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The Early Devonian ischnacanthiform acanthodian *Ischnacanthus gracilis* (Egerton, 1861) from the Midland Valley of Scotland

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ABSTRACT:

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Ischnacanthus gracilis (Egerton, 1861), the only ischnacanthiform acanthodian from the Lochkovian Lower Old Red Sandstone of Scotland, is known from hundreds of specimens in institutional collections worldwide. Despite this relative abundance, morphology and histology of its skeletal elements have rarely been investigated. Surface details of spines, dental elements, and scales are often not visible in specimens because they are usually split through the middle. We have examined a broad size range of fish, from 35 mm to 250 mm long. Several intact (not split) specimens have been collected in recent years and acid-prepared to show fine details of the dermal and dental elements. We have also used scanning electron microscopy of scales, jaws and dental elements, denticles and fin spines, and serial thin sectioning of articulated specimens, to document their structure. Some of our notable observations include: identification of ventral lateral lines, double-layered subtessellate calcified cartilage forming the jaws, and the probable occurrence of extraoral tricuspid denticles on the jaws of most fish. Examination of the size range, body proportions and dentition of institutional specimens gives no support for recognising more than one species in the Midland Valley localities.

Key words: Acanthodii; *Ischnacanthus*; Lochkovian; Palaeohistology; Dentition.

INTRODUCTION

Ischnacanthus gracilis (Egerton, 1861), from the Lochkovian of the Midland Valley, Scotland, was the first ischnacanthiform acanthodian to be described based on articulated specimens. The only ischnacanthiform taxon described prior to *I. gracilis* is *Plectrodus mirabilis* Agassiz, 1839, erected for isolated jaw bones from the upper Silurian Ludlow Bonebed of the West Midlands, England. Numerous genera have since been erected based on isolated dentigerous jaw bones, but only four were based on articulated fish. Of these, two taxa – *Acanthodopsis* Hancock and Atthey, 1868 and *Uraniacanthus* Miles, 1973 – have since been recognized as an acanthodiform (Long 1986) and diplacanthiform (Hanke *et al.* 2001; Burrow 2004a; Hanke and Davis 2008), respectively. Of the other two taxa, the type material of

Onchus graptolitarum Fritsch, 1907 (upper Silurian, Czech Republic) has been long lost, and *Atopacanthus*? sp. of Jessen (1973) from the Frasnian of Germany, is known from just one specimen. Only in recent decades have other articulated fish been assigned to the ischnacanthiforms. These include *Zemlyacanthus menneri* (Valiukevičius, 1992), *Acritolepis ushakovi* Valiukevičius, 2003, and *Acritolepis urvantsevi* Valiukevičius, 2003 from the Lochkovian of Severnaya Zemlya, and *Nerepisacanthus denisoni* Burrow, 2011 from the Pridoli of eastern Canada. The Lochkovian Man on the Hill (MOTH) locality in the Northwest Territories, Canada, is also known to have several ischnacanthiform taxa, originally all assigned by Bernacsek and Dineley (1977) to *Ischnacanthus gracilis*, but now all referred to other genera (Blais *et al.* 2015), or as yet undetermined.

Ischnacanthus gracilis is the type species for the Family Ischnacanthidae and the Order Ischnacanthiformes, and it is known from hundreds of specimens in major museums throughout the world, with the largest collection in the National Museums of Scotland (NMS). However, the histological structures of dentition, fin spines and scales have barely been documented. As part of our project focusing on the Lower and Middle Devonian acanthodians of Scotland, we document here analyses of both the morphology and histology of these structures, outlined by our presentation at the 14th International Symposium on Early and Lower Vertebrates (Burrow *et al.* 2017).

Acanthodians are proving to be a pivotal group in deducing relationships amongst early gnathostomes, with most recent analyses recovering them as stem chondrichthyans (e.g., Zhu *et al.* 2013; Coates *et al.* 2018), rather than stem osteichthyans (e.g., Miles 1973b) or a paraphyletic assemblage of stem osteichthyans and stem chondrichthyans (Davis *et al.* 2012). The cladistic analyses have been hampered by the lack of data on characters for most acanthodians other than *Acanthodes* Agassiz, 1833, a lack that we believe is partially filled by the information provided in this paper on the iconic *Ischnacanthus gracilis.*

HISTORY OF RESEARCH

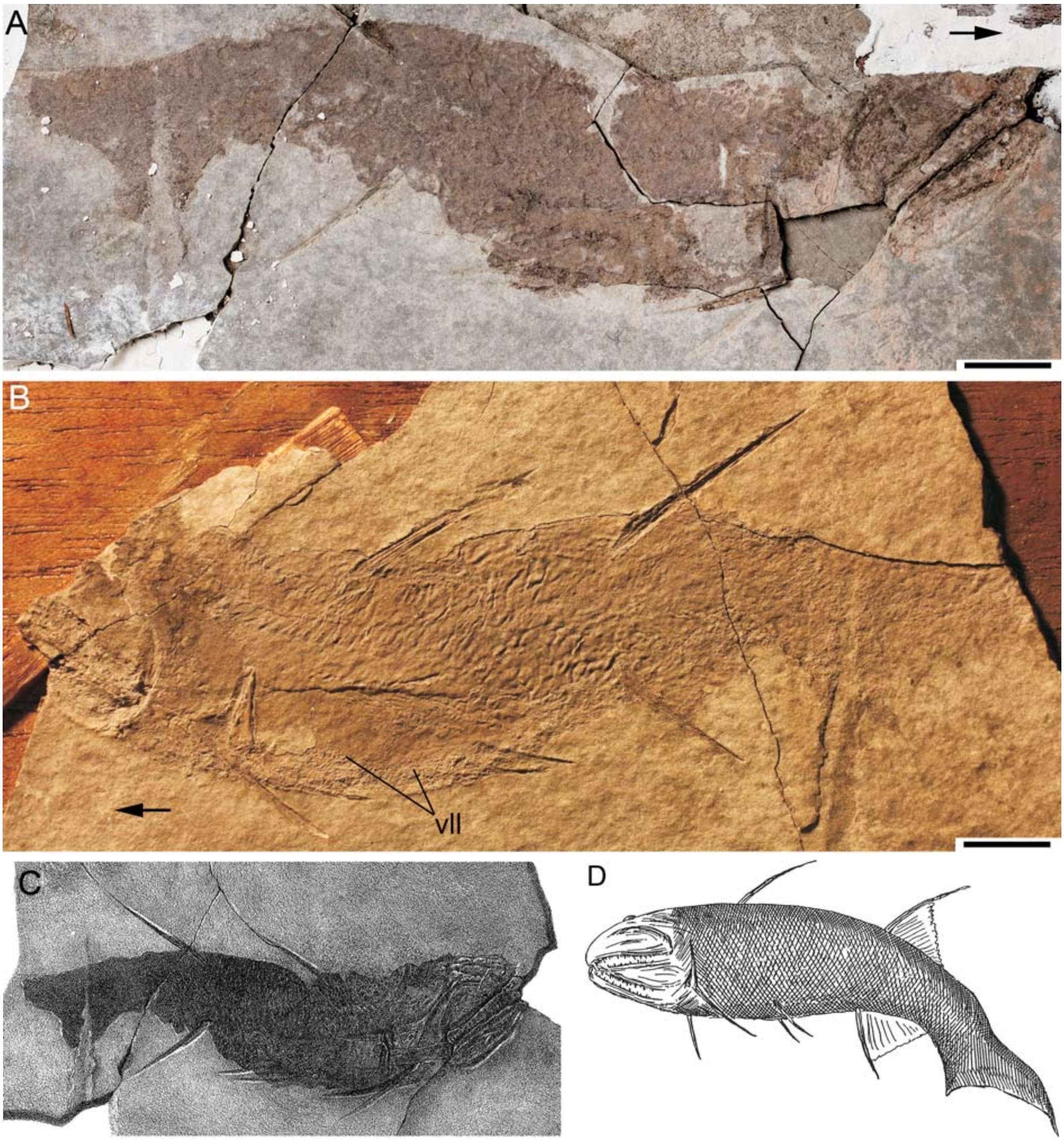
The species *Ischnacanthus gracilis* has been mentioned in numerous fossil lists and short descriptions, but it has only been described in detail in a limited number of articles. Fossil remains of *I. gracilis* were first recovered from Balruddery Den near the city of Dundee in Scotland. Page (1859) mentioned a specimen which he named *Ictinocephalus granulates*, but he provided no figures and little in the way of description other than to say that the specimen was "a small fish with fin spines and shagreen-like scales."

Egerton (1861) formally described the species as *Diplacanthus gracilis* based on an articulated specimen from the newly discovered locality of Farnell near Forfar (Text-fig. 1A–C). As was common at the time, the specimen was held in private hands, by the Reverend Henry Brewster of Farnell (1806–1866). James Powrie (1811–1895) arranged for delivery of the specimen to Egerton. Egerton (1861) considered the species belonged in the genus *Diplacanthus* Agassiz, 1841, known from the Middle Devonian of northern Scotland, and provided a brief description which included a number of mistakes, including considering the scale crowns to have a granular ornamentation (now known to be smooth).

Powrie (1864) redescribed the species in some detail based on new specimens from Turin Hill (Tillywhandland). He considered the species differed from *Diplacanthus* in the morphology of the head and the nature of the scale ornamentation and so erected a new genus *Ischnacanthus.* Powrie (1864) also suggested that a shorter, stouter species might also be present but declined naming it. He stated that he had seen Page's *Ictinocephalus granulates* specimen (they were evidently good friends as Powrie was executor of Page's will) which he considered conspecific with *I. gracilis*, and that he had permission from Page to substitute the name for something more appropriate. Powrie (1864) also mentioned that Page's specimen had jaws, further supporting his opinion that the specimens were conspecific, as no other ischnacanthids are known from the same strata. Powrie (1864) also pointed out that Egerton (1861) had erroneously listed *Ictinocephalus granulates* as a synonym of *Brachyacanthus scutiger* Egerton, 1861.

Later, Powrie (1870) reverted to the genus name *Diplacanthus* as he felt reluctant to multiply the genera, even though strangely stating that he still thought the species should be in its own genus. Powrie (1870, pl. 10, fig. 2) provided a pen and ink drawing of NMS G.1891.92.253 (Text-fig. 1D), a specimen from Turin Hill, where the best specimens have been collected.

Page and Lapworth (1888, fig. 85(3)) published the first reconstruction, although there was very little detail of the head. Traquair (1888, p. 512) recognised that the species belonged in its own genus due to the lack of intermediate fin spines and the "powerful dental armature of its jaws." Since then, the species has been formally known as *Ischnacanthus gracilis.* Woodward (1891, pl. 1, fig. 8) illustrated NHMUK



Text-fig. 1. *Ischnacanthus gracilis* (Egerton, 1861) from the Lochkovian of the Midland Valley, Scotland. A-C – type specimen from Farnell. A – Holotype NHMUK PV P.6987; B – NMS G.1891.92.251, counterpart of holotype; C – drawing of the holotype (Egerton 1861, pl. 9). D – drawing of NMS G.1891.92.253 (Powrie 1870, pl. 10, fig. 2), the first illustration to clearly show teeth. vll, ventrolateral lines. Scale bar = 1 cm. Arrows indicate anterior {fig. will be grayscale in printed version}

PV P.132 and described a number of specimens and their characters.

Dean (1907) described in detail the teeth on the dentigerous jaw bones of *I. gracilis* and their variation. He also discussed and figured sketches of jaw elements, and he was the first to recognise denticles on the side of the jaws, noting their shark-like nature. He was also the first author to figure and describe the vertebral column and its elements in *I. gracilis.* Goodrich (1909, text-fig. 160) subsequently figured a stylized drawing of a fragment of jaw, showing the denticles (redrawn in Ørvig 1973, text-fig. 1C).

In Graham-Smith's (1936) work on the morphological arrangement of the fins and lateral lines of all groups of fishes, he noted that the main lateral line of *I. gracilis* ran anteriorly into the head region. This is something he had not noted in the majority of other fish groups.

Watson (1937) published an in-depth description of *I. gracilis* and it is his reconstructions that are mostly reproduced in text books. Most of the later descriptions of the species are based on his work.

Gross (1947) made a brief description of the histology of the scales of *I. gracilis*, the first author to do so. Gross (1967, fig. 1D) provided a rather stylised sketch lacking detail of a lower jaw of *I. gracilis* in his paper on the dentition of acanthodians and placoderms. In the same volume, Ørvig (1967) described and figured the morphology of the teeth, including the loose denticles. In his paper describing the acanthodians of the Baltic upper Silurian–Lower Devonian, Gross (1971) compared the umbellate scale form of *Nostolepis striata* Pander, 1856 with the scales lining the sensory canals on the head of *I. gracilis*.

White (1961) erected a number of new species of *Ischnacanthus* based on jaw remains from the Anglo-Welsh Basin and made some brief comparisons with *I. gracilis*. Further work is required to determine if the Anglo-Welsh material really belongs in the genus *Ischnacanthus* (Newman *et al*. 2017).

Miles (1966) figured a head of *I. gracilis*, and described and discussed the dentition. Later, Miles (1970) commented on the vertebral column of *I. gracilis*, but mostly focused on the nature of the caudal fin, and the presence of ceratotrichia in the pectoral fin on one specimen. Shortly after, Moy-Thomas and Miles (1971) summarised the knowledge on *I. gracilis* expanding on Moy-Thomas's (1939) very brief earlier work. Miles (1973a) published a lengthy work on acanthodians and noted that *I. gracilis* had a region of enlarged scales on the ventral lobe of the caudal fin. However, the majority of his attention was focussed on the shoulder girdle, which he described in detail.

Long (1986) discussed the jaw morphology of *I. gracilis* as well as its phylogeny, based principally on the Scottish material. He noted that there is a well developed posterodorsal process on the articular region of the lower jaw cartilage, and he attempted a reconstruction of the ischnacanthiform jaw mechanism (Long 1986, fig. 6I).

Young (1995, fig. 3) sketched the crowns of *I. gracilis* scales, but finding them featureless she concluded they were not of much use in biostratigraphy. Dineley (1999) briefly described *I. gracilis*, as well as providing some Scottish locality details.

Burrow (1996) noted the length to depth ratio in a small selection of *I. gracilis* specimens, and later (Burrow 2004a) described the jaws of *I. gracilis* in detail. Valiukevičius and Burrow (2005) noted that histologically, *I. gracilis* scales are similar to *Gomphonchus sandelensis* (Pander, 1856). Burrow and Turner (2010) described elements of the head in *I. gracilis*, and subsequently Burrow and Turner (2012) illustrated the anatomical distribution and form of teeth, head, lateral line scales and other elements. Burrow and Rudkin (2014) described features on the head of *I. gracilis* figuring NMS G.1890.6.27, particularly noting the arrangement of the circum-naral bones; Burrow (2017, fig. 6d, e) showed the structure of the scapulas.

Trewin and Davidson (1996) provided an extensive investigation of the species distribution and deposition conditions for the fish beds at Tillywhandland Quarry, listing *I. gracilis* as one of the two most commonly occurring taxa. In his book on the best Scottish fossils, Trewin (2013) briefly described *I. gracilis* and figured a superb acid prepared specimen, as well as an in-life reconstruction of the species.

A major surprise came when Bernacsek and Dineley (1977) described remains collected from the Delorme Formation in the Canadian Northwest Territories in the 1960s, which they assigned to *I. gracilis*. They wrote that no specific variation could be found with the Scottish material other than the smaller size of the Canadian specimens, which they put down to sampling issues. However, they also noted that there seemed to be a greater variation in jaw morphology compared with the Scottish specimens. Soon after, Denison (1979) expressed doubt on the attribution of the Delorme Formation specimens by Bernacsek and Dineley (1977) to *I. gracilis*, but he did not give his reasons. More material was collected from the Delorme Formation in the 1980s, which led Gagnier and Wilson (1995) to suggest that at least three different forms of ischnacanthids were present. This conclusion was principally based on the jaw morphology. Further material was collected from the Delorme Formation in the 1990s, and this with the earlier material allowed Sahney and Wilson (2001) to describe the labyrinth infillings in a number of fish species. They referred the ischnacanthids they described to *Ischnacanthus* cf. *I. gracilis*, being unsure of the true affinities of their material. Hermus and Wilson (2001) noted that ontogenetic series were preserved at the site, and that there was more than one species, and all differed from the Scottish *I. gracilis*. Hanke and Wilson (2004) described a number of elements of *I. gracilis* which they used in their phylogeny matrix in classifying the acanthodians. Hanke and Wilson (2006) referred to the Delorme ischnacanthids, noting many differences to the Scottish material. Blais *et al.* (2011) described the heads, particularly concentrating on the jaws and teeth, of some of the Delorme ischnacanthids. They stated that there is more than one species present but did not raise any new species. The first published work since Bernacsek and Dineley (1977) to attempt a systematic description of these fish was by Blais *et al.* (2015), focussing on isolated ischnacanthiform jaw sets, all of which were referred to new genera and species.

MATERIAL AND METHODS

Specimens that were already in the UK museum collections (National Museums of Scotland prefixed NMS G; Natural History Museum London prefixed NHMUK PV P) before the project was undertaken were photographed by MJN and JLdB using a Canon Digital Rebel 450D camera, with microphotographs of squamation taken under normal light using a Wild M420 binocular microscope with a Sony DSC-H2 camera.

NMS G.2016.22.3 (Text-fig. 2A) was sacrificed for serial thin sections. It was washed with acetone, and then part and counterpart were glued together with Araldite. Sections were made through the specimen with a diamond saw as illustrated by the lines in Text-fig. 2B, and then were polished on one side and mounted with Araldite to glass slides. The head slices 46 to 54 were polished on both sides of the slice, then photographed under water with a Wild M420 binocular microscope with a Sony DSC-H2 camera, slices 50–54 were cut in half and numbered as, for example, 51 and 51A. Some of the thicker slices (46, 49–54) were sandwiched between two microscope glasses and sliced lengthwise with a diamond saw to obtain two sections from one slice, then labelled as, for example, 51X and 51XA. Specimens NMS G.2016.22.4 (Text-fig. 2C, D) and 2016.22.5 were also serially thin sectioned. Thin sections were ground by JdB using various grain sizes of corundum grinding powder down to 4 µm, with sections photographed using a Sony DSC-H2 camera attached to a Nikon Eclipse E 400 microscope. Disarticulated head and pectoral region specimen QM F 58851 (Text-fig. 2D) was prepared using 8% buffered acetic acid to release individual scales and dental elements from the calcareous mudstone matrix for scanning electron microscopy. QM F specimens were photographed using an Olympus SD40 binocular microscope with DP-12 imaging system. SEM images were made with the Queensland Museum Hitachi Tabletop TM-1000 Environmental scanning electron microscope. NMS G.2017.23.4 specimen (Text-fig. 2F) was prepared using 2% acetic acid buffered with calcium phosphate; Paraloid was used to stabilise and glue the specimen during the treatment. Figures were compiled using Adobe Photoshop.

SYSTEMATIC PALAEONTOLOGY

Class Acanthodii Owen, 1846
Order Ischnacanthiformes Berg, 1940
Family Ischnacanthidae Berg, 1940

TYPE GENUS: *Ischnacanthus* Powrie, 1864.

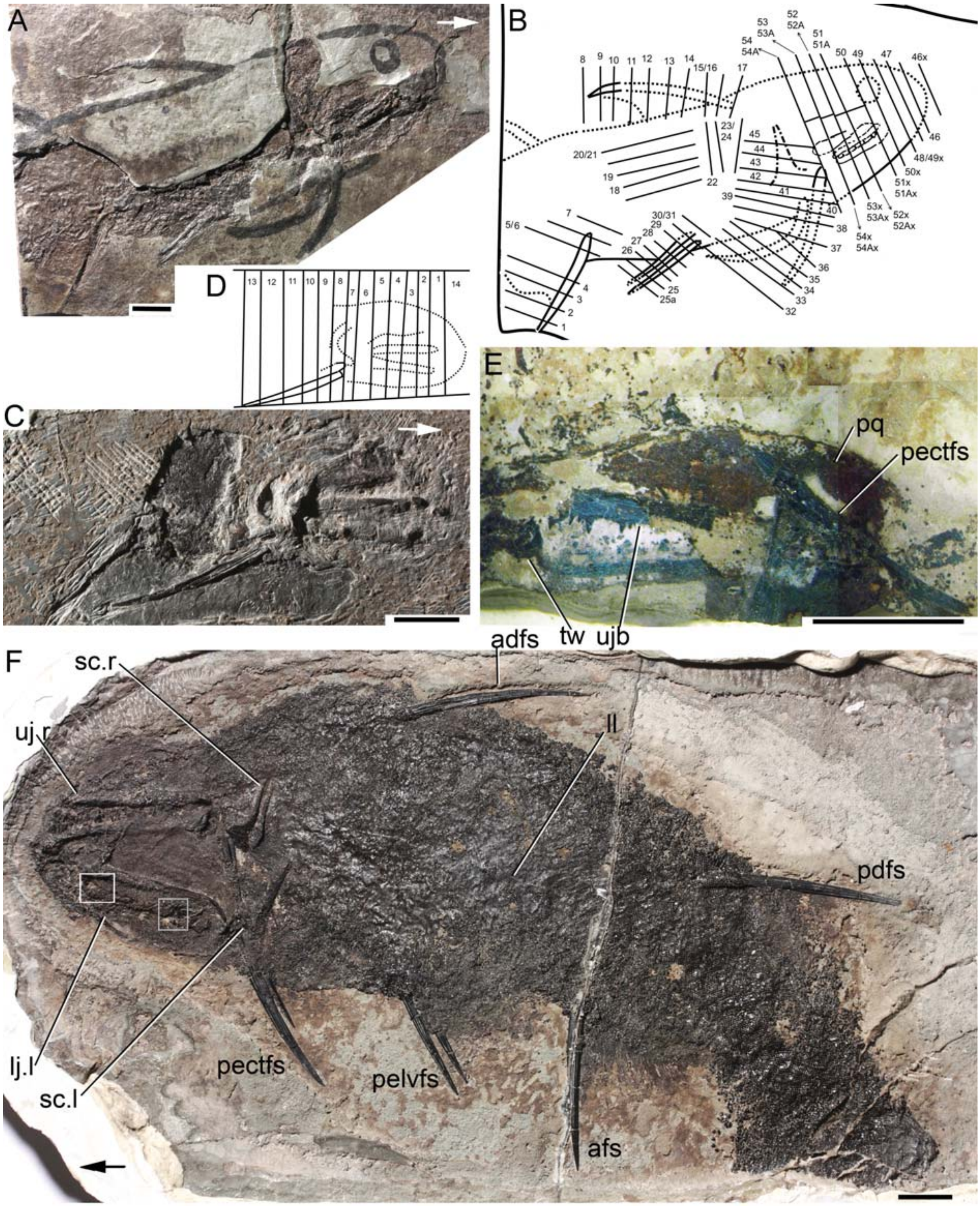
REVISED DIAGNOSIS: Ischnacanthiform acanthodians with a slender fusiform body; branchial region short relative to head length; scapula c. half body depth with broad U-shaped cross section, widening and flattening towards base; slender fin spines ornamented with up to four smooth longitudinal ridges which extend whole length of each side of spines; uniquely, ornament ridges continue to proximal end of spine, with spines inserted shallowly in the musculature; anterior dorsal spine between the pectoral and pelvic spines, posterior dorsal behind the anal spine; scales with a smooth crown lacking a pore canal system, having superposed crown growth zones formed of *Gomphonchus*-type dentine (*sensu* Gross 1971).

Ischnacanthus Powrie, 1864

TYPE SPECIES: *Diplacanthus gracilis* Egerton, 1861.

DIAGNOSIS: As for *I. gracilis*, type and only species.

REMARKS: Other species (all Lochkovian) that have been assigned to *Ischnacanthus* are now considered to belong to different genera. *Ischnacanthus*? *anglicus*, *I. kingi* and *I. wickhami*, all species from the Anglo-Welsh Basin erected by White (1961), are now considered to belong to indeterminate ischnacanthiform genera (Newman *et al.* 2017); *Ischnacanthus*? *scheii* Spjeldnaes, 1967 from Ellesmere Island, Canada is now assigned to *Poracanthodes* Brotzen, 1934 (Burrow 2013).



Text-fig. 2. *Ischnacanthus gracilis* (Egerton, 1861), newly prepared specimens, all from Tillywhandland. A, B – Specimen NMS G.2016.22.3, sacrificed for serial thin sectioning. A – specimen before sectioning, position of buried structures marked; B – map of thin section slices (TS1–TS54). C, D – NMS G.2016.22.4, sacrificed for serial thin sectioning. C – specimen before sectioning; D – map of thin section slices (TS1–TS14). E – QMF 58851, composite image of disarticulated specimen, partly disaggregated for scales and dental elements for scanning electron microscopy. F – NMS G.2017.23.4, articulated fish prepared by acetic acid treatment. adfs, anterior dorsal fin spine; afs, anal fin spine; lj.l, left lower jaw; ll, lateral line; pdfs, posterior dorsal fin spine; pectfs, pectoral fin spine; pelvfs, pelvic fin spines; pq, palatoquadrate; sc.l, left scapula; sc.r, right scapula; tw, tooth whorl; ujb, upper jaw dentigerous bone; uj.r, right upper jaw. Scale bar = 1 cm. Arrows indicate anterior {fig. will be grayscale in printed version}

Ischnacanthus gracilis (Egerton, 1861)
(Text-figs 1–13)

1859. *Ictinocephalus granulates*; D. Page, p. 105 (nomen nudum).
1861. *Diplacanthus gracilis*; P. Egerton, pp. 69–71, pl. 9.
1864. *Ischnacanthus gracilis*; J. Powrie, pp. 419, 420.
1865. *Ischnacanthus Gracilis*; Anonymous, p. 4, fig. 2.
1870. *Diplacanthus gracilis*, Eg.; J. Powrie, pp. 287, 289, 290, pl. 10, fig. 2.
1888. *Diplacanthus gracilis*; D. Page and C. Lapworth, p. 185, fig. 85(3).
1888. *Ischnacanthus gracilis* Eger.; R. Traquair, p. 512.
1890. *Diplacanthus gracilis*, Egerton; A. Woodward and C. Sherborn, p. 65.
1891. *Ischnacanthus gracilis* (Powrie); A. Woodward, pp. 21, 22, pl. 1, fig. 8.
1892. *Diplacanthus gracilis*; H. Coates and P. MacNair, p. 3.
1892. *Ischnacanthus gracilis* Powrie; R. Traquair, pp. 33, 37.
1902. *Ischnacanthus gracilis*; A. Geikie, pp. 30, 358.
1907. *Ischnacanthus gracilis*; B. Dean, pp. 209–211, 213, 214, figs 1–10, 13, 16, 17.
1909. *Ischnacanthus*; E. Goodrich, text-fig. 160.
1912. *Ischnacanthus gracilis* Pow.; G. Hickling, table 1.
1936. *Ischnacanthus*; W. Graham-Smith, pp. 596, 597.
1937. *Ischnacanthus gracilis*; D. Watson, pp. 52, 77–84, figs 10, 11, pl. 9.
1939. *Ischnacanthus*; J. Moy-Thomas, p. 35.
1947. *Ischnacanthus gracilis* (Egerton); W. Gross, p. 124.
1961. *I. gracilis*; E. White, pp. 263, 265, 286.
1966. *Ischnacanthus gracilis* EG; R. Miles, pp. 172, 173, fig. 11.
1967. *Ischnacanthus gracilis* EG.; W. Gross, pp. 122, 123, fig. 1D.
1967. *Ischnacanthus gracilis* Egert.; T. Ørvig, pp. 145–148, pl. 3, figs 3–5.
1970. *Ischnacanthus gracilis* (Egerton); M. Armstrong and I. Paterson, p. 23.
1970. *Ischnacanthus gracilis* (Egerton); R. Miles, pp. 344, 350, 356, 358, fig. 8, appendix.
1971. *Ischnacanthus gracilis*; W. Gross, p. 7.
1971. *Ischnacanthus*; J. Moy-Thomas and R. Miles; pp. 61, 73, 74, fig. 4.14.
1973. *Ischnacanthus gracilis* Egerton; T. Ørvig, pp. 122, 133, text-fig. 1C, pl. 16, fig. 1.
1973a. *Ischnacanthus gracilis* (Egerton); R. Miles, pp. 121, 150, 160, 161, fig. 24.
1976. *Ischnacanthus gracilis* (Egerton 1861); R. Paton, pp. 14, 15.
1976. *Ischnacanthus gracilis*; J. Zidek, p. 18.
?1977. *Ischnacanthus gracilis* (Egerton, 1861); G. Bernacsek and D. Dineley, pp. 2, 10–13, 20, 22, 24, text-fig. 8, pl. 5.
non 1977. *Ischnacanthus gracilis* (Egerton, 1861); G. Bernacsek and D. Dineley, pp. 2, 10–13, 20, 22, 24, text-figs. 9–11, 20, pl. 6.
1979. *Ischnacanthus gracilis* (Egerton) 1861; R. Denison, pp. 1–13, 16, 17, 32, 37–41, 45, 56, figs 4D, 25A, 26I, 28G.
1979. *Ischnacanthus gracilis*; C. Fergusson *et al*., p. 102.
1986. *Ischnacanthus*; J. Long, pp. 330–331, 333–335, fig. 7A.
1990a. *Ischnacanthus gracilis* (Egerton) 1861; J. Vergoossen, p. 132, fig. 2A.
1990b. *Ischnacanthus gracilis* (Egerton) 1861; J. Vergoossen, p. 137, fig. 1.
1991. *Ischnacanthus gracilis* (Egerton); K. Frickhinger, p. 244, fig. 1.
1995. *Ischnacanthus gracilis*; C. Burrow, p. 331.
1995. *Ischnacanthus gracilis* in part; P.-Y. Gagnier and M. Wilson, pp. 140, 142.
non 1995. *Ischnacanthus gracilis* in part; P.-Y. Gagnier and M. Wilson, p. 138.
1995. *Ischnacanthus gracilis* (Egerton, 1861); V. Young, pp. 65, 66, figs 1, 3.
1996. *Ischnacanthus gracilis*: C. Burrow, pp. 224–226.
1996. *Ischnacanthus gracilis*; N. Trewin and R. Davidson, table 1.
1997. *Ischnacanthus gracilis*; V. Young, p. 48.
1999. *Ischnacanthus gracilis*; C. Burrow *et al*., p. 357.
1999. *Ischnacanthus gracilis* (Egerton, 1861); D. Dineley, pp. 154, 155, 158, 159, figs 5.6A, 5.8A.
1999. *Ischnacanthus gracilis*; P.-Y. Gagnier *et al*., p. 95.
2001. *Ischnacanthus gracilis*; G. Hanke *et al*., p. 740.
non 2001. *Ischnacanthus* cf. *I. gracilis*; S. Sahney and M. Wilson, figs. 2A, 3C, 3D.
2004a. *Ischnacanthus gracilis* (Egerton, 1861); C. Burrow, pp. 8–13, figs 1A, 4.
2004b. *Ischnacanthus gracilis* (Egerton, 1861); C. Burrow, p. 257.
2004. *Ischnacanthus gracilis*; G. Hanke and M. Wilson, pp. 207, 210, figs 11, 12, app. 2.
2004. *Ischnacanthus gracilis*; J. Long *et al*., p. 15.
2005. *Ischnacanthus gracilis*; C. Burrow and G. Young, p. 20.
2005. *Ischnacanthus gracilis* (Egerton, 1861); J. Valiukevičius and C. Burrow, p. 643.
non 2006. *Ischnacanthus* cf. *I. gracilis*; G. Hanke and M. Wilson, p. 527, fig. 2A.
2007. *Ischnacanthus gracilis* (Egerton, 1861); C. Burrow, p. 831.
2008. *Ischnacanthus gracilis*; G. Hanke and S. Davis, p. 326.
2010. *Ischnacanthus gracilis* Powrie, 1864; C. Burrow and S. Turner, pp. 124, 128, 134, 136, figs 6E, 7, appendix 2.

non 2011. *Ischnacanthus gracilis*; S. Blais *et al*., p. 1191.
2011. *Ischnacanthus gracilis*; C. Burrow, pp. 1331, 1338.
2011. *Ischnacanthus gracilis*; M. Newman *et al.*, pp. 102, 103, 110.
2012. *Ischnacanthus gracilis*; C. Burrow and S. Turner, pp. 202, 203, fig. 6.
2012. *Ischnacanthus gracilis*; V. Voichyshyn and H. Szaniawski, p. 879.
2013. *Ischnacanthus gracilis*; C. Burrow *et al*., p. 411.
2013. *Ischnacanthus gracilis*; N. Trewin, p. 79, fig. 76a, b.
2014. *Ischnacanthus gracilis*; C. Burrow and D. Rudkin, pp. 3, 5, 6, fig. 5.
2014. *Ischnacanthus gracilis* Egerton, 1861; H. Botella *et al*., p. 1067.
2015. *Ischnacanthus gracilis* (Egerton, 1861); S. Blais *et al*., pp. 2, 4, 6, 10, 11.
2015. *Ischnacanthus gracilis*; J. Long *et al*., p. 13.
2015. *Ischnacanthus gracilis* (Egerton, 1861); C. Burrow *et al*., pp. 7, 12.
2016. *Ischnacanthus gracilis*; C. Burrow *et al*., p. 8.
2017. *Ischnacanthus gracilis* (Egerton, 1861); M. Newman *et al*., pp. 4, 6, table 1.
2018. *Ischnacanthus*; M. Coates *et al*., figs. 3a (ii), b, 4.

REVISED DIAGNOSIS: Slender body with maximum depth to length ratio 1:4; dentigerous jaw bones with conical main teeth having a circular parabasal section and smaller cusps anterior and posterior, with the jaw bone lacking a lingual ridge and tuberculation; lower jaw symphysial tooth whorl with single cusped teeth, plus parasymphysial tooth whorls with multicuspid teeth; tricuspid denticles lingual to the jaw bones and tooth whorl-like structures on the rostrum; no dentition cones; branchial region with four to six branchiostegal plates posterior to jaw joint and lines of thin narrow plates over the gill septa above the branchiostegals; anterior dorsal fin spine more curved and shorter than posterior dorsal fin spine; fin webs are shorter than the spines on the median fins.

TYPE SPECIMEN: NHM PV P.6987, counterpart NMS G.1891.92.251 (Text-fig. 1A, B), from Farnell, Scotland.

TYPE LOCALITY: Pow Burn near Farnell, Brechin (British grid reference NO 628 553), Scotland, UK.

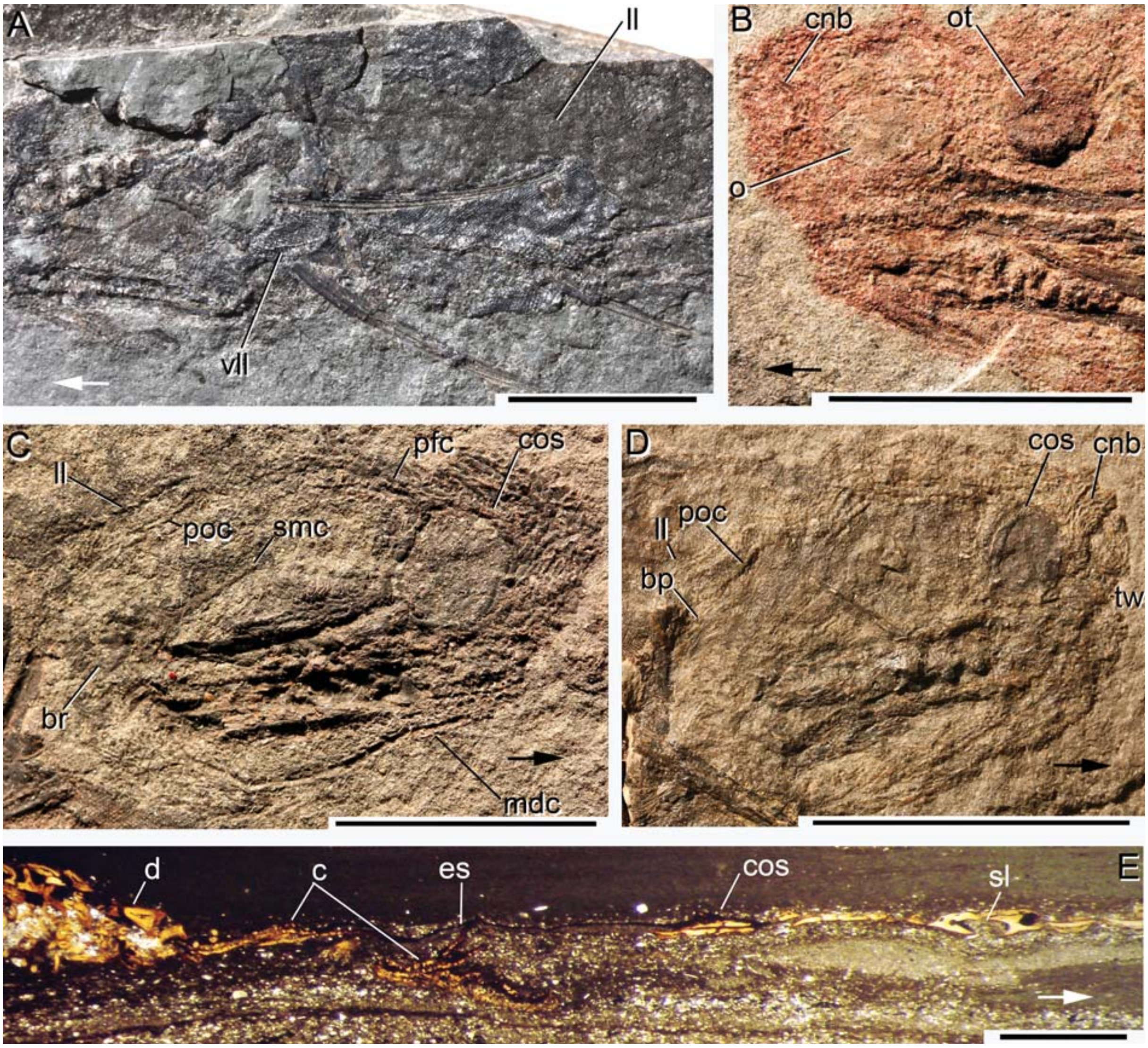
STRATIGRAPHICAL HORIZON: *Ischnacanthus gracilis* comes from the lower part of the Arbuthnott Group of the Lower Devonian (Lochkovian) of the Strathmore region of Scotland.

DISTRIBUTION: As well as the type locality, Balruddery Den near Dundee (British grid reference NO 310 328), Canterland Den near Montrose (British grid reference NO 708 644), Duntrune Quarry near Dundee (British grid reference NO 437 353), Haining Burn near Dundee (British grid reference NO 353 419), Middleton Quarry (now known as Legaston Quarry) near Friockheim (British grid reference NO 589 487), Mirestone Quarry near Forfar (British grid reference NO 496 535), Tillywhandland Quarry near Forfar (British grid reference NO 530 536), Whitehouse Den (Tealing) near Dundee (British grid reference NO 426 397), Wormit Bay near Dundee (British grid reference NO 385 258).

MATERIAL EXAMINED: All specimens previously lodged in the NMS and the NHMUK were examined and photographed. Specimens described or figured herein include: from Farnell: NMS G.1891.92.252; from Tillywhandland Quarry: NMS G.2017.30.1, NMS G.2017.27.7, NMS G. 2017.27.6, NMS G.2017.27.5, NMS G.2017.23.4, NMS G.2017.23.2, NMS G.2017.23.1, NMS FR1710, NMS FR1711, QMF 58848–58852; from Turin Hill: NHM UK PV OR.46305, NMS G.1881.5.64, NMS G.1887.35.2A, NMS G.1890.6.27, NMS G.1891.92.266, NMS G.1891.92.258, NMS G.1892.92.265; from Tealing: NMS G.1956.14.16; from Mirestone Quarry: NMS G.1973.16. Specimens from Tillywhandland Quarry sacrificed for thin sections: NMS G.2016.22.3, NMS G.2016.22.4, NMS G.2016.22.5; specimen acid etched for scales and dental elements: QMF 58851.

Note: Watson (1937) referred in his description of *I. gracilis* to a number of specimens in his private collection. These specimens are now housed in the University Museum of Zoology, Cambridge (prefixed GN) and the Grant Museum of Zoology, University College London (prefixed LDUCZ) and are alluded to below. The relevant specimens include P.297 now GN.28, P.298 now LDUCZ-V1676, P.311 now GN.32, P.478 now GN.597, and P.481 now GN.58. The whereabouts of the specimen referred to by Watson (1937) as C.4 is unknown.

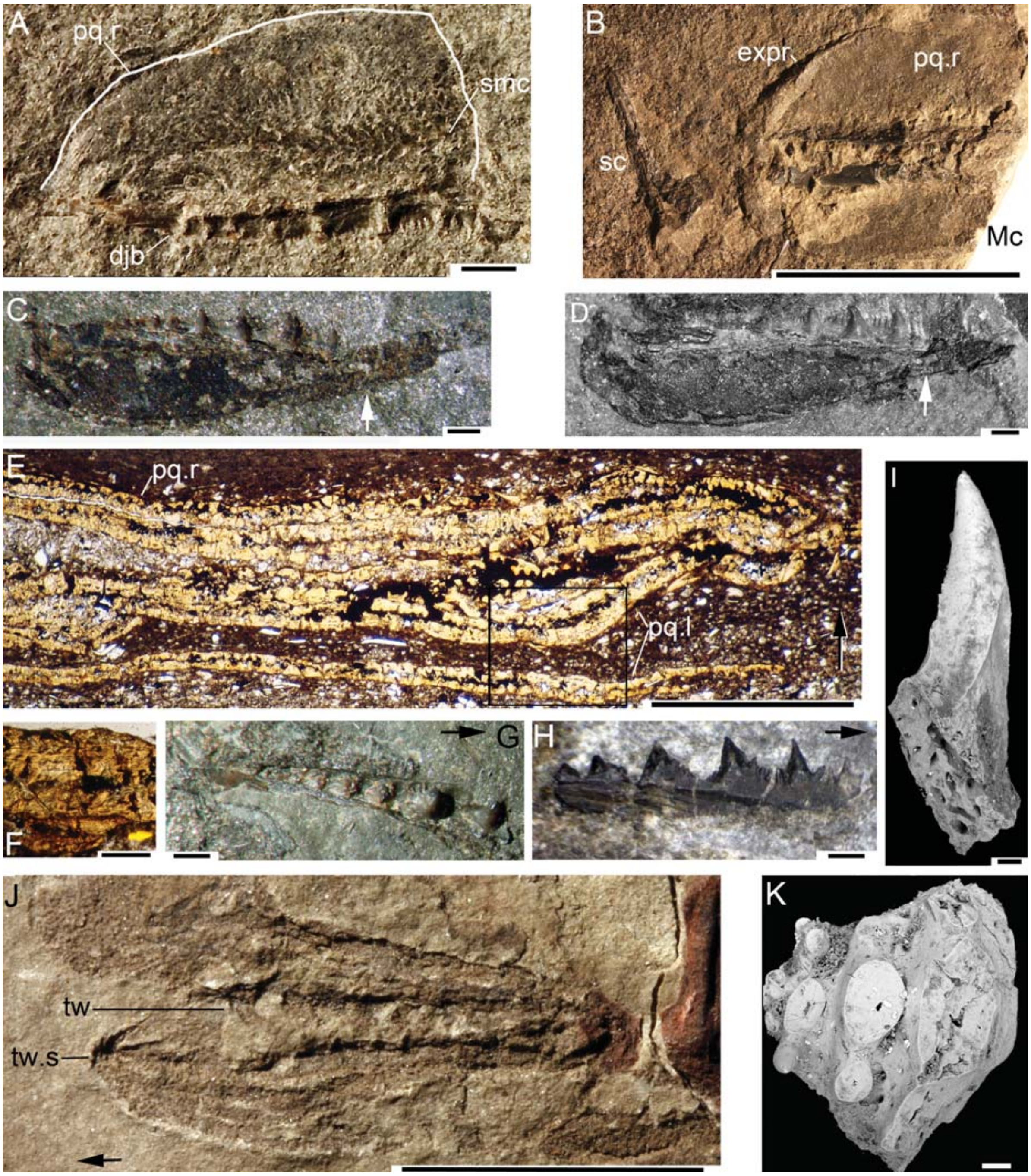
DESCRIPTION: Many of the morphological features of *I. gracilis* were thoroughly described by Watson (1937) and Miles (1973a), therefore we will focus on revising some of their observations, plus provide a description of previously undescribed features, in particular the histological structure of the teeth, endoskeleton, scales and spines. One general body feature in *I. gracilis*, not illustrated by previous authors, is a ventrolateral sensory line on each side of the fish,



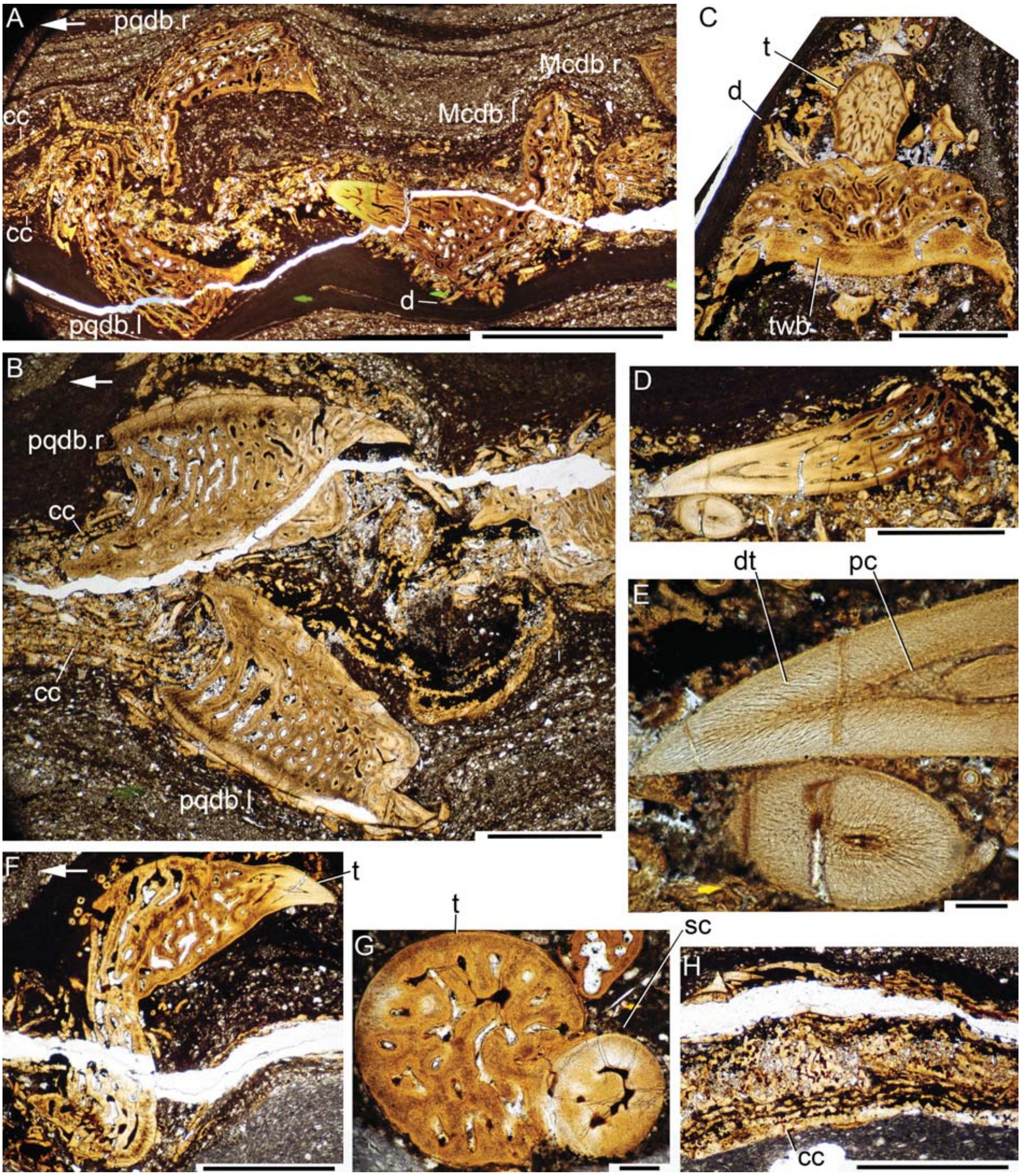
Text-fig. 3. *Ischnacanthus gracilis* (Egerton, 1861), sensory lines and dermal head plates. A – NMS G.2017.27.7 from Tillywhandland, showing ventrolateral line. B – NMS G.1891.5.266 from Turin Hill. C – NMS G.1890.6.27c (counterpart) from Turin Hill. D – NMS G.1956.14.16 from Tealing. E – NMS G.2016.22.3 TS47, vertical section through right orbit, dorsal to right, ventral to left. bp, branchial plates; br, branchiostegal plates; c, cartilage; cnb, circumnaral bones; cos, circumorbital scales/platelets; d, denticles; es, eye stain; ll, lateral line; mdc, mandibular canal; o, orbit; ot, otic capsule; pfc, profundus canal; poc, preopercular canal; sl, sensory line; smc, supramaxillary canal; tw, tooth whorl; vll, ventrolateral line. Scale bar = 1 cm in A-D, 1 mm in E. Arrows indicate anterior in A-D, dorsal in E

medial to the paired fins (Text-figs 1B, 3A). These lines coalesce into the median ventral canal which extends over the gular region to the symphysial region (Denison 1979).

Head region. Dermal plates and general features. Behind the eye in NMS G.1891.92.266 (Text-fig. 3B) is a large, round protruding area that we interpret as the infilling of the otic capsule. This capsule is a similar size to the orbit, which is close to the anterior end of the fish. Watson (1937, fig. 11) described and figured a sclerotic ring in the orbit, however we have not observed such a ring in any of the fish examined. Specimen NMS G.1890.6.27 (Text-fig. 3C) shows the orbit delineated by short wide scales/platelets aligned around the margin; on NMS 1956.14.16 (Text-fig. 3D) a line of narrow platelets run around the posterodorsal quadrant, and the impressions of other circumorbital platelets are also visible. These two specimens also show that the fish had a 'preopercular' canal running down and back from the main lateral line to-



Text-fig. 4. *Ischnacanthus gracilis* (Egerton, 1861), jaws and dentigerous jaw bones. A – disarticulated right upper jaw on NMS FR1710 from Tillywhandland, impression of palatoquadrate, with teeth and the scales around the sensory line external to the pq preserved. B – Impression of lateral surface of articulated set of right upper and lower jaws, with remnants of dentigerous jaw bones, on NMS G.1881.5.64, disarticulated fish from Turin Hill. C – NMS G.2017.23.2, lower jaw and dentigerous bone, mesial view, white arrow points to separation in cartilage(s). D – QMF 58849a, lower jaw with dentigerous bone, mesial view, white arrow points to separation in cartilage(s). E – NMS G.2016.22.3 TS52, vertical section through two jaw cartilages near the rostrum. F – NMS G.2016.22.2 TS51A, close-up of calcified cartilage blocks in vertical jaw section near the rostrum, showing lines of Liesegang. G – NMS G.2017.27.5, dentigerous jaw bone, occlusal view. H – NMS G.2017.23.1, dentigerous jaw bone, mesial view, with obliquely oriented small cusps. I – QMF 58851.20, SEM of large tooth cusp broken off dentigerous jaw bone. J – NMS G.1891.92.252 from Farnell, with symphysial tooth whorl in situ and smaller tooth whorl on upper jaw. K – QMF 58851.08, SEM of detached tooth whorl with cusps broken off, showing central pulp canals. djb, dentigerous jaw bone; expr, extrapalatoquadrate ridge; Mc, Meckel's cartilage; pq.l, left palatoquadrate; pq.r, right palatoquadrate; sc, scapulocoracoid; smc, supramaxillary canal; tw, tooth whorl; tw.s, symphysial tooth whorl. Scale bar = 1 cm in A, B, J, 1 mm in C-E, G-I, K, 0.1 mm in F. Black arrows indicate anterior {fig. will be gray-scale in printed version}



Text-fig. 5. *Ischnacanthus gracilis* (Egerton, 1861), histology of dentigerous jaw bones and tooth whorls; dorsal to left in sections through jaw bones. A-E – NMS G.2016.22.3. A – TS50, vertical section through jaws just posterior to the anterior limit of the dentigerous bones; B – TS53A, vertical section close to the posterior limit of the dentigerous bones; C – TS46, transverse section through symphysial tooth whorl; D, E – TS49, vertical section through the ?anteriormost main cusp on the dentigerous bone, with dentine tubules visible in E. F–H – NMS G.2016.22.4. F – TS3, transverse section through anterior end of jaw bone; G – TS4, horizontal basal section through main cusp and contiguous secondary cusp of jaw bone; H – TS4, transverse section through posterior end of jaw cartilage with multiple outer subtessellate layers and inner disorganised region. cc, subtessellate calcified cartilage; d, denticles; dt, dentine tubules; Mcdb, dentigerous bone on Meckel's cartilage; pc, pulp canal; pqdb.l, dentigerous bone on left palatoquadrate; pqdb.r, dentigerous bone on right palatoquadrate; sc, secondary cusp; t, main tooth cusp; twb, tooth whorl base. Scale bar = 1 cm in A, B, 1 mm in C, D, F, H, 0.1 mm in E, G. White arrows indicate dorsal direction in A, B, F wards the top of the scapula (Text-fig. 3C, D), not previously identified in the species. We have only found evidence for a single pair of nares, each surrounded by rings of platelets. This is best illustrated on NMS G.1956.19.14 (Text-fig. 3D, cnb), the specimen on which Watson (1937, p. 83) based his description: "The nostril is perfectly shown in a specimen belonging to the Dundee Natural History Society. It is a small circular hole placed far above the border of the mouth and forms the centre of a series of concentric rings of dermal bones." A vertical section through the orbit (Text-fig. 3E) shows a thin black stain, the remnant of the eye itself, edged by thin platelets. Pieces of calcified cartilage underlying the eye have an extension towards the middle of the eye.

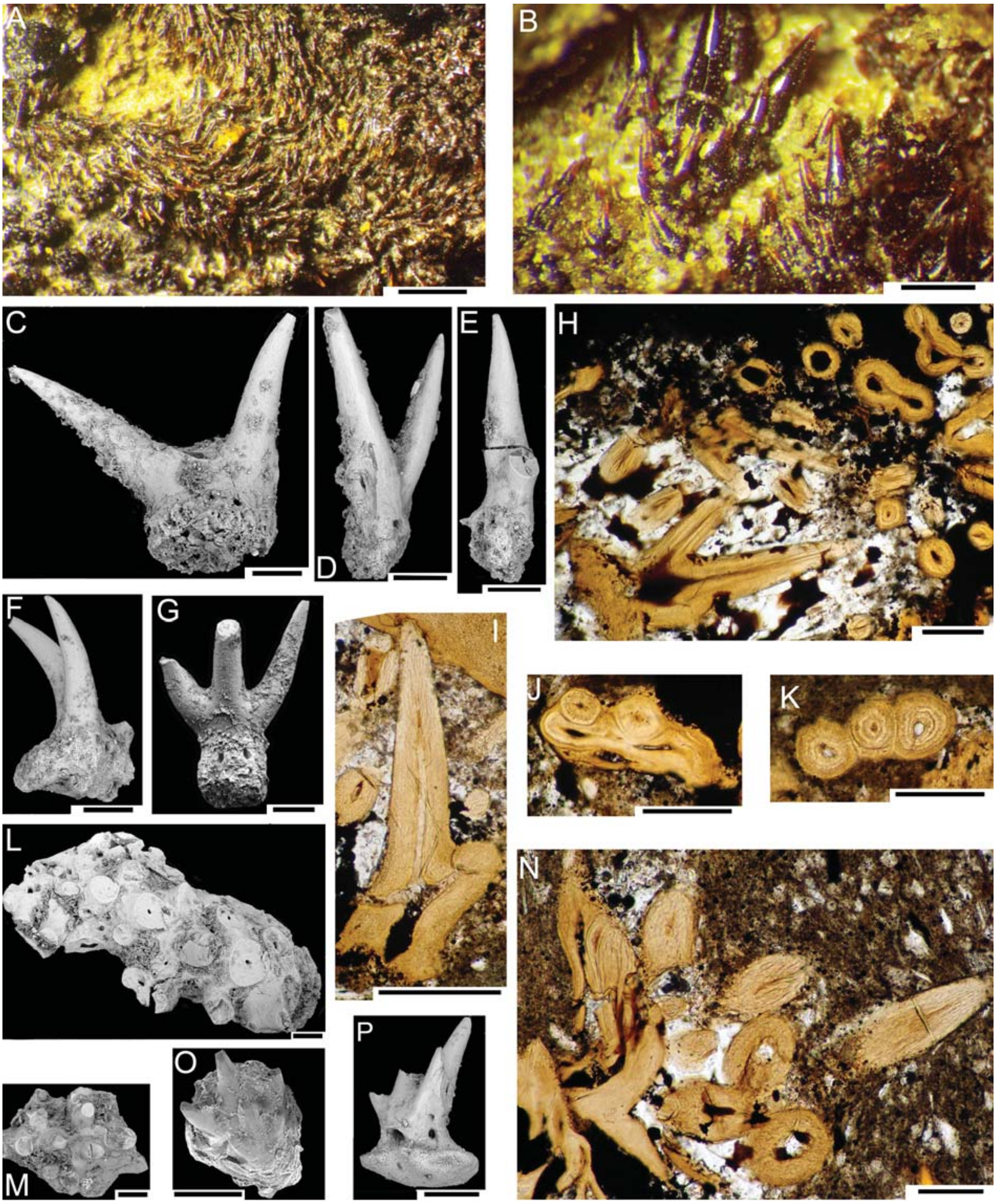
Jaws. Most surface features of the palatoquadrate cartilage (Text-fig. 4A, B) were described by Watson (1937). Brazeau (2009, suppl. notes, character 52) observed that there is an oblique ridge or groove along the medial face of the palatoquadrate (Watson 1937, pl. 9, fig. 3a, b). Regarding the Meckel's cartilage, Watson (1937, p. 79) stated that it was "quite clear" that a posterior and an anterior cartilage form the lower jaw. If there are in fact two cartilages, the separation between them occurs just anterior to the dentigerous jaw bone (Text-fig. 4C, D), although one must question if this apparent separation is rather a break in the cartilage between the posterior part, splinted by the dentigerous bone, and the 'free' anterior part, which just bears separate tooth whorls (as noted by Watson in some large fish including P.311 [now GN.32] in his collection). The mineralised surface of the jaw appears to be formed of a double layer of irregularly shaped calcified cartilage blocks (Text-fig. 4E), presumed to have originally overlain an uncalcified cartilage core. Lines of Liesegang are visible in the tissue at all depths within the layers (Text-fig. 4F), indicating that it is a variant of globular calcified cartilage.

The morphology and mode of growth of dentigerous jaw bones of ischnacanthiforms, and in particular *I. gracilis*, have been described by previous authors (Dean 1907; Watson 1937; Ørvig 1973; Burrow 2004a). As originally noted by Dean (1907), there is some variation in the shape of the teeth. The most common form is illustrated in Text-fig. 4C, D, with slightly incurved main cusps with a smooth apex and circular cross section (Text-fig. 4G) flanked by two or three smaller cusps that decrease slightly in height away from the main cusp. Another form has 'splayed out' secondary cusps that are angled away from the main cusp (Text-fig. 4H). Although the main cusps have a circular cross-section towards the apex, they are often more compressed laterally towards the base (Text-fig. 4I).

These tooth-bearing bones show the same change in transverse section profile from posterior to anterior as observed in other Silurian–Early Devonian ischnacanthiforms (e.g., Burrow 2004a, fig. 2A), with a shallow flattish bone base anteriorly (Text-fig. 5A, F) and a deep bone with a concave base posteriorly (Text-fig. 5B). The dentigerous jaw bones have a histological structure similar to that described for *Gomphonchus* Gross, 1971 (Gross 1957, fig. 3I; 1971, figs 9J, 22F), with a spongiose bone base and a vascular network extending into the main cusps (Text-fig. 5D, E, G). In the older, posterior end of the dentigerous bone, the base is very thick and shows bone trabeculae more or less parallel to the concave base, indicating that successive bone growth layers were added over the underlying cartilage (Text-fig. 5B). This type of layering has previously been illustrated in the younger ischnacanthiform *Atopacanthus* Hussakof and Bryant, 1918 from the Givetian of Spitsbergen (Ørvig 1957, figs 14, 15). At the anterior end of the dentigerous bones, there is a boundary between the teeth and underlying bone (Text-fig. 5A). The vascular network is dense in the base of the tooth cusps (Text-fig. 5G), and diminishes towards the apex of the main teeth (Text-fig. 5A, B, D–F). There is no evidence of an outer enameloid layer overlying the orthodentine extending out from the pulp canals to the external surface of the tooth cusps (Text-fig. 5D, E).

Tooth whorls. A relatively large symphysial tooth whorl was positioned between the lower jaws, although this is only rarely preserved in situ (Text-fig. 4J). Its histological structure (Text-fig. 5C) is similar to that of the dentigerous bones, with a vascular network in the base of the cusps and spongiose bone forming most of the base, but with a denser basal bone layer below the spongiosa. This basal layer is traversed by rare canals that penetrate the lower surface. It is unclear if there are any bone cell lacunae in the bone base; cross-cut Sharpey's fibres are preserved through most of the denser innermost layer. At least some fish also had smaller tooth whorls on the occlusal surface of the lower and upper jaws,

Text-fig. 6. *Ischnacanthus gracilis* (Egerton, 1861), multicuspid denticles, 'Borstenplattchen' and denticulate scales. A, B – NMS G.2017.23.4; extraoral denticles arranged in tooth whorl-like rows, in situ towards the anterior end of the left lower jaw bone (white box in Text-fig. 2F). C-G – tricuspid denticles from QMF 58851, SEM images. C – QMF 58851.12, central cusp broken off; D – QMF 58851.27, lateral cusp broken off; E – QMF 58851.10, two lateral cusps broken off; F – QMF 58851.22, lateral cusp broken off; G – QMF 58851.30, showing all three cusps →



and pore canal openings in base. H-K – NMS G.2016.22.3 denticle thin section images. H – TS52A vertical section and transverse sections of denticles showing single pulp cavity in each cusp; I – TS49, transverse section showing three cusps each with central pulp cavity and centripetal growth lines; J – TS46X, transverse section through cusp bases; K – TS46, vertical section showing pulp canal leading into basal central pulp cavity. L-O – 'Borstenplattchen', or 'cheek scales'. L – NMS G.2017.23.4, plates above and below posterior end of dentigerous bones (grey box in Text-fig. 2F); M – SEM image QMF 58851.02, crown view of plate with broken cusps; N – thin section TS46, oblique section through element. O – QMF 58851.36, pair of short tricuspid denticles on common base, SEM image. P – QMF 58851.19, denticulate scale showing sharp cusps on a base with Sharpey's fibre bundles, SEM image. b, denticle base; 'cs', 'cheek scale'; gz, growth zone; lc, lateral cusp; mc, median cusp; nc, neck canal; pc, pulp canal. Scale bar = 1 mm in A, B, L, 0.1 mm in C-K, M-P {fig. will be grayscale in printed version} between the dentigerous bone and the symphysis (Text-fig. 4J).

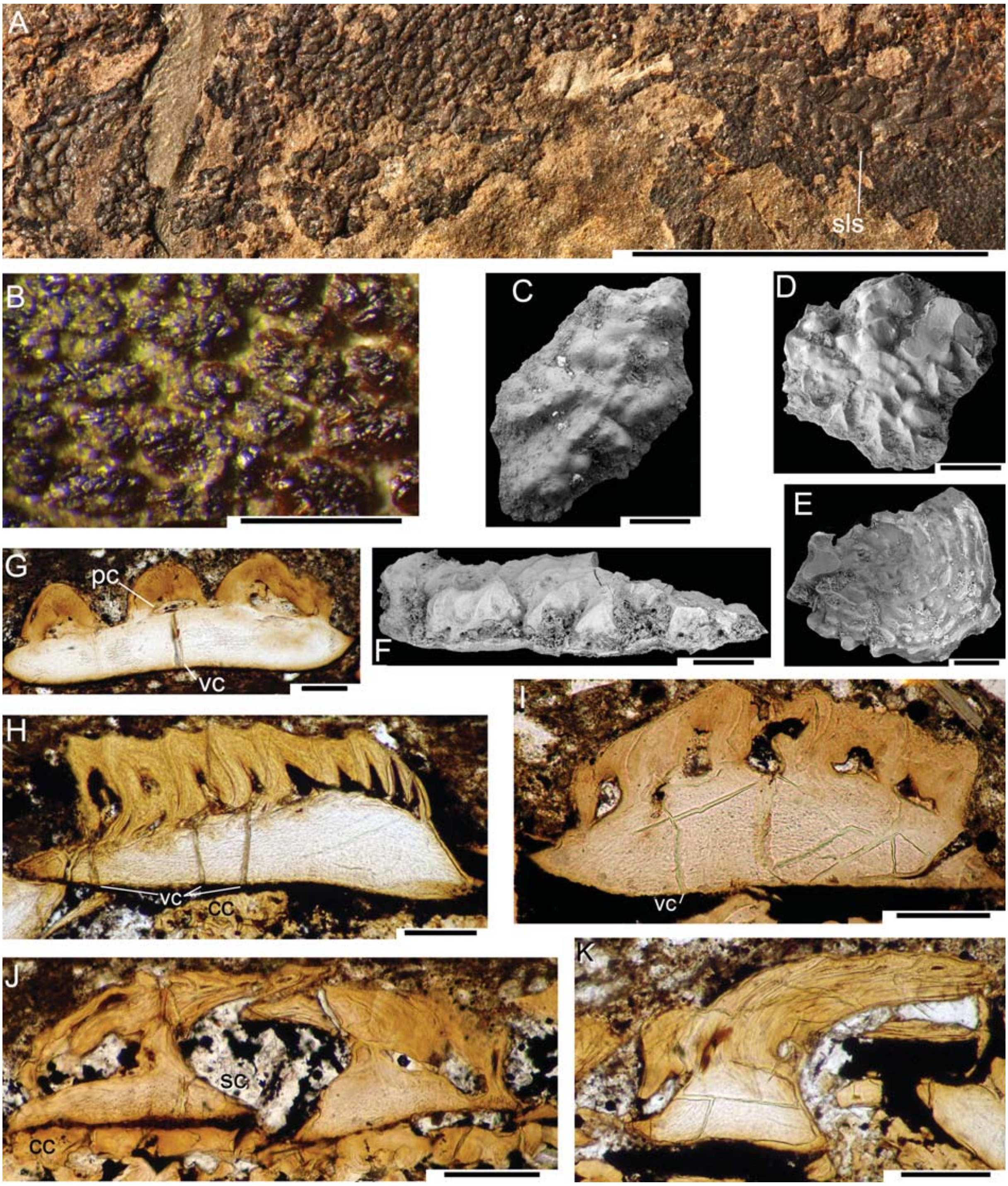
Denticles. Watson (1937, p. 79) noted that on the labial edge of the dentigerous bone on the lower jaw, outside the large tooth cusps, there "arises an extremely deep ridge..." which "bears a series of small denticles." He also observed that some large (NMS G.1887.35.2) and 'normal' sized (NHM PV P.46305) fish have small tricuspid denticles in the anterior part of the mouth. Our acid-prepared specimen NMS G.2017.23.4 (Text-fig. 2F) clearly shows the distribution of the denticles, on the labial rather than lingual side of the dentigerous jaw bones (Text-fig. 6A, B). Most of these are arranged in more or less labiolingual rows, with the cusps directed towards the mouth. Each of these denticles appears to have been tricuspid, with all cusps having a circular cross-section; the lateral cusps are slightly shorter than the medial cusp (Text-fig. 6C–G). The denticles have a bone base, and a central canal extends from near the tip of each cusp into a pulp cavity in the base (Text-fig. 6H–K), with openings halfway up the base (Text-fig. 6G). Growth lines are visible in the cusp dentine (Text-fig. 6J, K), with orthodentine tubules extending from close to the surface into the central canal (Text-fig. 6I). There does not appear to be a superficial enameloid layer. As well as the tricuspid denticles, we also identify scales or platelets with tooth cusp-like odontodes (Text-fig. 6L, M) which have the same shape and structure as the denticle cusps. These platelets are comparable with the 'Borstenplättchen' (= tesserae hirsutae), which Gross (1971, pl. 4, figs 24–29) assigned to *Gomphonchus* sp. indet.? from the Beyrichienkalk, Germany, as well as some of the 'cheek scales' identified by Blais *et al.* (2011, figs 5B, 6A–C) in ischnacanthids from the Lochkovian MOTH locality in Northwest Territories, Canada. The histological structure of the cusps (Text-fig. 6N) appears identical to that of the tricuspid denticles. Smaller scales with similar cusp-like odontodes (Text-fig. 6O, P) resemble the rostral scales figured by Blais *et al.* (2011, fig. 5D), on one of the unnamed MOTH ischnacanthids.

Head tesserae. Most of the head is covered with areal growth tesserae of various forms (Text-fig. 7A). Other small areal-growth scales are distributed below the jaws (Text-fig. 7B). The circumnaral platelets, and other tesserae/platelets posterodorsal to these, are elongate and slightly curved (Text-fig. 7C). Other tectal tesserae are subpolygonal with a stellate arrangement of odontodes (Text-fig. 7D), or with an apparent haphazard arrangement (Text-fig. 7E, F). All these tesserae show a similar histological structure, with a dense acellular bone base (Text-fig. 7G–I). Canals penetrate the basal surface and rise up to the single large pulp canal in the base of each odontode. Scales beside the sensory canals (Text-fig. 7A, E) are of the 'umbellate' form *sensu* Gross (1971), with the posterior crown formed of appositional growth zones which overly the sensory canal (Text-fig. 7J, K). These scales also have wide canals at the base of the growth zones, but these do not penetrate the flat base.

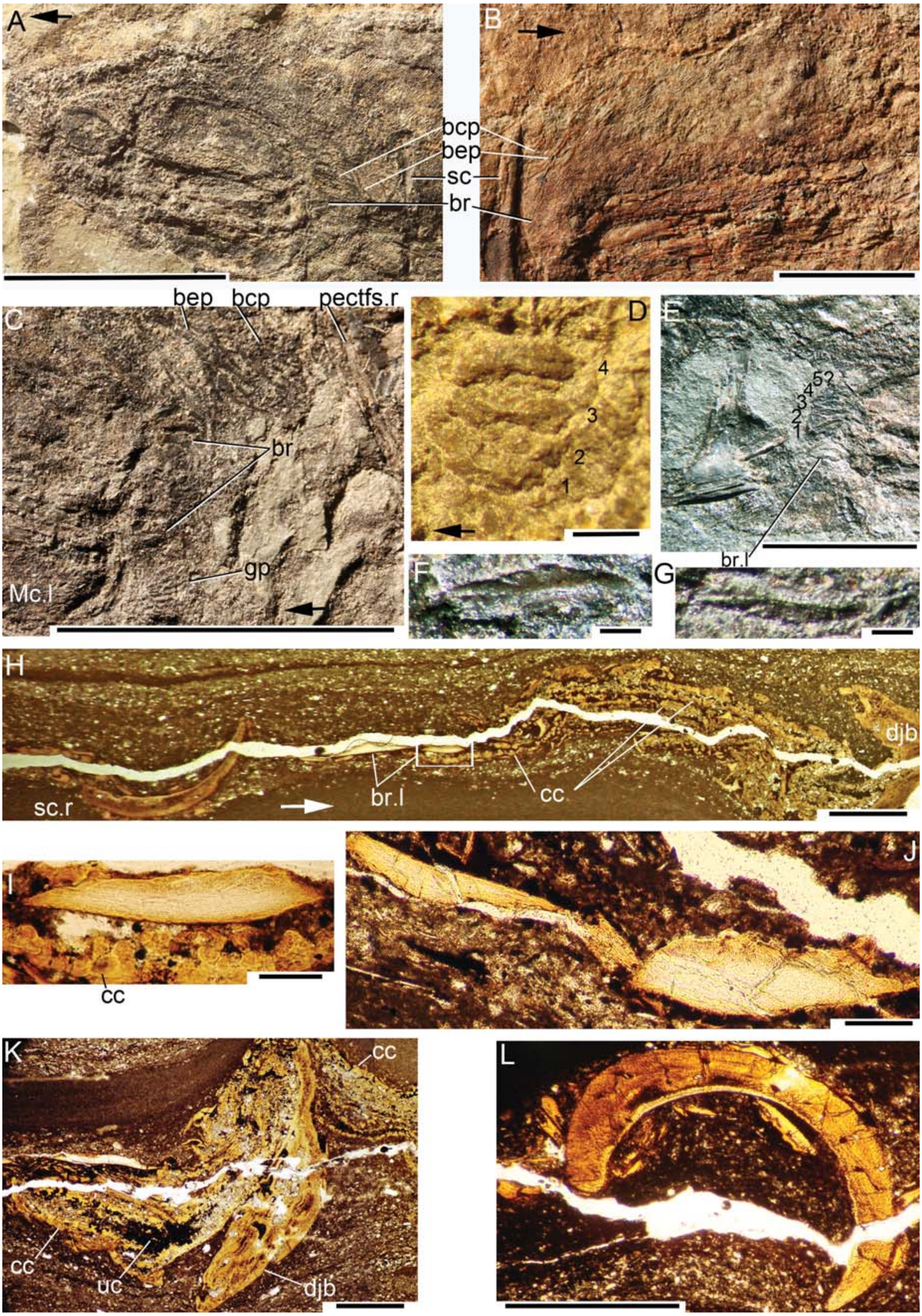
Branchial region. This is the area of *I. gracilis* that was least well-described in previous literature, mostly due to poor preservation of this area and the tendency of the small thin branchial plates to become detached from the fish. Based on specimens in his collection (P.481, 298), Watson (1937) recognised three branchial arches extending from dorsal to the posterior half of the palatoquadrate to near the level of the jaw articulation. The anterior edges of the gill septa are strengthened by staggered oblique thin, long, bony plates (e.g., Text-fig. 8A, bep). NMS G.1891.92.258 (Text-fig. 8B) and NMS G.1891.92.265 (Text-fig. 8C) show their layout, with the plates overlapping at each end. Behind these subvertical plates, the gill septa are covered with subhorizontal, short, thin bony plates, as seen in NMS G.1890.92.265 (Text-fig. 8A) and NMS G.1956.14.16 (Text-fig. 3C). Although shorter than the subvertical plates, they are up to twice as thick. Below these septa is a series of four to six horizontal, fairly broad, thin branchiostegal plates (Text-fig. 8A, D–G), marking the ventral limit of the gill chamber. The branchiostegal plates have a median longitudinal ridge, with short oblique ridges trending back from the ridge towards the edges, and small tubercles intercalated between the ridges (Text-fig. 8D, F, G). The histological structure of the branchiostegals resembles that of the head tesserae, with a flat or slightly convex acellular bone base (Text-fig. 8H, I). The anterior ends of the lower branchiostegals overlie the posterior end of the jaw cartilage (Text-fig. 8J). Very thin, short gular plates lie posteroventral to the lower jaw under the gill chamber (Text-fig. 8C).

Head and branchial region reconstruction. We have revised the reconstruction proffered by Watson (1937, fig. 11) based on our new observations (Text-fig. 9).

Pectoral girdle. The pectoral girdle is fairly simple in form as clearly shown on NMS G.2016.22.5 (Text-fig. 10A), which preserves the pectoral spines articulated with the endoskeletal scapulocoracoids (both in lateral view). The scapulocoracoid is relatively short, with the height being slightly more than twice its base length, and about a third the body depth; the shaft



Text-fig. 7. *Ischnacanthus gracilis* (Egerton, 1861), head tesserae. A – left side of head above the jaws on NMS G.1887.35.2A, showing 'tectal' tesserae and umbellate scales lining the supramaxillary sensory line. B – NMS G.2017.23.4, scales below the jaws (near left lower corner of white box on Text-figure 2E). C-F – stellate tesserae from QMF 58851, SEM images. C – QMF 58851.18 with rounded tubercles, crown view; D – QMF 58851.04, with overlapping tubercles, crown view; E – umbellate scale QMF 58851.40, crown view; F – elongate QMF 58851.24, anterior view. G-K – thin sections of tesserae on NMS G.2016.22.3. G – TS46X, vertical section of tessera with separate, rounded tubercles; H – TS48, vertical longitudinal section of tessera with overlapping tubercles; I – TS49, vertical transverse section of tessera with overlapping tubercles; J – TS53AX, vertical longitudinal section of 'umbellate' scales bordering sensory line showing apposed growth zones of posterior crown; K – TS53A, vertical longitudinal section of 'umbellate' scale. cc, calcified cartilage; pc, pulp canal; sc, sensory canal; sls, sensory line scale; vc, vascular canal. Scale bar = 1 cm in A, 1 mm in B, 0.2 mm in C-F, 0.1 mm in G-K {fig. will be grayscale in printed version}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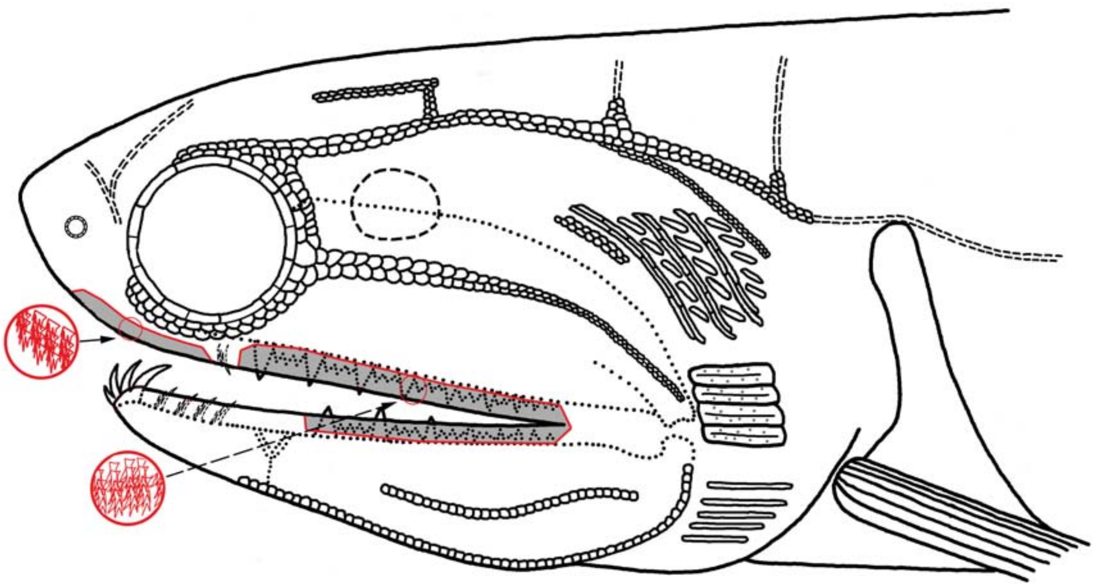


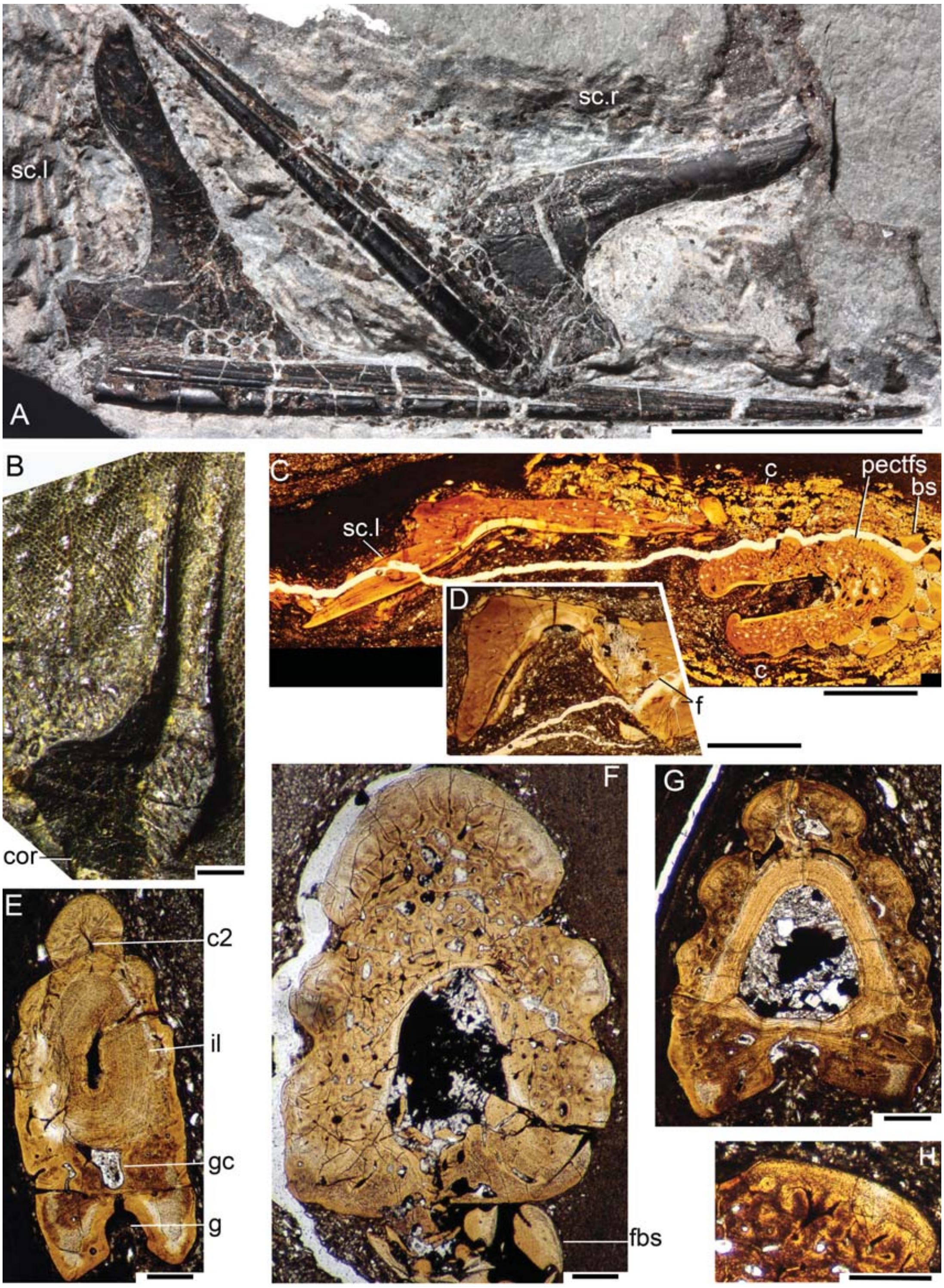
Text-fig. 9. Reconstruction of the head of *Ischnacanthus gracilis* (Egerton, 1861), lateral view, after Watson (1937, fig. 10). Magnified drawings in circles show layout of rostral and 'lip' denticles {fig. will be grayscale in printed version}

widens and flattens to form the scapular blade. The scapular shaft is sigmoid in profile along its anterior edge but with a fairly straight profile on the posterior edge. The whole shaft is inclined to the anterior. The exterior surface is anteroposteriorly convex and the medial surface concave (Text-fig. 10B), giving a U-shaped cross section. The scapular blade is aligned along the pectoral fin spine with its flat base lying flush along the dorsal edge of the spine (Text-fig. 8E). The anterior edge of the shaft is straight and vertical towards its base, below the sigmoidal outline. This anteriormost limit of the scapulocoracoid is level with the proximal end of the pectoral spine, and was presumed by Miles (1973a) to have articulated with an unossified procoracoid. The coracoid region of the scapulocoracoid appears to usually be unossified in *I. gracilis*. However, the visible base of the right scapulocoracoid on NMS G.2016.22.5 is unusual in having an ossified coracoid extending down medial to the spine (Text-figs 2F, 10B).

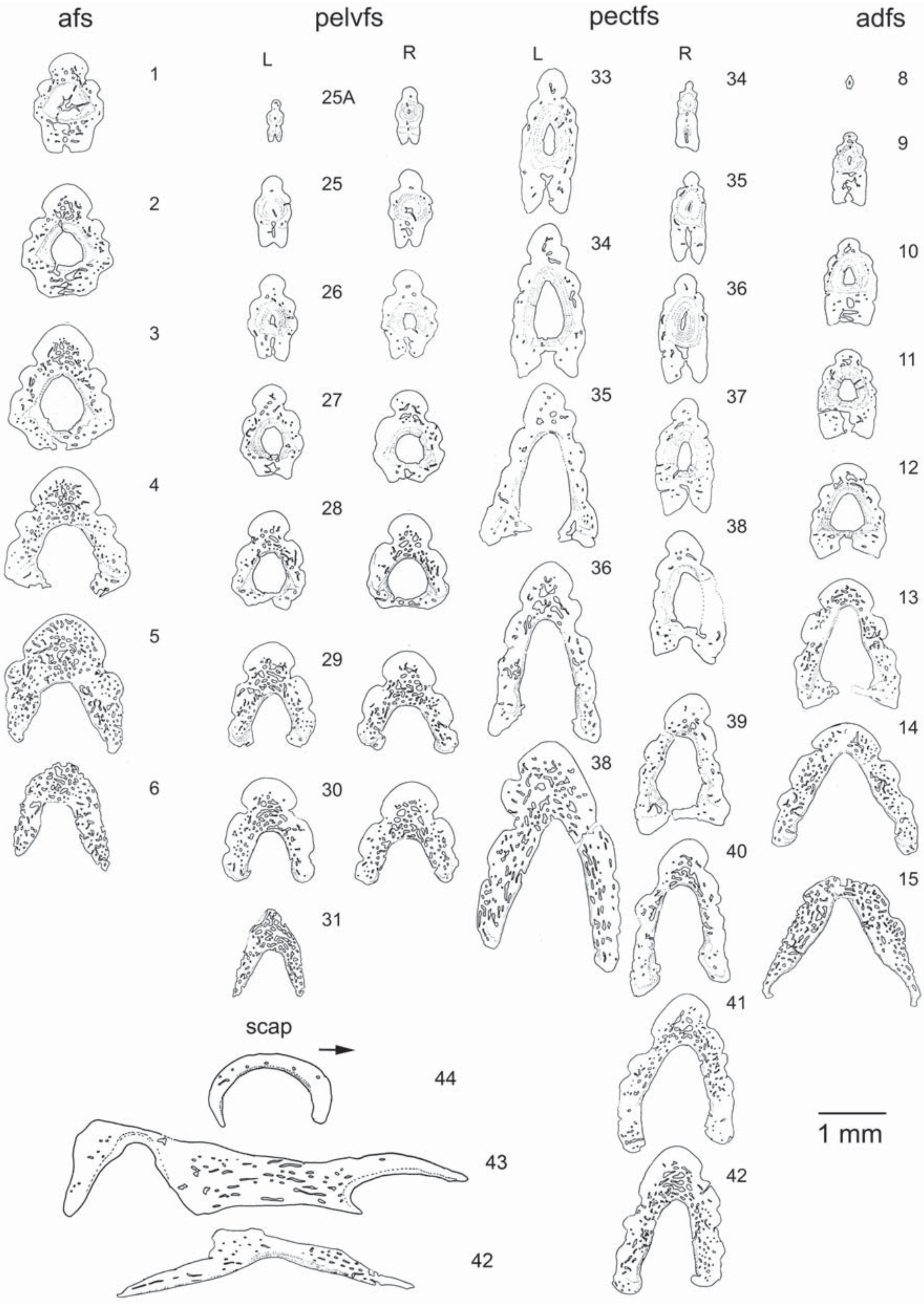
The internal structure of the scapulocoracoid is shown in anteroposterior oriented sections through the pectoral region. NMS G. 2016.22.3 TS42 (Text-fig. 10C) is a section through the base of the left coracoid and disarticulated pectoral spine, and the posterior end of the jaw cartilages. It shows that the internal surface layer of the scapulocoracoid is thin dense laminar bone, with the rest of the element formed of bone with a network of vascular canals, the same structure as in the scapular shaft (Text-fig. 8L). Serial sections through the scapulocoracoid (Text-fig. 11, scap, TS42–44) show its ventrodorsal change in cross-sectional shape, from slightly arched, to a more complex shape presumed to be where it abuts the pectoral fin spine, to the semicircular shape along the shaft (Text-fig. 8L). This specimen appears to have a healed fracture revealed on NMS G. 2016.22.3 TS43 (Text-fig. 10D).

Fin spines. The morphology of the fin spines is best seen on the acid-prepared NMS G.2017.23.4 (Text-fig. 2F); NMS G. 2016.22.5 (Text-fig. 10A)

← Text-fig. 8. *Ischnacanthus gracilis* (Egerton, 1861), branchial region. A – NMS G.1890.6.27p, head and branchial region exposed in left lateral view. B – NMS G.1891.92.258, branchial region exposed in right lateral view. C – NMS G.1891.92.265 showing branchiostegal plates of left and right sides, and branchial and gular plates of the left side. D – NMS FR1711, branchiostegal plates 1–4. E-G – NMS G.2017.30.1. E – pectoral and branchial regions with impressions of left branchiostegal plates 1–4/5 on part; F – left branchiostegal plate 1 impression on part; G – left branchiostegal plate 1 on counterpart. H, I – NMS G.2016.22.3 TS45. H – oblique section, through right scapula shaft, branchial region and posterior end of jaws; I – branchiostegal plate and calcified cartilage in box on H. J-L – NMS G.2016.22.3 TS44 oblique section. J – through branchiostegal plates from each side of the body; K – through posterior end of jaw cartilage and flange of dentigerous jaw bone; L – left scapula shaft, convex medially. bcp, branchial cover plate; bep, branchial edge plate; br, branchiostegal plate; br.l, left branchiostegal plate; djb, dentigerous jaw bone; cc, subtessellate calcified cartilage; gp, gular plates; Mc.l, left Meckel's cartilage; pectfs.r, right pectoral fin spine; sc, scapulocoracoid; sc.r, right scapulocoracoid; uc, uncalcified core of jaw cartilage. Scale bar = 1 cm in A-C, E; 1 mm in D, F, G-L



Text-fig. 10. *Ischnacanthus gracilis* (Egerton, 1861), pectoral girdle and fin spines, all from Tillywhandland. A – NMS G.2016.22.5, left and right pectoral fin spines articulated with scapulocoracoids. B – NMS G.2017.23.4, medial face of right scapulocoracoid. C-H – NMS G.2016.22.3. C – TS42, through base of pectoral spine and scapulocoracoid; D – TS43, posterior end of fractured scapular blade; E – TS36 pectoral spine 2/3 distal from base; F – TS4 middle anal spine; G – TS11 anterior dorsal spine; H – TS30 pelvic spine, lateral ridge. bs, body scale; c, cartilage; cor, coracoid; c2, secondary canal; f, ?pathologic fracture; fbs, large fin base scale; g, posterior groove; gc, canal pinched off posterior groove; il, inner lamellar bone layer; pectfs, pectoral fin spine; sc.l, left scapulocoracoid; sc.r, right scapulocoracoid. Scale bar = 1 cm in A, 1 mm in B-D, 0.1 mm in E-H {fig. will be grayscale in printed version}



Text-fig. 11. *Ischnacanthus gracilis* (Egerton, 1861), fin spines, drawings of serial transverse sections from NMS G.2016.22.3 with numerals denoting the relevant TS section. adfs, anterior dorsal spine; afs, anal spine; pectfs, pectoral spines; pelvfs, pelvic spine; scap, left scapulocoracoid. Scale bar = 1 mm also shows the pectoral fin morphology well. All the spines are long and slender, showing only slight curvature, with three or four smooth, longitudinal ridges extending the length of the spine, including the insertion, on each side, and a robust smooth leading edge ridge. The spines are only shallowly inserted into the musculature. The paired pectoral fin spines are the longest and most robust spines. The posterior dorsal fin spine is the next longest, with the anterior dorsal and anal fin spines being roughly equal in length, and slightly shorter than the posterior dorsal spine. The anterior dorsal fin spine is more strongly curved than the other spines, particularly near the distal end. The shortest spines are the paired pelvic fin spines. The anterior dorsal fin spine is at a level between the pectoral and pelvic fin spines and the posterior dorsal fin spine is posterior to the anal fin spine.

The pectoral spines have a wide-open pulp cavity at the proximal end (Text-figs 10C, 11), with a thin dense lamellar inner layer, a wide middle osteodentine layer extending into the ridges, and a narrow outer layer of orthodentine. The inner layer increases in thickness distally, filling more than half the width of the spine towards the tip with only a small main pulp canal; a secondary pulp canal is sometimes formed in the leading edge ridge (Text-figs 10E, G, 11). Towards the distal end of the median and paired spines, the inner part of the deep posterior (trailing edge) groove becomes enclosed to form a subsidiary canal or canals (Text-figs 10E, 11). The median spines show the same change in relative thicknesses of layers along the spine as in the pectoral spine (Text-figs 10F, G, 11). Unfortunately, the dentine tubules are not well preserved in the sections (Text-fig. 10H); there is no evidence for bone cell lacunae.

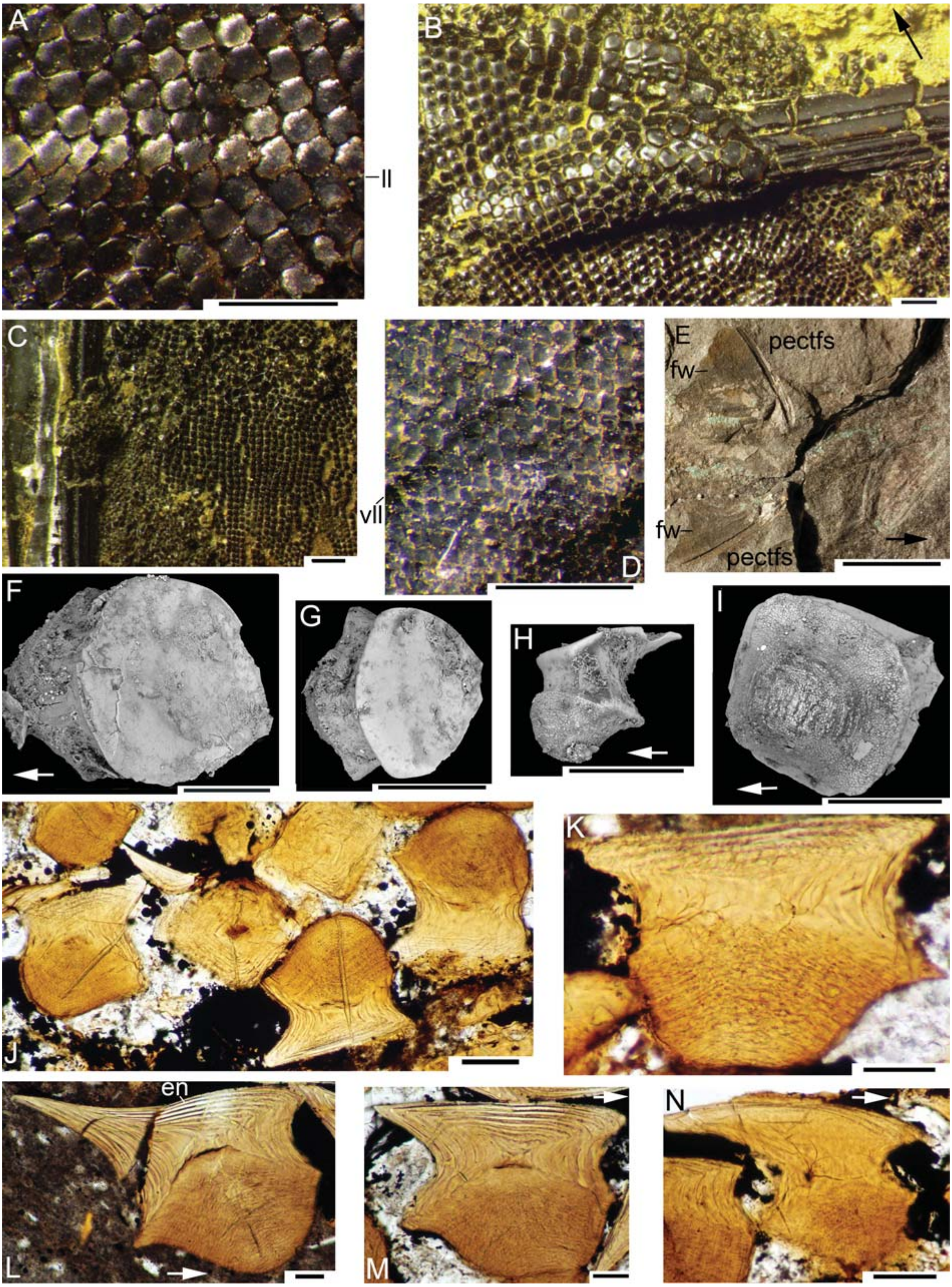
Squamation. As noted by Watson (1937) and others, the scales covering the body show little variation in morphology; most have a smooth rhombic crown less than 0.3 mm wide (Text-fig. 12A). The dorsal, anal and pelvic spines have enlarged scales around the base (Text-figs 2E, 12B). The lateral and ventrolateral lines are only distinguishable by a raised ridge in the squamation (Text-figs 2E, 12A, D), with no other surface evidence of the sensory canal. As noted by Watson (1937), scales on the fins are much smaller than the body scales, with a clear demarcation between the fins and the body (Text-figs 2E, 12B, C). All the fin spines have fin webs, which are shorter than the spines on the median fins. Pectoral fin webs are rarely preserved, but one specimen NMS G.1973.16 from the sandstone of Mirestone Quarry shows that the web extends beyond the spine tip (Text-fig. 12E). Large smooth polygonal scales like those around the fin bases are also distributed along the dorsal margin of the caudal peduncle, extending back along the dorsal edge of the caudal fin (Watson 1937).

Scanning electron micrographs of individual scales (Text-fig. 12F–I) show the subrhombic smooth crown. The neck is concave all round, and of a similar height to the convex base. The base is deepest under the anterior part of the crown. The distribution of fibre bundles through the base is evidenced by the circular microstructures visible on the surface (Text-fig. 12H, I). Histological structure of the flank scales shows an acellular lamellar bone base, and orthodentine and enameloid forming the superposed crown growth zones (Text-fig. 12J–N). The crown has up to 10 growth zones, all of equal width, with the upper central region of each zone formed of enameloid, overlying a thin layer of dentine (Text-fig. 12L, M). Narrow dentine canals extend inwards from neck pores, with dentine tubules branching off and extending up into the crown growth zones, and sometimes also down into the base (Text-fig. 12K). The primordial (oldest central) growth zone often retains a pulp cavity (Text-fig. 12J, N).

DISCUSSION

As part of our investigation, and considering the wide size range of specimens, we evaluated the possibility that more than one *Ischnacanthus* species was represented in the Midland Valley localities. We found no taxonomically significant differences in the morphology or structure of skeletal elements; the only notable variation was in the relative body depth of larger individuals, with rare fish (e.g., NMS G.2017.23.4) being ‘fatter’ than the average, but showing no other distinctive characters. By compar-

Text-fig. 12. *Ischnacanthus gracilis* (Egerton, 1861), squamation. A-C – squamation on NMS G.2017.23.4. A – around the lateral line, posterior to the pelvic spine level; B – around the base of the posterior dorsal fin spine; C – the base of the anal fin spine. D – squamation around the ventrolateral line on NMS G.2017.27.6. E – NMS G.1973.16 from Mirestone Quarry, ventral surface exposed showing extent of pectoral fin webs. F-I – scales from QMF 58851, SEM images. F – QMF 58851.06, anterocrown view; G – QMF 58851.13, anterocrown view; H – QMF 58851.11, lateral view; I – QMF 58851.07, basal view. J-N – thin sections of scales on NMS G.2016.22.3. J – TS54A, vertical longitudinal and horizontal sections; K – TS23, vertical oblique section; L – TS18, vertical longitudinal section; M – TS18, oblique section; N – TS54A, vertical longitudinal section. en, enameloid; fw, fin web; ll, lateral line; pectfs, pectoral fin spine; vll, ventrolateral line. Scale bar = 1 mm in A-E; 0.2 mm in F-I, 0.1 mm in J-N. Arrow indicates anterior →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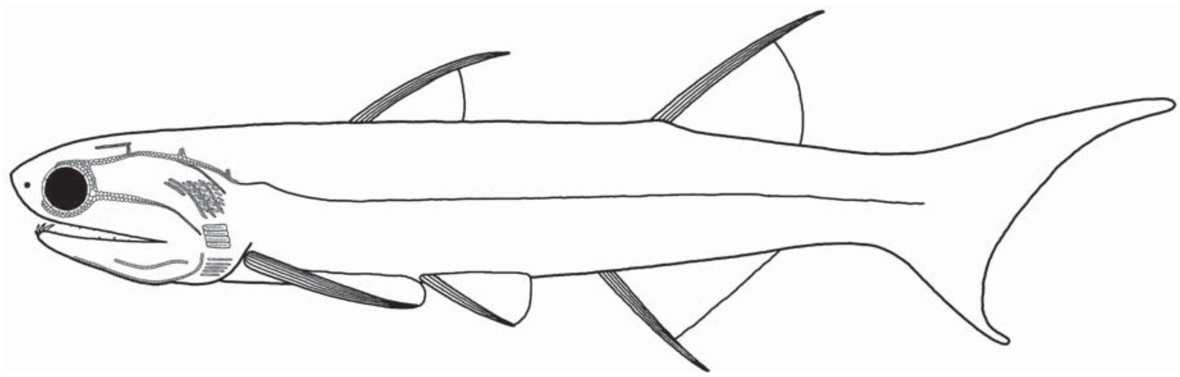


Text-fig. 13. Reconstruction of *Ischnacanthus gracilis* (Egerton, 1861) (after Watson 1937, fig. 11)

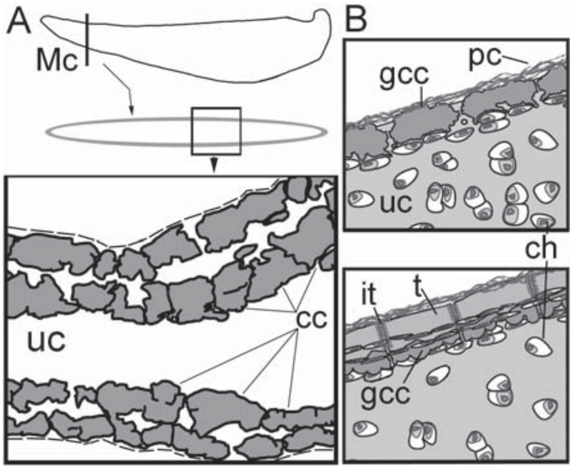
ison with modern fish, we speculate that these individuals are gravid females, but – not surprisingly – we can find no evidence for eggs. Text-fig. 13 is our reconstruction of the whole fish in lateral view.

A number of skeletal features were newly discovered or revised. Given that a bony sclerotic ring is considered a general gnathostome character (Burrow *et al.* 2011), and they are found in most acanthodians, it is understandable that previous reconstructions of *I. gracilis* (e.g., Watson 1937, fig. 10) appear to show a sclerotic ring. (Note that Watson described these rings of bones in all acanthodians as circum-orbitals, even though they are now regarded as sclerotic bones – Burrow *et al.* 2011). However, our investigations have revealed no evidence for sclerotic bones in the orbit; none of the acid-prepared specimens have any such bones preserved, indicating their absence is not just due to the elements detaching during splitting.

Perhaps the most interesting elements investigated here are the extraoral tricuspid denticles on the labial side of the jaw cartilages. Watson (1937) noted their presence in several specimens, but as Goodrich (1909, fig. 160) had done before him, he misinterpreted their position as being inside the mouth, rather than outside. Watson noted that their morphology resembled that of "*Diplodus*" Agassiz, 1843 and *Doliodus* Traquair, 1893 (taxa erected for isolated teeth). Our thin sections show that the histological structure of their cusps is much more 'shark-like' than the structure of the dentigerous jaw bone and tooth whorl cusps, with the denticle cusps having a single central pulp cavity rather than the vascular network seen in the occlusal dental elements. Osteichthyan fishes are characterised by having two fields of 'biting' teeth, an inner and an outer dental arcade (e.g., Rosen *et al.* 1981), whereas gnathostomes on the chondrichthyan lineage only have functional teeth borne on the jaw cartilages, considered homologous to the inner dental arcade in osteichthyans (Zhu *et al.* 2013). Perhaps the labial denticles in ischnacanthids are the equivalent of the outer dental arcade borne on the dermal bones lateral to the jaw cartilages in osteichthyan fishes.

A variety of forms of extraoral denticles and denticulated plates have been observed in the MOTH ischnacanthids (Blais *et al.* 2011), but because the denticle fields tend to obscure the dentigerous bone cusps these variants have not been associated with any of the species newly named by Blais *et al.* (2015). Although Blais *et al.* (2015) considered none of the MOTH fish were *I. gracilis*, MOTH specimen CMN 22727 (Bernacsek and Dineley 1977, text-fig. 8, pl. 5) only shows features identical to those on Scottish *I. gracilis* specimens, and UALVP 45014 (Blais *et al.* 2011, fig. 2A; 2015, fig. 2B) shows some similarities with *I. gracilis*. It has the five or six branchiostegals behind the jaw hinge somewhat similar to the arrangement illustrated by Watson (1937, fig. 10). Another specimen UALVP 45020, designated *Ischnacanthus* cf. *I. gracilis*, shows otic labyrinth infillings (Sahney and Wilson 2001, fig. 2A,3C) as seen in NMS G.1891.92.266 (Text-fig. 3B), but also in other MOTH ischnacanthids (Blais *et al.* 2011, fig. 3A; 2015, fig. 2A) as well as other gnathostomes and osteostracans from the MOTH locality (Sahney and Wilson 2001). Other acanthodians/stem chondrichthyans also have specialised scales or tesserae edging the mouth, including the adentate *Obtusacanthus corronis* Hanke and Wilson, 2004, and *Parexus recurvus* Agassiz, 1844 (Burrow *et al.* 2013, fig. 10), but these structures are not tooth-like.

One of the other interesting features revealed in our study is the structure of the jaw cartilages in



Text-fig. 14. Organisation of calcified cartilage blocks in the lower jaw of *Ischnacanthus gracilis* (Egerton, 1861). A – sketch of Meckel's cartilage (Mc) and stylised cross-section showing the position of the area illustrated (this is the area in the black box on Text-fig. 4E); dashed line represents position of perichondrium in life. B – ontogenetic stages in the development of tessellated calcified cartilage in modern sharks (after Dean *et al*. 2009, fig. 6, stages pre- and post-tesseral formation). cc, calcified cartilage; ch, chondrocyte; gcc, globular calcified cartilage; it, intertesseral joint; pc, perichondrium; t, tessera; uc, uncalcified cartilage (not preserved in fossil)

I. gracilis, with a double layer of cartilage blocks overlying a mostly uncalcified cartilage core. The composition of these blocky cartilage 'sheets' is interpreted as a double layer rather than a single layer of blocks with an unmineralised centre, because the separation between the blocks is not aligned across the two layers (Text-figs 4E, 14A), and these layers sometimes separate from each other. The structure appears identical to that of the jaws in *Climatius reticulatus* Agassiz, 1845 (Burrow *et al*. 2015, fig. 6D). An interesting comparison can be made with the ontogenetic development of the tesserae in tessellate calcified cartilage (TCC) in modern sharks. There, they form in two pieces, with the outer part directly under the perichondrium made of prismatic cartilage and the inner part formed by coalescence of calcified cartilage globules (Dean *et al*. 2009; Text-fig. 14B). With the cartilage in *I. gracilis* comprising rounded blocks rather than globules, its structure seems transitional to the tessellate arrangement of calcified cartilage characterising crown chondrichthyans. Recent work on Devonian stem chondrichthyans indicates marked variation in the cartilage structure exhibited in different taxa, including *Gogoselachus* Long, Burrow, Ginter, Maisey, Trinajstic, Coates, Young and Senden, 2015 and *Gladbachus* Heidtke and Krätschmer, 2001 (Coates *et al*. 2018), suggesting a complex history accompanying the evolution of tessellated calcified cartilage.

The branchial region of *I. gracilis* shows previously unrecorded similarities with that in other Early Devonian acanthodians from Scotland, in particular the presence of subrectangular branchiostegal dermal plates of a similar form to those in *Euthacanthus macnicoli* Powrie, 1864 and *Climatius reticulatus*, rather than the irregularly shaped plates described and illustrated for *I. gracilis* by Watson (1937, fig. 10). In *E. macnicoli*, these plates are quite robust and much longer and more numerous than in *I. gracilis*. They are covered with tubercles and long sinuous ridges in *E. macnicoli* (Newman *et al*. 2014, figs 5D, 6E, 9), whereas in *I. gracilis* they have a sparser, more regular ornament of separated oblique ridges converging on a median longitudinal ridge, with small tubercles between the ridges. *Climatius reticulatus* has a similar number of branchiostegal plates (five or six) as in *I. gracilis*; the plates are robust with a median ridge and ornamented with ridged tubercles (Miles 1973a, text-fig. 7C). *Parexus recurvus* has six or seven branchiostegal plates ornamented with a longitudinal ridge and fine tubercles (Burrow *et al*. 2013, fig. 11G) somewhat similar to *I. gracilis. Euthacanthus macnicoli*, *C. reticulatus* and *I. gracilis* have fields of thin dermal plates covering at least three branchial arches, posterodorsal to the branchiostegal plates. In all three species, the cover comprises long diagonal plates presumably along the anterior edge of each arch with short more horizontal plates behind. The anterior plates are much shorter in *I. gracilis* than in *E. macnicoli* (Newman *et al*. 2014, fig. 9) and *C. reticulatus* (Miles 1973a, text-fig. 5). Of the other less well known Scottish LORS species, *Uraniacanthus curtus* (Powrie, 1870) has four branchiostegals plates ornamented with fine ridges in a loose chevron pattern; no other gill cover plates have been observed in this taxon (Newman *et al*. 2012). *Brachyacanthus scutiger* (Egerton, 1861) and *Mesacanthus mitchelli* (Egerton, 1861) were last described by Watson (1937) and are in need of revision. However, both species have well-formed branchiostegal plates and branchial arch dermal cover. The other Scottish Early Devonian acanthodian known from whole articulated specimens is *Vernicomacanthus uncinatus* (Powrie, 1864 ex Egerton MS), which has not been described in any detail since being erected by Powrie, and is in desperate need of revision.

The fin spines of *I. gracilis* differ from those of most acanthodians in that the ornament ridges extend almost to the proximal end of the spine. Some fin spine fragments that Gross (1971, pl. 8, fig. 29, pl. 9, fig. 1) assigned to *Gomphonchus* sp. indet. conform to the morphology of *I. gracilis* spines, and the histological structure of *I. gracilis* spines is identical to that of *Gomphonchus* as described by Gross (1971, figs 24E–G, 25, 26A), as far as it is possible to tell given the limited preservation of dentine tubules and ultrafine details in the Scottish *I. gracilis* material.

The smooth-crowned flank scales of *I. gracilis* also appear indistinguishable from the *Gomphonchus* type species, *G. sandelensis* Pander, 1856. Not surprisingly, histological structure of *I. gracilis* scales is of the *Gomphonchus*-type *sensu* Gross (1971), with an acellular bone base, thin orthodentine-type canals and tubules extending through the crown base and into the growth zones, and an enameloid layer superficially in the middle of each growth zone. This enameloid layer is less prominent in the inner (older) growth zones. Whereas Chevrinais *et al.* (2017) regarded similar enameloid layers in scales of the Late Devonian acanthodiform *Triazeugacanthus affinis* (Whiteaves, 1887) as separate layers of ganoine added after the concentric addition of dentine layers, we maintain the traditional interpretation (e.g., Gross 1971) that the enameloid layers in acanthodians are an intrinsic part of each growth zone, with each formed before the superposition of the next growth zone.

Regarding scale variation over the body, contra Watson (1937), enlarged scales surround some of the fin spine bases, as also seen in many other acanthodians (Hanke and Wilson 2004, app. 2, characters 31, 32). Thin sections through the lateral line show no difference in scale shape or histology between scales along the line and elsewhere on the flank, and no evidence of a canal infilling or vacuity. The caudal fin shows scale zonation of the typical form exhibited by most acanthodians (Miles 1970); this was described by Watson (1937).

CONCLUSIONS

Our investigation has highlighted several features in *Ischnacanthus gracilis*, including the branchial arch cover platelets and branchiostegals and the structure of the jaw cartilages, which support the interrelationships between different acanthodian orders and families. Some features – in particular, the structure of the extraoral denticles and subtessellate organisation of the cartilage forming the jaws – further support the position of ischnacanthiform acanthodians with 'climatiiform' acanthodians as stem chondrichthyans, as determined by recent cladistic analyses. Although the denticle fields have been described as 'extraoral' (Blais *et al.* 2011), perhaps they are rather the equivalent of the outer dental arcade recognized in osteichthyan fishes, as the dentigerous jaw bones and occlusal tooth whorls are considered homologous to the inner dental arcade in osteichthyans (Zhu *et al.* 2013).

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REFERENCES

Agassiz, L. 1833–43. Recherches sur les poissons fossiles. 5 vols and atlas, 1–1420. Imprimerie de Petitpierre et Prince; Neuchâtel.

Agassiz, J.L.R. 1844–45. Monographie de poissons fossils des Vieux Grès Rouge ou Système Dévonien (Old Red Sandstone) des Iles Britanniques et de Russie, 171 p. Jent et Grassman; Neuchâtel.

Anonymous. 1865. Report of the Directors for 1864, 3–7. Montrose Museum; Scotland.

Armstrong, M. and Paterson, I.B. 1970. The Lower Old Red Sandstone of the Strathmore Region. *Institute of Geological Sciences, report*, **70/12**, 1–23.

Berg, L.S. 1940. Classification of fishes both recent and fossil. *Travaux de l'Institut de Zoologie de l'Academie des Sciences de l'URSS*, **5**, 85–517.

Bernacsek, G.M. and Dineley, D.L. 1977. New acanthodians from the Delorme Formation (Lower Devonian) of N.W.T., Canada. *Palaeontographica Abteilung A*, **158**, 1–25.

Blais, S.A., Hermus, C.R. and Wilson, M.V.H. 2015. Four new Early Devonian ischnacanthid acanthodian from the Mackenzie Mountains, Northwest Territories, Canada: an early experiment in dental diversity. *Journal of Vertebrate Paleontology*, **35**, e948546 (13 pp.).

Blais, S.A., MacKenzie, L.A. and Wilson, M.V.H. 2011. Toothlike scales in Early Devonian eugnathostomes and the 'outside-in' hypothesis for the origins of teeth in vertebrates. *Journal of Vertebrate Paleontology*, **31**, 1189–1199.

Botella, H., Manzanares, E., Ferrón, H.G. and Martínez-Pérez, C. 2014. *Obruchevacanthus ireneae* gen. et sp. nov., a new ischnacanthiform (Acanthodii) from the Lower Devonian of Spain. *Paleontological Journal*, **48**, 1067–1076.

Brazeau, M.D. 2009. The braincase and jaws of a Devonian 'acanthodian' and modern gnathostome origins. *Nature*, **457** (7227), 305–308.

Brotzen, F. 1934. Erster Nachweis von Unterdevon im Ostseegebiete durch Konglomeratgeschiebe mit Fischresten. II Teil (Paläontologie). *Zeitschrift Geschiebeforschung*, **10**, 1–65.

Burrow, C.J. 1995. Acanthodian dental elements from the Trundle beds (Lower Devonian) of New South Wales. *Records of the Western Australian Museum*, **17**, 331–341.

Burrow, C.J. 1996. Taphonomy of acanthodians from the Devonian Bunga Beds (late Givetian/early Frasnian) of New South Wales. *Historical Biology*, **11**, 213–228.

Burrow, C.J. 2004a. Acanthodian fishes with dentigerous jaw bones: the Ischnacanthiformes and *Acanthodopsis*. *Fossils and Strata*, **50**, 8–22.

Burrow, C.J. 2004b. A redescription of *Atopacanthus dentatus* Hussakof and Bryant, 1918 (Acanthodii, Ischnacanthidae). *Journal of Vertebrate Paleontology*, **24**, 257–267.

Burrow, C.J. 2007. Early Devonian (Emsian) acanthodian faunas of the western USA. *Journal of Paleontology*, **81**, 824–840.

Burrow, C.J. 2011. A partial articulated acanthodian from the Silurian of New Brunswick, Canada. *Canadian Journal of Earth Sciences*, **48**, 1329–1341.

Burrow, C.J. 2013. Reassessment of *Ischnacanthus*? *scheii* Spjeldnaes (Acanthodii, Ischnacanthiformes) from the latest Silurian or earliest Devonian of Ellesmere Island, arctic Canada. *Canadian Journal of Earth Sciences*, **50**, 945–954.

Burrow, C.J. 2017. Reassessment of a mid-Palaeozoic vertebrate assemblage from Laúndos, Portugal. *Journal of Iberian Geology*, **43**, 97–110.

Burrow, C., den Blaauwen, J., Newman, M. and Davidson, R. 2016. The diplacanthid fishes (Acanthodii, Diplacanthiformes, Diplacanthidae) from the Middle Devonian of Scotland. *Palaeontologia Electronica*, **19.1.10A**, 1–83.

Burrow, C.J., Davidson, R.G., den Blaauwen, J.L. and Newman, M.J. 2015. Revision of *Climatius reticulatus* Agassiz, 1844 (Acanthodii, Climatiidae), from the Lower Devonian of Scotland, based on new histological and morphological data. *Journal of Vertebrate Paleontology*, **35**, e913421 (15 p.).

Burrow, C., Newman, M., den Blaauwen, J., Jones, R. and Davidson, R. 2017. The Early Devonian ischnacanthiform acanthodian *Ischnacanthus gracilis* from the Midland Valley of Scotland. In: Ginter. M. (Ed.), 14th International Symposium on Early and Lower Vertebrates University of Warsaw, Chęciny, Poland, 3–8 July 2017, p. 25. Warszawa.

Burrow, C.J., Newman, M.J., Davidson, R.G. and den Blaauwen, J.L. 2011. Sclerotic plates or circumorbital bones in early jawed fishes? *Palaeontology*, **54**, 207–214.

Burrow, C.J., Newman, M.J., Davidson, R.G. and den Blaauwen, J.L. 2013. Redescription of *Parexus recurvus*, an Early Devonian acanthodian from the Midland Valley of Scotland. *Alcheringa*, **37**, 392–414.

Burrow, C.J. and Rudkin, D. 2014. Oldest near-complete acanthodian: the first vertebrate from the Silurian Bertie Formation Konservat-Lagerstätte, Ontario. *PLoS ONE*, **9** (8), e104171 (7 pp.).

Burrow, C.J. and Turner, S. 2010. Reassessment of "*Protodus*" *scoticus* from the Early Devonian of Scotland. In: Elliott, D.K., Maisey, J.G., Yu, X. and Miao, D. (Eds), Morphology, Phylogeny and Paleobiogeography of Fossil Fishes, pp. 123–144. Verlag Dr. Friedrich Pfeil; München.

Burrow, C.J. and Turner, S. 2012. Fossil Fish Taphonomy and the Contribution of Microfossils in Documenting Devonian Vertebrate History. In: Talent, J.A. (Ed.), Earth and Life, pp. 189–223. Springer; Dordrecht, Heidelberg, London, New York.

Burrow, C.J., Vergoossen, J.M.J., Turner, S., Uyeno, T.T. and Thorsteinsson, R. 1999. Microvertebrate assemblages from the Upper Silurian of Cornwallis Island, Arctic Canada. *Canadian Journal of Earth Sciences*, **36**, 349–361.

Burrow, C.J. and Young, G.C. 2005. The acanthodian fauna of the Craven Peaks Beds (Early to Middle Devonian), western Queensland. *Memoirs of the Queensland Museum*, **51**, 3–25.

Chevrinais, M., Sire, J.-Y. and Cloutier, R. 2017. From body scale ontogeny to species ontogeny: Histological and morphological assessment of the Late Devonian acanthodian *Triazeugacanthus affinis* from Miguasha, Canada. *PLoS ONE*, **12** (4), e0174655.

Coates, M.I., Finarelli, J.A., Sansom, I.J., Andreev, P.S., Criswell, K.E., Tietjen, K., Rivers, M.L. and La Riviere, P.J. 2018. An early chondrichthyan and the evolutionary assembly of a shark body plan. *Proceedings of the Royal Society B: Biological Sciences*, **285** (1870), 1–10.

Coates, H. and MacNair, P. 1892. The Old Red Sandstone of Perthshire. *Transactions of the Perthshire Society of Natural Science*, **1**, 1–11.

Davis, S.P., Finarelli, J.A. and Coates, M.I. 2012. *Acanthodes* and shark-like conditions in the last common ancestor of modern gnathostomes. *Nature*, **486** (7402), 247–250.

Dean, B. 1907. Notes on acanthodian sharks. *American Journal of Anatomy*, **7**, 209–222.

Dean, M.N., Mull, C.G., Gorb, S.N. and Summers, A.P. 2009. Ontogeny of the tessellated skeleton: insight from the skeletal growth of the round stingray *Urobatis halleri*. *Journal of Anatomy*, **215**, 227–239.

Denison, R. 1979. Acanthodii. In: Schultze, H.-P. (Ed.), Handbook of Paleoichthyology, vol. 5, pp. 1–62. Gustav Fischer Verlag; Stuttgart.

Dineley, D.L. 1999. Early Devonian fossil fishes sites of Scotland. In: Dineley, D.L. and Metcalf, S.J. (Eds), Fossil Fishes of Great Britain, pp. 145–165. Joint Nature Conservation Committee; Peterborough, UK.

Egerton, P. de M.G. 1861. British fossils. (Descriptions of *Tristichopterus*, *Acanthodes*, *Climatius*, *Diplacanthus*, *Cheiracanthus*). *Memoirs of the Geological Survey of the United Kingdom (British Organic Remains)*, Decade **10**, 51–75.

Fergusson, C.L., Cas, R.A.F., Collins, W.J., Craig, G.Y., Crook, K.A.W, Powell, C.M., Scott, P.A. and Young, G.C. 1979. The Upper Devonian Boyd volcanic complex, Eden, New South Wales. *Journal of the Geological Society of Australia*, **26**, 87–105.

Frickhinger, K.A. 1991. Fossilien-Atlas Fische, 1088 p. Mergus Verlag; Melle.

Fritsch, A. 1907. Miscellanea palaeontologica. I. Palaeozoica, 23 p. Fr. Rivnác; Prague.

Gagnier, P.-Y., Hanke, G.F. and Wilson, M.V.H. 1999. *Tetanopsyrus lindoei* gen. et sp. nov., an Early Devonian acanthodian from the Northwest Territories, Canada. *Acta Geologica Polonica*, **49**, 81–96.

Gagnier, P.-Y. and Wilson, M.V.H. 1995. New evidences on jaw bones and jaw articulations in acanthodians. *Geobios*, mémoire special, **19**, 137–143.

Geikie, A. 1902. The Geology of Eastern Fife. Memoirs of the Geological Survey of Great Britain (Scotland), 421 p. HMSO; Edinburgh.

Goodrich, E.S. 1909. Vertebrata Craniata (First Fascicle: Cyclostomes and Fishes). In: Lankester, R. (Ed.), A Treatise on Zoology, Part IX, pp. 1–518. Adam and Charles Black; London.

Graham-Smith, W. 1936. The tail of fishes. *Proceedings of the Zoological Society*, **1936**, 595–608.

Gross, W. 1947. Die Agnathen und Acanthodier des obersilurischen Beyrichienkalks. *Palaeontographica Abteilung A*, **96**, 91–158.

Gross, W. 1957. Mundzähne und Hautzähne der Acanthodier und Arthrodiren. *Palaeontographica Abteilung A*, **109**, 1–40.

Gross, W. 1967. Über das Gebiss der Acanthodier und Placodermen. *Journal of the Linnean Society, Zoology*, **47**, 121–130.

Gross, W. 1971. Downtonische und dittonische Acanthodier-Reste des Ostseegebietes. *Palaeontographica Abteilung A*, **136**, 1–82.

Hancock, A. and Atthey, T. 1868. Notes on the remains of some reptiles and fishes from the shales of the Northumberland coal field. *Annals and Magazine of Natural History*, **1**, 266–278, 346–378.

Hanke, G.F. and Davis, S.P. 2008. Redescription of the acanthodian *Gladiobranchus probaton* Bernacsek and Dineley, 1977, and comments on diplacanthid relationships. *Geodiversitas*, **30**, 303–330.

Hanke, G.F., Davis, S.P. and Wilson, M.V.H. 2001. New species of the acanthodian genus *Tetanopsyrus* from northern Canada, and comments on related taxa. *Journal of Vertebrate Paleontology*, **21**, 74–753.

Hanke, G.F. and Wilson, M.V.H. 2004. New teleostome fishes and acanthodian systematics; In: Arratia, G., Wilson, M.V.H. and Cloutier, R. (Eds), Recent Advances in the Origin and Early Radiation of Vertebrates, pp. 189–216. Verlag Dr. Friedrich Pfeil; München.

Hanke, G.F. and Wilson, M.V.H. 2006. Anatomy of the early Devonian acanthodian *Brochoadmones milesi* based on nearly complete body fossils, with comments on the evolution and development of paired fins. *Journal of Vertebrate Paleontology*, **26**, 526–537.

Heidtke, U.H.J. and Krätschmer, K. 2001. *Gladbachus adentatus* nov. gen. et sp., ein primitiver hai aus dem oberen Givetium (Oberes Mitteldevon) der Bergisch Gladbach-Paffrath-Mulde (Rheinisches Schieffergebirge). *Mainzer Geowissenschaftliche Mitteilungen*, **30** (4), 105–122.

Hermus, C.R. and Wilson, M.V.H. 2001. Early Devonian ischnacanthid acanthodians from the Northwest Territories of Canada. *Journal of Vertebrate Paleontology*, **21**, suppl. 3, 61A.

Hickling, G. 1912. On the geology and palaeontology of Forfarshire. *Proceedings of the Geologists' Association*, **23**, 303–311.

Hussakof, L. and Bryant, W.L. 1918. Catalog of the fossil fishes in the Museum of the Buffalo Society of Natural Sciences. *Bulletin of the Buffalo Society of Natural Sciences*, **12**, 1–346.

Jessen, H. 1973. Weitere Fischreste aus dem Oberen Plattenkalk der Bergisch-Gladbach – Paffrather Mulde (Oberdevon, Rheinisches Schiefergebirge). *Palaeontographica Abteilung A*, **143**, 159–187.

Long, J.A. 1986. New ischnacanthid acanthodians from the Early Devonian of Australia, with comments on acanthodian interrelationships. *Zoological Journal of the Linnean Society*, **87**, 321–339.

Long, J.A., Burrow, C.J., Ginter, M., Maisey, J.G., Trinajstic, K.M., Coates, M.I., Young, G.C. and Senden, T.J. 2015. First shark from the Late Devonian (Frasnian) Gogo Formation, Western Australia sheds new light on the development of tessellated calcified cartilage. *PLoS ONE*, **10** (5), e0126066.

Long, J.A., Burrow, C.J. and Ritchie, A. 2004. A new Late Devonian acanthodian fish from the Hunter Formation near Grenfell, New South Wales. *Alcheringa*, **28**, 147–156.

Miles, R.S. 1966. The acanthodian fishes of the Devonian Plattenkalk of the Paffrath Trough in the Rhineland. *Arkiv för Zoologi*, **18**, 147–194.

Miles, R.S. 1970. Remarks on the vertebral column and caudal fin of acanthodian fishes. *Lethaia*, **3**, 343–362.

Miles, R.S. 1973a. Articulated acanthodian fishes from the Old

Red Sandstone of England, with a review of the structure and evolution of the acanthodian shoulder-girdle. *Bulletin of the British Museum (Natural History). Geology*, **24**, 111–213.

Miles, R.S. 1973b. Relationships of acanthodians. In: Greenwood, P.H., Miles, R.S. and Patterson, C. (Eds), Interrelationships of Fishes, pp. 63–103. Linnean Society; London.

Moy-Thomas, J.A. 1939. Palaeozoic Fishes, 149 p. Methuen and Co.; London.

Moy-Thomas, J.A. and Miles, R.S. 1971. Palaeozoic Fishes, 2nd Edition, 259 p. Chapman and Hall Ltd; London.

Newman, M.J., Burrow, C.J., den Blaauwen, J.L. and Davidson, R.G. 2014. The Early Devonian acanthodian *Euthacanthus macnicoli* Powrie, 1864 from the Midland Valley of Scotland. *Geodiversitas*, **36**, 321–348.

Newman, M.J., Burrow, C.J., Davidson, R.G., den Blaauwen, J.L. and Jones, R. 2017. Comparison of the vertebrate faunas of the Lower Old Red Sandstone of the Anglo-Welsh Basin with contemporary faunas in Scotland. *Proceedings of the Geologists' Association*, **128**, 447–459.

Newman, M.J., Davidson, R.G., den Blaauwen, J.L. and Burrow, C.J. 2011. The Early Devonian acanthodian *Euthacanthus gracilis* from the Midland Valley of Scotland. *Scottish Journal of Geology*, **47**, 101–111.

Newman, M.J., Davidson, R.G., den Blaauwen, J.L. and Burrow, C.J. 2012. The Early Devonian acanthodian *Uraniacanthus curtus* (Powrie, 1870) n. comb. from the Midland Valley of Scotland. *Geodiversitas*, **34**, 739–759.

Ørvig, T. 1957. Notes on some Paleozoic lower vertebrates from Spitsbergen and North America. *Norsk Geologisk Tidsskrift*, **37**, 285–354.

Ørvig, T. 1967. Some new acanthodian material from the Lower Devonian of Europe. *Journal of the Linnean Society, Zoology*, **47**, 131–153.

Ørvig, T. 1973. Acanthodian dentition and its bearing on the relationships of the group. *Palaeontographica Abteilung A*, **143**, 119–150.

Owen, R. 1846. Lectures on the comparative anatomy and physiology of vertebrate animals delivered at the Royal College of Surgeons, England in 1844 and 1846. Part 1, Fishes, 308 p. Longman, Brown, Green and Longman; London.

Page, D. 1859. Farther contributions to the palaeontology of the tilestones or Silurio-Devonian strata of Scotland. In: Report of the Twenty-Eighth Meeting of the British Association for the Advancement of Science held at Leeds in September 1858. Transactions of the Sections, pp. 104–105. John Murray; London.

Page, D. and Lapworth, C. 1888. Introductory text-book of Geology, 12th edition, 316 p. William Blackwood and sons; Edinburgh.

Pander, C.H. 1856. Monographie der fossilen Fische des silurischen Systems der Russisch-Baltischen Gouvernements. Obersilurische Fische, 91 p. Buchdruckerei der Kaiserlichen Akademie der Wissenschaften; St. Petersburg.

Paton, R.L. 1976. A catalogue of fossil vertebrates in the Royal Scottish Museum, Edinburgh. Part 5 Acanthodii, 40 p. Royal Scottish Museum; Edinburgh.

Powrie, J. 1864. On the fossiliferous rocks of Forfarshire and their contents. *Quarterly Journal of the Geological Society of London*, **47**, 413–429.

Powrie, J. 1870. On the earliest known vestiges of vertebrate life; being a description of the fish remains of the Old Red Sandstone rocks of Forfarshire. *Transactions of the Edinburgh Geological Society*, **1**, 284–301.

Rosen, D.E., Forey, P.L., Gardiner, B.G. and Patterson, C. 1981. Lungfishes, tetrapods, paleontology, and plesiomorphy. *Bulletin of the American Museum of Natural History*, **167** (4), 159–276.

Sahney, S. and Wilson, M.V.H. 2001. Extrinsic labyrinth infillings imply open endolymphatic ducts in Lower Devonian osteostracans, acanthodians, and putative chondrichthyans. *Journal of Vertebrate Paleontology*, **21**, 660–669.

Spjeldnaes, N. 1967. Acanthodians from the Siluro-Devonian of Ellesmere Island. In: Oswald, D.H. (Ed.), International symposium on the Devonian system, II, pp. 807–813. Alberta Society of Petroleum Geologists, Calgary.

Traquair, R.H. 1888. Old Red Sandstone fishes. *Geological Magazine*, Decade III, **5**, 507–517.

Traquair, R.H. 1892. List of the Type and Figured specimens in the "Powrie Collection" of fossils. *The Annals of Scottish Natural History*, **1**, 31–39.

Traquair, R.H. 1893. Notes on the Devonian fishes of Campbelltown and Scaumenac Bay in Canada – No. 2. *The Geological Magazine*, Decade III, **10**, 145–149.

Trewin, N.H. 2013. Scottish Fossils, 118 p. Dunedin Academic Press; Edinburgh.

Trewin, N.H. and Davidson, R.G. 1996. An Early Devonian lake and its associated biota in the Midland Valley of Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **86**, 233–246.

Valiukevičius, J.J. 1992. First articulated *Poracanthodes* from the Lower Devonian of Severnaya Zemlya. In: Mark-Kurik, E. (Ed.), Fossil Fishes as Living Animals, pp. 193–214. Academy of Sciences of Estonia; Tallinn.

Valiukevičius, J.J. 2003. Devonian acanthodians from Severnaya Zemlya Archipelago (Russia). *Geodiversitas*, **25**, 131–204.

Valiukevičius, J. and Burrow, C.J. 2005. Diversity of tissues in acanthodians with *Nostolepis*-type histological structure. *Acta Palaeontologica Polonica*, **50**, 635–649.

Vergoossen, J. 1990a. De visfauna's van vijf Boven-Silurische kalkstenen uit het Mirdumer klif. *Grondboor en Hamer*, **44**, 132–136.

Vergoossen, J. 1990b. Over enn grote tandspiraal uit de Groningse keileem. *Grondboor en Hamer*, **44**, 136–138.

Voichyshyn, V. and Szaniawski, H. 2012. Acanthodian jaw bones from Lower Devonian marine deposits of Podolia, Ukraine. *Acta Palaeontologica Polonica*, **57**, 879–896.

Watson, D.M.S. 1937. The acanthodian fishes. *Philosophical Transactions of the Royal Society of London*, **228B**, 49–146.

White, E.I. 1961. The Old Red Sandstone of Brown Clee Hill and the adjacent area. II. Palaeontology. *Bulletin of the British Museum (Natural History). Geology*, **5**, 245–310.

Whiteaves, J. 1887. Illustrations of the fossil fishes of the Devonian rocks of Canada. *Proceedings and Transactions of the Royal Society of Canada*, **4** (iv), 101–110.

Woodward, A.S. 1891. Catalogue of the fossil fishes in the British Museum (Natural History), 2, 1–567. British Museum (Natural History); London.

Woodward, A.S. and Sherborn, C.D. 1890. A catalogue of British fossil vertebrate, 396 p. Dulau and Co.; London.

Young, V.T. 1995. Micro-remains from Early and Middle Devonian acanthodian fishes from the U.K. and their biostratigraphic possibilities. *Ichthyolith Issues*, **1**, 65–68.

Young, V.T. 1997. Early Palaeozoic acanthodians in the collection of the Natural History Museum, London. *Ichthyolith Issues Special Publication*, **3**, 46–50.

Zhu, M., Yu, X., Ahlberg, P.E., Choo, B., Lu, J., Qiao, T., Qu, Q., Zhao, W., Jia, L., Blom, H. and Zhu, Y.A. 2013. A Silurian placoderm with osteichthyan-like marginal jaw bones. *Nature*, **502**, 188–193.

Zidek, J. 1976. Kansas Hamilton Quarry (Upper Pennsylvanian) *Acanthodes*, with remarks on the previously reported North American occurrences of the genus. *The University of Kansas Paleontological Contributions*, **83**, 1–41.

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