The Early Devonian Acanthodian *Uraniacanthus curtus* (Powrie, 1870) n. comb. from the Midland Valley of Scotland

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ABSTRACT
The acanthodian originally described as *Euthacanthus curtus* Powrie, 1870 from the Early Devonian (Lochkovian) of Scotland was tentatively reassigned to *Diplacanthus* Agassiz, 1844 later in the nineteenth century, although doubt was cast on this revision. In 1976 Paton suggested that specimens comparable with the single type could belong to *Uraniacanthus* Miles, 1973, based on similarities with the type species *U. spinosus* Miles, 1973 from the Lochkovian of England. Hanke *et al.* (2001) noted that the Canadian Lochkovian species *Gladiobranchus probaton* Bernacsek & Dineley, 1977 was also very similar to *U. spinosus*. Our investigations indicate that all three species belong to the genus *Uraniacanthus* (which has priority over *Gladiobranchus* Bernacsek & Dineley, 1977) in the family Gladiobranchidae Bernacsek & Dineley, 1977, order Diplacanthiformes Berg, 1940 (revised). This identification supports a biogeographical connection between the Canadian, Scottish and English Early Devonian based on the common presence of the genus *Uraniacanthus*, as well as other acanthodian genera, including *Ischnacanthus* Powrie, 1864. *Uraniacanthus* could also be represented by isolated scales in coeval deposits in the Baltic.

KEY WORDS
Lochkovian,
Acanthodii,
Diplacanthiformes,
Gladiobranchus,
Euthacanthus,
biogeography.

RÉSUMÉ
L'acanthodien Uraniacanthus curtus *(Powrie, 1870) n. comb. du Dévonien inférieur de la vallée Midland, Écosse.*
L'espèce d'acanthodien originellement décrite en tant qu'*Euthacanthus curtus* Powrie, 1870 du Dévonien inférieur (Lochkovien) d'Écosse a été assignée au cours du dix-neuvième siècle au genre *Diplacanthus* Agassiz, 1844 bien que des doutes aient été émis sur la validité de cette révision. Paton (1976) suggère alors que des spécimens comparables au type pourraient appartenir au genre *Uraniacanthus* Miles, 1973, sur la base de similarités avec l'espèce-type *U. spinosus* Miles, 1973 du Lochkovien d'Angleterre. Hanke *et al.* (2001) ont noté que l'espèce lochkovienne canadienne *Gladiobranchus probaton* Bernacsek & Dineley, 1977 est aussi très similaire à l'espèce *U. spinosus*. Nos investigations montrent que ces trois espèces appartiennent toutes au genre *Uraniacanthus* (qui a priorité nomenclaturale sur *Gladiobranchus* Bernacsek & Dineley, 1977), de la famille des Gladiobranchidae Bernacsek & Dineley, 1977, ordre des Diplacanthiformes Berg, 1940 (révisé). Cette identification supporte l'hypothèse d'une connexion biogéographique entre le Canada, l'Écosse et l'Angleterre au cours du Dévonien inférieur, repose sur la présence commune de ce genre *Uraniacanthus*, et également d'autres genres d'acanthodiens tel que *Ischnacanthus* Powrie, 1864. D'après la présence d'écailles isolées, le genre *Uraniacanthus* pourrait également être représenté dans les dépôts du même âge de la région Balte.

MOTS CLÉS
Lochkovien,
Acanthodii,
Diplacanthiformes,
Gladiobranchus,
Euthacanthus,
biogéographie.

INTRODUCTION

The history of the discovery of Lower Devonian fossil fishes in the Strathmore region of the Midland Valley of Scotland has recently been discussed by Newman *et al.* (2011). James Powrie was a preeminent collector and author of the Lower Old Red Sandstone acanthodian taxa in the nineteenth century. Powrie erected the genus *Euthacanthus* Powrie, 1864, with one species, *Euthacanthus macnicoli* Powrie, 1864 and later erected a new species, *Euthacanthus curtus* Powrie, 1870. Until the present paper, the only published figure of this species was in the original description by Powrie (1870: pl. 12, fig. 7), a rather crude pen and ink drawing of NMS G.1891.92.249 reproduced here in Figure 1. Powrie (1881) later briefly described *E. curtus* in a general description of the fossils of Forfarshire. No further mention was made of *E. curtus* until Woodward & Sherborn (1890) tentatively placed the species in the genus *Diplacanthus* Agassiz, 1844, as they considered it differed appreciably from the other *Euthacanthus* species. Traquair (1892) recorded the type and figured material in the Powrie collection and noted Woodward & Sherborn's (1890) assignment of *E. curtus* to ?*Diplacanthus.* However, he noted that a second specimen from Turin Hill (NMS G.1891.92.250) which was catalogued as *E. curtus* exhibited more than one pair of intermediate spines, thus excluding it from *Diplacanthus*, and removed the species back to *Euthacanthus*. Although Paton (1976) retained this classification for the holotype of *E. curtus*, she referred NMS G.1891.92.250 to ?*Uraniacanthus* sp., thereby casting doubt on the generic assignment of *E. curtus.* Paton (1976) also placed NMS G.1964.31.30A/B in ?*Uraniacanthus* sp. Denison (1979) stated that *E. curtus* did not belong in *Euthacanthus* and questioned its reference to *Diplacanthus* by Woodward & Sherborn (1890), but he did not provide an alternative classification. This was the last mention of this species until the present paper.

In recent years there has been a renewed interest in Early Devonian acanthodians centred on excellent new material collected in the Northwest Territories of Canada. A substantial amount of work has been published describing these new specimens, as well as preliminary phylogenetic analyses of the

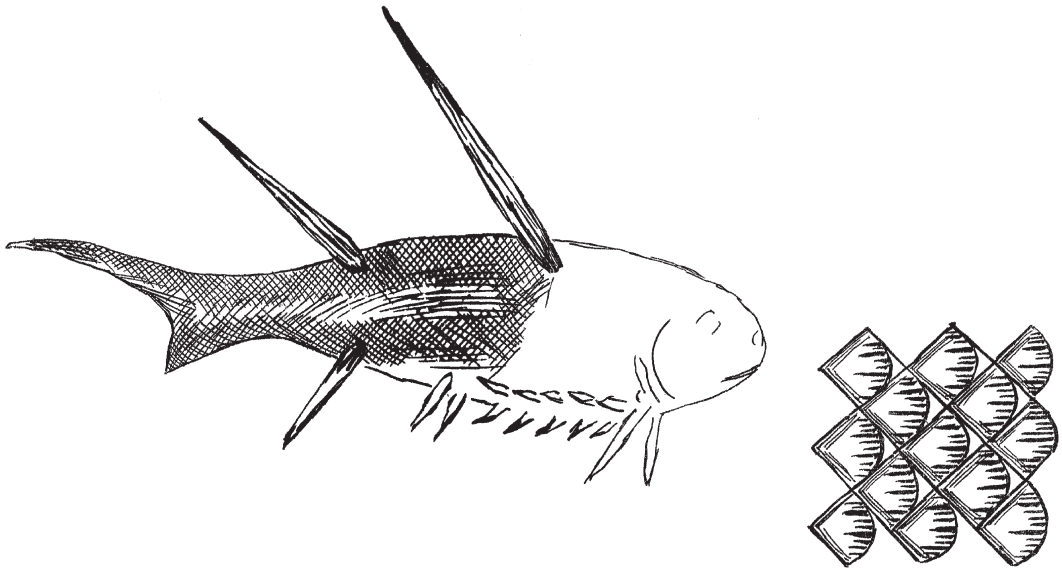

FIG. 1. — *Uraniacanthus curtus* (Powrie, 1870) n. comb. NMS G.1891.92.249, holotype from Farnell. A reproduction of Powrie's figure (1870: pl. 12, fig. 7) of the complete specimen and his enlargement of the scales (Powrie 1870: pl. 12, fig. 7a).

Acanthodii (e.g., Hanke & Wilson 2004, 2006 and references therein) followed more recently by a broader analysis of relationships amongst all early jawed fishes (Brazeau 2009). The present authors have conducted extensive fieldwork in Scotland and researched collections in most of the museums where Scottish Early Devonian acanthodians are housed. Two of the authors (MJN and JdB) visited the Natural History Museum in London (2007) and the National Museums of Scotland (NMS) in Edinburgh (2009) where most Scottish acanthodians are housed and took photographs of all the Scottish Devonian acanthodians. This task was undertaken with a view to re-examine and if necessary redescribe all the Scottish Devonian acanthodians, to allow comparison with the Canadian material referred to above, and articulated specimens of new taxa described in recent decades from Severnaya Zemlya, Russia (e.g., Valiukevičius 2003) and other regions. A redescription of *U. curtus* (Powrie, 1870) n. comb. was chosen as a preliminary article in this project as there has recently been a redescription of "*Gladiobranchus*" *probaton* Bernacsek & Dineley, 1977 by Hanke & Davis (2008). As part of our redescription of *U. curtus* n. comb. and evaluation of its relationships, it was necessary to address the diagnostic characters of the order Diplacanthiformes. Whilst two of the three specimens of *U. curtus* n. comb. at our disposal are badly preserved, the third juvenile specimen shows a surprising amount of detail. The photographs display details previously unknown, allowing a more comprehensive comparison with other species, particularly *U. probaton* (Bernacsek & Dineley, 1977) n. comb. Also, for the first time we have been able to do some invasive analysis on *U. curtus* n. comb. as a small number of scales were removed from NMS G.1964.31.30A for both ESEM (environmental scanning electron microscopy) and thin section work.

MATERIAL AND METHODS

Three specimens of *Uraniacanthus curtus* (Powrie, 1870) n. comb. were available for study. All are laterally compressed; no preparation was allowed on the specimens collected by Powrie. The holotype, NMS G.1891.92.249 from Farnell, is preserved as a naturally red-stained cast with well-preserved scale impressions but minus the head which is cut

off at the edge of the slab; NMS G.1891.92.250 is a small, mostly complete, specimen from Turin Hill (Tillywhandland); both these specimens were collected in the nineteenth century. The third specimen, NMS G.1964.31.30A/B, was collected from Hayston Hill in the 1960s by C. D. Waterston (C. D. Waterston pers. comm. 1997); it is an articulated specimen, lacking the head, with well preserved body scales. Small patches of scales were removed from three regions of this specimen for ESEM and thin section preparation. Immersion of the patches in weak acetic acid aided separation of the scales, producing 15 salvageable scales for ESEM work and eight scale fragments for thin sectioning (an excellent result for the limited amount of material at our disposal). The ESEM machine used was an Hitachi TM-1000 Tabletop housed in Queensland Museum, Australia. Scales were embedded with Crystalbond® on a glass slide, ground using 2000 grit wet and dry sandpaper, and cover slips attached using Entellan New®. The thin sections were imaged using an Olympus BX50 transmission microscope and DP12 imaging system. Macro-photographs were taken of all specimens using a Canon Digital Rebel 450D. Microphotographs were taken of squamation on the two larger specimens under normal light using a Wild M420 binocular microscope with a Sony DSCH2 camera. Figures were compiled using Adobe Photoshop®.

Burrow & Turner (2010: fig. 1) discussed the general stratigraphy of the Early Devonian of the Midland Valley of Scotland, and figured a locality map with the important fish beds. More precise stratigraphical and geological information was later provided by Newman *et al.* (2011).

SYSTEMATICS

Class ACANTHODII Owen, 1846
Order DIPLACANTHIFORMES Berg, 1940

Revised diagnosis. — Acanthodians with a short mouth and cheek region (< ⅕ body length), and a deep body (> ⅓ body length); inserted portion of the median fin spines with narrow, closely spaced parallel ridges; anterior dorsal fin spine with long inserted portion and fin supported by large basals with short radials; pair of admedian spines; paired pinnal plates with or without spines, or prepectoral spines without plates; scapulocoracoid with a prominent ridge separating the postbranchial lamina from the posterior flange; large postorbital plate; circumorbital ring of small plates plus large anterior and/or posterior plates; plate-like hyoidean gill covers; no true teeth; ossified dental plates on lower jaws; scales with an acellular bone base pierced by branching canals of Williamson, and long branching ascending vascular and dentine canals in the crown (i.e. *Diplacanthus*-type histological structure *sensu* Valiukevičius 1995).

Remarks

As noted by Young & Burrow (2004), few characters have been recognised as uniquely diagnostic for the order. Hanke & Davis (2008) assigned *Gladiobranchus probaton* to the suborder Diplacanthoidei Miles, 1966 within the order Climatiiformes Berg, 1940 but did not revise the last published diagnosis by Denison (1979), who assigned all diplacanthiforms/diplacanthoids to the family Diplacanthidae (also within the Climatiiformes). Only a few of the characters listed by Denison are probably diagnostic: lack of teeth, and scale structure (*Diplacanthus*-type *sensu* Valiukevičius 1995). We propose two previously unrecognised diagnostic characters, one of which is a smooth ossified prearticular plate on the Meckel's cartilage. Before Hanke & Davis's (2008) description of the lower jaw ossifications in *Uraniacanthus probaton* n. comb., smooth bones in the lower jaw of many other diplacanthiforms were interpreted as mandibular splints, homologous to the bones reinforcing the ventral margins of the Meckel's cartilages in acanthodiforms. The latter bones wrap around the posterior end of the cartilage and taper to a point anteriorly. In diplacanthiforms other than *Uraniacanthus*, however, the bones in the lower jaw are blade-like (e.g., *Milesacanthus antarctica* Young & Burrow, 2004) or spatulate (e.g., *Diplacanthus horridus* Woodward, 1892 and *Diplacanthus ellsi* Gagnier, 1996 [Gagnier 1996: figs 1, 7]). Ossified dental plates have also been recognised by the authors in the type species *Diplacanthus crassisimus* Duff, 1842 (e.g., NMS G.1892.8.5 from Gamrie, Banffshire, Scotland), and *Diplacanthus longispinus* Agassiz, 1844 (e.g., NMS G.1891.92.338 from Gamrie; Fig. 2A, B). Hanke & Davis's (2008) description of deep thin ossified plates on the lower jaws in *U. probaton* n. comb., without similar plates on the occluding

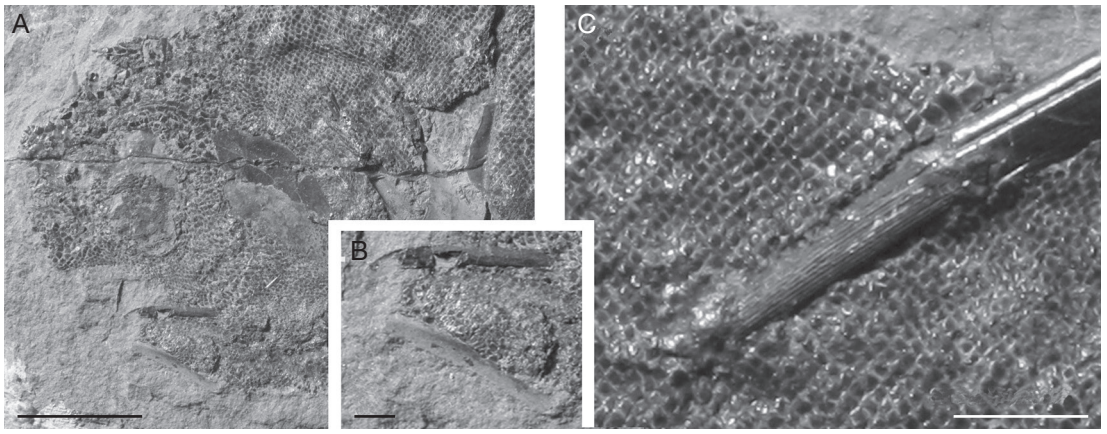

FIG. 2. — *Diplacanthus longispinus* Agassiz, 1844, NMS G.1891.92.338, a complete specimen from Gamrie, Banffshire, Scotland: **A**, detail of the head showing the position of the jaw plates; **B**, close up of the tooth plate positioned on the upper surface of the lower jaw; **C**, detail of the posterior dorsal fin spine showing the deep base of insertion with fine, parallel ridges Scale bars: A, 10 mm; B, 1 mm; C, 5 mm.

upper jaws, encouraged our reinterpretation of the bones associated with lower jaws in other diplacanthiforms as homologous to those of *U. probaton* n. comb. The other recently recognized diagnostic character for the diplacanthiforms is the narrow, closely spaced parallel ridges on the deep bases of insertion on the median fin spines (Burrow 2007: 835), seen for example on the posterior dorsal fin spine of *Diplacanthus longispinus* (Fig. 2C).

Family GLADIOBRANCHIDAE Bernacsek & Dineley, 1977

TYPE AND ONLY GENUS. — *Uraniacanthus* Miles, 1973.

DIAGNOSIS. — As for the type genus.

Genus *Uraniacanthus* Miles, 1973

TYPE SPECIES. — *Uraniacanthus spinosus* Miles, 1973, original designation, from the Lochkovian of Herefordshire, England.

REVISED DIAGNOSIS. — Diplacanthiform acanthodians with two pairs of prepectoral fin spines; anterior dorsal fin spine with a marked posteriorly-pointing curvature at the tip; postorbital plates with rounded to spiky raised tubercles; broad, spatulate opercular covers ornamented with fine ridges in a loose chevron pattern; smooth gnathal bone with a subtriangular dorsal process, on Meckel's cartilage; scales, when ornamented, with three to eight grooves extending the whole length of the scale crown.

REMARKS

This diagnosis is mostly based on the diagnosis for *Gladiobranchus* given by Hanke & Davis (2008). As originally noted by Hanke *et al.* (2001), Miles (1973: text-fig. 17A, pl. 12, fig. 1) mistakenly identified *Uraniacanthus spinosus* as an ischnacanthiform based on the association of one of his figured specimens with a dentigerous jaw bone, and misidentification of a postorbital plate as a jaw element (Hanke & Wilson 2004). Bernacsek & Dineley (1977) erected a new taxon *Gladiobranchus probaton* for partial specimens lacking the rostrum and jaws from the Lochkovian MOTH locality, Northwest Territories, Canada. They placed both *Uraniacanthus* and *Gladiobranchus* in a new family Gladiobranchidae Bernacsek & Dineley, 1977 indicating a close relationship between the two genera. Prepectoral spines have not previously been identified in *U. spinosus*, but spines anterior to the pectoral fin spine and close to the branchiostegal plates that Miles (1973: pl. 13, figs 1, 2) identified as isp. 1 (intermediate spines) could rather be prepectoral spines: the laterally compressed holo-

type (Miles 1973: pl. 11) shows isp. 1 posteriorly positioned, close to the pelvic spines. The only clear differences between specimens assigned to the two genera are the ornamentation of the postorbital plates and the more robust posterior dorsal fin spine of *G. probaton*. As previously suggested by Hanke & Davis (2008; also Hanke pers. comm. 2009), these differences are too minor to support separate genera. As described below, *Euthacanthus curtus* and *G. probaton* show even closer similarity.

Uraniacanthus curtus (Powrie, 1870) n. comb. (Figs 1; 3-13)

Euthacanthus curtus Powrie, 1870: 293, pl. 12, figs 7, 7a. — Woodward 1891: 32. — Traquair 1892 : 34. — Paton 1976: 6. — Denison 1979: 27.

?*Diplacanthus curtus* – Woodward & Sherborn 1890: 65, 81.

Euthacanthus Curtus – Powrie 1881: 169.

?*Uraniacanthus* sp. – Paton 1976: 15.

TYPE SPECIMEN. — Powrie (1870) mentioned two syntypes when he first erected the species but described and figured only one, namely NMS G.1891.92.249 (Figs 1; 3) from Farnell, the headless specimen which Traquair (1892) considered the type (and hence the lectotype). Paton (1976) described NMS G.1891.92.249 as the syntype.

REFERRED SPECIMENS. — Traquair (1892) also registered NMS G.1891.92.250 (Figs 4, 5), a very small complete specimen from Turin Hill. Although it is from Powrie's collection, we cannot be certain it is the other one mentioned by Powrie (1870), as he provided no description. The third specimen NMS G.1964.31.30A/B (Fig. 6), from Hayston Hill, is a partial articulated fish lacking the head. NMS G.1964.31.30B is the counterpart of the above but is less well-preserved

TYPE LOCALITY. — Pow Burn near Farnell, Brechin, Angus, Scotland (National Grid reference NO 622 549).

STRATIGRAPHIC HORIZON AND AGE. — *Uraniacanthus curtus* n. comb. occurs in the Arbuthnott Group of the Early Devonian (Lochkovian) of the Midland Valley of Scotland.

OCCURRENCE. — Apart from the type locality, *Uraniacanthus curtus* n. comb. has been collected from Turin Hill (probably Tillywhandland Quarry), Forfar (National Grid reference NO 528 537) and from a small, in-filled quarry north of Hayston Hill near Glamis, Dundee (National Grid reference NO 413 460).

REVISED DIAGNOSIS. — Short, deep bodied diplacanthiform acanthodians; dorsal fin spines have numerous longitudinal grooves and ridges, with the anterior dorsal fin spine having up to eleven ridges and the posterior up to nine ridges per side; four opercular covers on each side; flank scales are from 0.2 to 0.5 mm long; all body and fin scales are ornamented: scales have a flat crown with deep, wide, U-shaped grooves that sometimes extend the length of the crown, fanning out towards the anterior edge; large multiple pores in the anterior half of the grooves open into wide ascending canals that lead into wide circular canals, interconnected by short radial canals, in the lower crown; branched dentine tubules extend within each crown growth zone into the vascular canals; a row of 1-3 pores are on each side of the scale neck constriction.

DESCRIPTION

General structure

Specimens are from 20 mm to an estimated 110 mm long. Whilst all three specimens are deep bodied, they are not complete enough to give an accurate depth to length range. All three specimens are preserved in lateral view suggesting the body was deeper than wide. The lateral sensory line is visible only on NMS G.1891.92.249 (Fig. 3A) as a shallow depression running between the scales. Nothing is known of the sensory lines of the head. The endoskeleton is not preserved, and is presumed to be unmineralized.

Head

On NMS G.1964.31.30A (Fig. 6) the head region is mostly missing except for some scattered broken dermal plates visible at the edge of the slab, but these are too fragmentary to be recognisable or reconstructed into their original arrangement. The plates are larger than the body scales. The head is completely missing from the holotype NMS G.1891.92.249 (Fig. 3A). As the outline of the head is not preserved on any of the specimens we cannot ascertain the slope of the head between the rostrum and the anterior dorsal fin. NMS G.1891.92.250 (Fig. 4) is the only specimen with recognisable, intact structures in the head region, but they are extremely small and the head is slightly disarticulated and rotated dorsally. Four spatulate opercular covers are preserved (Fig. 4C)

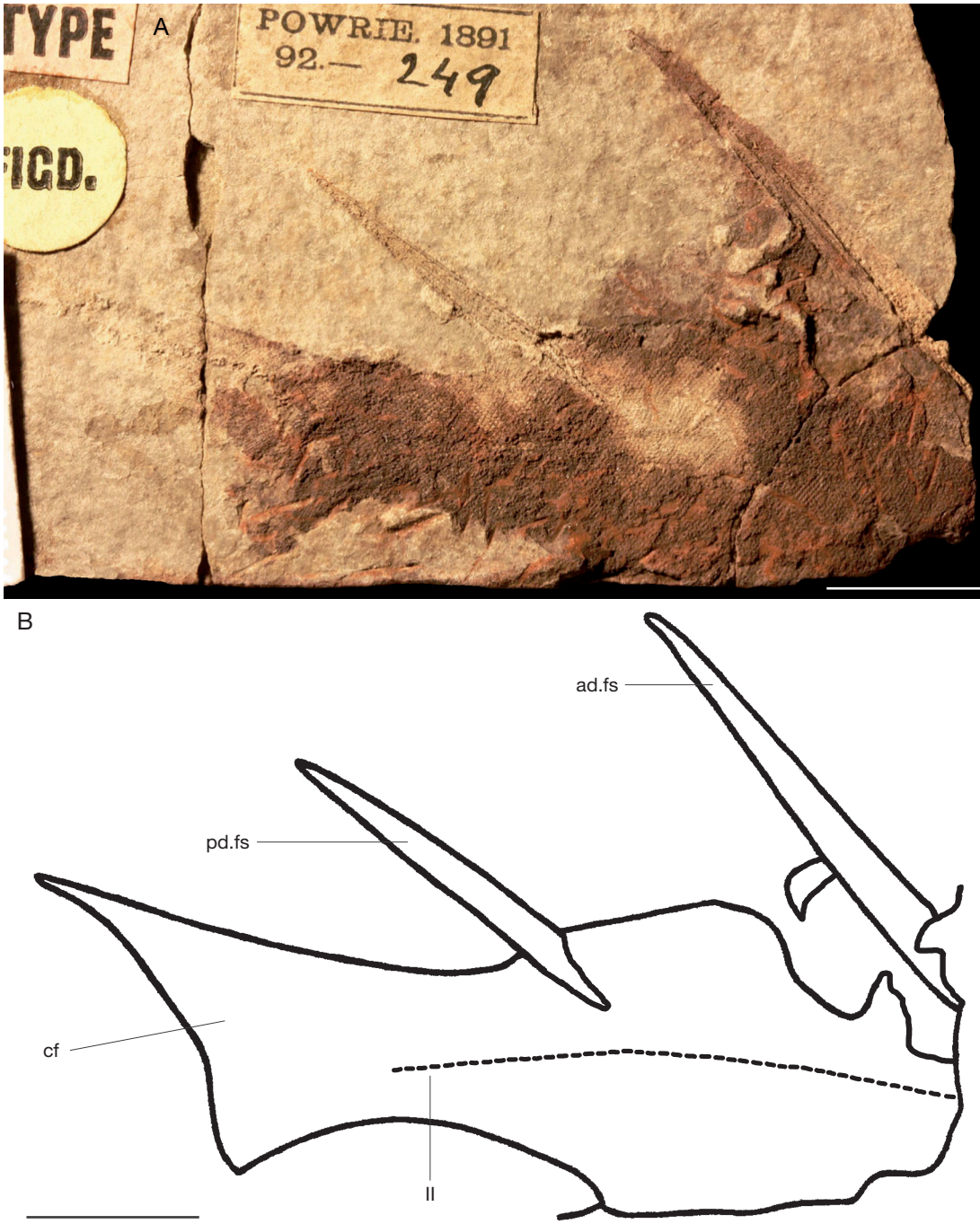

FIG. 3. — *Uraniacanthus curtus* (Powrie, 1870) n. comb., NMS G.1891.92.249, holotype from Farnell: **A**, photograph of the specimen; **B**, line drawing of the specimen. Abbreviations: **ad.fs**, anterior dorsal fin spine; **cf**, caudal fin; **ll**, lateral line; **pd.fs**, posterior dorsal fin spine. Scale bars: 10 mm.

FIG. 4. — *Uraniacanthus curtus* (Powrie, 1870) n. comb., NMS G.1891.92.250, a very small complete individual from Turin Hill (Tillywhandland), Angus, Scotland: **A**, complete specimen; **B**, ossification of the right Meckel's cartilage with the coronoid process visible on the upper surface; **C**, external view of the spatulate opercular plates with a trace of thin ridge ornamentation; **D**, scapulocoracoids; **E**, possible prepectoral spines with the posterior one being larger; **F**, internal surface of a postorbital plate. Scale bars: A, 5 mm; B-D, F, 1 mm; E, 0.1 mm.

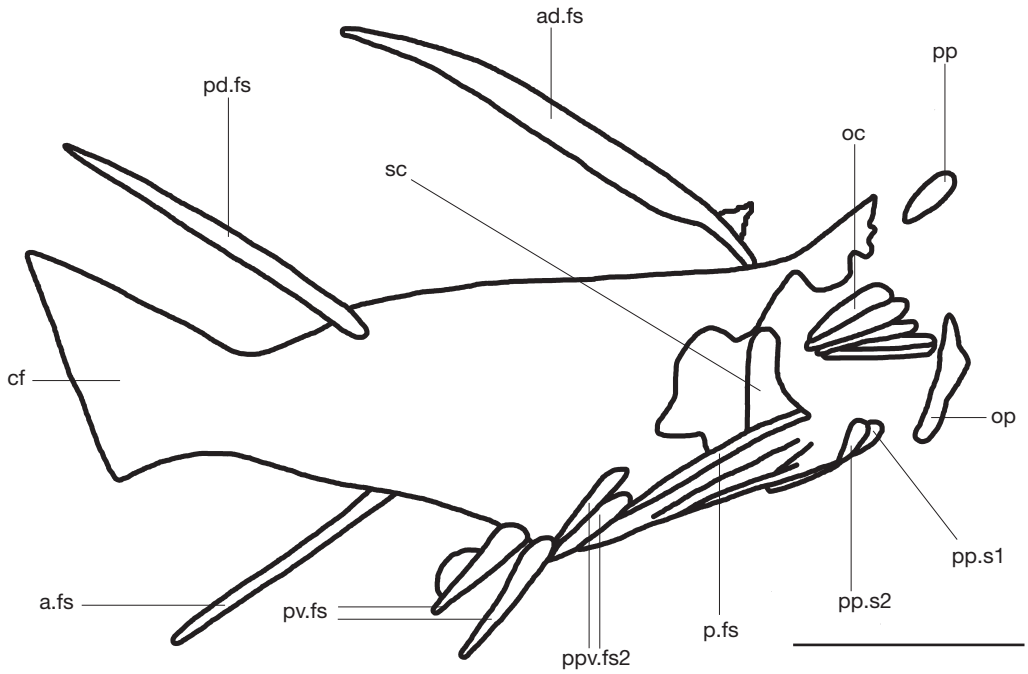

FIG. 5. — *Uraniacanthus curtus* (Powrie, 1870) n. comb., NMS G.1891.92.250, a very small complete individual from Turin Hill (Tillywhandland), Angus, Scotland: Line drawing of the specimen. Abbreviations: **ad.fs**, anterior dorsal fin spine; **a.fs**, anal fin spine; **cf**, caudal fin; **sc**, scapulocoracoid; **oc**, opercular covers; **op**, occlusal plate; **pd.fs**, posterior dorsal fin spine; **p.fs**, pectoral fin spine; **pp**, postorbital plate; **pp.s1**, first prepectoral spine; **pp.s2**, second prepectoral spine; **ppv.fs2**, second prepelvic fin spine; **pv.fs**, pelvic fin spine. Scale bar: 5 mm.

with the larger ones in the middle of the series. They are broader towards the anterior, tapering to a point at the posterior end. Their ornamentation is difficult to discern, but appears to consist of concentric, thin ridges. The opercular series has rotated slightly dorsally and would have originally been closer to the scapulocoracoid.

A small bone 3 mm long, interpreted as an occlusal plate on the right lower jaw (Fig. 4B) of NMS G.1891.92.250, has been displaced anterodorsally and is seen in lateral view. It is fairly well preserved and is a single ossified element with an antero-posterior axis that is slightly convex dorsally. Midway along the upper edge is a sub-triangular dorsal 'coronoid' process. Anterior of this process the bone is thickened on the dorsal edge. The posterior end of the bone forms a spoon-shaped blade. A shallow trough runs anteriorly from the posterior blade; the ventral edge of the bone is thickened.

Towards the dorsal anterior of the head is an impression of a thick triangular bone (Fig. 4F). If it had rotated in the same direction as the rest of the bony elements of the head, it would have been positioned originally just behind the orbit. This element is thus interpreted as a postorbital plate, although no ornamentation can be observed because the internal rather than the external surface is exposed.

Scapulocoracoid

The dorsal end of the scapulocoracoid, a simple cylindrical shaft, is just visible on the edge of the slab of NMS G.1964.31.30A (Fig. 6). The scapulocoracoid of NMS G.1891.92.250 (Fig. 4D), whilst being very small at only 2 mm high is more complete and the following description is based on this specimen. The scapulocoracoid is a perichondrally-ossified structure. The scapular shaft is shorter in NMS G.1891.92.250 than *U. probaton* n. comb.,

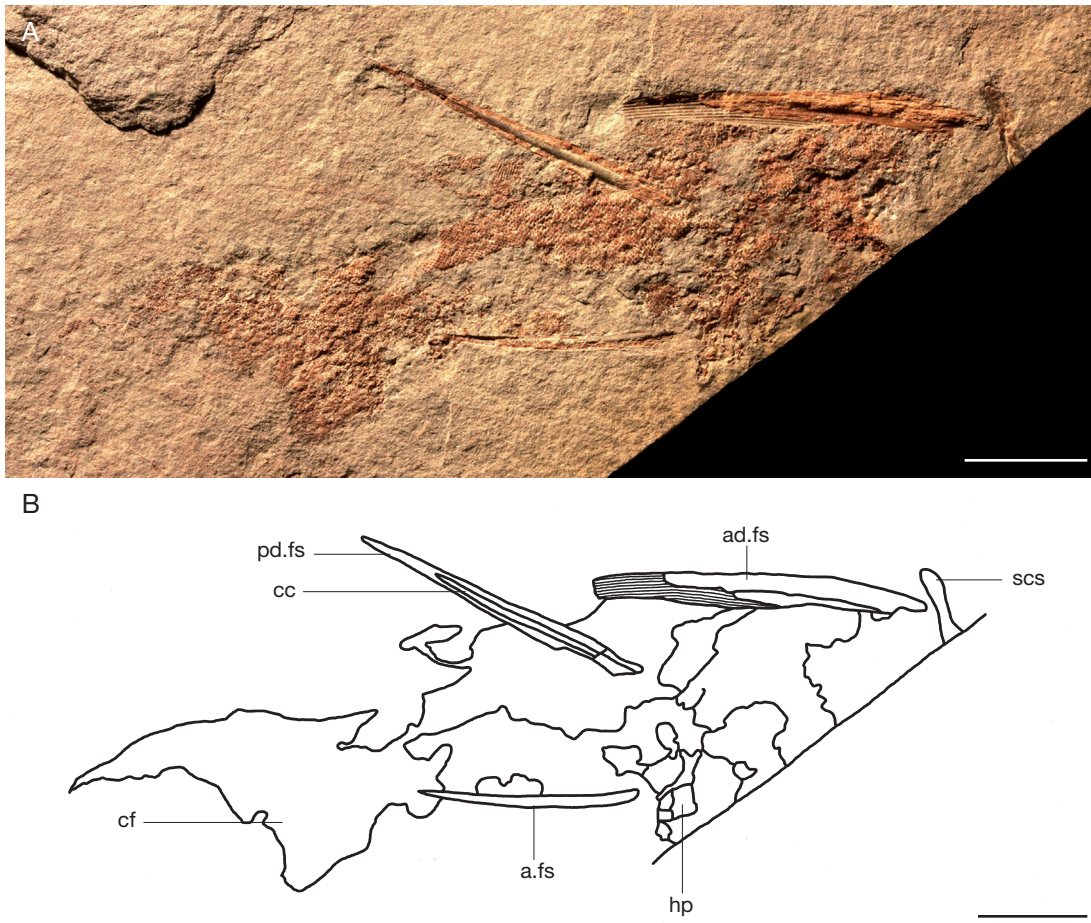

FIG. 6. — *Uraniacanthus curtus* (Powrie, 1870) n. comb., NMS G.1964.31.30A, the part of an incomplete, moderate sized specimen from Hayston Hill, Angus, Scotland: **A**, photograph of the specimen; **B**, line drawing of the specimen. Abbreviations: **ad.fs**, anterior dorsal fin spine; **a.fs**, anal fin spine; **cc**, central canal; **cf**, caudal fin; **hp**, head plates; **scs**, scapula shaft; **pd.fs**, posterior dorsal fin spine. Scale bars: 10 mm.

but this may be an ontogenetic feature as the partial remains in NMS G.1964.31.30A indicate the scapulocoracoid was longer and had a thin dorsal tip in the adult form (Fig. 6). The cylindrical shaft extends down toward the contact with the pectoral fin spine. The anterior edge of the scapulocoracoid is concave, as the element widens anteroventrally. It is not clear if an anterior lamina is present; the scapula flares out posteriorly toward the pectoral spine contact (Fig. 4D). The scapulocoracoid is tilted forward. Poor preservation obscures details of the articulation to the pectoral fin spine.

Spines

The dorsal, anal and pectoral fin spines are long and slender. The ornamentation consists of straight, smooth, deep grooves and rounded longitudinal ridges. The grooves and ridges terminate on the inner (trailing) edge of all the fin spines, as clearly evident on the anterior dorsal fin spines of both NMS G.1964.31.30A and NMS G.1891.92.250 (Fig. 7). The posterior dorsal fin spine is about four-fifths the length of the anterior dorsal fin spine. In the holotype NMS G.1891.92.249 (Fig. 3) these are the only two spines preserved, with the base of

FIG. 7. — *Uraniacanthus curtus* (Powrie, 1870) n. comb. anterior dorsal fin spines: **A**, NMS G.1964.31.30A, from Hayston Hill, Angus, Scotland; **B**, NMS G.1891.92.250, from Turin Hill (Tillywhandland), Angus, Scotland. Abbreviation: **scs**, scapula shaft. Scale bars: A, 10 mm; B, 5 mm.

the anterior dorsal fin spine missing at the edge of the slab. In this specimen the spines are preserved as coarse moulds and it is impossible to count the number of grooves and ridges, although it is clear that the anterior dorsal fin spine is quite broad at the base and has a distinctive posterior-pointing curvature at the tip. The spines are better preserved in NMS G.1964.31.30A (Figs 6; 7A) but only the dorsal and anal fin spines are present. The tip of the slightly curving anterior dorsal fin spine is buried in matrix and the base is broken, but it appears to have a deep base of insertion. This spine is fairly broad with at least 11 thin ridges and grooves visible on one side (Fig. 7A). The posterior dorsal fin spine of NMS G.1964.31.30A is straight and also fairly robust. Although not as well preserved as the anterior dorsal fin spine, nine thin ridges and furrows are visible on one side; the inserted end is covered in scales. The central canal of the spine has been mineralized and exposed towards the base of the spine, showing that it was about half the radius of the original spine. The anal fin spine is slightly curved, shorter (about 60%) and thinner than the posterior dorsal fin spine. Whilst not particularly well preserved, four ridges and grooves are visible on one side.

The small specimen NMS G.1891.92.250 (Figs 4; 5; 7B) is only 20 mm long. The fin spines are poorly preserved, but correspond to the relative dimensions and shapes of the spines on the two larger specimens while having fewer grooves and ridges. The anterior dorsal fin spine (Fig. 7B) has six grooves present on one side as well as a posterior-pointing curvature at the tip.

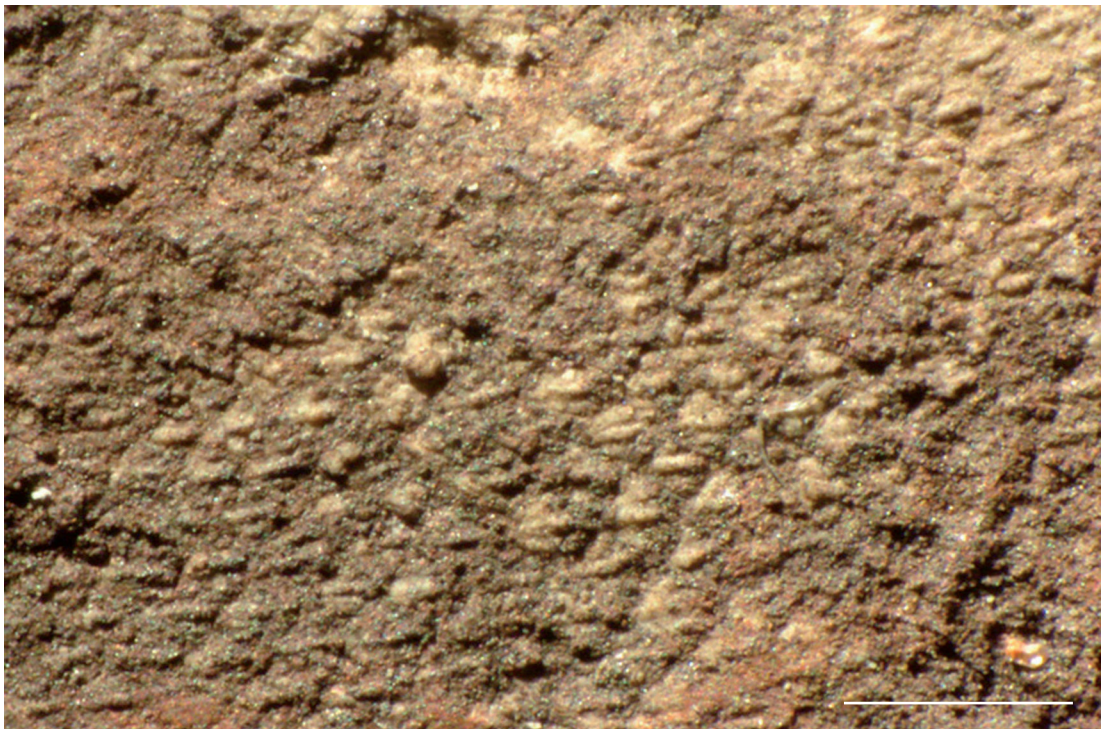

FIG. 8. — *Uraniacanthus curtus* (Powrie, 1870) n. comb., NMS G.1891.92.249, holotype from Farnell: Magnified impressions of the body scales. Scale bar: 1 mm.

The base of insertion is very deep. The posterior dorsal fin spine is too broken and crushed to be described. This is the only known specimen where the pectoral, pelvic and prepelvic fin spines are preserved. A pair of pelvic fin spines are present with the right spine being better preserved, showing three or four grooves and ridges on one side. The pelvic spines are about 75 percent the length of the anal spine. The pectoral fin spines are too crushed and broken to be described in detail and are jumbled up with another pair of crushed, broken fin spines. The latter must represent the anteriormost pair of intermediate (i.e. either admedian or first prepelvic) fin spines observed by Traquair (1892), but they cannot be visually separated from the pectoral spines. Some deterioration possibly has occurred since the specimen's collection over 130 years ago, the rock matrix being susceptible to damage particularly from humidity. The second pair of prepelvic spines just anterior to the pelvic spines are better preserved, with three grooves and ridges visible on the side of one spine; they are about half the length of the anal fin spine.

The only other visible spines, positioned in front of the scapulocoracoids (Fig. 4E), are the right first and second prepectoral spines, the latter being larger. They appear to be isolated, with no attachment to any dermal bone, and surrounded by scales. The preservation is not good enough to allow further description.

Caudal fin

The caudal fin of *Uraniacanthus curtus* n. comb. is not well preserved in any of the specimens. In NMS G.1891.92.249 and NMS G.1964.31.30A the dorsal surface is only slightly deflected from the body. The tail is heterocercal as in all acanthodians, with the main or chordal lobe longer than the hypochordal lobe. At first glance, the caudal fins on

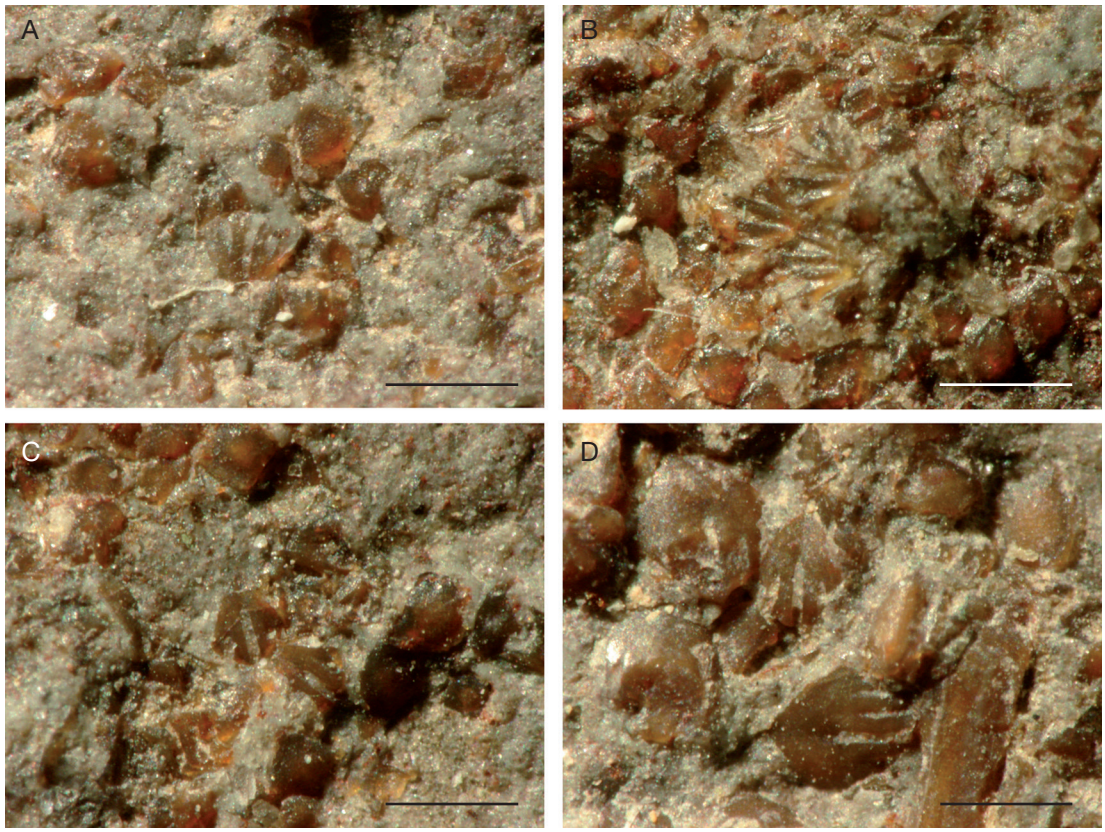

FIG. 9. — *Uraniacanthus curtus* (Powrie, 1870) n. comb., an incomplete moderate sized specimen from Hayston Hill, Angus, Scotland: **A**, **B**, NMS G.1964.31.30B, *in situ* but scattered body scales on the counterpart; **C**, **D**, NMS G.1964.31.30A, *in situ* scattered scales in the tail region of the part. Scale bars: 0.5 mm.

NMS G.1891.92.249 and NMS G.1891.92.250 appear trilobed, but this is an artefact of the folding of the fin web and sediments. The tail has a slightly forked appearance.

Squamation

The scales in NMS G.1891.92.250 are not well enough preserved to be described while in NMS G.1891.92.249 (Fig. 8) they are only preserved as coarse impressions. In NMS G.1964.31.30A/B most of the scales are preserved with their bases showing, as often occurs when a specimen is split into two halves. Where exposed (Fig. 9), the well preserved scale crowns have three to five grooves that are either quite close (Fig. 9B) or widely separated (Fig. 10D). Scales are from 0.2-0.5 mm long and wide with straight lateral crown edges converging to a single posterior point (Figs 9B-D). On mid-flank scales the grooves extend the length of the scale crown, fanning out from the posterior corner to the anterior edge of the crown. Scales of the caudal fin have a crown ornament similar to body scales, but with grooves only on the anterior end of the crown (Fig. 9D). ESEM study of individual scales (Fig. 10) from three regions on NMS G.1964.31.30A – dorsal caudal (Fig. 10A-E), dorsal posterior to the pdfs (Fig. 10F-K), and mid-flank below the posterior dorsal fin spine (pdfs) (Fig. 10L-O) – shows that the crown ornament is formed by 2-5 deep U-cross section grooves in the flat crown. The posterior point extended beyond the base (Figs 9D; 10J). Crowns on some scales

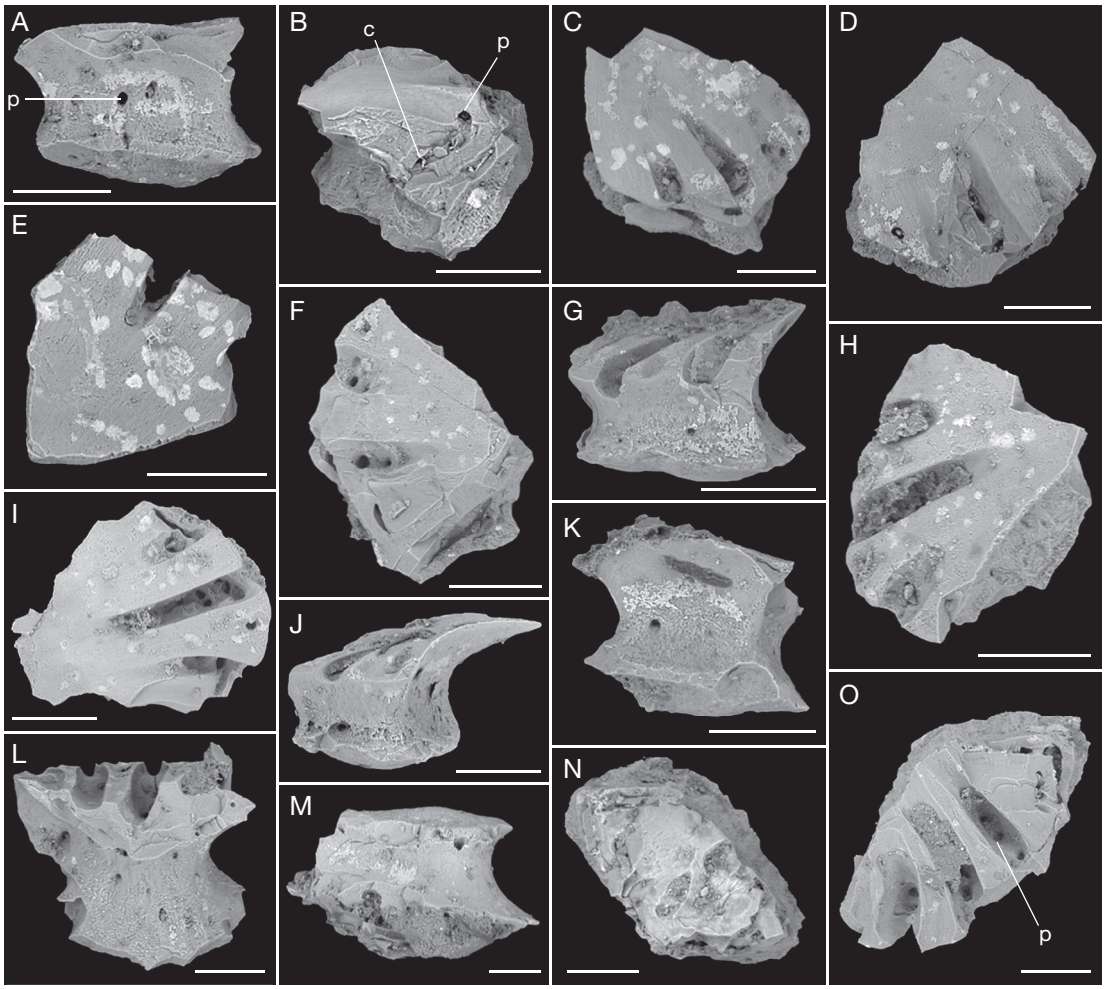

FIG. 10. — *Uraniacanthus curtus* (Powrie, 1870) n. comb., NMS G.1964.31.30A, an incomplete moderate sized specimen from Hayston Hill, Angus, Scotland. Scales removed from the dorsal caudal region (**A**-**E**), posterior to the pdfs (**F**-**K**), and mid-flank (**L**-**O**), photographed under ESEM: **A**, lateral view; **B**, anterolateral view; **C**, posterocrown view; **D**, anterocrown view; **E**, posterior view with the back of the scale crown broken off.; **F**, crown view; **G**, crown view; **H**, posterior view; **I**, lateral view; **J**, crown view; **K**, basal view; **L**, laterocrown view; **M**, lateral view; **N**, crown view; **O**, crown view. Abbreviations: **c**, canal; **p**, pore opening. Scale bars: 0.1 mm.

show short shallow incipient grooves along the anterior margin (Fig. 10G, H). The number of grooves increases with size of the scale (Fig. 10E, O). Several wide pores open out in the anterior part of the crown grooves (Fig. 10A, C, D, F, O), and also around the "waist" of the deep scale neck (Fig. 10A, G, J-L). The pores in the crown grooves lead into wide canals within the crown, as exposed in the fracture on the scale in Figure 9B. The base is shallow or flat. Thin sections of the scales reveal a well-developed network of wide circular canals in the lower crown (Fig. 11A-F), interconnected by short radial canals which also lead to the pore openings in the neck (Fig. 11A, E, F); ascending canals lead to the pore openings in the crown grooves (Figs 11C, D). Other wide longitudinal canals extend back from the anterior of the ring canals towards the poste-

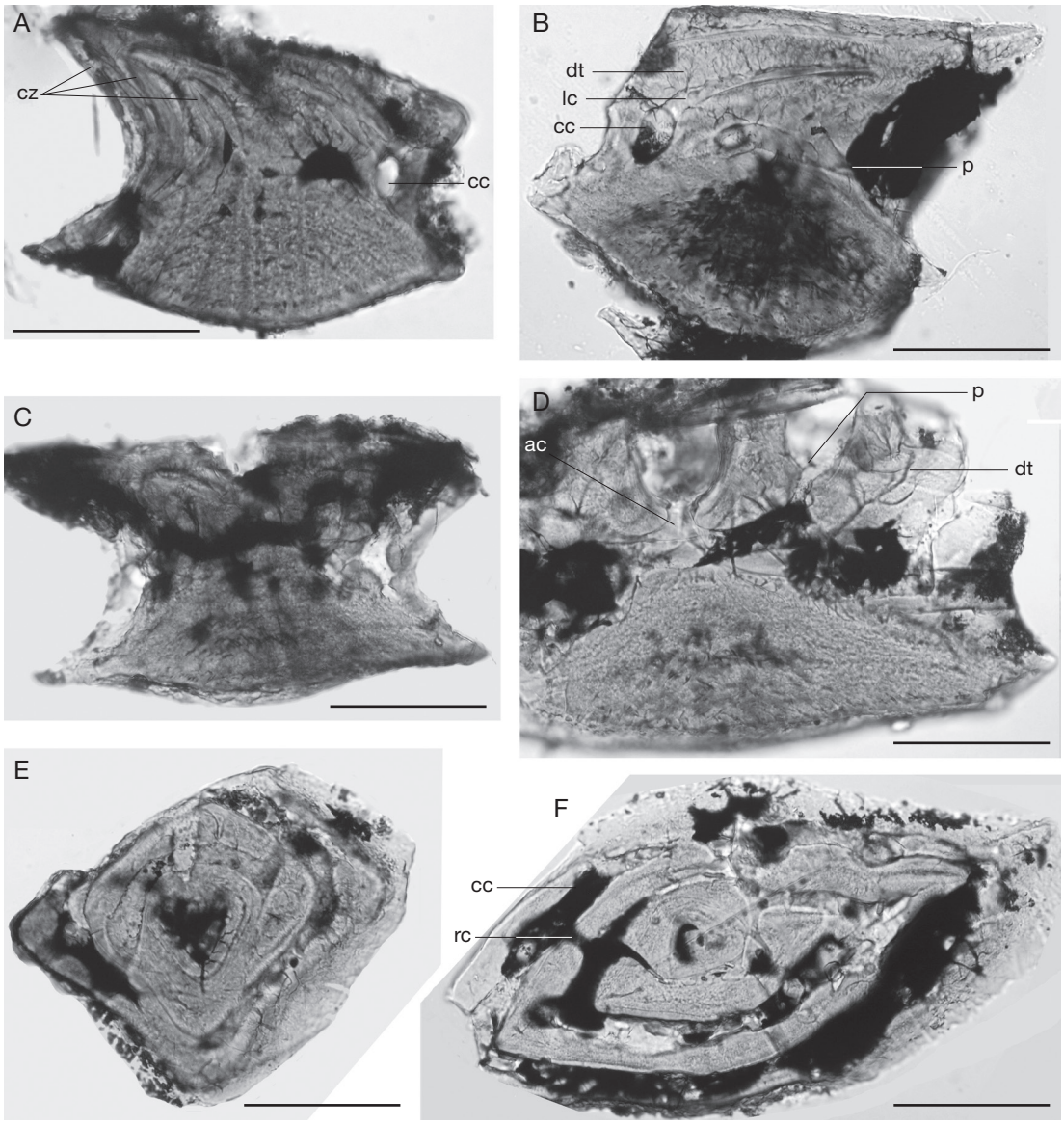

FIG. 11. — *Uraniacanthus curtus* (Powrie, 1870) n. comb., NMS G.1964.31.30A, an incomplete moderate sized specimen from Hayston Hill, Angus, Scotland. Various thin sections of scales: **A**, vertical longitudinal section; **B**, vertical longitudinal section with the anterior of the crown missing; **C**, vertical transverse section; **D**, vertical transverse section; **E**, mid crown horizontal section; **F**, low crown horizontal section. Abbreviations: **ac**, ascending canal; **cc**, circular canal; **cz**, crown growth zone; **dt**, dentine tubules; **lc**, longitudinal canal; **p**, pore opening; **rc**, radial canal. Scale bars: 0.1 mm.

rior tip of each growth zone (Fig. 11B). All the wide canals are interconnected to form a single network, rather than separate "pore" canal and vascular canal systems. Dentine tubules extend from the wide canals through each crown growth zone; each scale has 2-4 growth zones (Fig. 11A, B, D). Sharpey's fibre canals extend through the acellular base (Fig. 11A-D).

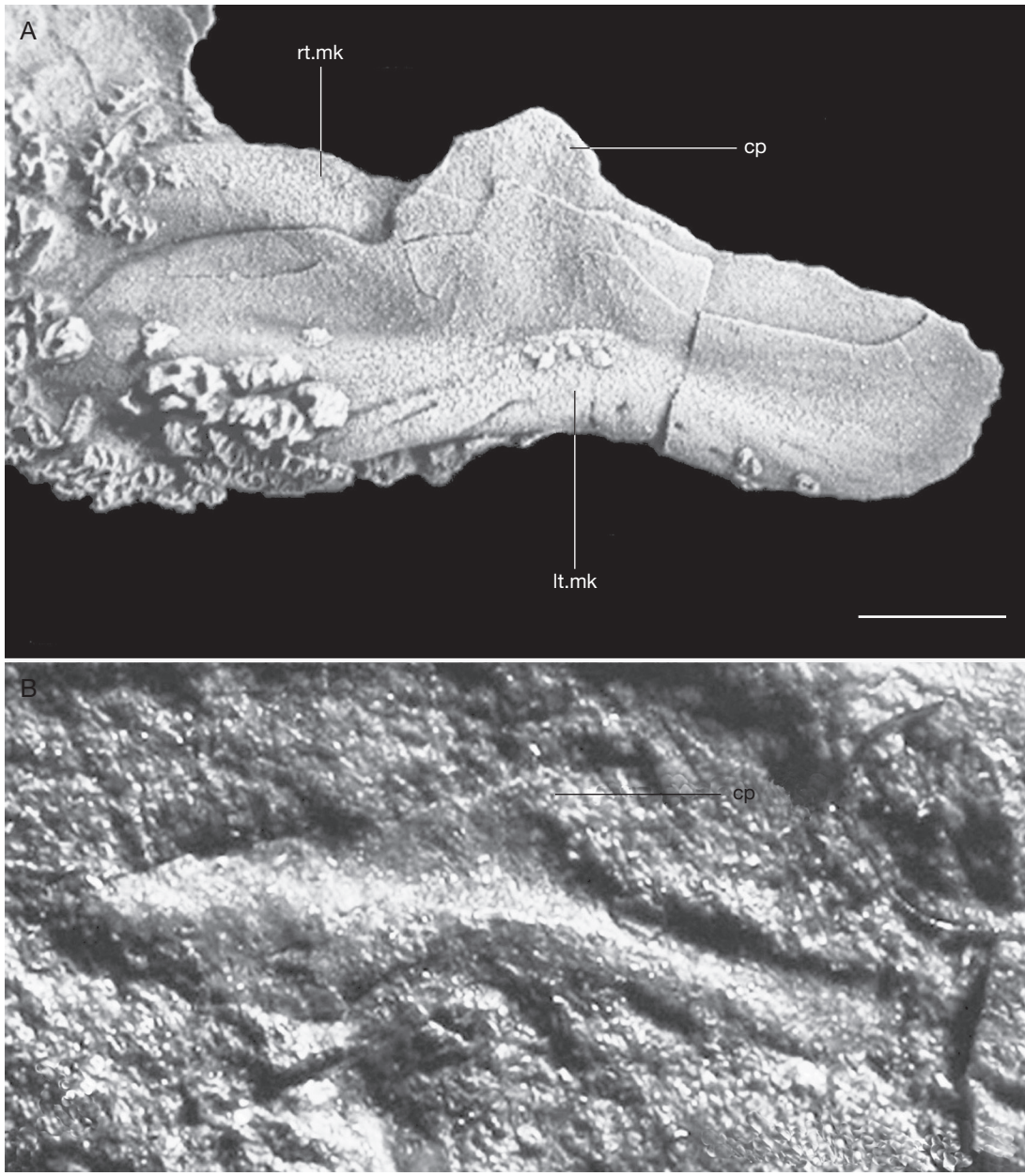

Fig. 12. - *Uraniacanthus* Meckel's cartilage: **A**, *U. probaton* (Bernacsek & Dineley, 1977) n. comb., UALVP42095. Modified from Hanke & Davis (2008: fig. 9D) by being flipped horizontally 180 degrees and relabelled; **B**, *U. curtus* (Powrie, 1870) n. comb., NMS G.1891.92.250. Abbreviations: **cp**, coronoid process; **lt.mk**, left Meckel's cartilage; **rt.mk**, right Meckel's cartilage. Scale bars: 1 mm.

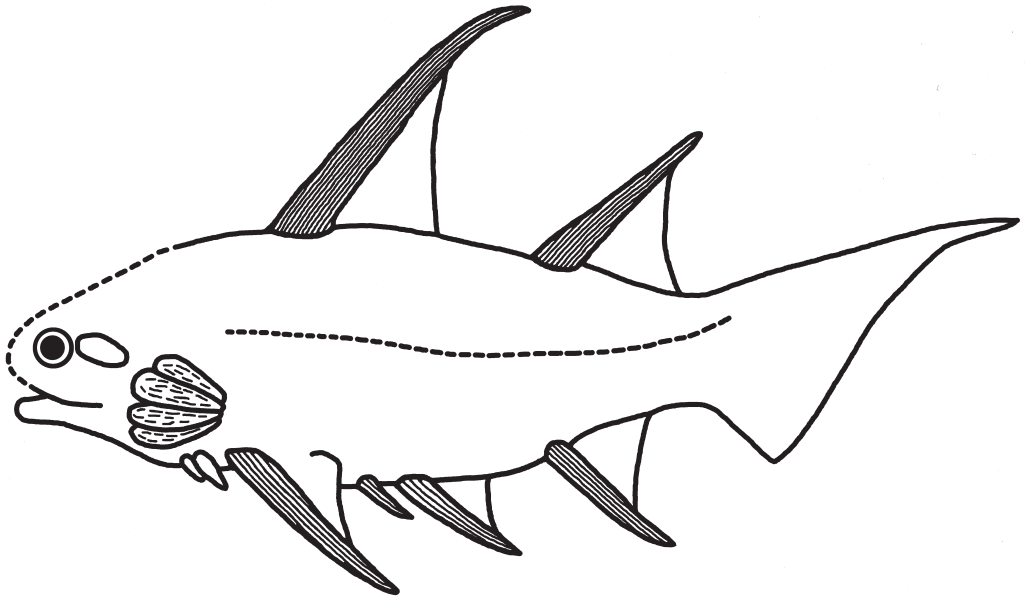

FIG. 13. — Reconstruction of *Uraniacanthus curtus* (Powrie, 1870) n. comb.

DISCUSSION

Powrie (1870) justified the assignment of *Uraniacanthus curtus* n. comb. to the genus *Euthacanthus* based on the shape of the spines and scales. However *U. curtus* n. comb. is a much shorter, deep bodied fish than *Euthacanthus* with an anterior dorsal fin spine that is longer than the posterior dorsal fin spine. *Uraniacanthus curtus* n. comb. also has far fewer prepelvic fin spines and opercular covers than *Euthacanthus*, and has a smooth bony plate on the occlusal surface of the Meckel's cartilage. Our re-examination of the three specimens of *U. curtus* n. comb. reveals its close similarity to *Uraniacanthus spinosus* and particularly to *Uraniacanthus probaton* n. comb. which has the best preservation of the three species. Unfortunately, the head and shoulder girdle are very poorly preserved in *U. spinosus* and so direct comparison of this area is mostly made with *U. probaton* n. comb.

Certain details of the original description by Miles (1973) of the type species of *Uraniacanthus*, *U. spinosus*, have been challenged by Hanke & Wilson (2004). They stated that the jaw fragments identified on the body fossils of *U. spinosus* (Miles 1973: pl. 13, fig.1) were not jaw elements but spiny postorbital plates similar to those on *Uraniacanthus probaton* n. comb. (e.g., Hanke & Davis 2008: fig. 7E, F). They also stated that the isolated jaw described by Miles (1973: pl. 12, fig. 1), whilst found at the same outcrop, was not part of an articulated fish and that therefore, there was no evidence for *U. spinosus* having dentigerous jaw bones, and the jaw structure in *U. spinosus* is unknown. This is important to note as the most striking similarity between *Uraniacanthus curtus* n. comb. and *U. probaton* n. comb. is the almost identical ossification on their lower jaws (Fig. 12; Hanke & Davis 2008: fig. 9D). The difference is minor, with the posterior end of the jaw forming a spoon-shaped blade in *U. curtus* n. comb., and a blade with a shallow depression in *U. probaton* n. comb. However, as the only specimen of *U. curtus* n. comb. with the Meckel's cartilage preserved is a juvenile (NMS G.1891.92.250), it is possible that the adult fish might have had a depression at the posterior end of the jaw as in *U. probaton* n. comb. Hanke & Davis (2008) noted that *U. probaton*

n. comb. does not have dermal mandibular splint bones supporting the ventral edge of the Meckel's cartilage (previously described in many other diplacanthiforms), and these are also absent in *U. curtus* n. comb. As noted earlier, we propose that the supposed mandibular splints in other diplacanthiforms are smooth prearticular dental plates like those in *Uraniacanthus*, but lacking the coronoid process diagnostic of the Gladiobranchidae. The actual jaw cartilages are unmineralized in all diplacanthiforms, so it is unclear if the occlusal plates are of dermal origin (like the dentigerous jaw bones of ischnacanthiforms) or perichondral ossifications as found in acanthodiforms. Thin layers visible in *U. probaton* n. comb. plates (Fig. 12A) could suggest the latter, but the ossifications do not envelop the whole Meckel's cartilage as in acanthodiforms. The presumed position of the plates in *Uraniacanthus* mirrors that of the toothed prearticular bone in osteichthyans, some of which also have a dorsal coronoid process, but this structural similarity is surely functional not homologous. While Brazeau's (2009) coding of placoderm gnathal plates, ischnacanthiform dentigerous bones and osteichthyan palatine/coronoid series as homologous structures in his cladistic analysis of early gnathostomes is contentious, it seems possible that ischnacanthiform, diplacanthiform and osteichthyan prearticular plates could be homologous structures.

The postorbital bone is quite well preserved in *Uraniacanthus probaton* n. comb. (Hanke & Davis 2008: fig. 7E, F) and *Uraniacanthus spinosus* (Miles 1973: pl. 13, fig. 1: labelled as dg.b, dentigerous bone). Surface ornamentation on the bone differs between the species, but they are similar otherwise (Hanke & Davis 2008). In *Uraniacanthus curtus* n. comb. the postorbital bone is only preserved in NMS G.1891.92.250 as a triangular internal impression (Fig. 4F). It was clearly robust for the size of fish but the external ornament is not exposed.

All three species share very similar shaped and ornamented spatulate opercular plates. The opercular plates in *Uraniacanthus spinosus* (Miles 1973: pl 13. fig. 1; Hanke & Davis 2008: fig. 8) are virtually identical to those of *Uraniacanthus probaton* n. comb. as noted by Hanke & Davis (2008: figs 6A, 7H). Although not so well preserved, the *Uraniacanthus curtus* n. comb. plates show no obvious difference to those of the other two species (Fig. 4C).

The scapulocoracoid of *Uraniacanthus curtus* n. comb. (Fig. 4D) is a perichondrally-ossified structure closely resembling the scapulocoracoid of *Uraniacanthus probaton* n. comb. (Hanke & Davis 2008: fig. 8B). However, the preservation is insufficient to identify whether there is a high posteriorly directed flange or an anterior lamina present as described in *U. probaton* n. comb. (Hanke & Davis 2008). As in *U. probaton* n. comb. (and most acanthodians), the scapulocoracoid is tilted forward in *U. curtus* n. comb. but poor preservation obscures the articulation to the pectoral fin spine, although the two structures appear similarly associated in both species. Although poorly preserved, the scapulocoracoid of *Uraniacanthus spinosus* closely resembles that of the two other species (Miles 1973: pl. 13, fig. 1).

The median fin spines of the three *Uraniacanthus* species all have very deep bases of insertion (like all diplacanthiforms), particularly the dorsal spines. The fin spines of *Uraniacanthus spinosus* and *Uraniacanthus probaton* n. comb. are essentially identical. *Uraniacanthus curtus* n. comb. differs slightly in that the dorsal fin spines have more grooves and ridges than in the other two species, relative to the size of the fish. The deep bases of insertion are not well preserved in either *U. spinosus* or *U. curtus* n. comb., but in *U. probaton* n. comb. close set parallel ridges are preserved (Hanke & Davis 2008), a characteristic of all diplacanthiforms.

Ornamented scales cover the entire body of *Uraniacanthus curtus* n. comb., including the caudal fin (Fig. 8), thus differing to *Gladiobranchus probaton* which has both ornamented and smooth scale crowns (Hanke & Davis 2008: fig. 11). The scale crowns are very poorly preserved in *Uraniacanthus spinosus* and only visible in isolated areas (Miles 1973: text-fig. 17B; Young 1995: fig. 2). It is therefore unclear if smooth crowned scales are present or not in this species.

Hanke & Davis (2008) comprehensively revised the description of *Uraniacanthus probaton* n. comb. based on new material. They noted the close similarity between *U. probaton* n. comb. and *Uraniacanthus spinosus* and placed them in the

same family, the Gladiobranchidae, but did not synonymize the genera. They concurred with the earlier assertion by Hanke & Wilson (2004) that the Gladiobranchidae were diplacanthoid rather than ischnacanthiform taxa, contra Miles (1973). Miles (1973) considered that *U. spinosus* was quite similar to the diplacanthoids, but due to the misidentification of dentigerous jaws placed them in the Ischnacanthiformes.

Because the order Climatiiformes Berg, 1940 is now considered a paraphyletic group by most workers (Hanke & Wilson 2006 and references therein), we have reverted to recognising the order Diplacanthiformes first erected by Berg (1940).

The composite reconstruction of *Uraniacanthus curtus* n. comb. in Figure 13 is based on all three specimens available to us, with the general outline based on the reconstruction of *Uraniacanthus probaton* n. comb. by Hanke & Davis (2008: fig. 1). All three specimens conform very well to the outline of this species in the areas where they are preserved. As the pectoral fin web and the profile of the dorsal surface of the head are not known for *Uraniacanthus curtus* n. comb., the reconstruction has been extrapolated from *Uraniacanthus probaton* n. comb., the species with greatest similarity to *U. curtus* n. comb. A similar body/head profile is a feature of most Middle Devonian diplacanthiforms. The only significant discernable differences between these two species is the greater number of grooves and ridges on both dorsal fin spines of *U. curtus* n. comb. and its lack of smooth-crowned scales on posterior areas of the body. These differences are very minor and not enough to warrant genus separation. Similarly, *U. probaton* n. comb. and *U. curtus* n. comb. differ from *Uraniacanthus spinosus* in only minor characters, plus the lack of evidence for a smooth dental plate on the lower jaw of *U. spinosus*.

BIOGEOGRAPHY

We have shown here that the genus *Uraniacanthus* occurs in the Lower Old Red Sandstone of the Welsh Borderland of England and the Midland Valley of Scotland, and the Delorme Formation of Canada. All these deposits are considered to be Lochkovian (earliest Devonian) in age (Galbrielse *et al.* 1973; Allen 1977; Trewin & Davidson 1996). Articulated remains of the ischnacanthiform acanthodian *Ischnacanthus gracilis* (Egerton, 1861) also occur in the Delorme Formation and the Midland Valley (e.g., Powrie 1864; Bernacksek & Dineley 1977) with disarticulated remains of the genus described from the Welsh Borderland (e.g., White 1961). The acanthodian genus *Parexus* Agassiz, 1844-1845 long known from the Midland Valley is also known from the Welsh Borderland (e.g., Traquair 1894; Ørvig 1967). The above areas clearly share several acanthodian genera, but further consideration on overall correlation must await the completion of further descriptions of the fauna of these deposits.

Many acanthodian genera have been erected based on isolated scales in the Early Devonian deposits of the Baltic region. In the preparation of this paper, we have observed that *Euthacanthus* is present in both the Baltic region and the Midland Valley of Scotland and that *Uraniacanthus* is also probably present. Some of the scales from the Lochkovian of Lithuania that Valiukevičius (1998: pl. 5, figs 11, 12) assigned to *Nostolepis gracilis* Gross, 1947 closely resemble scales from *U. probaton* n. comb. and differ to the type material of *N. gracilis* (Gross 1947: pl. 7, figs. 1-4) in having a flat crown with deep grooves, and sometimes "warts" or large bumps low on the posterior neck (a feature diagnostic, but not present on all scales, of diplacanthiform taxa), and appearing to lack large pore openings in the crown grooves. Other scales with broad ridges from the Lochkovian Severnaya Zemlya Formation, arctic Russia which Valiukevičius (2003: figs 27A, B, 28M) ascribed to *Nostolepis* sp. cf. *Nostolepis gracilis* are also very similar to those of *Uraniacanthus*. Unfortunately the histological structure of those figured scale forms is not known.

Further afield, Forey *et al.* (1992) referred incomplete isolated fin spines from the Emsian (late Early Devonian) Jawf Formation of Saudi Arabia to *Uraniacanthus spinosus*. We do not consider there are sufficient characters preserved in these remains to allow generic or specific identification. Most diplacanthiforms have a similar spine ornament of equal width, smooth longitudinal ridges, often with a slightly

wider leading edge ridge, on the exserted part, and fine closely spaced ridges on the inserted part (e.g., Young & Burrow 2004: figs 5C, 6F). The scales of *Milesacanthus ancestralis* Burrow, Lelievre & Janjou, 2006, also from the Jawf Formation, have some superficial resemblance to *Uraniacanthus* scales, but scales of *Milesacanthus* differ in having many more grooves on the crown. Also, the type species *Milesacanthus antarctica* Young & Burrow, 2004 from the Givetian of Antarctica which is based on articulated specimens, does not have spatulate opercular covers or a robust postorbital plate, diagnostic features for *Uraniacanthus*. *Milesacanthus* also has a blade-like bone in the lower jaw, rather than the occlusal plate with a coronoid process present in *Uraniacanthus probaton* n. comb. and *Uraniacanthus curtus* n. comb. The revelation that scales of *U. curtus* n. comb. and *Milesacanthus* spp. have a canal system opening out to the surface via pores in the crown grooves is likely to be significant both phylogenetically and functionally.

CONCLUSIONS

Reassignment of "*Euthacanthus*" *curtus* to *Uraniacanthus* marks the first "new" genus of acanthodians recognised in the Lochkovian strata of the Lower Old Red Sandstone in Scotland since Miles (1973) referred "*Climatius*" *uncinatus* Powrie, 1864 to *Vernicomacanthus* Miles, 1973. Our re-examination of *U. curtus* n. comb. specimens reveals features including a cone-like postorbital plate, spatulate opercular covers, a smooth gnathal bone with a coronoid process on the lower jaw, and ornamented scales which ally the species with "*Gladiobranchus*" *probaton* from the Lochkovian of Canada and *Uraniacanthus spinosus*, from the Lochkovian of England, although the nature of the gnathal bones is unknown in the latter. The minor differences between the species indicate that they should all be assigned to the one genus *Uraniacanthus* by priority, giving biogeographical support for faunal exchanges between Canada, England and Scotland during the earliest Devonian based on distribution of articulated fish, and probably also with the Baltic and arctic Russia based on our re-identification of isolated scales.

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