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Acanthorhachis, a new genus of shark from the Carboniferous (Westphalian) of Yorkshire, England

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Abstract – An association of diverse hollow spines and dermal denticles (ichthyoliths) from the Carboniferous (Westphalian) of Todmorden, Yorkshire, England are attributed to a new genus of enigmatic shark that may lie close to *Listracanthus* Newberry & Worthen, 1870. Scanning electron microscopy shows that denticle morphology is highly variable, but forms a morphocline including elongate multi-spined elements as well as robust dome-like stellate denticles and recurved spinose elements. Histological analysis suggests an absence of enameloid. Continuous variation of form between elongate multi-cusped spines to boss-like circular denticles shows that all previously described Palaeozoic species of *Listracanthus* are probably junior synonyms of the type species *L. hystrix* Newberry & Worthen, 1870. The status of *Listracanthus* as a surviving 'Lilliputian' taxon after the Permian extinction is questioned. Although the new specimen has affinities with *Listracanthus*, significant differences in the form of the posterior spines on elongate denticles warrants its placement in the new genus *Acanthorhachis* gen. nov. The family Listracanthidae is erected to accommodate *Listracanthus* and *Acanthorhachis*.

Keywords: *Acanthorhachis* gen. nov., Carboniferous, Chondrichthyes, dermal denticles, England.

1. Introduction

Listracanthus Newberry & Worthen, 1870 is a 'form' taxon representing an enigmatic chondrichthyan known only from its mostly small but elaborate spines and a few dermal denticles (ichthyoliths). It ostensibly ranges from the Carboniferous to the Triassic (Mutter & Neuman, 2006) and was first described from Carboniferous strata in Illinois, USA (Newberry & Worthen, 1870). Elsewhere in the United States it has been reported from Ohio, Indiana, Missouri and Kansas (Newberry, 1873, 1875; Newberry & Worthen 1870; Hibbard, 1938; Chorn & Reavis, 1978; Schultze *et al.* 1982; Hamm & Cicimurri, 2005), while in Europe the genus has been reported from the Carboniferous of England (Stobbs, 1905; Edwards & Stubblefield, 1948), Scotland (Woodward, 1891, p. 149), Belgium (Woodward, 1891; Koninck, 1878; Derycke *et al.* 1995), Germany (Bolton, 1896; Schmidt, 1950) and the Czech Republic (Lang, 1979; Štamberg & Lang, 1979). In Asia *Listracanthus* has been reported from the Carboniferous of northern China (Lu *et al.* 2002, 2005) and also from the Permian of the Ural region of Russia (Ivanov, 2005). Turner (1993) reported *Listracanthus* in the Carboniferous of Queensland, Australia (the first occurrence in the southern Hemisphere) on the basis of a single spine, but several dermal denticles figured by her as 'hybodontid' also resemble those of *Listracanthus*. *Listracanthus* has also been considered present in the Triassic of Canada where its occurrence has been considered a part of the so-called Lilliputian recovery fauna after the Permian mass extinction event (Mutter & Neuman, 2009). Although enigmatic, *Listracanthus* was considered by Patterson (1965) to be a junior synonym of the holocephalan *Deltoptychius*, but recent workers accept that *Listracanthus* represents an early, although somewhat unusual, elasmobranch (e.g. Mutter & Neuman, 2006). Here we describe a new specimen of elasmobranch with associated spines and denticles that resembles *Listracanthus* but displays a wide variety of dermal denticle morphotypes as well as several significant differences in spine structure from the holotype of *Listracanthus*.

Institutional abbreviations. UALVP – Laboratory for Vertebrate Paleontology – University of Alberta – Edmonton – Canada; YPM – Yale Peabody Museum – USA; NHMUK – Natural History Museum – London.

2. Locality

Material examined in this study was collected by one of the authors (PdS) on the east side of an old colliery spoil dump on Todmorden Moor, Calderdale District, West Yorkshire (NGR SD 89292 24865) (Fig. 1a). This spoil dump was generated from mine workings of the Sandy Road Colliery belonging to the East Lancashire Brick Co. Ltd., abandoned in 1966. It appears to be located close to the boundary between the Millstone Grit and the Lower Coal Measures (Wright *et al.*

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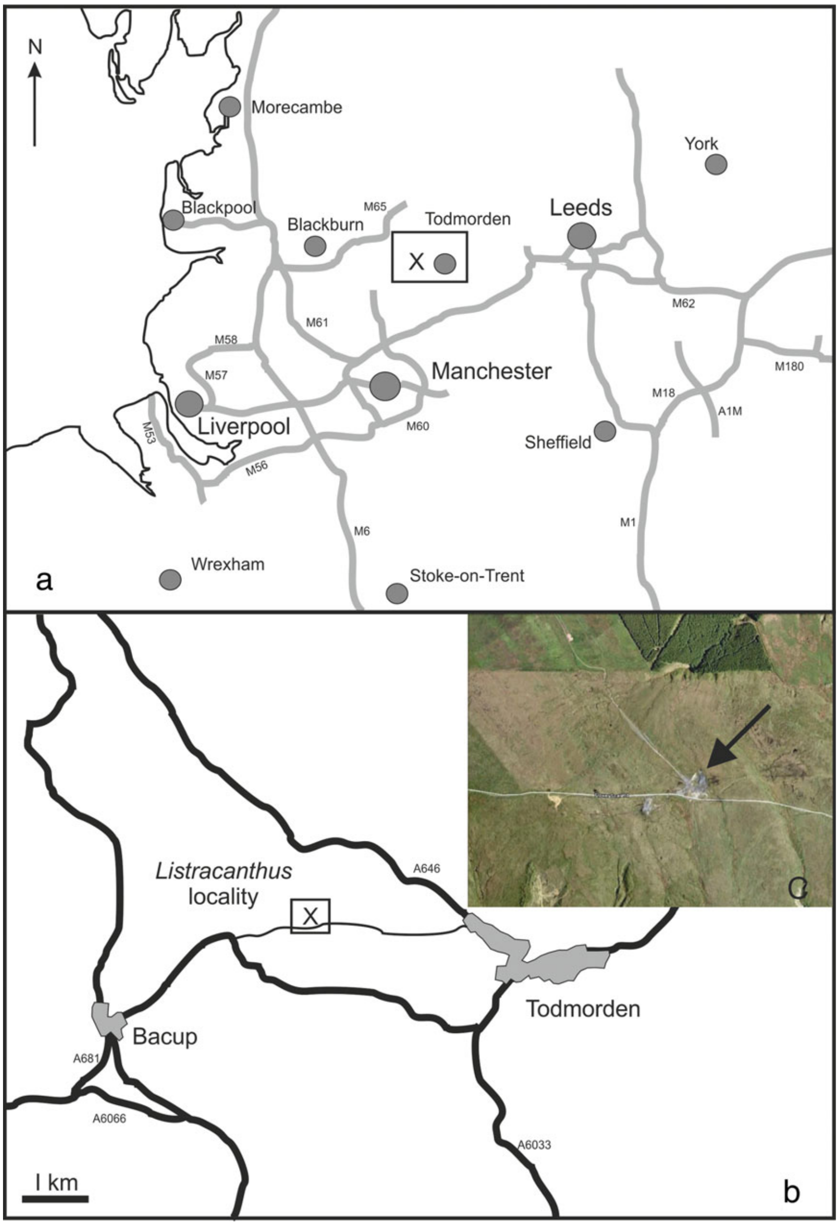

Figure 1. (Colour online) Locality maps for the Todmorden *Acanthorhachis* occurrence. (a) Generalized map of central England showing the location of Todmorden with respect to main commercial centres. (b) The *Acanthorhachis* locality is an abandoned mine dump by the field road between Todmorden and Bacup. (c) Insert showing Google Earth image of abandoned mine dump.

1927) (Fig. 2). Presently there is very little exposure of the fossiliferous strata in this region, but the spoil dump is well-known for yielding so-called ‘coal balls’, carbonate concretions rich in 3D plant remains (Stopes & Watson, 1908), and goniatites from the *Gasteroceras listeri* marine band. There are few accounts of vertebrate remains from this locality; an early exception is the report of fish remains by Bolton (1889) who described coelacanth and indeterminate fish bones from a locality east of Bacup and an occurrence of *Listracanthus* in shales above the Bullion Coal, also at Bacup (Fig. 1), but this specimen was lost at the time of its discovery (Bolton 1896). The abundance of ‘coal balls’ at this locality has made it an important historic site, which was collected by palaeobotanist Mary Stopes in 1903 (Briant, 1962). Todmorden Moor is currently registered as a site of Local Geological Interest by the West Yorkshire Geology Trust.

3. Material and methods

The associated spines and denticles examined in this analysis were all obtained from a concentration in a layer within a dark grey limestone fragment measuring *c.* 160 × 90 × 40 mm. Part of the fragment was broken and placed in acetic acid at 7–10 % concentration until all the matrix had dissolved (approximately one month). A second piece was placed in acetic acid, but with an acid-resistant coating

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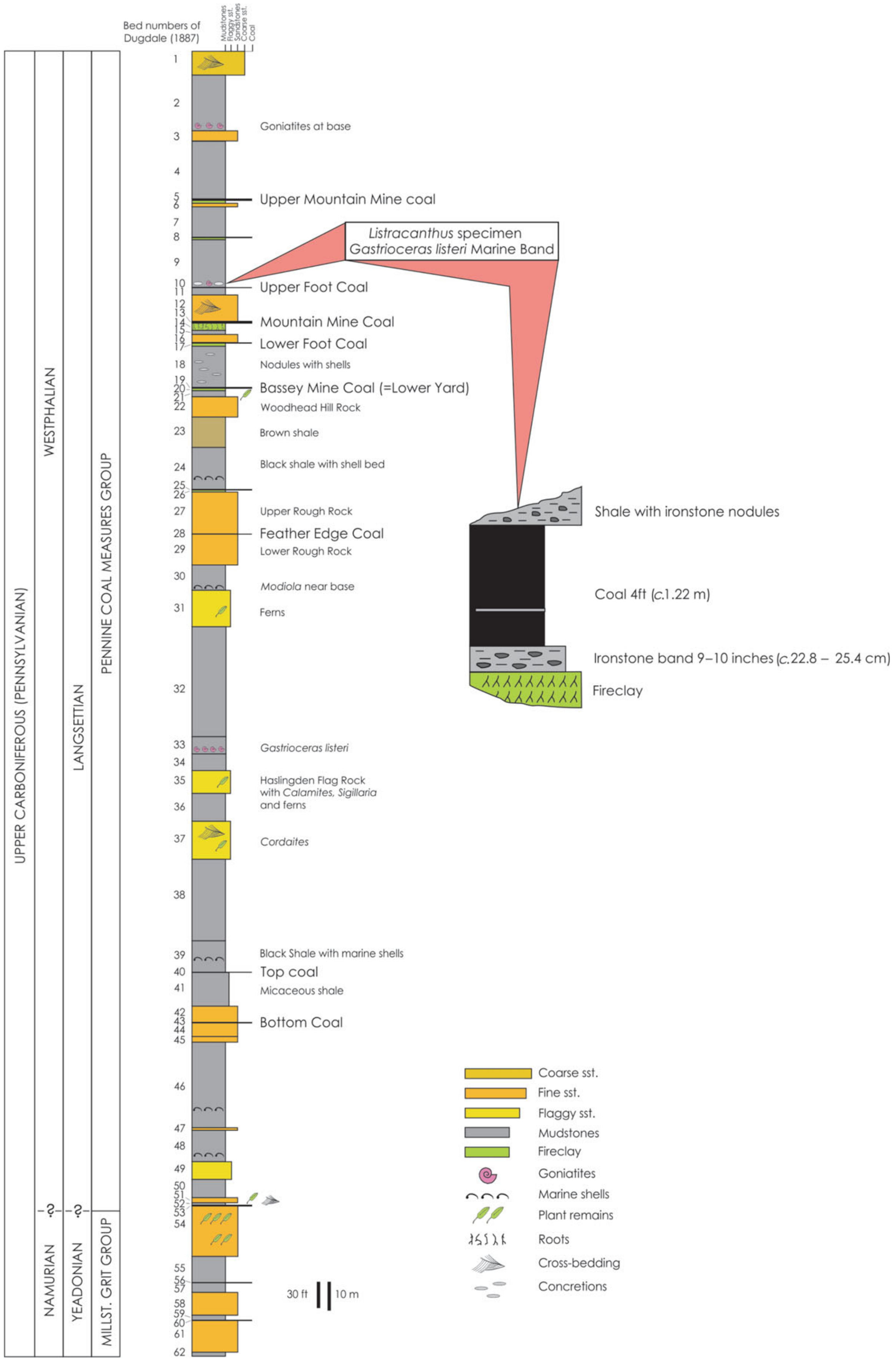

Figure 2. (Colour online) A generalized stratigraphic section for the Westphalian sequence in the vicinity of Todmorden. The insert (arrowed) is a more detailed section seen in the abandoned coal mine that yielded the *Acanthorhachis* specimen, from Dugdale (1887).

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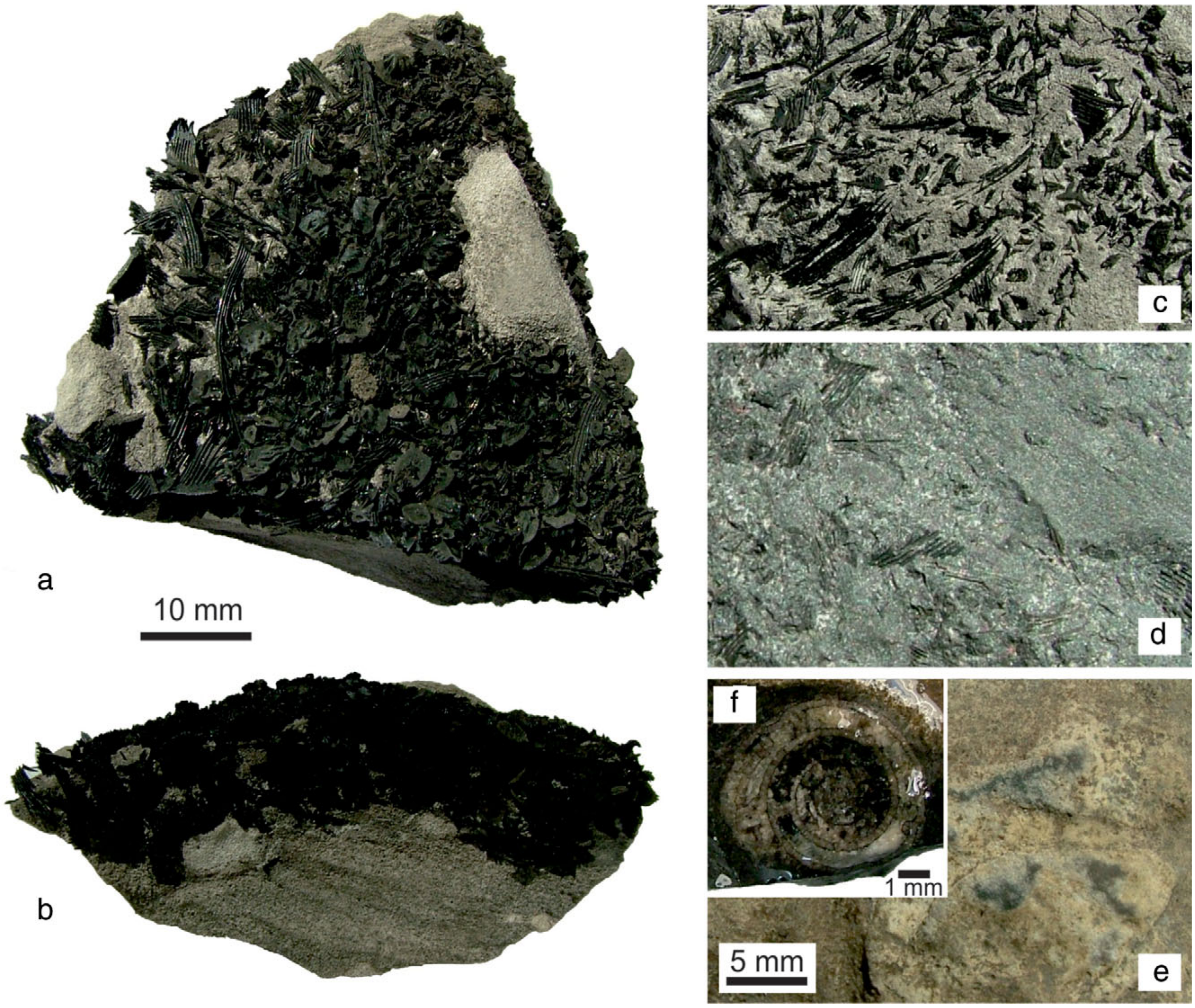

Figure 3. (Colour online) A portion of the specimen yielding the *Acanthorhachis* denticles after partial dissolution in 10 % acetic acid: (a) looking down onto bedding plane surface (NHMUK P73205a); (b) etched section through the portion (NHMUK P73206b); (c) detail of the distribution of denticles on bedding after etching and (d) before etching showing fresh, unweathered colour of the matrix; (e) weathered surface showing cream colouration; and (f) goniatite cf. *Gastrioceras listeri* photographed under alcohol. The specimen is seen in sagittal section, showing this was not the original outer surface of the concretion.

(paraloid) applied to the sides so that a bedding plane surface was partially etched to reveal several large spines without complete separation from the matrix. Acid-resistant residues were rinsed initially in tap water, with a final rinse in distilled water. Suspended clay was decanted off and the remaining insoluble residue contained only dermal denticles and did not require sieving. A similar process was also performed on pieces of Dinantian crinoidal limestone from Steeplehouse Quarry, Wirksworth, Derbyshire containing *Petrodus* denticles for comparative purposes. Specimens for electron microscopy analysis were mounted on flat aluminium stubs, sputter coated with gold and examined using a JEOL JSM 6100 machine.

Thin-sections were produced from remaining fragments and examined using a petrological microscope and photographed with an Olympus digital camera. Images have been manipulated using Corel Photo-Paint X5 and CorelDraw X5.

4. Geological setting and stratigraphy

4.a. Geological setting

The geology of Rossendale and Todmorden Moor is described by Aitken (1868) and Wright *et al.* (1927) with a more recent, though general, account provided by Aitkenhead *et al.* (2002). The fossiliferous strata are located on the eastern flank of the Rossendale Sub-basin of the Pennine Basin and are part of an anticline associated with the so-called Todmorden Smash Belt, where they dip gently to the SW. Exposures of the fossiliferous strata are rare on Todmorden Moor due to extensive cover by Holocene peat deposits, but a good section can be seen in the small stream on the eastern

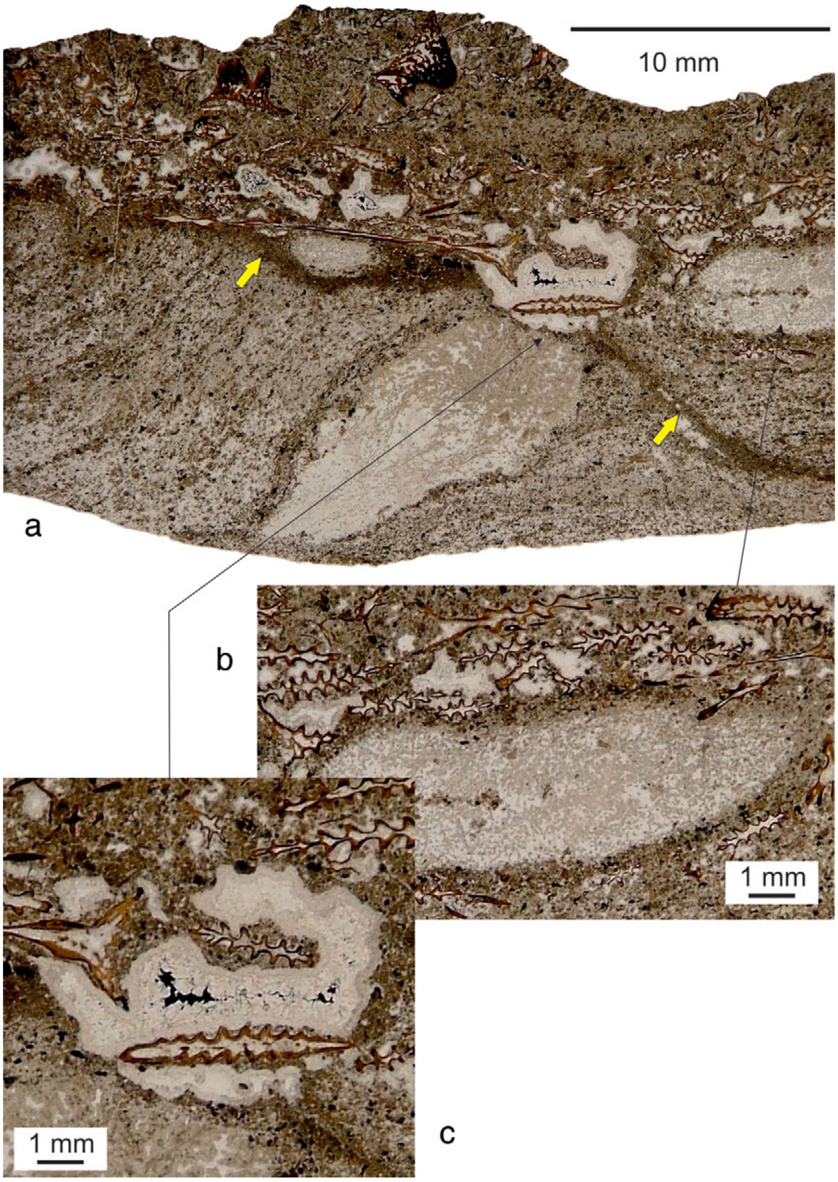

Figure 4. (Colour online) Thin-section through the *Acanthorhachis* -bearing nodule (NHMUK P73207c). (a) Laminated mudstone with microspar cement overlain by non-laminated mudstone rich in *Acanthorhachis* denticles. The yellow arrows highlight the contact. (b) Ellipsoid carbonate 'clast' perhaps representing pinched-out lamina, overlain by denticle-bearing sediment. The flat-sided elongate spines of *Acanthorhachis* lie parallel to the bedding surface. (c) A vuggy cavity within the denticle-bearing lamina lined with at least three generations of calcite.

side of the Calder Valley at national grid reference [SD 90762 27215] near Coal Clough Farm.

4.b. Stratigraphy

A complete stratigraphic log for Todmorden Moor has not been published, but generalized accounts of the sequence of Coal Measures of Rossendale are given by Dugdale (1887) and are presented diagrammatically here (Fig. 2). The lithostratigraphy of the British Coal Measures, with details of the Pennine Basin and the scheme followed here, is given by Waters *et al.* (2007).

Although the material described here was not found *in situ*, there are very good reasons for being able to provide reasonable stratigraphic data for their occurrence. The material was found on a mine spoil dump derived from the working of coal seams lying towards the base of the so-called Lower Coal Measures (Westphalian, Langsettian) of the Pennine Coal Measures Group (Fig. 2) that are exposed on the summit of Todmorden Moor. Here a heterolithic sequence of shales, clays sandstones and thin coals overlies the Kinderscoutian (Stainmore Formation = Midgely Grit = Pule Hill Grit Formation = Todmorden Grit of earlier authors) of the Millstone Grit Group (Aitkenhead *et al.* 2002). Several of the coal seams were worked, with the Sandy Lane Colliery working the Union Seam, a combination of the Lower Mountain and Upper Foot coal seams (Fig. 2). These two seams are

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indicated separately in the log described by Dugdale (1887) and occur towards the top of his section (Fig. 2).

4.b.1. Biostratigraphy

Much of the UK Westphalian is in non-marine facies and has been zoned using non-marine bivalves, with the lower part of the Lower Coal Measures of the Pennine Coal Measure Group lying within the *Lenisculacata* biozone. However, a number of marine bands occur within the Lower Coal Measures in the Pennine Basin, allowing more refined zonation and permitting correlation with marine sequences elsewhere. Nodules containing goniatites occur in the strata immediately overlying the Union Coal at Todmorden Moor, where they could be seen in the roof of the galleries (the miners calling them 'Baum pots'; Wright *et al.* 1927). Brown (1841) and Wright *et al.* (1927) record a number of fossils from the Baum pots, including the goniatites *Gastrioceras subcrenatum*, *G. listeri*, the bivalves *Posidoniella* sp. and *Pterinopecten* sp. and plant remains. During field work, we also found orthoconic nautiloids in these concretions.

4.b.2. Chronostratigraphy

The presence of the goniatites *Gastrioceras subcrenatum* and *G. listeri* permits correlation with sequences elsewhere, and indicates a Lower Westphalian, Langsettian (Bashkirian of Gradstein *et al.* 2004) age for the sequence at Todmorden Moor, with an age of *c.* 315 Ma (Davydov *et al.* 2004).

5. Sedimentology, diagenesis, taphonomy and palaeoenvironment

5.1. Sedimentology

The observations made here are limited because of the 'extra situ' context of the sample containing the ichthyoliths, and are based solely on the hand specimen and petrographic sections taken from it. The matrix of the sample is a dark grey mudstone with numerous black, reflective ichthyoliths adding to its dark appearance (Fig. 3). Weathered surfaces are cream coloured, and mild etching by humic acids has revealed some fine-scale sedimentary structures including laminae and possible cross-stratification (Fig. 3e). Bedding is clearly present giving the specimen a tabular aspect. The way 'up' is not so easy to discern. The ichthyoliths are concentrated into a single layer of 10–20 mm thick. Contact of the ichthyolith layer with layers either side is well-defined, but the matrix of the bounding layers appears similar to that of the ichthyolith layer. Fine laminae of 1–2 mm revealed on an etched surface are evident, while a thin section reveals them to be truncated by the ichthyolith layer (Fig. 4a). This truncation suggests that the laminated layer predates the ichthyolith layer.

5.2. Diagenesis and taphonomy

Cementation of the clays to a carbonate mudstone appears to be of a relatively early diagenetic origin as there is no crushing and fracturing of the ichthyoliths or enclosed goniatites. The matrix of the ichthyolith layer comprises clays with a flocculated or pelletal texture cemented by calcite microspar (Fig. 4c). Two elongate, clast-like bodies may be a relic of a 'pinched-out' layer, suggesting some soft sediment deformation (Fig. 4b). It is therefore possible that the ichthyoliths occur in a small scour, or are part of an individual that sank into soft sediment in a similar manner to that reported for fishes from the Cretaceous Santana Formation of NE Brazil (Martill, 1997). All of the ichthyolith remains pertain to a single taxon in which dermal denticle variation is considerable. The largest elements in the assemblage are spine-like denticles of up to 40 mm length associated with denticles of less than 1 mm diameter. There is a preferred orientation in that the laterally flattened spine-like denticles lie in the plane of the bedding, but otherwise do not appear to have a preferred directional orientation. All of the denticles are in excellent condition with numerous spines with unbroken tips. Damaged spines seen in acid prepared residues have been broken during preparation, as thin-sections show the spines to be intact. There are no examples with signs of physical abrasion.

5.3. Palaeoenvironment

Although shark remains usually occur more abundantly in marine strata, the occurrences of freshwater elasmobranchs both in the past (e.g. Sweetman & Underwood, 2006) and today (e.g. J. McEachran, unpub. data, 2004: http://www.fishbase.org) make isolated occurrences

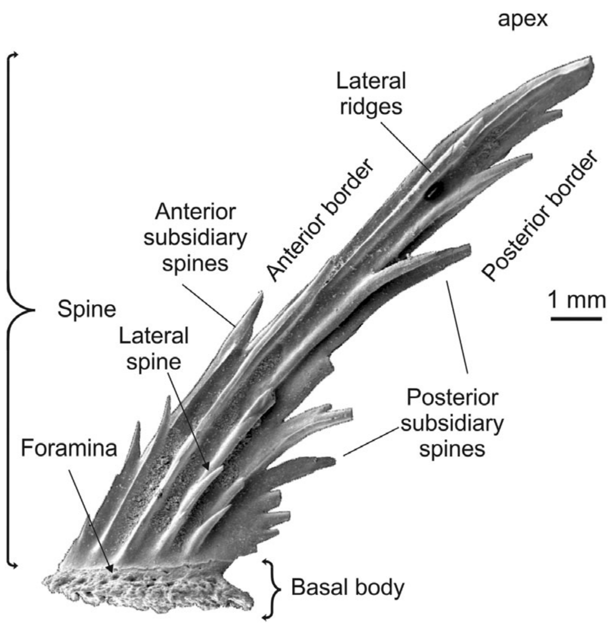

Figure 5. A spine-like dermal denticle of *Acanthorhachis* gen. nov. showing main features and nomenclature used in text.

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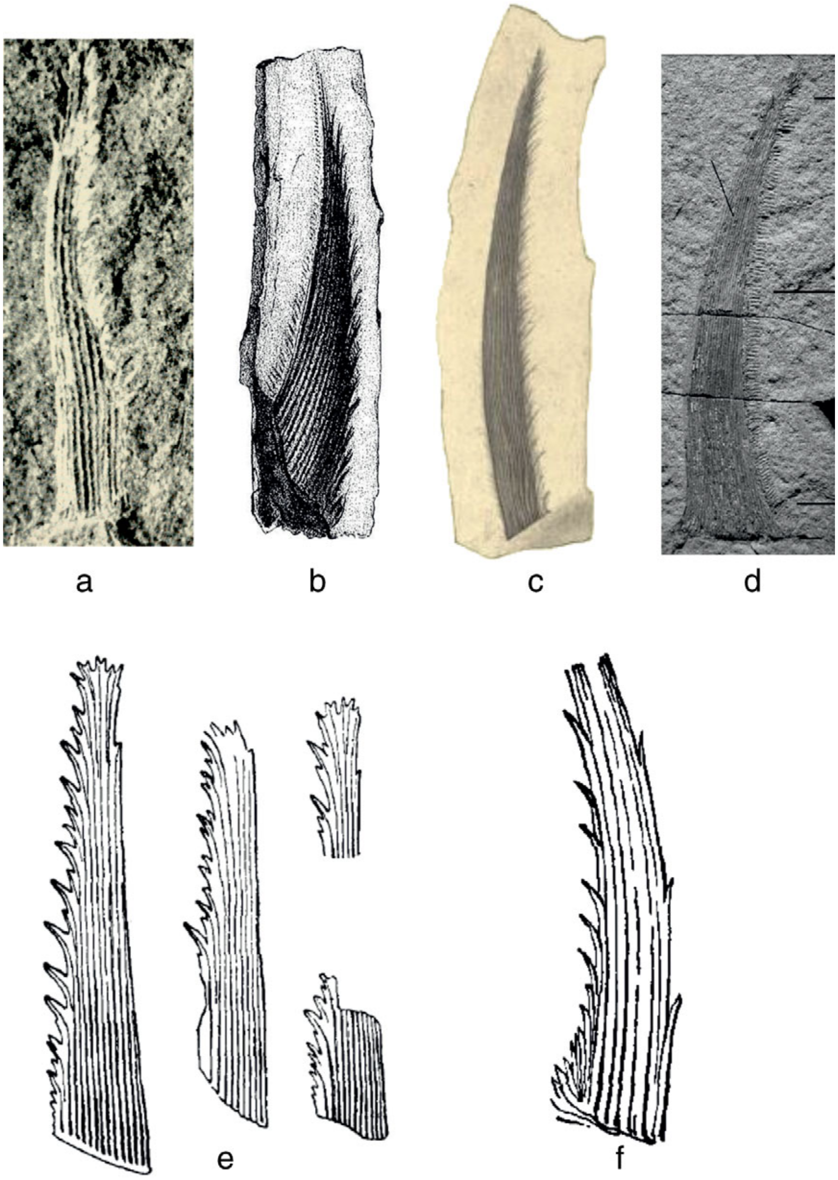

Figure 6. (Colour online) Spines of the different species of *Listracanthus* and *Acanthorhachis*: (a) *Listracanthus eliasi* after Hibbard (1938); (b) *Listracanthus beyrichi* after von Könen (1879); (c) *Listracanthus hystrix* after Newberry & Worthen (1870); (d) *Listracanthus pectenatus* Mutter & Neuman (2006), elongate dermal spine of holotype series UALVP 46551 from the Lower Triassic of western Canada (this spine compares closely with the type species of the genus from the Carboniferous of Illinois); (e) *Acanthorhachis wardi* after Woodward (1903); (f) *Acanthorhachis spinatus* after Bolton (1896). Not drawn to scale.

of sharks unreliable palaeosalinity indicators. The presence of a small (10 mm diameter) goniatite on the margin of the specimen however indicates a marine origin for the sample (Fig. 3f). The fine-grained nature of the matrix and the lack of abrasion and sorting of the ichthyoliths suggests a quiet, perhaps deepish, water setting for the sample. Water depth for a marine band associated so intimately with coal seams would probably not be excessively deep. The disaggregated but associated nature of the fish remains, all pertaining to a single taxon and most probably a single individual, suggests either disaggregation due to very gentle winnowing or, perhaps more likely, due to carcase collapse during decomposition in very quiet conditions.

6. Systematic palaeontology

CHONDRICHTHYES Huxley, 1880
?ELASMOBRANCHII Bonaparte, 1838
Family LISTRACANTHIDAE fam. nov.

Diagnosis. Dermal denticles and spines of osteodentine with broad, flatish basal body, conically hollowed basally and spine most-likely lacking enameloid outer layer. Elongate spines typified by rounded lateral ridges with occasional subsidiary lateral spines terminating in subsidiary spine at posterior and sometimes anterior margins. Spines and lateral ridges hollow. Other dermal denticles highly variable.

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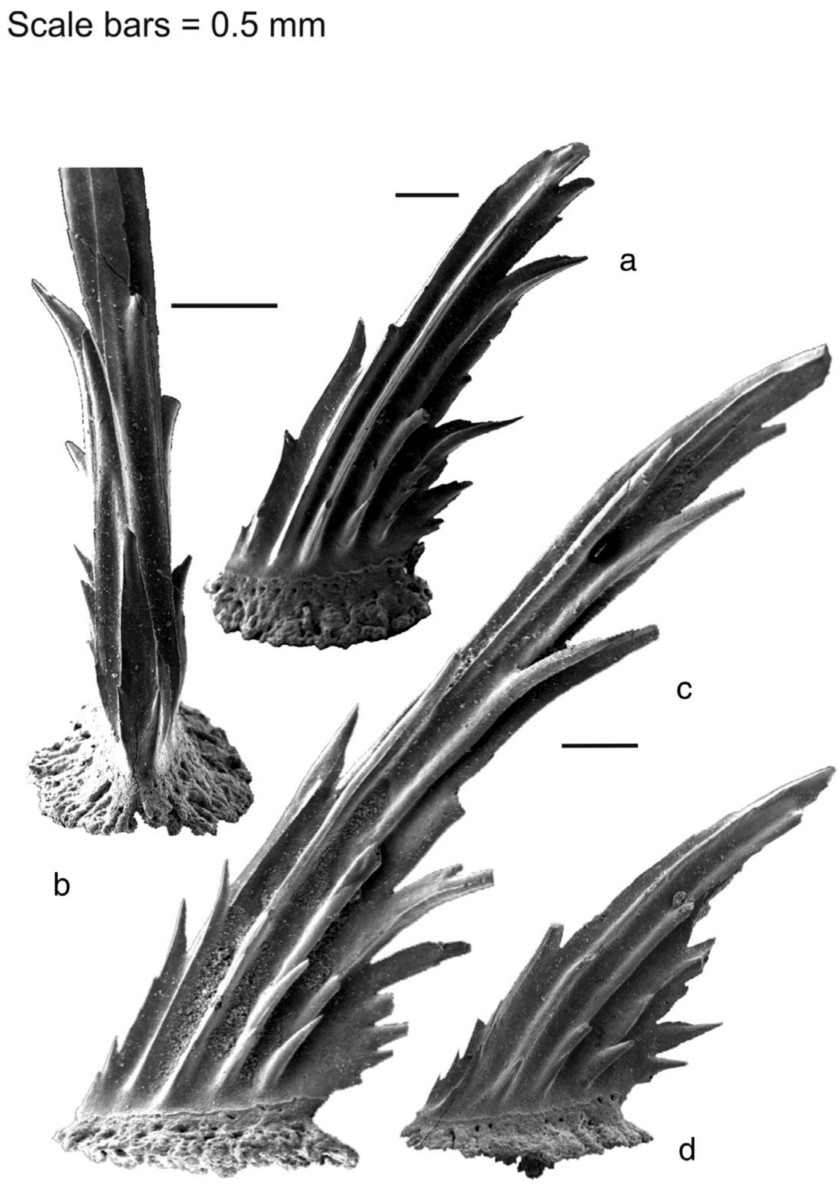

Figure 7. *Acanthorhachis spinatus* (Bolton, 1896). Scanning electron micrographs of elongate dermal denticles elongated into spines, possibly from dorsal surface of the animal (NHMUK P73208d): (a, b) medium height spine; (c) highly elongate spine; (d) short spine. (a, c, d) seen in left lateral aspect, (b) seen in anterior aspect. Scale bars 1 mm.

Content. Listracanthus Newberry & Worthen, 1870 and *Acanthorhachis* gen. et sp. nov. (see below).

Genus *Listracanthus* Newberry & Worthen, 1870

Type species. Listracanthus hystrix Newberry & Worthen, 1870.

Content. Listracanthus hystrix Newberry & Worthen, 1870; *Listracanthus hildrethi* Newberry, 1875; *L. eliasi* Hibbard, 1938, *Listracanthus pectenatus* Mutter & Neuman, 2006. Perhaps also *L. beyrichi* von Könen, 1879 and *L. woltersi* Schmidt, 1950.

Geographic and temporal range. Global within the palaeotropics and high latitudes in Australia. Upper Carboniferous – Lower Triassic.

Revised diagnosis. Hollow, tapered, gently recurved spine with numerous parallel lateral ridges, terminating at posterior border progressively apically. 'Fringe' of small spines form continuous posterior border and extend over spine apex to continue a short distance along anterior border. Overall morphology (e.g. number of lateral ridges, number of spines, height/width ratio) variable. Morphological terminology is given in Figure 5.

Discussion. The genus *Listracanthus* was erected by Newberry & Worthen (1870) for a distinctive tapered spine fine characterized by being gently posteriorly curved and having lateral margins with prominent parallel ridges extending from a broad basal body to the tip of the spine. Those ridges that reached the posterior

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border before reaching the apex of the spine were deflected posteriorly and projected beyond the spine margin. The anterior-most lateral ridges reach the apex and form a 'bristle-like tuft' of spines which extend a little way down the anterior border of the spine. For this distinctive spine Newberry & Worthen (1870) erected the species *L. hystrix*. Newberry (1875) assigned an additional species, *L. hildrethi* to *Listracanthus* that differed mainly in being considerably smaller than *L. hystrix*. Later authors referred additional material to *Listracanthus*, erecting several new species including: *L. wardi* erected by Woodward (1903) for material from the British Isles; *L. beyrichi* erected by von Könen (1879) for an example from Belgium; *L. spinatus* erected by Bolton (1896) for specimens from the Lancashire coalfield; and *L. woltersi* erected by Schmidt (1950) and *L. eliasi* erected by Hibbard (1938) for spines from Missouri, USA. *Listracanthus* was also reported from Russia and China, but these examples were not assigned to new or existing species (Ivanov, 2005; Lu *et al.* 2002, 2005). A series of ichthyoliths from the Triassic of western Canada were assigned to a new species of *Listracanthus*, *L. pectenatus* Mutter & Neuman (2006). This occurrence was particularly noteworthy, as it had been considered that *Listracanthus* had become extinct at or before the end of the Permian.

The holotype spine of *Listracanthus* (Fig. 6d) is highly distinctive, particularly for the presence of a large number of posteriorly located spines that form a 'comb-like' posterior margin extending from the basal body to the apex and then passing over the spine apex and continuing a short way along the distal anterior border. We consider this aspect of its anatomy to be diagnostic for the genus. Other species referred to *Listracanthus* that display this morphology include *L. hildrethi* Newberry, 1875 and *L. eliasi* Hibbard, 1938. We have not seen figures of *L. woltersi* or *L. beyrichi* to comment on the validity of their placement in the genus.

On account of the variability, we regard most of the species erected and placed within *Listracanthus* to be synonyms of the type species *L. hystrix*, excluding *L. pectenatus* Mutter & Neuman, 2006, which we consider valid (see below).

Listracanthus hystrix Newberry & Worthen, 1870
Figure 6c

1870 *Listracanthus hystrix* Newberry & Worthen.
1875 *Listracanthus hildrethi* Newberry, p. 56, pl. LIX, fig. 6.
1938 *Listracanthus eliasi* Hibbard.
1978 *Listracanthus* (probably) *hystrix* Newberry & Worthen; Chorn & Reavis, p. 5, figures 2, 3c.
2005 '*Listracanthus*' Ivanov, p. 132, figure 5k, l.

Holotype. YPM VP 007343.

Figure 8. (Colour online) *Acanthorhachis spinatus* (Bolton, 1896). Longitudinal section through highly elongate spine showing hollow interior (NHMUK P73209e). Within matrix associated with other spines on left. On right digitally removed from matrix.

Revised diagnosis. Spines as for genus, but subsidiary spines of posterior border directed posteroapically and of variable length.

Discussion. The holotype of *Listracanthus hildrethi* Newberry, 1875 from Ohio was based on an incomplete spine distinguished from *L. hystrix* on account of being somewhat broader, slightly more curved and 'sharply marked' (whatever that may mean). The variation found in the spines described here suggests strongly

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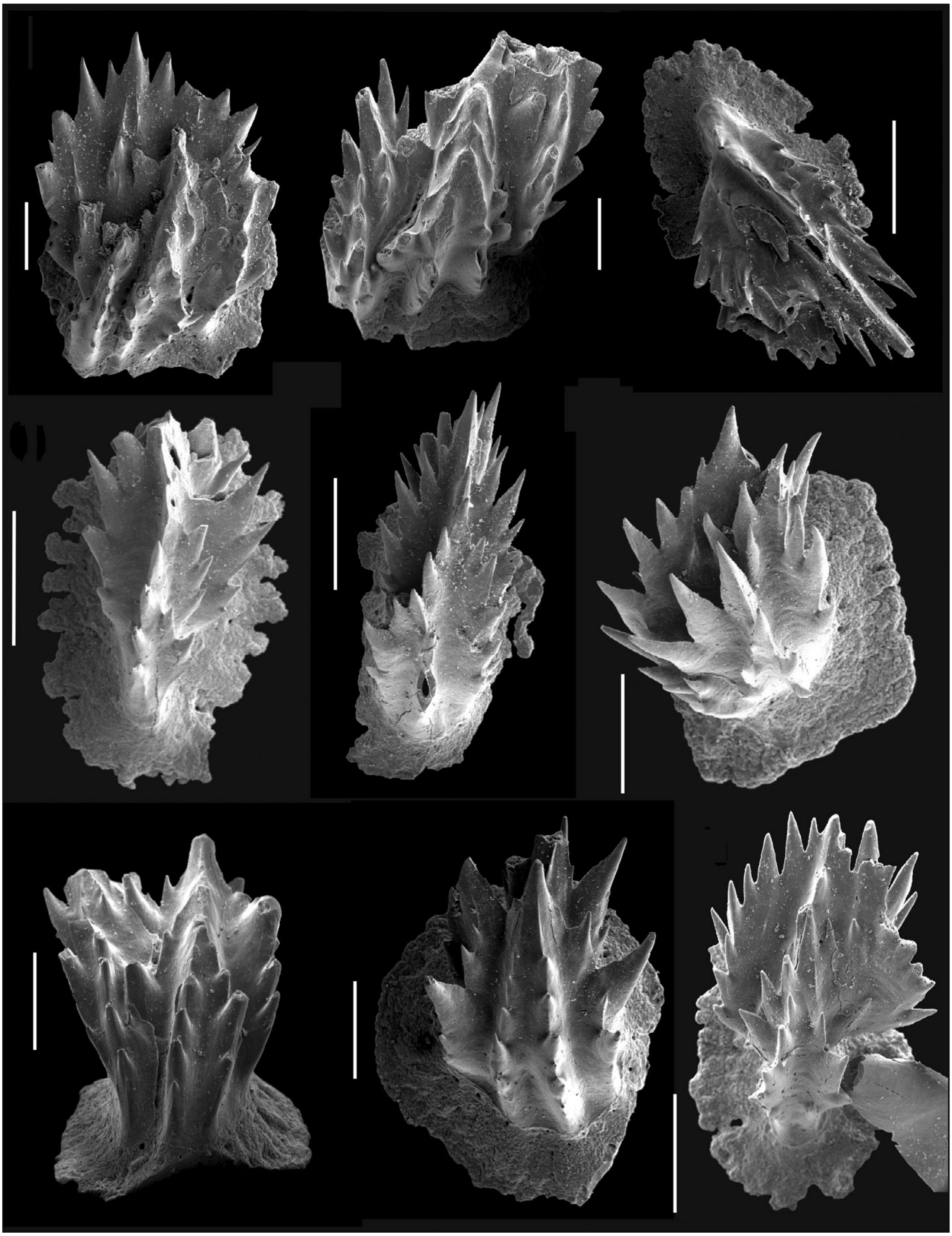

Figure 9. *Acanthorhachis spinatus* (Bolton, 1896). Variation in morphology of short, composite dermal denticles, assumed to be from flanks of animal (NHMUK P73210f).

that spines of *Listracanthus* would also be similarly variable and we consider *L. hildrethi* to be a morph, and therefore junior synonym of *L. hystrix*. *L. eliasi* Hibbard, 1938 is similar to *L. hystrix*, differing only in being somewhat straighter, and is here regarded as a junior synonym of that taxon. We tentatively include

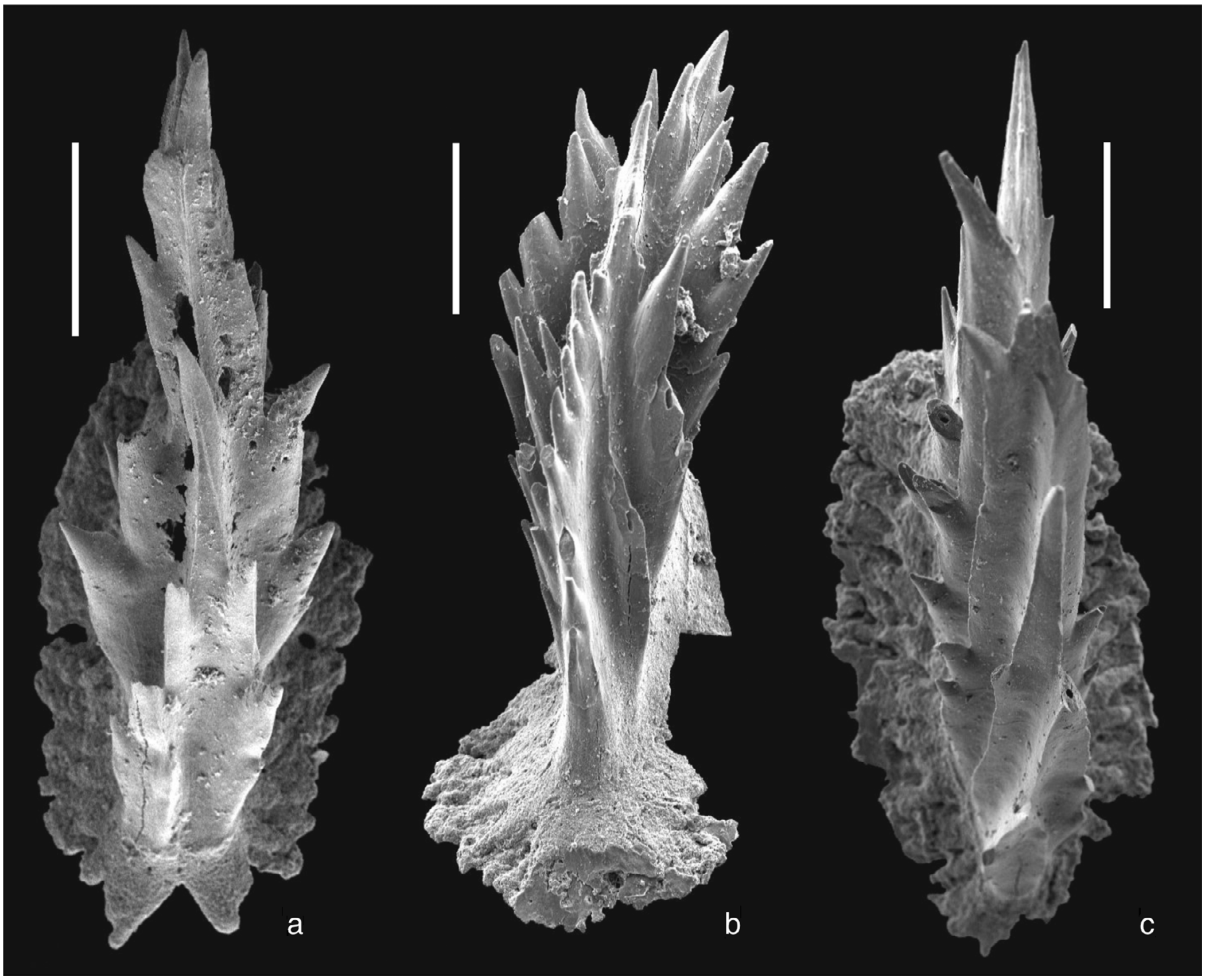

Figure 10. *Acanthorhachis spinatus* (Bolton, 1896). Dermal denticles intermediate between spines and short denticles (NHMUK P73211g). (a, c) in dorsal view, (b) in anterior view. Scale bars 1 mm.

L. beyrichi Könen, 1879 and *L. woltersi* Schmidt, 1950 within *L. hystrix*.

Listracanthus pectenatus Mutter & Neuman, 2006
Figure 6d

Holotype. UALVP 47002.

Revised diagnosis. Spines as for genus but with subsidiary spines of posterior border uniform in length, closely adpressed and directed posteriorly. Subsidiary spines of posterior border solid. Composite spines may occur, which Mutter & Neuman (2006) regard as aberrant. It is quite possible that these spines are simply specialized elements located in specific parts of the animal, perhaps as elaborate cephalic elements.

Discussion. This taxon was erected for spines similar to those of *L. hystrix*, but from the base of Triassic (probably Lower Smithian) of western Canada. This record was the first occurrence of *Listracanthus* in the Mesozoic. Measurements of numerous spines suggest that *L. pectenatus* was considerably smaller than Palaeozoic forms of *Listracanthus*. Consequently, Mutter & Neuman (2006) considered *L. pectenatus* to represent a 'Lilliputian' taxon surviving the biotic crisis at the end of the Permian. However, the largest spines of *L. pectenatus* (*c.* 40–70 mm) are comparable with those from the Carboniferous.

Genus *Acanthorhachis* gen. nov.

Type species. Listracanthus spinatus Bolton, 1896

Content. Acanthorhachis spinatus (Bolton, 1896).

Derivation of name. Acanthos Gr. spine, and *rhachis* Gr. a suffix for spine, alluding to the numerous subsidiary spines on the spine-like dermal denticles of this shark.

Common name. The spiny spined shark.

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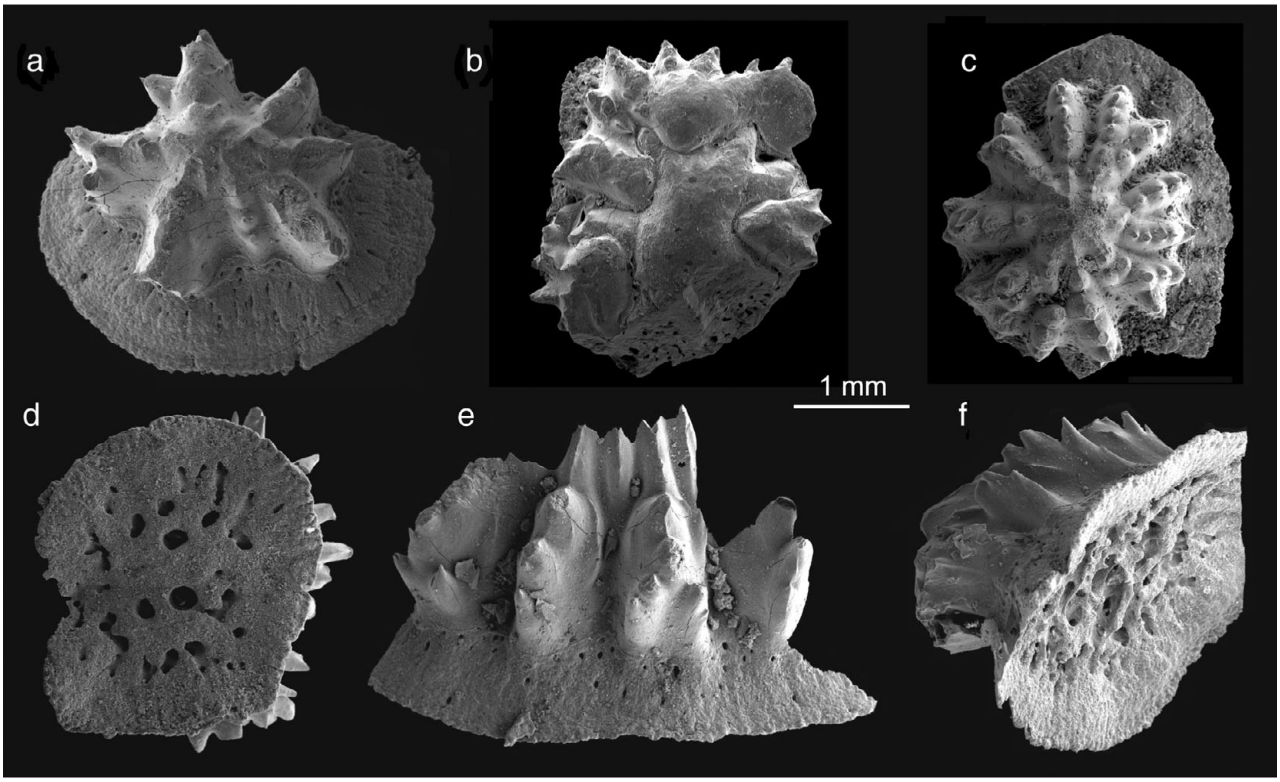

Figure 11. *Acanthorhachis spinatus* (Bolton, 1896). Robust, irregular and stellate denticles (NHMUK P73212h): (a) stellate with six main radials; (b) a robust, bulbous form, perhaps pathological; (c) stellate form with nine radial ridges, some of which are bifid; (d) view of basal body showing vascular ventral surface; (e) lateral view of stellate form; and (f) oblique view of stellate form showing characteristically dished ventral surface of basal body.

Diagnosis. As for type and only species, described below.

Acanthorhachis spinatus (Bolton, 1896)
Figures 6f, 7–14

Holotype. Present whereabouts unknown. Formerly housed in Salford Museum, Greater Manchester, where most fossils were transferred to other museums including Manchester, Fleetwood, Bolton, Stockport, Leeds and Liverpool during the 1980s.

Referred material described here. NHMUK P73205a, P73206b, P73207c, P73208d, P73209e, P73210f, P73211g, P73212h, P73215, P73216.

1896 *Listracanthus spinatus* Bolton, p. 425, unnumbered figure p. 425.
1903 *Listracanthus wardi* Woodward, p. 487, figs 1–8.

Geographic and temporal range. British Isles, Upper Carboniferous, Westphalian.

Revised diagnosis. Modified dermal spines resembling those of *Listracanthus*, but with irregular distribution of subsidiary spines on posterior border and not as many, and more widely spaced and of irregular length. Posterior subsidiary spines are hollow almost to their tips.

Discussion. The spine-like dermal denticles named *Listracanthus spinatus* by Bolton (1896) are here regarded as generically distinct from those of *Listracanthus hystrix* Newberry & Worthen, 1870 on account of the arrangement of subsidiary spines that branch from lateral ridges at the denticles posterior border, and are referred to the new genus *Acanthorhachis*. Histologically the spines of *Acanthorhachis* and *Listracanthus* are similar in that both are hollow (at least in the main body of the denticle) and both appear to lack enameloid (Figs 12–14).

Dermal denticle variation. A wide variety of dermal denticle morphologies are present in *Acanthorhachis* including elongate, posteriorly curved laterally ribbed spine-like elements (Figs 7, 8) which were the basis for the erection of the type species *A. spinatus*. These elements may have as few as 4 rounded and as many as 10 lateral ridges which periodically give rise to lateral subsidiary spines and, where they reach the posterior margin, give rise to one or more subsidiary posterior spines. Some denticles are shorter multi-bladed elements with multiple branching lateral ribs and subsidiary spines (Figs 9, 10) giving them a ‘bushy’ appearance. There are also short flat-based boss-like

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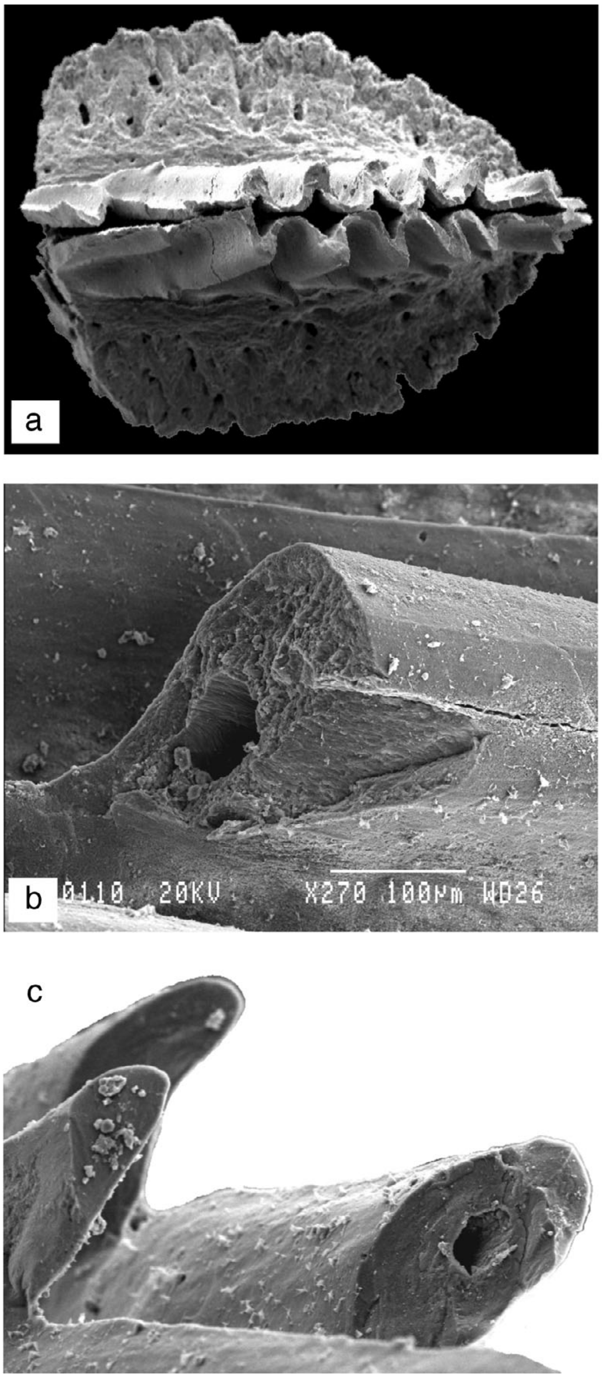

Figure 12. *Acanthorhachis spinatus* (Bolton, 1896): (a) broken surface of tall spine revealing hollow interior (pulp cavity); (b) broken lateral ridge just prior to branching away from main body revealing that hollow interior extends into subsidiary spines; and (c) tip of spine broken, revealing hollow interior extending almost to tip (right side of image). The broken tip on the left does not have a hollow interior (NHMUK P73216).

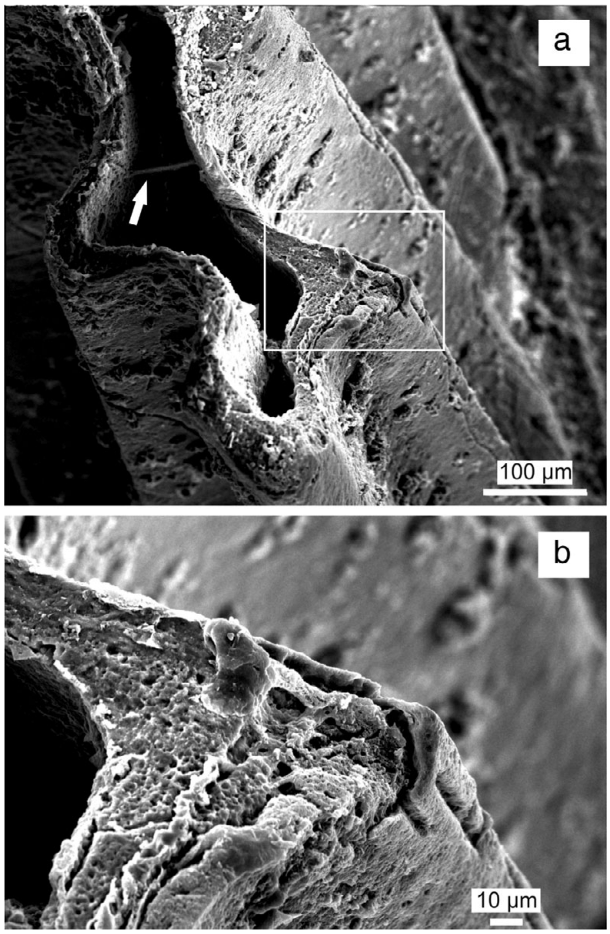

Figure 13. *Acanthorhachis spinatus* (Bolton, 1896). (a) Scanning electron micrographs of etched surface revealing internal tissue structure (NHMUK P73216). There appears to be a cross-strut internally traversing the internal cavity (arrow). (b) High-magnification image of spine wall in (a) showing a thin outer non-enameloid layer and thin inner layer sandwiching a vascular internal layer.

elements (Fig. 11), some of which are similar to those called *Petrodus* (see Chorn & Reavis, 1978; Elliot *et al.* 2004 for similar denticles in *Listracanthus*). These shorter elements are also highly variable, with some being stellate having 5–8 radial spiny ridges, some of which bifurcate distally (Fig. 11a, c). Irregular bulbous forms also occur (Fig. 11b). The degree of variation suggests a near continuum of form between denticle morphs.

In section many of the subsidiary spines contain a sub-endosteal network of fine capillaries that extend from the deep interior of the denticle and converge just beneath the tip of the subsidiary spine (Fig. 14). These may represent an arrangement of dentine tubules and provide the dermal denticle with an electrosensory or chemosensory function, but this remains to be examined further. The dermal denticles of sharks appear to be mainly concerned with protection from macro predators and parasites, drag reduction and, with modified elements, sexual display and reproduction (Raschi & Tabit, 1992). A role in dismembering prey has also been discovered for elongate dermal denticles in the dogfish *Scyliorhinus canicula* (Southall & Sims, 2003). An electro-potential or chemosensory role has yet to be reported for the denticles themselves, although both chemo-sensing (Gardiner & Atema, 2007), electro-potential (Murray, 1960) and temperature-sensitive (Brown, 2010) organs are well known in sharks.

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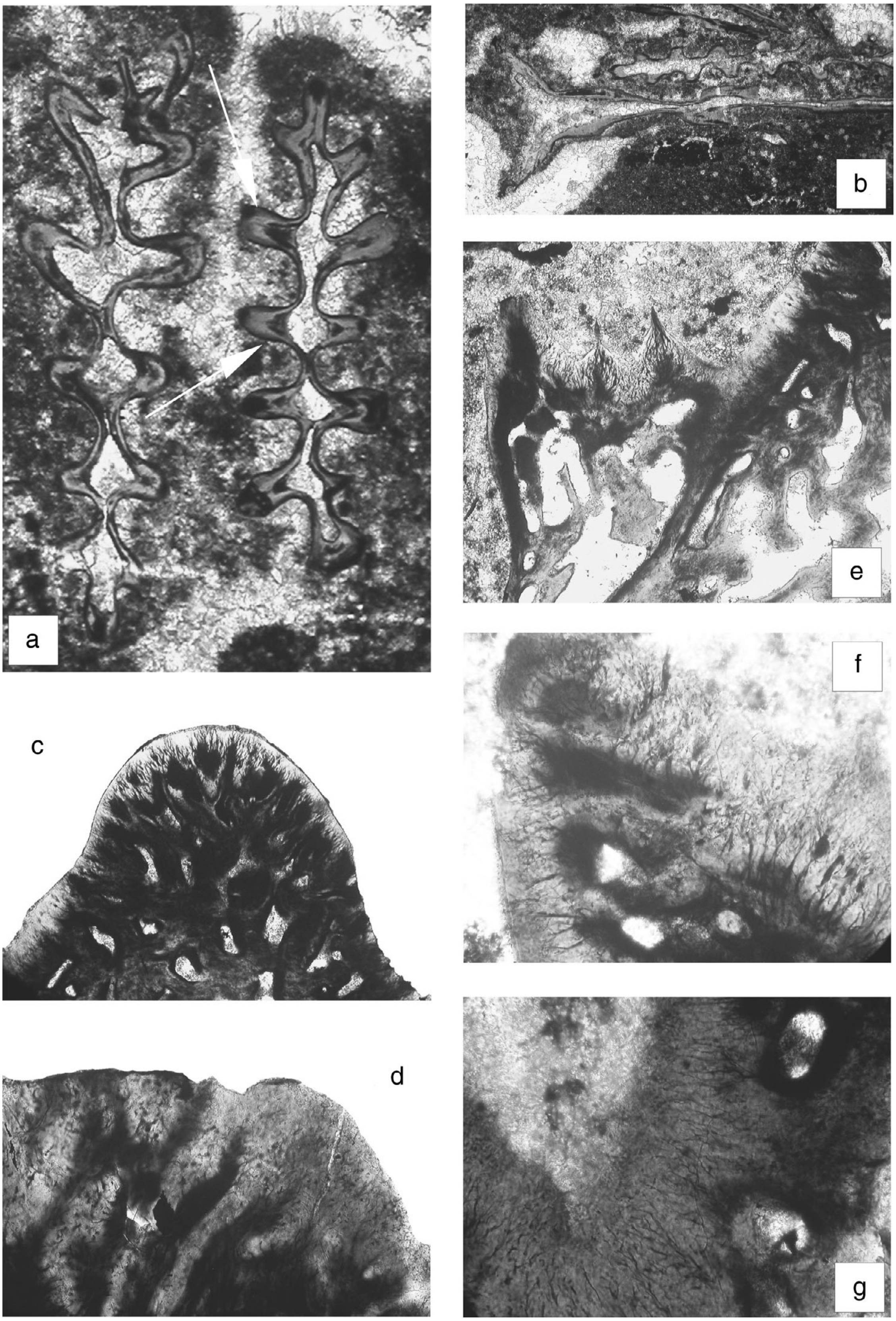

Figure 14. *Acanthorhachis spinatus* (Bolton, 1896). Thin-sections through spines showing internal 'osteo' histology (NHMUK P73215): (a) two elongate spines sectioned transversely revealing dark outer (arrows) and inner layers, sandwiching a lighter-coloured middle layer; (b) section through basal body of spine showing extent of internal void (pulp cavity); (c, d) distribution of mineralized tissue within one of the bulbous spines; (e, f) dense network of micro canals reaching periphery of denticle, suggestive of chemo- or electro-sensory function (note how the canals converge on the sharpened microspine in (e)); and (g) network of branching micro-canals within dentine.

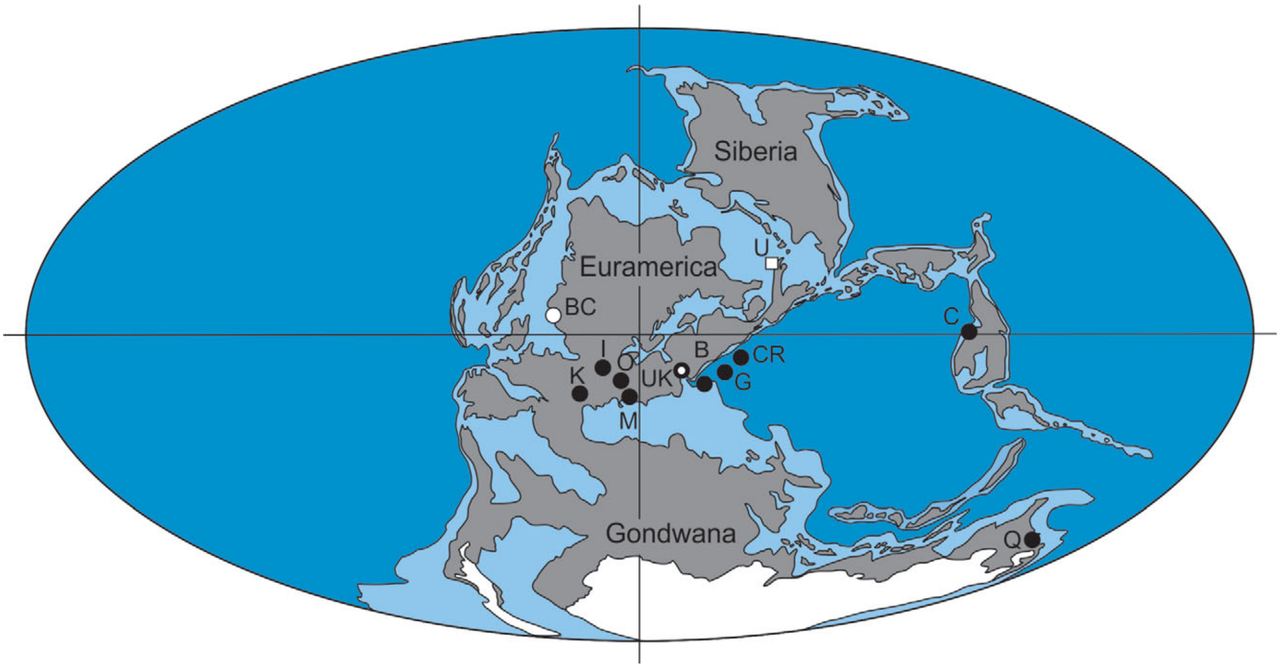

Figure 15. (Colour online) Distribution of *Listracanthus* and *Acanthorhachis* plotted onto a global palaeogeographic map for the Late Carboniferous, based mainly on a global map produced by Professor Ron Blakey, NAU Geology. Grey – land; light blue – shelf and epeiric seas; dark blue – deeper seas and ocean basins; white – glaciated terrain; black circles – Carboniferous occurrences of *Listracanthus*; B – Belgium; C – China; CR – Croatia; G – Germany; I – Illinois; K – Kansas; M – Missouri; O – Ohio; Q – Queensland; black and white circle – occurrence of *Acanthorhachis* in UK; white circle – Triassic occurrence; BC – British Columbia; square – Permian occurrence; U – Urals.

7. Discussion

The enigmatic shark genera *Acanthorhachis* and *Listracanthus* are considered closely related on account of similarities in their overall morphology, the range of variation of their various ichthyoliths from spinose spines to short stellate forms with continuous variation. In addition, similarities in their histology, including hollow interiors and lack of enameloid, also suggest a close relationship. The two genera can be united within a family Listracanthidae nov., but the relationships of this clade within the Elasmobranchii remain unclear, and their affinities within the group must await the discovery of articulated material with well-preserved cranial cartilages. The two genera occur widely distributed with most occurrences in the equatorial belt, but an isolated occurrence in Queensland, Australia suggests at least periodic expansion of the range into waters of higher latitudes (Fig. 15). Survival of the family into the Mesozoic of western Canada represents one of only a few documented occurrences of fish genera surviving the end Permian extinction event. The claim by Mutter & Neuman (2009) that this represents the survival of a Lilliput taxon is not well supported however, as spines of Carboniferous forms are in the same size range as those from the Canadian Early Triassic.

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