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Acanthodians from the Lower Devonian (Emsian) 'Placoderm Sandstone', Holy Cross Mountains, Poland

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ABSTRACT:

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The Lower Devonian 'Placoderm Sandstone' in the Holy Cross Mountains (HCM) is filled with abundant impressions of disarticulated vertebrate remains. The only acanthodian macroremains named to date are fin spines of *Machaeracanthus polonicus* Gürich. Fin spine impressions in slabs from the Winna Formation (Emsian) at Podłazie Hill (near Daleszyce) in the southern HCM, and also the Barcza Formation (?Lochkovian) at Barcza Quarry, Miedziana Góra Conglomerate (?Lochkovian), Gruchawka, and Zagórze Formation (middle–upper Emsian) at Bukowa Mountain in the northern HCM, reposited in the University of Warsaw, Polish Geological Institute-National Research Institute, Warsaw, and Natural History Museum, London collections, have been cast and studied in order to better document this poorly known taxon. As noted in other *Machaeracanthus* species, we have found that *M. polonicus* has two different morphotypes of spines, which abut lengthwise to form a pair of spines. Our investigations show that the fin spine assemblage includes *Onchus overathensis* as well as *M. polonicus*, and probably another undetermined acanthodian. The affinities of *O. overathensis* are reassessed. It is here considered to be a diplacanthiform, and reassigned to the genus *Striacanthus*, as *S. overathensis*. Acanthodian scapulocoracoids have also been identified, as well as tightly spiralled toothwhorls which could be from an acanthodian.

Keywords: Acanthodii; *Machaeracanthus*; *Striacanthus*; *Onchus*; Emsian; Poland.

INTRODUCTION

Acanthodian stem gnathostomes are rare in the Polish Devonian, or at least only rarely described. The only acanthodian taxon erected to date, based on specimens from the Lower Devonian of Poland, is *Machaeracanthus polonicus* Gürich, 1901. Unfortunately, the holotype fin spine is lost, but it was figured by Gürich (1901, fig. 8), and Zidek (1981) regarded *M. polonicus* as a valid taxon because the cross-sectional shape of the spine differs from that in other *Machaeracanthus* species (see Burrow *et al.* 2010, fig. 1). Otherwise there are very few other acanthodian records. Many microvertebrate assemblages with acanthodian scales have been described from the Upper Silurian–lowest Devonian subsurface deposits which extend from Lithuania into northern Poland, mainly from Lithuanian boreholes (e.g. Valiukevičius 2005). Märss (1997, pl. 4) first figured acanthodian scales from uppermost Silurian–lowermost Devonian core sections in northern and eastern Poland (Märss 1997, fig. 7: acanthodian taxa assigned to *Nostolepis alta*, *N. gracilis*, *N. striata*, *Gomphonchus hoppei*, and *G. sandelensis*). Liszkowski and Racki (1993, fig. 6A–F) described scales from the Givetian of the Holy Cross Mountains which they assigned to *Acanthoides*? *dublinensis* Stauffer, 1938 and *Cheiracanthoides comptus* Wells, 1944. They also figured a dermal bone fragment they considered to possibly be an acanthodian jaw fragment (Liszkowski and Racki 1993, fig. 6G), however the specimen looks more like part of a placoderm spinal plate.

The 'Placoderm Sandstone' vertebrate fauna is long known (Gürich 1896), particularly for placoderms as indicated by the common name, but also for heterostracans (e.g. Halstead-Tarlo 1965; Blieck 1980) and one sarcopterygian record (Kulczycki 1960). Perhaps surprisingly, the first placoderm from the Lower Devonian of Poland, a homosteidid arthrodire, was described by Szrek *et al*. (2015). That specimen was collected from an active sandstone quarry in the Bukowa Mountain, northern Holy Cross Mountains (the Łysogóry Region) about 20 km north of Kielce (Szrek *et al*. 2015, fig. 1), in an allochthonous shelly concentration in the Zagórze Formation (Lower Devonian, upper? Emsian). Other vertebrates present at that locality include a *Guerichosteus*-like psammosteid heterostracan, small unidentified placoderms, and *Machaeracanthus* fin spine fragments (Szrek *et al*. 2015). The first placoderm assemblage from the 'Placoderm Sandstone' unit (Winna Fm.) at Podłazie Hill (Kielce Region) was also formally described only recently (Szrek and Dupret 2017). Although *Machaeracanthus polonicus* is the only acanthodian fin spine form recorded from the Zagórze and Winna formations (northern and southern HCM respectively), collections by PS and colleagues in 2011–2013 include specimens of other acanthodian taxa as well as *Machaeracanthus*. L.B. Halstead (a.k.a. Tarlo, also Halstead-Tarlo) deposited specimens catalogued as *Machaeracanthus* sp. in the Natural History Museum, London (NHM UK) collection. These specimens are described herein, and their affinities and geographic distribution are discussed, as outlined in our presentation at the 14th International Symposium on Early and Lower Vertebrates (Burrow and Szrek 2017).

MATERIAL AND METHODS

The NHM UK specimens described here are from an abandoned quarry in the Winna Formation, popularly referred to as the 'Placoderm Sandstone', at Podłazie Hill near Daleszyce, 15 km east of Kielce, central Poland (Szrek and Dupret 2017, fig. 1). They were collected by H. Łobanowski and Halstead in the 1950s and donated to the NHK UK in 1971. More specimens were collected from the same site in 2011–13 by PS and coworkers (Szrek *et al*. 2014) and reposited in the Geological Museum of the Polish Geological Institute-National Research Institute, Warsaw (Muz PGI). Specimen Muz PGI 1733.II.172 was collected from the Barcza Quarry, and Muz PGI 1733.II.354, 1733.II.175-6 from Gruchawka. University of Warsaw (UW) specimens are from the Podłazie Hill locality.

All the spine fossils are preserved as impressions in the sandstone. Silicon casts were made of the specimens, and the casts were whitened with ammonium chloride sublimate for photography. Whole cast specimens in the Muz PGI were photographed using a Nikon D80 with lens AF Micro Nikkor 60 mm 1:2,8D. Other images were taken with an Olympus SZ40 dissecting microscope and DP12 imaging system at the Queensland Museum (QM), Brisbane. The NHM UK specimens were cast in-house, then whitened and photographed at the QM using the Olympus equipment. Text-figures were compiled in Adobe Photoshop; composite images were made of large specimens.

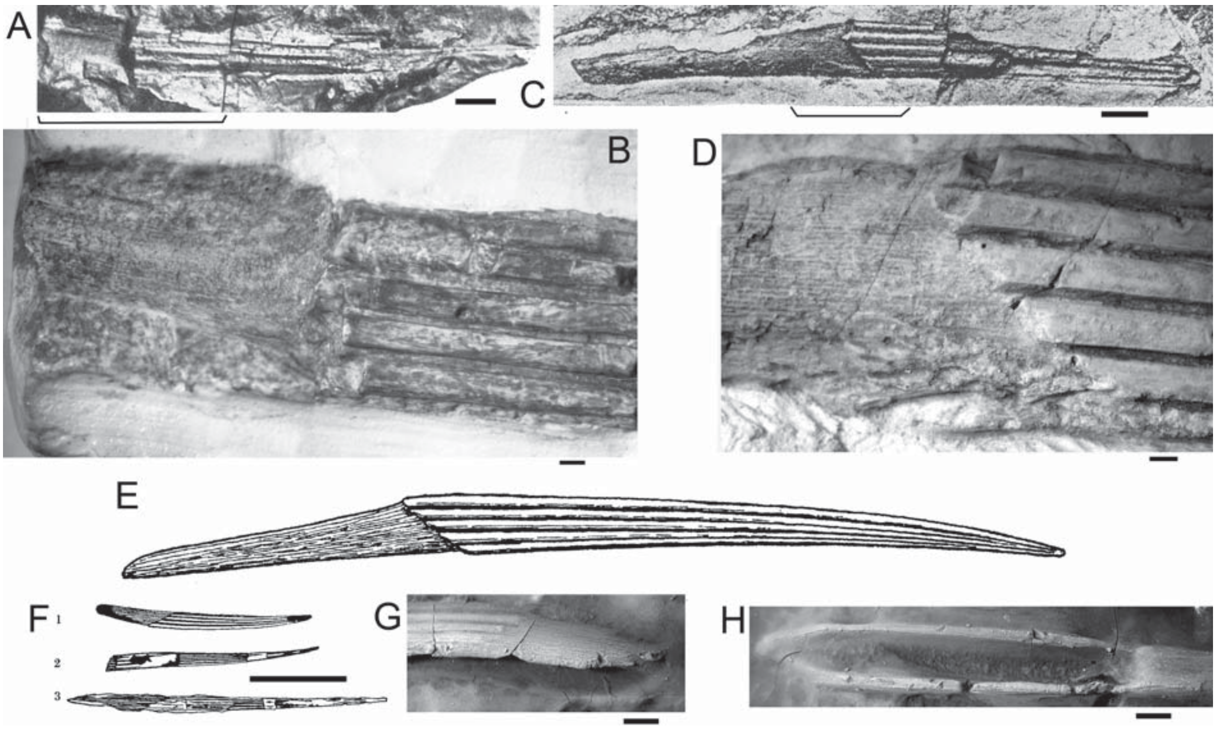
SYSTEMATIC PALAEONTOLOGY

Acanthodii Owen, 1846
Order Diplacanthiformes Berg, 1940

DIAGNOSIS: (Fin spines, after Newman *et al*. 2012): fin spines ornamented with longitudinal ridges paralleling the leading edge; inserted portion of median fin spines with narrow, closely spaced parallel ridges; anterior dorsal fin spine with long inserted portion.

Family indet.

REMARKS: Although *Striacanthus* can be assigned to the diplacanthiforms based on the surface structure of the inserted area, it cannot be assigned to any recognised diplacanthiform family. The Middle Devonian (Eifelian) Scottish Diplacanthidae have fin spines with an accessory pulp canal above the main pulp cavity (Burrow *et al*. 2016), which is lacking in *Striacanthus* spines. As in *Striacanthus*, dorsal fin spines of *Diplacanthus crassisimus* (Duff, 1842) have a concave anterior edge to the insertion, but they differ in having many more, narrow longitudinal ridges on the exserted part and an insertion/exsertion boundary (IEB) perpendicular to the spine axis. Dorsal fin spines of *Diplacanthus tenuistriatus* Traquair, 1894 also have a similar profile, but have more ridges, plus fine striations on the ridge surfaces. *Rhadinacanthus*



Text-fig. 1. *Striacanthus overathensis* nov. comb. and *Striacanthus*-like fin spines. A-E – *Striacanthus overathensis*: A – holotype specimen MBf 705 from Overath, Germany (specimen figured by Gross 1933, fig. 11C as *Onchus major*); B – inserted area impression and exserted area near the IEB on cast of holotype spine (level indicated on A); C – spine MBf 772 from Overath, Germany (specimen figured by Gross 1937, pl. 8 fig. 8); D – cast of MBf 772, closeup image of inserted and exserted area near the IEB (level indicated on C); E – reconstruction of a whole spine (Gross 1937, fig. 29). F – *Striacanthus sicaeformis* spine impressions (after Hills 1931, fig. 4.1–3). G, H – *Striacanthus*-like fin spines (lacking distinctive insertion shape) on whitened cast of AMF 61297 from the ?Emsian Merrimerriwa Formation, western New South Wales, Australia: G – lateral, and H – trailing edge impression moulds. Scale bar = 1 cm in A, C, F, 1 mm in B, D, G, H. Distal end to right in A-F, H, to left in G

longispinus (Agassiz, 1844) dorsal fin spines differ in having smooth sides separated from a large leading edge ridge by a deep groove, and the anterior edge of the insertion is almost straight. They resemble *Striacanthus* spines in having narrow canals running the length of the spine paralleling the pulp cavity, that appear to lead into the grooves between the narrow ridges of the insertion area (Burrow *et al*. 2016, fig. 27). Dorsal spines of the Late Devonian (Frasnian) "*Diplacanthus*" *ellsi* Gagnier, 1996, "*Diplacanthus*" *horridus* Woodward, 1892 and *Florestacanthus morenoi* Burrow, Janvier and Villaroel, 2003, and the Famennian *Diplacanthus acus* Gess, 2001, seem to have an almost straight anterior edge on the insertion, as do those of the Lower Devonian (Lochkovian) Gladiobranchidae (*Uraniacanthus spinosus* Miles, 1973, *U. curtus* (Powrie, 1870) and *U. probaton* (Bernacsek and Dineley 1977); see Miles 1973, pl. 11; Newman *et al*. 2012, fig. 6B; Hanke and Davis 2008, fig. 2 respectively) as well as the Middle–Late Devonian Culmacanthidae (Long 1983, fig. 1). The Frasnian *Devononchus concinnus* (Gross, 1930), presumed also to be a diplacanthiform based on the narrow parallel ridges on the insertion, has a similar number of smooth longitudinal ornament ridges on the exserted area, radially arranged longitudinal vascular canals, and an even more markedly concave leading edge on the insertion, but it has a subcostal canal as well as the main pulp canal.

In summary, the only other acanthodian species known from articulated specimens which have a concave anterior edge to the dorsal spine insertion are the diplacanthids *Diplacanthus crassissimus* and *D. tenuistriatus*, plus *Devononchus concinnus*, but they differ from *Striacanthus* in other features.

Genus *Striacanthus* Hills, 1931

TYPE SPECIES: *Striacanthus sicaeformis* Hills, 1931.

DIAGNOSIS: Diplacanthiform acanthodian with long gently curved median fin spines with an elongate insertion c. one quarter the length of the whole spine; inserted part with a concave leading edge and straight trailing edge; exserted part with four or five smooth longitudinal ridges on each side separated by narrow grooves, and a wider leading edge ridge; a single wide pulp cavity extends the length of the spine, with no other large pulp canals; narrow canals are arranged concentrically around the pulp cavity parallel to its length.

INCLUDED SPECIES: *Striacanthus overathensis* (Gross, 1933) nov. comb.

Striacanthus overathensis (Gross, 1933) nov. comb.
(Text-figs 1A–E, 2A–H, ?2I–L)

1933a. *Onchus major*; W. Gross, pp. 65–66, fig. 9, fig. 11A–C, pl. 5.
1933b. *Onchus major*; W. Gross, p. 64.
?1933. *Onchus* sp.; H. Schmidt, fig. 5c, d.
1937. *Onchus overathensis*; W. Gross, fig. 29, pl. 8, fig. 8.
1961. *Onchus overathensis*; E. White, p. 286.
?1967. '*Onchus*' *overathensis* Gross; T. Ørvig, p. 148, pl. 1, fig. 5.
?1969. '*Onchus*' *overathensis* Gross; T. Ørvig, p. 303.
1979. *Onchus overathensis* Gross 1937A [*O. major* Gross 1933C, non Etheridge in Symonds 1872C]: R. Denison, p. 53, figs 32B, 33B.
1980. «*Onchus*» *overathensis* Gross, 1937; A. Blieck *et al*., p. 147, fig. 7B.
2004. *Onchus overathensis*; G. Young and C. Burrow, p. 25, 35, 41.
2007. '*Onchus overathensis*'; R. Mutter and M. Richter, p. 220.

HOLOTYPE: Germany: the Overath spine nominated by Gross (1933, pl. 5 fig. 9) as the holotype of *Onchus major* is MB f705 (Text-fig. 1A, B).

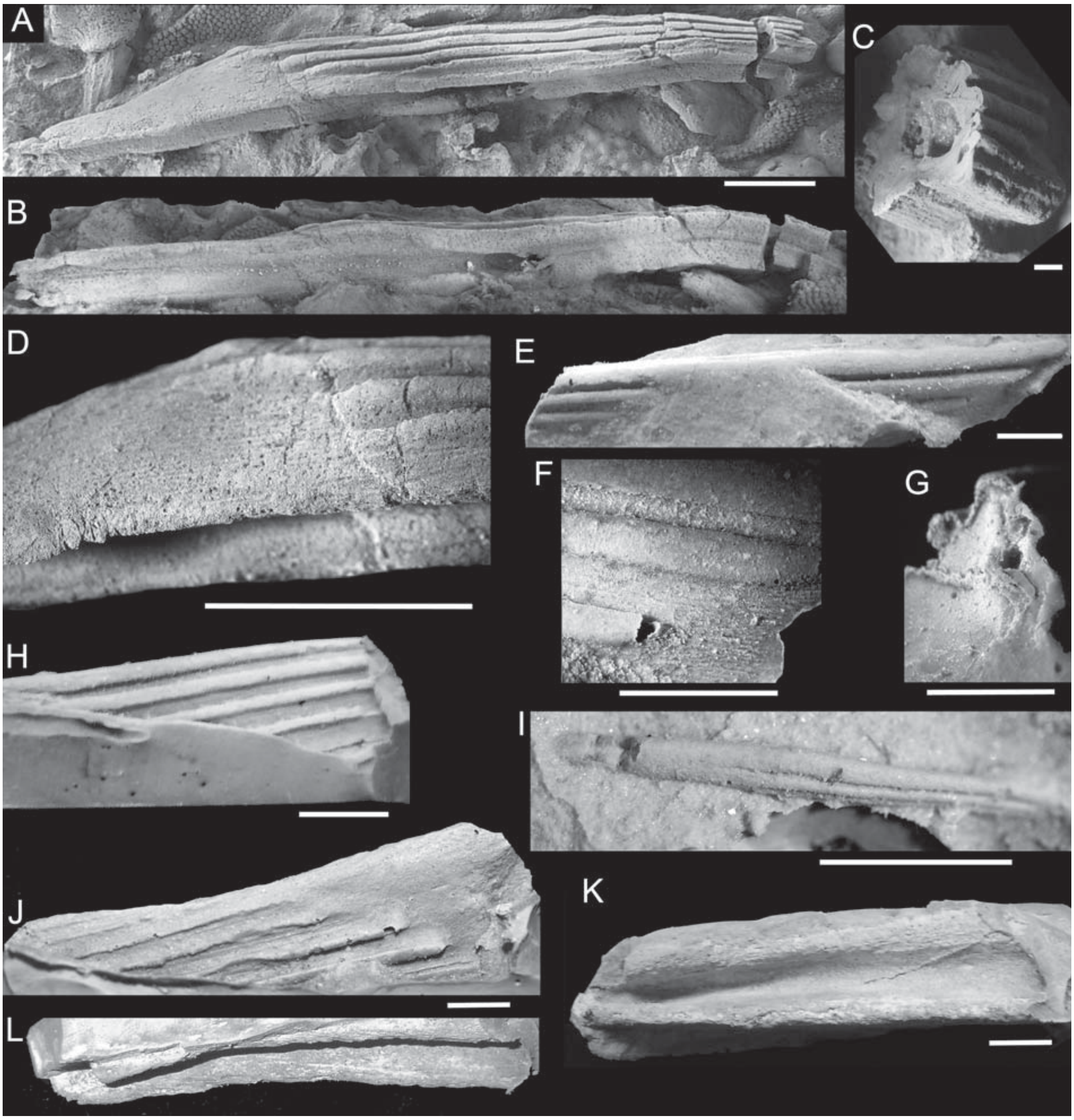
DIAGNOSIS: Spines up to (at least) 14 cm long, with only a slight curvature longitudinally; spongiose tissue between the wide pulp cavity and the leading edge ridge, with radiating canals extending up to the leading edge and highest lateral ridges.

MATERIAL EXAMINED: Germany: Gross (1937, pl. 8, fig. 8) figured a more complete spine MB f772 (Text-fig. 1C, D) when he renamed the species as *O. overathensis* (*O. major* was preoccupied); the Taunus Quarzite *Onchus* sp. asymmetrical spine figured by Schmidt (1933, fig. 5c, d) is possibly a pectoral fin spine of *Striacanthus overathensis*. Poland: MZ.VIII.Vp.438, spine lacking the distal tip; MZ.VIII.Vp.447, fragment of large spine just distal to IEB; D19UW, small spine, almost complete; MZ.VIII.Vp.431, fragment of very large spine, area around the IEB.

REMARKS: After Hills (1931) erected the new genus and species *Striacanthus sicaeformis* for isolated fin spines in micaceous sandstones from Freestone Creek, Victoria, Australia, Gross (1932) remarked that the new genus was unwarranted, as the fin spines resembled spines from the Baltic and American Devonian assigned to the form taxon *Onchus* Agassiz, 1837. Hills (1936, p. 168) however maintained the validity of the new genus because of two distinctive characters: a 'distinct longitudinal ribbing' on the inserted portion of the spines, rather than the fine striations of *Onchus*, and a histological structure comprising 'several small canals running through the spine parallel to the large central pulp cavity', a structure 'not shown by any *Onchus* spine'. *Onchus* was erected as a form taxon for isolated spines with smooth longitudinal ribs with a short, inserted base without parallel ribbing (see Newman *et al*. 2017). For this reason, "*Onchus*" *overathensis*, which shows the two generic characters for *Striacanthus* as well as having the distinctively shaped insertion, is reassigned to *Striacanthus*.

STRATIGRAPHIC AND GEOGRAPHICAL DISTRIBUTION: Upper Pragian: Wahnbachschichten and Gemünd Conglomerate, Germany; ?Kapp Kjeldsen Formation, Barmfjellet, Spitsbergen (age based on Pernègre and Blieck 2016, fig. 6); middle Emsian: Winna Formation ('Placoderm Sandstone'), Holy Cross Mountains, Poland.

DESCRIPTION: Spine MZ.VIII.Vp.438 (Text-fig. 2A–D), the most complete specimen, is 87.5 mm long, lacking the distal end; it has five longitudinal ridges on each side with a wider leading edge ridge. Narrow parallel longitudinal ribs (c. 6 per mm) extend over the insertion, and are also visible along the trailing edge distally (Text-fig. 2C). A single large central pulp cavity is revealed by the natural fracture at the distal end of the spine; this pulp cavity is wide open along the posterior/trailing edge for 50 mm from the proximal end of the spine (Text-fig. 2B). The spine is higher than wide along its length, being 5 mm wide and 6 mm high at the distal fracture, and 8 mm high at its deepest at the IEB. Spine fragment MZ.VIII.Vp.447 (Text-fig. 2E–H) lacks both the inserted and distal ends; it is 85 mm long, and 12 mm high by about



Text-fig. 2. Fin spines from the 'Placoderm Sandstone', Podłazie Hill, Holy Cross Mountains, Poland; whitened casts of spine impressions. A-H, ?I-L – *Striacanthus overathensis* nov. comb.: A-D – MZ.VIII.Vp.438: A – lateral view; B – trailing edge view; C – fracture surface showing cross section; D – inserted and exserted areas near the IEB; E-H – large spine fragment MZ.VIII.Vp.447: E – leading edge view; F – IEB (box in E); G – transverse section distal end (to left in E); H – ornament ridges on distalmost end (side not visible in E). I – small spine D19UW. J-L – large spine fragment MZ.VIII.Vp.431: J – lateral view, trailing edge to top, showing IEB; K – posterior view, wide open pulp cavity; L – posterolateral view, showing bone texture. Scale bar = 1 cm in A, B, D-L, 1 mm in C. Proximal end to left in A, B, D, to right in E, F, G

12 mm wide on the distalmost fracture surface. A small area of the insertion, visible near the IEB (Text-fig. 2F), shows fine parallel ridging, which is also visible between the ornament ridges. All ornament ridges are smooth; only the leading edge and two lateral ridges are visible on one side, with four lateral ridges visible on the other side (Text-fig. 2H). The ridges are more widely separated than on MZ.VIII.Vp.438, with narrower ridges towards the posterior/trailing face. The almost complete spine D19UW (Text-fig. 2I) is the smallest spine found, at about 30 mm long and 3 mm maximum width. The insertion is c. 9 mm

long, ornament ridges are smooth with a wide leading edge ridge and parallel lateral ridges, but the posterior part of the spine is not exposed. Unfortunately, the preservation is rather coarse, and it is not possible to discern any parallel ribbing on the inserted part. Spine fragment MZ.VIII.Vp.431 (Text-fig. 2J–L) appears to be from a very large spine; it is 80 mm long, and 18 mm at its widest, at the level of the IEB; the pulp cavity is wide open (Text-fig. 2K). Ornament ridges are smooth and narrow relative to the width between them. Thin parallel ribbing is not visible on the inserted area, but is seen between the ornament ridges, and on the posterolateral edges (Text-fig. 2L).

DISCUSSION: The Polish spines show comparable morphological features to the type and other spines from Germany; unfortunately, as the specimens are only casts, their internal histology is unknown.

The type stratum for *Striacanthus sicaeformis*, which Hills (1931) regarded as Late Devonian is now considered to be latest Givetian or earliest Frasnian (Young 1996). Isolated spines from the older (?Emsian) Merrimerriwa Formation (Mulga Downs Group) in western New South Wales, Australia (Text-fig. 1F, G), which show very similar morphology and histology, were referred by Rade (1964, pl. 149, fig. 3) and Burrow (2002, figs 13D, E, 14L) to *Striacanthus* sp., but these spines differ in lacking the strongly tapered, subtriangular insertion with a concave leading edge, and are here referred to Diplacanthiformes fam., gen., sp. indet. Although some spines of *S. overathensis* are markedly larger than those of *S. sicaeformis* from its type locality, being almost six times as long, they show the characters recognized here as diagnostic for the genus. In fact, the main distinguishing character for the species is the length of the spines, inadequate as this character may be, given that both juvenile and adult fish are presumed to have borne them. However, Gross (1937) considered at least one short spine 2 cm long from Willwerath also belonged to the species, and it seems likely that the one small Polish spine does as well.

The spine from Spitsbergen that Ørvig (1967, p.148) considered to belong to '*Onchus*' *overathensis* "with certainty" is large like the type specimens, with a long insertion and five smooth longitudinal ridges on each side of the exserted part, but the insertion surface does not appear visible on the specimen. Some doubt must therefore be cast on its assignment to the species.

Acanthodii order indet.
Family Machaeracanthidae Burrow and Young, 2005

Genus *Machaeracanthus* Newberry, 1857

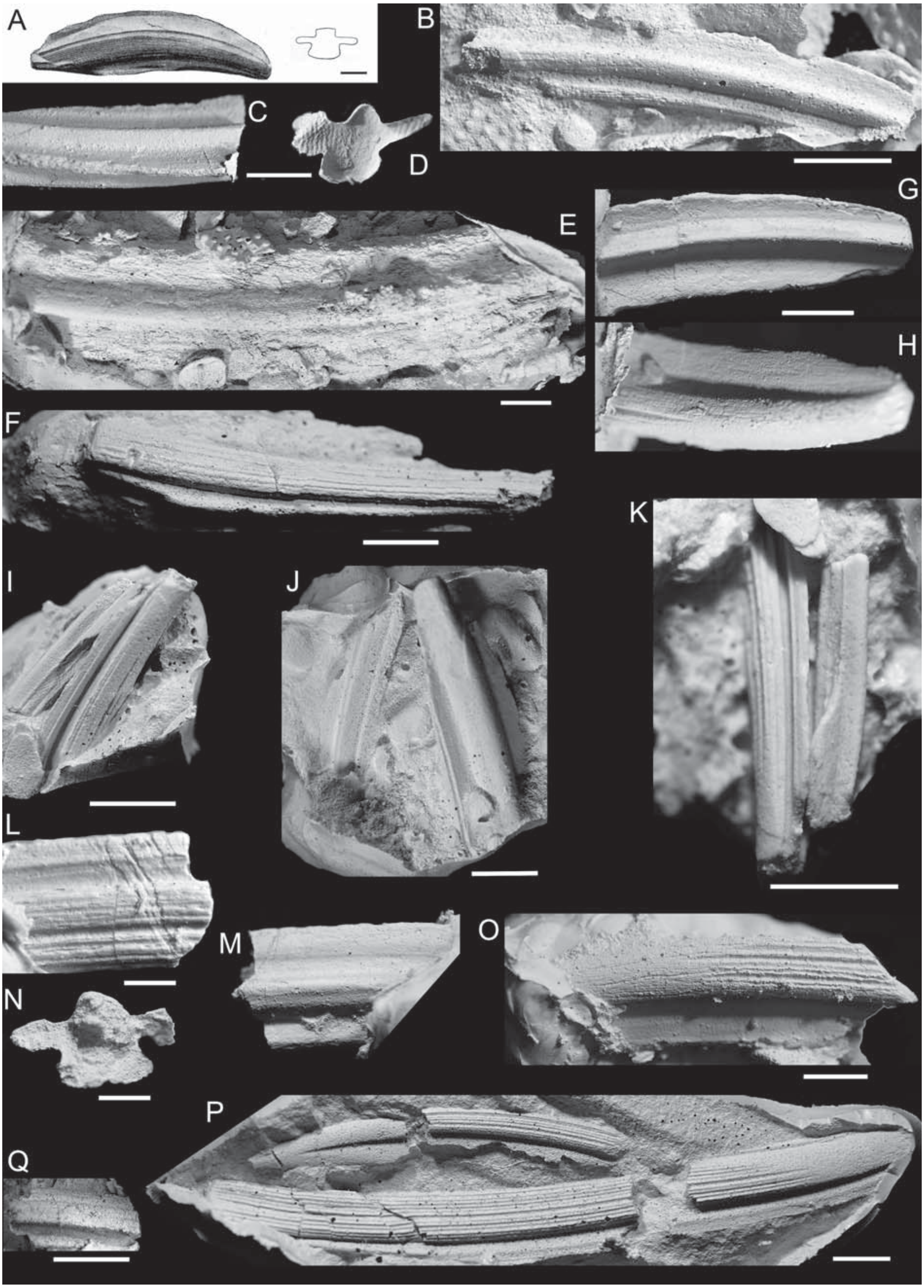
TYPE SPECIES: *Machaeracanthus peracutus* Newberry, 1857.

Machaeracanthus polonicus Gürich, 1901
(Text-figs 3, 4)

1901. *Machaeracanthus polonicus*; G. Gürich, pp. 366–367, fig. 8a, b.
1957. *Machaeracanthus polonicus* Gürich; L.B. Tarlo, p. 227.
1979. *Machaeracanthus polonicus* Gürich 1901; R. Denison, p. 52.
2010. *Machaeracanthus polonicus* Gürich, 1901; C. Burrow *et al*., pp. 60, 78, fig. 1E.
2012. *Machaeracanthus polonicus* Gürich, 1901; H. Botella, C. Martínez-Pérez, R. Soler-Gijón, pp. 763, 776.
2014. *Machaeracanthus* sp.; P. Szrek, G. Niedźwiedzki, M. Dec, p. 802, fig. 7E.

TYPE MATERIAL: The holotype was a rubber cast of a negative impression of the lower surface of a spine; paratype was a cast of a spine fragment showing the whole cross-section (Gürich 1901, fig. 8a, b respectively). Specimens originally in the Kontkiewicz and Gürich collection, from the 'Placoderm Sandstone' (Emsian), Beiliny, Holy Cross Mountains, Poland – now lost. As we do not have specimens from the

Text-fig. 3. *Machaeracanthus polonicus* fin spine casts from the 'Placoderm Sandstone' (Winna Formation), Podłazie Hill (A-O), Barcza Formation (P), near Bukowa Mountain, and Miedziana Góra Conglomerate (Q), Gruchawka, Holy Cross Mountains, Poland; Polish institute specimens. A – original illustration of type material (Gürich 1901, fig. 8a, b). B – Muz. PGI 173.II.360, upper surface of morphotype 2 spine, previously illustrated by Szrek *et al*. (2014, fig. 7E). C, D – Muz PGI 1733.II.210, ?morphotype 1 midspine fragment: C – upper surface; D – 3D cross section view. E – UW 25 D, ?morphotype 1 spine, upper surface. F – Muz PGI 1733.II.155, midspine fragment, lower surface. G-H – MZ.VIII.Vp.430, abraded distal segment of morphotype 1 spine: G – upper surface; H – lower surface. I – Muz PGI 1733.II.156, pair of midspine fragments. J – Muz PGI 1733.II.161, pair of midspine fragments, morphotype 1 and 2. K – UW 35 D, pair of midspine fragments. L-N – Muz PGI 1733.II.367, morphotype 2 midspine fragment: L, lower surface; M – upper surface; N – end-on view showing cross-sectional shape. O – Muz PGI 1733.II.157, distal end of spine, lower surface showing tip wear. P – Muz PGI 1733.II.172, large almost complete spine, distal end to right, and smaller spine, distal end to left, both showing lower surfaces with gradationally abraded tips. Q – Muz PGI 1733.II.354, short spine fragment, lower surface. Scale bar = 1 cm →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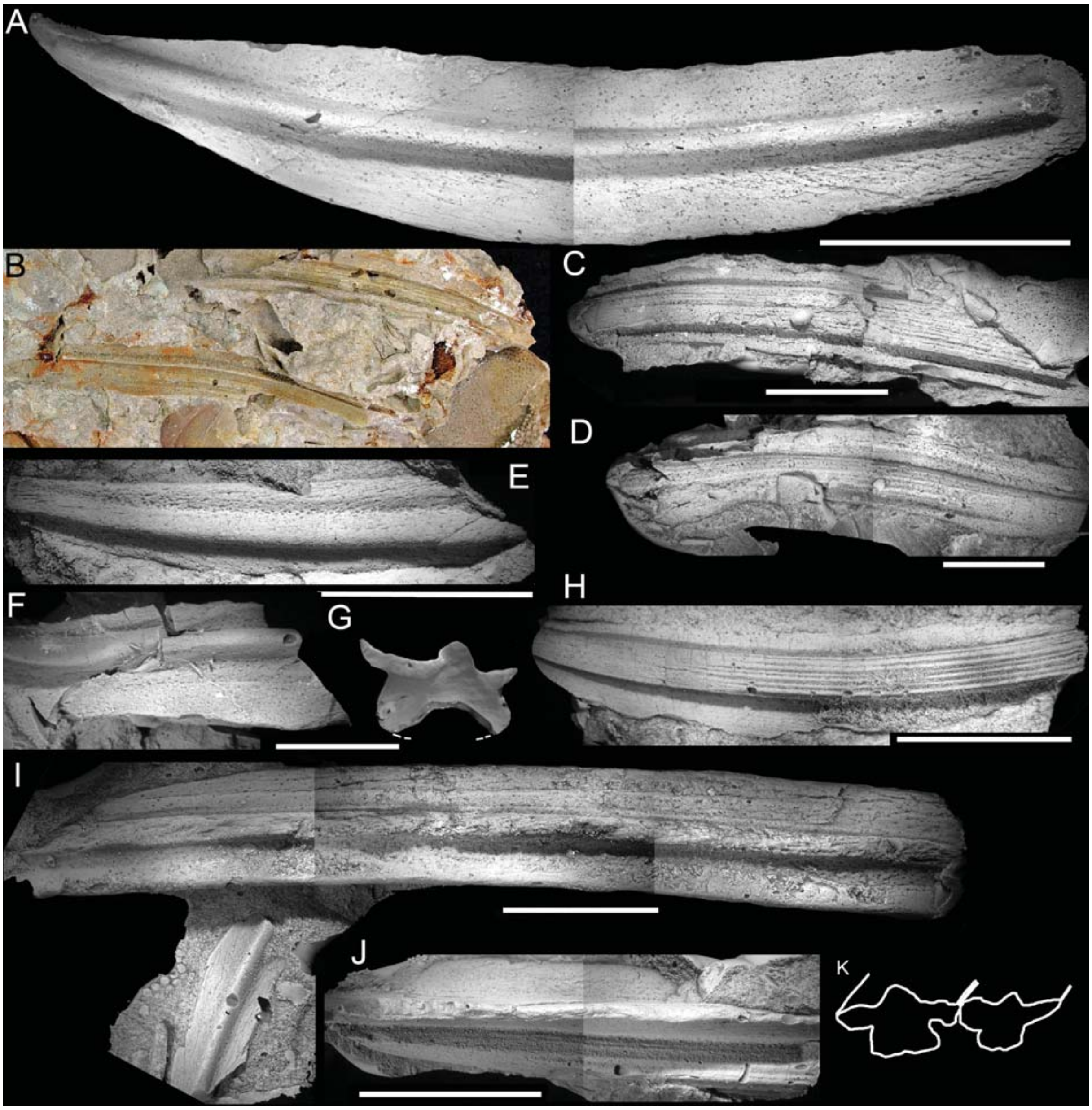


Text-fig. 4. *Machaeracanthus polonicus* fin spine casts from the 'Placoderm Sandstone', Daleszyce, Poland; NHM UK specimens. A – NHM UK PV P.56914, complete morphotype 1 spine; B-D – NHM UK PV P.51855, pair of incomplete spines: B – original impressions of lower surfaces; C – cast of lower spine; D – cast of upper spine. E – NHM UK PV P.51976, upper surface of distal half of morphotype 2 spine. F,G – NHM UK PV P.56916, damaged cast of 3D morphotype 1 spine. H – NHM UK PV P.51857, lower surface of spine lacking the proximal end. I – NHM UK PV P.51853, lower surface of large incomplete spine, and upper surface of small morphotype 1 spine fragment; J – NHM UK PV P.51977, lateral view of large morphotype 2 spine fragment, upper surface uppermost. K – reconstruction of possible association of paired spines (based on Text-fig. 3D, N). Scale bar = 1 cm

type locality, we have refrained from nominating a neotype.

DIAGNOSIS: *Machaeracanthus* with spines up to 150 mm long and 24 mm wide, having a broad quadrangular axial ridge on the lower surface with up to eight longitudinal carinae and sulci. Two morphotypes: one has a narrow smooth axial ridge on the upper surface and a strong longitudinal carina near the thick inner (concave) edge of the wing on the lower surface; the second has a relatively broad axial ridge on the upper surface and a strong longitudinal carina near the thick outer (convex) edge of the keel on the lower surface.

MATERIAL EXAMINED: From Podłazie Hill: Muz PGI 1733.II.12, distal spine fragment; Muz PGI 1733. II.35, pair of small midspine fragments; Muz PGI 1733.II.155, midspine fragment; Muz PGI 1733.II.156, pair of spine fragments (exUW D 35); Muz PGI 1733. II.157, spine tip; Muz PGI 1733.II.158, midspine fragment; Muz PGI 1733.II.159, spine fragment, 3D; Muz PGI 1733.II.160, midspine fragment; Muz PGI 1733. II.161, pair of midspine fragments; Muz PGI 1733. II.163, midspine fragment; Muz PGI 1733.II.164, midspine fragment; Muz PGI 1733.II.165, midspine fragment; Muz PGI 1733.II.210, midspine fragment; Muz PGI 1733.II.360, spine lacking distal and proximal ends; Muz PGI 1733.II.363, midspine fragment; Muz PGI 1733.II.367, midspine fragment; MZ.VIII. Vp.430a, midspine fragment, 3D; UW D 25, midspine fragment; UW D 35, pair of spine fragments; spines and spine fragments on NHM UK PV P.51847, 51851, 51853, 51855, 51857, 51969, 51971, 51976, 51973, 51977, ?51981, 56912-3, 56914, 56916. From Bacza: Muz PGI 1733.II.172, pair of spines. From Gruchawka: Muz PGI 1733.II.175, short spine fragment; Muz PGI 1733.II.176, short spine fragment; Muz PGI 1733.II.354, two short midspine fragments.

DESCRIPTION: Because the spines are preserved as impressions, only rare specimens preserved as hollows in the rock – all of which are fragments – show the morphology of both the upper and lower surfaces (Text-figs 3C–D, G–H, L–N, 4F–G). The spines that are complete, or nearly complete, show a range of sizes. The largest are the larger spine on Muz PGI 1733.II.172 (Text-fig. 3O) which is 130+ mm long and 15+ mm at its widest; and UW 25 D (Text-fig. 3E) which must be from a larger spine as it is 110 mm long and 24 mm wide, but missing both ends. The smallest examined (NHM UK PV P.56914; Text-fig. 4A) is 43 mm long and 7 mm maximum width. The ratio of maximum width to length is estimated at c. 1:9 in larger spines and c. 1:6 in smaller spines. All spines have a broad longitudinal ridge with a square cross-section on the presumed lower surface, ornamented with up to eight longitudinal sulci and carinae (Text-figs 3F, L, N, O–Q, 4C, D, H, I). As observed by Burrow *et al.* (2010) in describing *M. sulcatus* spines, this surface is interpreted as the ventral/lower surface because it is gradationally abraded towards the tip (Text-figs 3H, I, O, P, 4H).

Text-fig. 5. Acanthodian scapula and tooth whorl casts from the 'Placoderm Sandstone', Poland. A, B – scapula D112,?lateral and posterior views; C – scapula Muz PGI 1733.II.269, ?lateral view; D – scapula MZ MZ.VIII.Vp.340, ?medial view; E – scapula Muz PGI 1733.II.386a, ?lateral view. F, G – tightly spiralled tooth whorl Muz PGI 1733.II.386b. Scale bar = 1 cm. Anterior to right in A, C, E, to left in D

The median sulcus on the ridge is often deeper than the flanking ones (Text-fig. 3D, L, N). Two morphotypes are recognized: on morphotype 1, the upper surface has a smooth narrow longitudinal axial ridge, the keel (outer convex expansion) has at least one strong longitudinal carina towards the outer edge on the lower surface (Text-fig. 3I, L, O), and the wing (inner concave expansion) is wider than the keel. On morphotype 2, the smooth median ridge on the upper surface is comparatively wide, the wing has a strong carina towards the outer edge on the lower surface, and the wing is slightly narrower than the keel (Text-fig. 3P). Based on the illustration by Gürich (1901, fig. 8a; Text-fig. 2A), the holotype spine, with its relatively wide upper ridge, and keel wider than wing, corresponds to morphotype 2. A few spines show a V-shaped osteodentine growth pattern, with oblique surficial short striae across the wing and keel, angled proximo-distally (Text-figs 3E, 4A, E).

DISCUSSION: The type specimen of *M. polonicus* was 90 mm long, and 21 mm at its widest, rather 'stouter' than the specimens examined. The cross-sectional shape illustrated by Gürich (1901, fig. 8b; Text-fig. 3A) is closest to that of the morphotype 2 spines. Our investigations support *M. polonicus* as a valid species. Only two other species have a strongly striated axial shaft: *M. sulcatus* and *M. kayseri*. *M. sulcatus* differs in having a narrow wing and keel, and a narrow axial shaft on the upper surface; *M. kayseri* differs mainly in having fewer, sharp crested, longitudinal ridges on the axial shaft. The oblique/chevron osteodentinal growth structure noted in some *M. polonicus* spines is also seen in the type species *M. peracutus* and some Pragian *M. bohemicus* spines (Burrow *et al.* 2010, figs 3A–D, 8G respectively).

Several *Machaeracanthus* species (*M. hunsrueckianum*, *M. longaevus*, *M. peracutus*, *M. polonicus*, *M. sulcatus*) are now recognized to have two morphotypes, and these species are interpreted to have had 'paired pairs' of pectoral spines, i.e. two spines articulating with each scapula, making it unlikely that the two spines are a pectoral and prepectoral, as the latter articulates with the procoracoid in climatiids and gyracanthids (e.g. Warren *et al.* 2000). While it seems possible that all *Machaeracanthus* species with the characteristic large spines had paired pairs, they have not yet been identified in all such species. In *M. polonicus*, it seems likely that morphotype 1 and 2 spines formed a pair by abutting lengthwise via the thickened edges and carinae on the wing of the morphotype 2 spine and on the keel of the morphotype 1 spine (Text-fig. 4K).

Acanthodii order indet.
Machaeracanthus polonicus?
(Text-fig. 5A–E)

MATERIAL: Scapulas Muz PGI 1733.II.269, Muz PGI 1733.II.386, MZ.VIII.Vp.340, D112 from Podłazie Hill.

DESCRIPTION: These small scapulas show typical endoskeletal bone surface texture of short oriented striations and dimples (Text-fig. 5A, C), and have a simple structure, with a slightly convex anterior edge and a concave posterior edge to the shaft. The shaft has a blunt rounded head and a laterally flattened, oval cross-section (Text-fig. 5B), and expands posteriorly towards the ventral edge (Text-fig. 5D). The smallest (Text-fig. 5E) is 24 mm high and 13 mm long at the base, and the largest (Text-fig. 5D) is 35 mm high and 17 mm long at the base. None of them show folded flaring towards the ventral edge. However, Szrek *et al.* (2014, fig. 5E) illustrated an in situ impression of a larger scapula, 86 mm high, which appears to show some folded flaring towards the base (to the top in their figure).

DISCUSSION: Burrow *et al.* (2010, fig. 5) described a characteristic folding of the lateral side of the scapula in several *Machaeracanthus* species, considered to be associated with the articulation of the pair of pectoral fin spines. It seems likely that this folding in the perichondral bone forming the scapula might only develop in adult fish, and the small scapulas we describe here are likely to be from juveniles. Although we only have a small number, the ventral expansion of the scapula appears to increase with size, supporting this speculation.

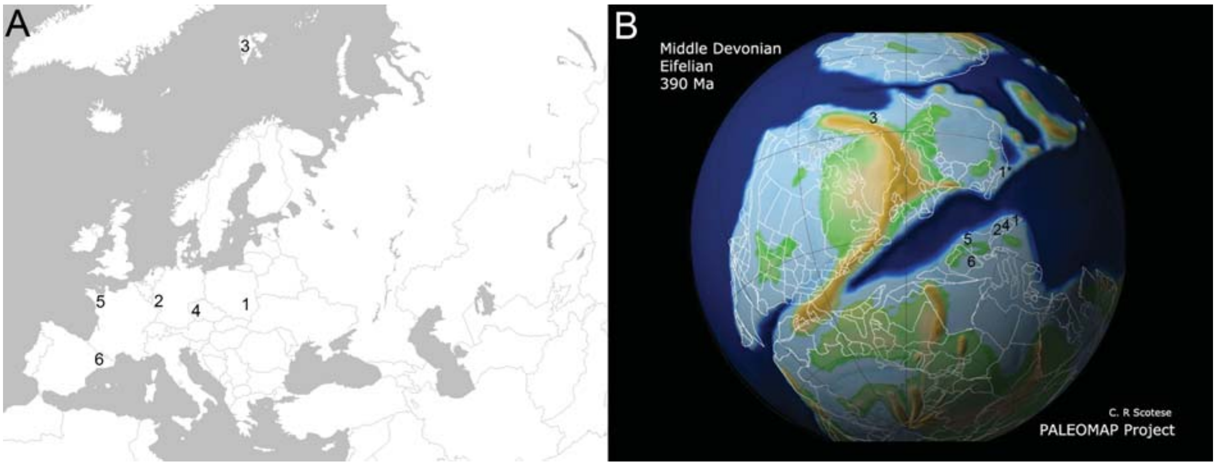
As *Striacanthus overathensis* is also found in these deposits, we considered that the scapulas could possibly be from juvenile fish of that species. No scapulas have been described or associated with *S. overathensis*, but scapulocoracoids described in other diplacanthiforms have a strong vertical ridge dividing a postbranchial lamina from a posterior flange (Newman *et al.* 2012), indicating that it is more likely the scapulas are from juvenile *M. polonicus*, or from the undetermined acanthodian. Although rare, the scapulas are more common than spines assigned to *S. overathensis*, which also indicates that they are more likely to be from *M. polonicus* given that acanthodians each had only two scapulas, but nearly all had at least six fin spines.

Acanthodii?
indet gen., sp.
(Text-fig. 5F, G)

MATERIAL: Tooth whorl Muz PGI 1733.II.386b from Podłazie Hill.

DESCRIPTION: The tightly scrolled whorl (Text-fig. 5F, G) is 13 mm wide, with three separated lines of short smooth conical tooth cusps; all exposed cusps are of a similar height, c. 1–2 mm.

DISCUSSION: The tight scrolling of the relatively large whorl is a significant feature. The scrolling indicates the whorl was symphysial, positioned between the jaw cartilages rather than on top of the cartilage. The element is unusual in having separate lines of equal-sized cusps aligned with the edges of the whorl, rather than having teeth with cusps having a common base, transversely oriented on the whorl. Gross (1957) illustrated a range of tooth whorl types from the upper Silurian Beyrichienkalk of northern Germany, which include specimens that enroll >360° (Gross 1957, pl. 2 fig. 1, pl. 3 fig. 1), and several specimens also appear to have the cusps



Text-fig. 6. European occurrences of *Striacanthus* and *Machaeracanthus*. A – present day map; B – palaeogeographic map (Paleomap Project http//:www.scotese.com). 1 – Holy Cross Mountains, Poland; 1* – alternate position for Holy Cross Mountains in the Devonian; 2 – western Germany; 3 – Spitsbergen; 4 – Czech Republic; 5 – western France; 6 – Celtiberia, Spain

arranged in three separate lines like the Polish specimen rather than in transverse teeth, but none of them have only equal-sized cusps. Of the acanthodian taxa found in the ‘Placoderm Sandstone’, *Striacanthus overathensis*, being a diplacanthiform, lacked dentition. Tooth whorls have never been assigned to *Machaeracanthus*: one of the only dental elements ever assigned to *Machaeracanthus* was a tooth tip which Zidek (1975, fig. 3C) found associated with *M. bohemicus* elements on a slab in the Czech National Museum. Goujet (1993) considered that *Leonodus* teeth and *Machaeracanthus* spines were from the same fish, based on the co-occurrence of these elements on a slab from the ?Pragian of western France. However, this association seems more likely to be casual, as an older slab from the Lochkovian of Spain preserves associated *Leonodus* teeth, an antarctilamnid type spine, and antarctilamnid type scales (Soler-Gijón and Hampe 2003), indicating that these three types of elements were from one animal. Subsequently, the tooth whorl is highly unlikely to be from either of the acanthodian taxa known from the deposit. Ginter *et al.* (2002, pl. 6S) illustrated a similar tightly scrolled tooth whorl from the Famennian of Morocco, captioned as an acanthodian symphysial tooth whorl, but perhaps such elements are chondrichthyan not acanthodian.

Machaeracanthus spp. have been recorded from several regions of Europe (Text-fig. 6A): *Machaeracanthus bohemicus* Barrande, 1872 from the Czech Republic and western Germany (Schmidt 1933), *M. kayseri* Kegel, 1913, *M. westfalicus* Pfeiffer, 1938 and *M. hunsruckianum* Südkamp and Burrow, 2007 from western Germany, *M. goujeti* Botella *et al.*, 2012 from Spain, and at least one species *M. bezieri* Burrow and Gendry, 2017 from western France. These other regions were all along the northern margin of Gondwana during the Early–early Middle Devonian; the Holy Cross Mountains were also on that margin (Text-fig. 6B), or else on the southern margin of Baltica (Szrek and Dupret 2017).

CONCLUSIONS

Our comprehensive investigation of dozens of specimens preserving acanthodian fin spines from the Emsian ‘Placoderm Sandstone’ in the Holy Cross Mountains, Poland show the presence of at least two acanthodian taxa, *Striacanthus overathensis* nov. comb. and *Machaeracanthus polonicus*. Rare spine fragments from the older, ?Lochkovian Barcza Formation are also assigned to *M. polonicus*. We confirm that *M. polonicus* is a valid taxon, distinguishable from other *Machaeracanthus* species by a combination of characters, in particular the closeset longitudinal ribbing on the quadrangular central axis on the lower surface of the fin spine. As for most other *Machaeracanthus* species, two spine morphotypes are recognized. *M. polonicus* is not known to occur elsewhere, but is one of several *Machaeracanthus* species recorded from the northern Gondwana margin, or possibly the southern margin of the Baltica terrane (Szrek and Dupret 2017). *S. overathensis* is recorded for the first time from this deposit; it is also found in the late Pragian of Germany, and has been recorded from Spitsbergen. However, the wide separation by land and ocean between Poland and Spitsbergen in the late Early Devonian (Text-fig. 6) suggests that the Spitsbergen occurrence could perhaps be attributed to a different diplacanthiform.

The latest work by Szrek and Dupret (2017) shows that the placoderm assemblage from the Winna Formation at Podłazie Hill comprises taxa relatively close to those in the contemporary assemblage from Podolia. The assemblage comprises the youngest representatives of the *Kujdanowiaspis*-fauna, as well as unspecified actinolepids and unidentified brachythoracid arthrodires. This occurrence indicates a close relationship between Podolia and the Holy Cross Mountains during the Early Devonian and suggests consideration of the Holy Cross Mountains as a refuge for the iconic Early Devonian *Kujdanowiaspis* assemblage.

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