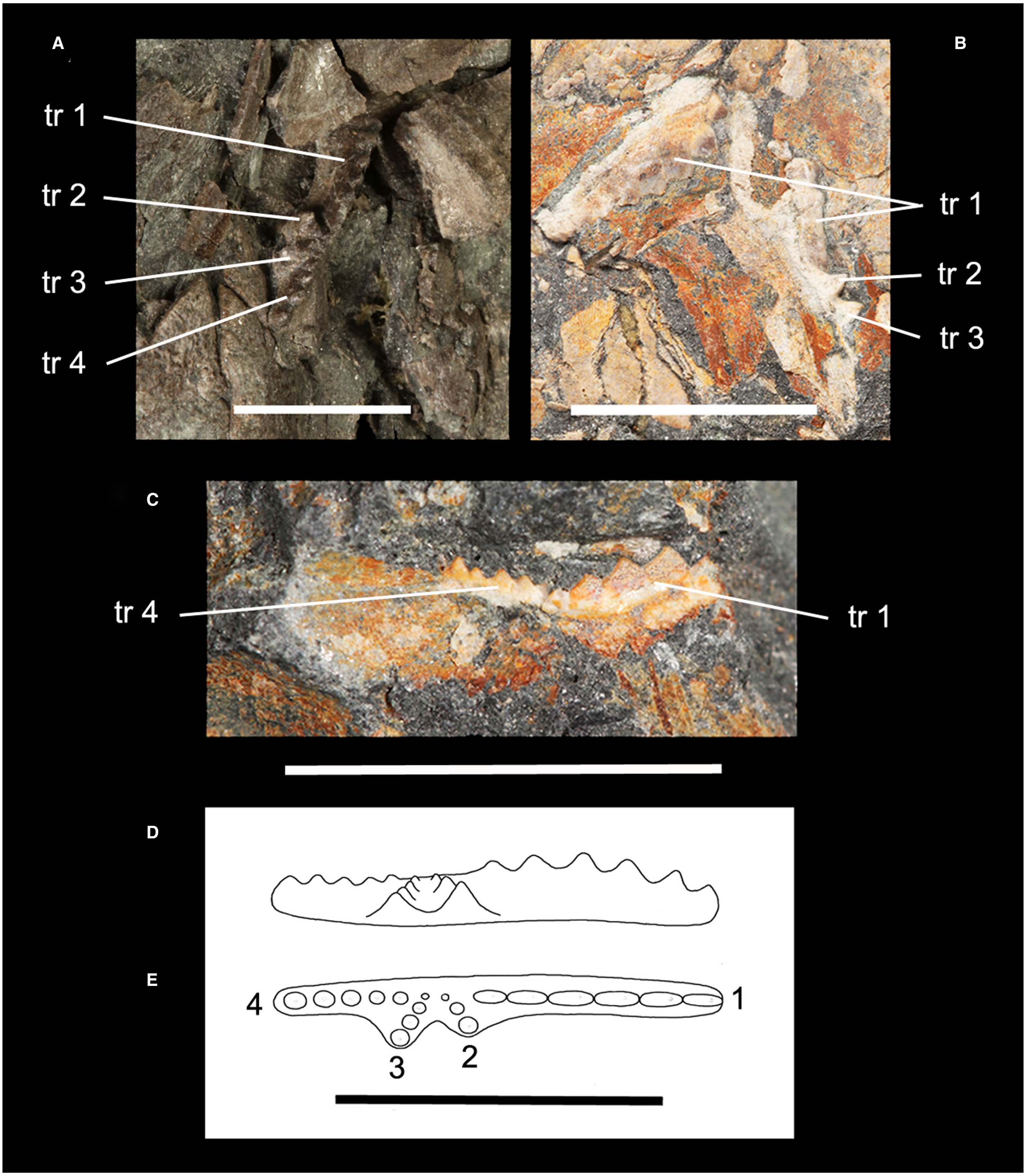

FIG. 5. Lungfish tooth plates from Romer's Gap; *Xylognathus macrustenus* gen. et sp. nov. from Burnmouth. A, UMZC 2014.1.3a, occlusal view. B, UMZC 2014.1.4a, labial view. C, UMZC 2014.1.5, lingual view. D–E outline restorations of left pterygoid tooth plate; D, labial view; E, occlusal view, with numbered tooth ridges. *Abbreviation*: tr, tooth ridge. Scale bars represent 10 mm. Colour online.

Derivation of name. From Ross, the most southerly of the four communities making up Lower Burnmouth and closest to the type locality.

Type material. UMZC 2014.1.1 left pterygoid tooth plate.

Material. UMZC 2014.1.2.

Type locality and horizon. Dark grey mudstone, midway between sandstones 5 and 6, Burnmouth, Scottish Borders, Scotland. (See Scrutton and Turner (2004) for horizon details.)

FIG. 6. Lungfish tooth plates from Romer's Gap, occlusal view. A, *Ballagadus caustrimi* sp. nov. NMS G 1896.81.45, left pterygoid plate from Coldstream. B, *Coccovedus celatus* gen. et sp. nov. UMZC 2014.2.1, right pterygoid plate from River Coquet. C, *Ballagadus rossi* gen. et sp. nov. UMZC 2014.1.1, left pterygoid plate from Burnmouth. D–E, *Occludus romeri* (Thomson, 1965); D, NMS G 1896.81.44, left prearticular plate from Coldstream; E, NMS G 2012.39.7, left pterygoid plate from Willie's Hole. All scale bars represent 10 mm. Colour online.

Diagnosis. Tooth plates with a length to width ratio of c 2.4:1. Seven radiating tooth ridges. Pterygoid tooth ridge angle *c.* 120°.

Description. This taxon is based on two pterygoid tooth plates. They are approximately triangular-shaped, and the most complete specimen, UMZC 2014.1.1 (Fig. 6C), is 18 mm long and 7.5 mm wide, with a length to width ratio of approximately 2.4:1. There are seven tooth ridges radiating from a point near the posterior end of the lingual edge. The tooth ridge angle is approximately 120°. Ridge 1 has seven laterally compressed teeth. The teeth on ridges 2–5 are longitudinally compressed. Ridges 2 and 3 have seven teeth, ridge 4 has six, and ridge 5 has eight. There are a number of small teeth beyond ridge 5 that may be the beginning of further tooth ridges. There is evidence of wear on the lingual edge of ridge 2 and in the groove between ridges 1 and 2.

The tooth plates were probably aligned as in *O. romeri* (Fig. 4D) and had a similar pattern of occlusion. Like *O. romeri* (see below), they are flat and do not show the curvature found in *Ctenodus*.

Stratigraphical range. Ballagan Formation, Tournaisian.

Ballagadus caustrimi sp. nov.
Figure 6A

LSID. urn:lsid:zoobank.org:act:6C483172-3060-4E1E-9D99-7414E5B3E1D1

Derivation of name. After Caustrim, the Scots name for Coldstream.

Type material. NMS G 1896.81.45 left pterygoid tooth plate.

Material. UMZC 2014.1.6.

Type locality and horizon. Dark grey, ostracod-rich mudstone, *c.* 400 m below Coldstream Bridge, right bank of the River Tweed, Northumberland, England.

Diagnosis. Tooth plates with a length to width ratio of c 2.3:1. Six radiating tooth ridges. Pterygoid tooth ridge angle *c.* 100°.

Description. A single tooth plate NMS G 1896.81.45 was collected at Coldstream at the same time as the specimens of *Occludus romeri* (Thomson 1965 and see below), but was never described. A smaller incomplete specimen UMZC 2014.1.6 probably belongs to this taxon. These pterygoid plates are small and triangular-shaped (Fig. 6A). The largest specimen is 8.5 mm long and 3.75 mm wide, with a length to width ratio of 2.3:1. There are six tooth ridges radiating from a point nearly three-quarters along the lingual edge. The tooth ridge angle is approximately 100°. Ridge 1 is damaged, but the last two preserved teeth are laterally compressed. The teeth on ridges 2–6 are longitudinally compressed. Ridge 2 has seven teeth and ridges 3–6 each have six teeth. There is occlusal wear on the oldest teeth in each ridge but little evidence of wear between the tooth ridges.

Remarks. The tooth plate of *B. caustrimi* is remarkably similar in shape and form to that of *B. rossi* (Fig. 6A, C). They both have seven teeth on tooth ridge 2 and six teeth on tooth ridges 3 and 4, and the shape of the teeth is almost identical. *B. rossi* has seven tooth ridges, whereas *B. caustrimi* has six, resulting in the former having a slightly larger length to width ratio (2.4:1 vs 2.3:1) and a larger tooth ridge angle (120° vs 100°), but the most striking difference is in their size. The tooth plate of *B. rossi* is more than twice the size of that of *B. caustrimi*. When the tooth plate of *B. caustrimi* is enlarged to the same dimensions of that of *B. rossi*, the two tooth plates are almost identical. However, in life, for the smaller tooth plate to attain the dimensions of the larger one, it would have to add tooth ridges and many more teeth. The size difference in the two tooth plates is presumably due either to sexual dimorphism (which has not previously been described in lungfish) or to inhibited growth (due to food shortage), or they are from separate species.

Stratigraphical range. Ballagan Formation, Tournaisian.

Family undesignated

Genus COCCOVEDUS nov.

LSID. urn:lsid:zoobank.org:act:8190AC18-9960-460C-A47E-1CCCF5600299

Derivation of name. From Coccoveda, the seventh century name for the River Coquet, the type locality.

Type species. *Coccovedus celatus* sp. nov.

Diagnosis. Small triangular-shaped tooth plates with length to width ratio c 2.4:1. Five radiating tooth ridges. Pterygoid tooth ridge angle *c.* 140°.

Coccovedus celatus sp. nov.
Figure 6B

LSID. urn:lsid:zoobank.org:act:320969EF-64D9-4396-B957-39BD9E03282D

Derivation of name. From the Latin *celatus* to conceal or hide, referring to the difficulty of finding small tooth plates.

Type material. UMZC 2014.2.1.

Material. UMZC 2014.2.2, UMZC 2014.3.1a, b.

Type locality and horizon. Black mudstones, 300 m below Kay Heugh, in the bed of the River Coquet, near Barrow Scar, Alwinton, Northumberland, England.

Diagnosis. As for genus.

Description. This new taxon is based on the material from two localities, Barrow Scar, Coquetdale; Northumberland and Cove, Scottish Borders. Three specimens that may also belong to this taxon have recently been described from the Ballagan on the Isle of Bute (Carpenter *et al.* 2014). The tooth plates are small and triangular-shaped. UMZC 2014.2.1 (Fig. 6B) is 6.67 mm long and 2.75 mm wide, with a length to width ratio of 2.4:1. There are five tooth ridges radiating from a point two-thirds along the lingual edge. The tooth ridge angle is approximately 140°. Ridge 1 has six laterally compressed teeth. Ridges 2–4 have four longitudinally compressed teeth. Ridge 5 has two small teeth. There is evidence of wear on the lingual edge of ridges 1 and 2, and in the grooves between ridges 1 and 2 and ridges 2 and 3, there are punctures from the opposing tooth ridges. The teeth are pointed and fused to each other in the tooth ridges. The tooth plates were probably aligned as in *O. romeri* (Fig. 4E) and had a similar pattern of occlusion.

Remarks. The tooth plates of *Coccovedus celatus* may at first sight be taken to belong to juveniles of *Ballagadus caustrimi*. However, if the tooth plates of *C. celatus* were juvenile versions of mature tooth plates of *B. caustrimi*, teeth from equivalent positions on the tooth plates would be similar in size and shape. The teeth in *B. caustrimi* are much larger and more longitudinally compressed than those from an equivalent position in the tooth plates of *C. celatus*.

Carpenter *et al.* (2014) suggested that similar tooth plates from the Isle of Bute may be those of juvenile *Sagenodus* sp. This taxon otherwise first appears in the Serpukhovian of Scotland (Traquair 1903). Based on a prearticular plate NMS G 1993.56.118 from the Dora Bone Bed (Smithson 1985), the earliest known *Sagenodus* tooth plates are relatively small, *c.* 12 mm long and *c.* 5 mm wide, with a length to width ratio of 2.4:1. The tooth ridge angle is approximately 140°, and there are typically five or six tooth ridges. The teeth on each tooth ridge are laterally compressed, and the grooves between the tooth ridges are relatively deep. The tooth plates of *C. celatus* are superficially similar to those of *Sagenodus*, but the tooth ridges are much shorter and have fewer teeth, and the teeth on ridges 2–5 are longitudinally compressed. It is therefore unlikely that specimens attributed to *C. celatus* are *Sagenodus*. Furthermore, given that these small tooth plates have now been discovered at three different, quite widely separated localities, and that larger examples of this type of tooth plate have not been found, they probably represent the tooth plates of small adult fish rather than those of juvenile larger fish.

Stratigraphical range. Ballagan Formation, Tournaisian.

Family undesignated

Genus OCCLUDUS nov.

LSID. urn:lsid:zoobank.org:act:E8EBEFA7-C072-478F-9CAF-6354759A6FC9

Type species. *Occludus romeri* (Thomson, 1965).

Occludus romeri (Thomson, 1965)
Figure 6D–E

1965 *Ctenodus romeri* Thomson, pp. 227–228, pl. III.
2013 *Ctenodus romeri* Thomson; Sharp and Clack, pp. 173–175, fig. 3.

Derivation of name. Refers to the complete occlusion of the tooth plates.

Type material. NMS. G. 1896.81.41.

Material. NMS G 1896.81.42-44, NMS G 2012.39.7 and NMS G 2012.39.427.

Type locality and horizon. Dark grey, ostracod-rich mudstone, *c.* 400 m below Coldstream Bridge, right bank of the River Tweed, Northumberland, England.

Diagnosis. Long, narrow, triangular-shaped tooth plates with length to width ratio *c.* 3:1. Up to 12 radiating tooth ridges. The tooth ridge angle *c.* 120°.

Stratigraphical range. Ballagan Formation, Tournaisian.

Remarks. The original material described by Thomson (1965) was recently redescribed by Sharp and Clack (2013). Additional comments are given here based on new material collected from the type locality at Coldstream on the River Tweed and Willie's Hole on Whiteadder Water (Smithson *et al.* 2012). The material is renamed *Occludus romeri* as it lacks the diagnostic features of the tooth plates of *Ctenodus* (see above).

Description. The tooth plates (Fig. 6D–E) are relatively long and narrow with a length to width ratio of approximately 3:1. The tooth ridge angle is approximately 120°. All the teeth are worn apart from the newest teeth on the labial edge of each row. The teeth are fused into a continuous crest except for the most recently added teeth. Worn teeth lack enamel and have a core lattice of petrodentine. The areas of greatest wear are along the lingual edge of the tooth plate and the rounded posterior end. The teeth on the elongated tooth ridge 1 are laterally compressed. Two most recent teeth show little wear, but behind them, the teeth are progressively more worn. In the posterior half of the row, they have been worn away completely creating a gently curved blade strengthened by petrodentine columns. On the pterygoid plate, tooth ridge 1 is worn on the labial surface only, but both the lingual and labial surfaces are worn on the prearticular tooth plate.

The tooth plates were probably aligned with the long tooth ridge 1 orientated anteroposteriorly as in *Dipterus* (Traquair 1878) (Fig. 4C). During jaw closure, the tooth ridges on the prearticular tooth plates were accommodated in the grooves between the tooth ridges on the pterygoid tooth plate and vice versa. The upper and lower tooth plates appear to have occluded completely when the jaws were closed. Cone-shaped depressions in the bases of the grooves between tooth ridges mark areas of wear by teeth from the opposing tooth plate.

RESULTS

A principal component analysis was undertaken using pterygoid tooth plates. PC1 is likely to represent a combination of length to width ratio and the angle between the first and the last tooth ridges (Fig. 7). *Xylognathus* has the highest PC1 value and is an extreme case of a long, narrow tooth plate with the highest angle between the first and the last tooth ridges, within the tooth plate sample. *Ctenodus roberti* presents the opposite condition as width is high in relation to length and the angle between the tooth ridges is low. PC2 is likely to represent the length of the posterior tooth ridge. *Occludus romeri*, *Ballagadus rossi* and *Coccovedus celatus* are similar in having very short posterior tooth ridges, whereas *Ctenodus williei* and *Xylognathus* have very long posterior tooth ridges.

Ballagadus rossi, *Coccovedus celatus* and *Occludus romeri* (prearticular) form a close group in this analysis. *Ctenodus roberti, C. whitropei* and *C. williei* (prearticular) also form a close group. *Xylognathus, Ballagadus caustrimi* and *C. williei* do not form any clear groupings within the sample. The two prearticular plates in the analysis both have relatively high PC2 scores (short posterior tooth row), but they do not share this trait to the exclusion of any other tooth plates. The prearticular plate of *Ctenodus williei* is closer to *C. roberti* and *C. whitropei* than to the pterygoid plate of *C. williei*. *Xylognathus* pterygoid and prearticular plates are separated by a marked difference in PC2; the prearticular has a longer posterior tooth ridge than the pterygoid. This suggests that tooth plates differ between jaws more than between some taxa. Future expansion of this landmark data set, subject to availability of fossil material, may be able to test and show whether the prearticular plates of a species tend to have shorter posterior tooth rows than the pterygoid plates of the same species. The pterygoid plate of *Occludus romeri* is shown in Figure 6E but was not included in this analysis as tooth ridge 1 is incomplete.

DISCUSSION

In the past, the taxonomic study of lungfish tooth plates has emphasized the number of tooth ridges and tooth number, shape and degree of separation or fusion (Ahlberg *et al.* 2006). We suggest that features such as the angle of divergence of the tooth rows, whether the plates are flattened or curved and their length to width ratios are all available as potential taxonomic characters. A principal component analysis on the shape of the tooth plates described above (Fig. 7A and Smithson *et al.* 2015) supports our conclusion that the eight different forms belong to different taxa. A comparison of tooth ridge number and tooth ridge angle in lungfishes from approximately equal time intervals of the Famennian (Late Devonian), Tournaisian and Visean (early Carboniferous) also reveals a rapid and previously unrecognized radiation in the Tournaisian (Fig. 7B).

Lloyd *et al.* (2011) listed 10 lungfish taxa in the Famennian. The dentition is unknown in two, four are either dentine-plated or denticulated (*sensu* Ahlberg *et al.* 2006), and four have typical tooth plates (see Smithson *et al.* 2015). To this list of tooth-plated forms can be added seven from the Oryol Region of Russia (Krupina 2000) and four from the Catskill Formation of Pennsylvania, USA (Friedman and Daeschler 2006).

Lloyd *et al.* (2011) listed three lungfish taxa in the Tournaisian. Two of these are *Delatitia* and *Parasagenodus* whose age is uncertain (see above), and they are not included in this analysis. The other is *Occludus romeri*. To this list can be added the seven new taxa from the Ballagan Formation described above.

Lloyd *et al.* (2011) listed three lungfish taxa in the Visean (see Smithson *et al.* 2015). The dentition is unknown in one, but the other two have tooth plates. To this list can be added two species of *Ctenodus* (Sharp and Clack 2013).

In the Famennian, most of the lungfish have tooth plates with a relatively low tooth ridge angle in the range 45–90° (Fig. 7B). Only two have a tooth ridge angle greater than this. In contrast, in the Tournaisian, none of the tooth plates has a tooth ridge angle in the range 45–90°. Instead, three have a tooth ridge angle in the range 0–45°, three have a tooth ridge angle in the range 90–135°, and two have a tooth ridge angle in the range 135–180°. In the Visean, lungfishes display tooth ridge angles from each of the four ranges.

The measured difference between the tooth plates of Famennian and Tournaisian lungfish is striking (Fig. 7B). Not only is there a greater range of tooth plate shape in Tournaisian taxa, but the most common tooth plate shape in the Famennian is absent from our sample of Tournaisian taxa. Two completely new shapes have evolved, one with a relatively low tooth ridge angle, no greater than 40°, in which most of the tooth ridges are essentially parallel, and the other with a much higher tooth ridge angle of up to 180° where the tooth ridges are highly divergent.

These differences in tooth plate shape may reflect different patterns of tooth plate growth. In most cases, the radiating pattern of tooth plate development seen in the modern lungfish *Neoceratodus* (Kemp 1977) probably applies, but in those forms with parallel rows of teeth seen in species of *Ctenodus*, a different pattern of growth is required. In these tooth plates, the anteroposterior axis probably dominates initially, to establish the number of tooth rows, followed by tooth development along the lingual–labial axis of each row. These ideas will be tested in future work.

The high level of diversity found in this geographically restricted area, over a narrow time period, suggests that there was a rapid and previously unrecorded radiation of lungfishes in the Tournaisian. Presumably, the tooth-plated lungfishes that survived the end-Devonian extinction were able to radiate into the gaps in ecospace created by the absence of non-tooth-plated lungfishes and other extinct major groups of fishes including arthrodires, anti-

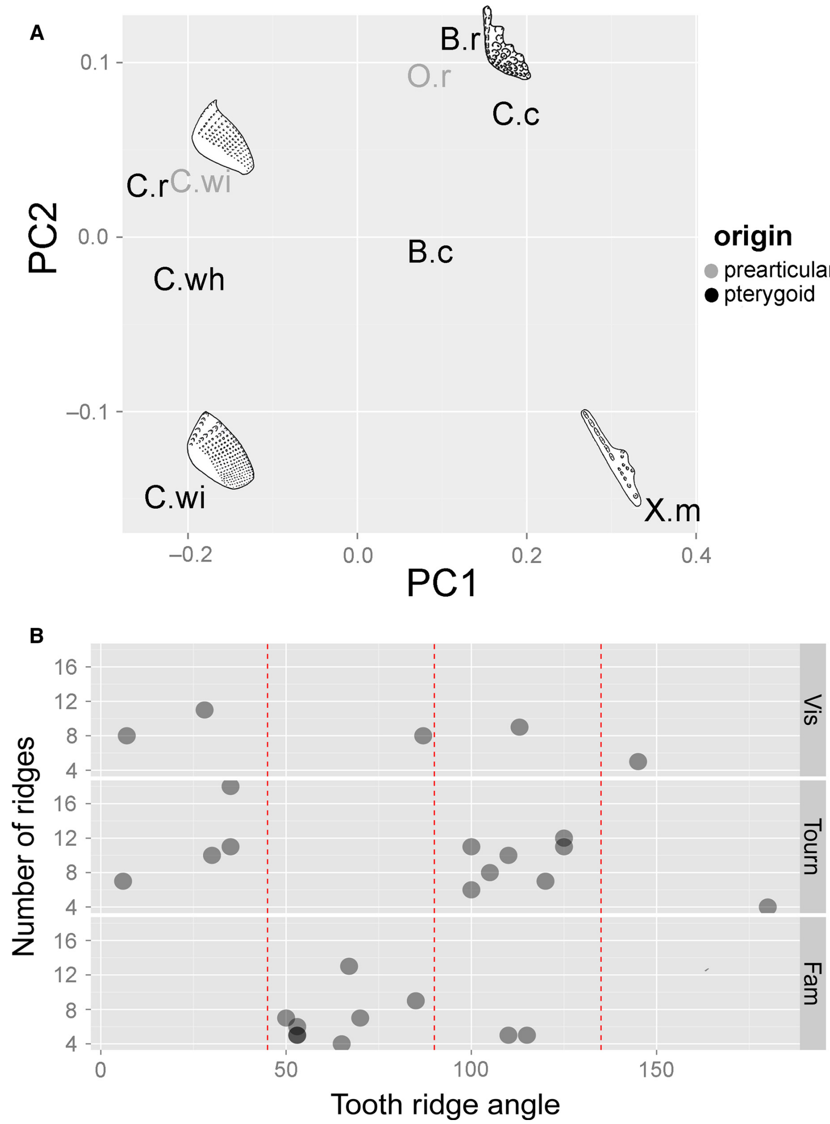

FIG. 7. Morphometric analysis of lungfish tooth plates. A, principal component analysis of tooth plates from Romer's Gap. B, comparison of tooth ridge number and tooth ridge angle in the tooth plates of lungfish from the Famennian (Upper Devonian) and the Tournaisian and Visean (early Carboniferous). (See Smithson *et al.* 2015). *Abbreviations*: B.c, *Ballagadus caustrimi*; B.r, *B. rossi*; C.c, *Coccovedus celatus*; C.r, *Ctenodus roberti*; C.wi, *Ctenodus williei*; C.wh, *Ctenodus whitropi*; O.r, *Occludus romeri*; X. m, *Xylognathus macrustenus*. Colour online

archs, porolepiformes and tristichopterids. They had to adapt to feeding on the surviving fish and invertebrates. The small size of two of these species is unusual for sarcopterygians in general and may indicate processes of paedomorphosis in their evolution.

The radiation of tooth-plated forms is consistent with the recent recognition of increasing durophagy in early Carboniferous chondrichthyans (Sallan *et al.* 2011) and actinopterygians (Sallan and Coates 2013). However, the discovery of *Xylognathus* (Fig. 5) from Burnmouth, which appears to have developed a marginal dentition from its tooth plates much like the younger *Uronemus* achieved, suggests that among lungfishes the pattern of radiation was not exclusively associated with durophagy.

Lungfish continued to diversify throughout the early Carboniferous. By the Visean, a variety of taxa existed in Australia (Turner *et al.* 1999), Europe and North America (Clack *et al.* 2009), with *Sagenodus* first appearing in the Serpukhovian of Britain (Traquair 1903). By the beginning of the late Carboniferous, the rate of appearance of new taxa had slowed down, with most tooth-plated lungfish being placed either in *Ctenodus* or in *Sagenodus*, and only a single non-tooth-plated form, *Conchopoma*, being known from that time (Clack *et al.* 2009). The *Ctenodus* type of tooth plate was eventually lost at the end of the Carboniferous, but the *Sagenodus* type, similar to that of the modern lungfish *Neoceratodus*, survived. *Neoceratodus* is a generalist feeder (Kemp 1987) and presumably, *Sagenodus* was likewise. The varied morphologies seen in the early Carboniferous suggest they were specialized for niches that were lost through the late Carboniferous and early Permian.

The discovery of a diverse fauna of lungfish in the early Carboniferous, displaying a mix of primitive and derived characters, challenges the hypothesis of low diversity following the end-Devonian extinction event. Future work will test current ideas on the rate of character change in lungfish evolution and contribute to a new hypothesis of their phylogeny. It will also explore the variation in morphology and size of lungfish tooth plates to test our current understanding of their patterns of growth and development.

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DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.66598

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APPENDIX: SPECIMENS EXAMINED

The specimens examined for this article are listed below:

Ctenodus williei *sp. nov.*

GSL 1312, right pterygoid tooth plate from the bank of the River Tweed near Wark, Northumberland, England. Collected by John Rhodes in 1883; UMZC 2011.7.5 right prearticular tooth plate and UMZC 2011.7.6 right pterygoid tooth plate from Willie's Hole, Whiteadder Water, near Chirnside, Berwickshire, Scotland. Collected by Stanley Wood in 2008; UMZC 2014.4.1 left pterygoid tooth plate from Crumble Edge, Whiteadder Water, near Preston, Berwickshire Scotland. Collected by Jennifer Clack in 2013.

Ctenodus whitropei *sp. nov.*

NMS G 2014.2.1 left pterygoid tooth plate from Whitrope Burn, near Hermitage, Hawick, Roxburghshire, Scotland. Collected by Stanley Wood in 2006.

Ctenodus roberti *sp. nov.*

UMZC 2014.10 left pterygoid tooth plate, preserved as a natural mould, from Heads of Ayr, Ayr, Ayrshire, Scotland. Collected by Robert Clack in 2014.

Xylognathus macrustenus *gen. et sp. nov.*

UMZC 2014.1.3a, b, c disrupted skull with tooth plates, UMZC 2014.1.4a, b three incomplete fish on single slab, one with tooth plates in labial view, and UMZC 2014.1.5 left prearticular tooth plate from Burnmouth, Berwickshire, Scotland. Collected by Stanley Wood in 2007.

Ballagadus rossi *gen. et sp. nov.*

UMZC 2014.1.1 left pterygoid tooth plate and UMZC 2014.1.2 incomplete left pterygoid tooth plate from Burnmouth, Berwickshire, Scotland. Collected by Jennifer Clack in 2012.

Ballagadus caustrimi *sp. nov.*

NMS G 1896.81.45 right pterygoid tooth plate from south bank of the River Tweed near Coldstream, Berwickshire, Scotland. UMZC 2014.1.6a left pterygoid tooth plate from Burnmouth, Berwickshire, Scotland. Collected by Stanley Wood in 2007. [Correction amended after initial online publication on 15 October 2015: The last sentence "Collected by . . . 2007." under the paragraph "*Ballagadus caustrimi* sp. nov." was corrected in the Appendix section.]

Coccovedus celatus *gen. et sp. nov.*

UMZC 2014.2.1 right pterygoid tooth plate and UMZC 2014.2.2 left pterygoid tooth plate from Barrow Scar, River Coquet, Near

Alwinton, Northumberland, England. Collected by Timothy Smithson in 2012; UMZC 2014.3.1a, b left pterygoid tooth plate from Cove, Berwickshire, Scotland. Collected by Timothy Smithson in 2012.

Occludus romeri *gen. nov.*

NMS G 1896.81.41 left pterygoid tooth plate, NMS G 1896.81.42 right pterygoid tooth plate, NMS G 1896.81.43 left prearticular tooth plate and NMS G 1896.81.44 left prearticular tooth plate from south bank of the River Tweed near Coldstream, Berwickshire, Scotland; NMS G 2012.39.7 left pterygoid tooth plate and NMS G 2012.39.427 small left pterygoid tooth plate from Willie's Hole, Whiteadder Water, near Chirnside, Berwickshire, Scotland. Collected by Stanley Wood in 2008.