



The Middle Devonian acanthodian *Orcadacanthus* n. gen. from the Orcadian Basin of Scotland

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ABSTRACT

Although first described more than 175 years ago and represented by many hundreds of specimens, the small (less than 60 mm long) mesacanthid acanthodiform originally named *Acanthodes pusillus* is the most poorly known acanthodian-grade vertebrate from the Middle Devonian of Scotland. The classification of the species received some attention in the late nineteenth century, but it is only in the last decade that more substantive interest has been shown in this little fish. Here we re-evaluate the type material for the species, and assess the validity of its putative junior synonym *Mesacanthus peachi* based on morphological and histological study of mesacanthid specimens from all levels of the Eifelian and Givetian from the Orcadian Basin. New information on the taxon revealed by these studies includes the shape of the jaw cartilages, ornamentation of the sclerotic plates, structure and morphology of the different fin spines, variation in scale shape and size over the body, and histological structure of the dermal elements. Our study supports synonymizing *M. pusillus* and *M. peachi* and erecting a new genus *Orcadacanthus*, type species *O. pusillus*. The depositional environment appears to have influenced the mode of preservation of the new taxon at different localities. Variability in the degree of mineralization, particularly in the head region, is linked to ontogenetic changes.

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INTRODUCTION

The early jawed vertebrates in the Order Acanthodiformes are distinguished from other ‘acanthodians’ by having one rather than two dorsal fin spines (Denison 1979). Of the four families recognised within the Acanthodiformes, the Mesacanthidae are mostly distinguished by features that are considered ‘primitive’ because they are shared with ‘Climatiiformes’ sensu lato – having one pair of prepelvic spines, a shallowly inserted dorsal spine, an unmineralised endocranium, and a simple mandibular joint (Burrow, 2021). As noted by Burrow et al. (2022), recent cladistic analyses (e.g., Zhu et al. 2022, extended data figure 9b) retrieve mesacanthids as the sister group to most other acanthodiforms.

Specimens of a small acanthodiform fish were first collected from the Middle Devonian nodule beds in the Moray Firth area of Scotland in the 1830s. Agassiz (1844, plate 28, figures 8-10) originally assigned the species name *Acanthodes pusillus* to this fish and figured as syntypes three poorly preserved specimens that he noted came from Gordon Castle. Later, Egerton (1861a) briefly discussed the species and noted that the specimens came from the Old Red Sandstone near Gordon Castle, from Tynet Burn, establishing that this was the type locality. All the syntypes were subsequently considered lost, although Andrews (1982) speculated on the possible identity of counterparts of two of the specimens figured by Agassiz. At the 1859 British Association for the Advancement of Science meeting held in Aberdeen, Mr. Charles Peach (see Taylor and Anderson, 2015 and references therein for information about Peach) showed a number of fossil fish specimens he collected in Caithness in the late 1850s. One of these was a small acanthodian from Barragill (now known as East Mey), Caithness which Egerton (1861b) named *Acanthodes peachi*. However, he provided no description or figures. It was not until later in the same year that Egerton (1861a) formally described *A. peachi* and another species (*Acanthodes coriaceus*) collected from near Thurso (probably Pennyland), Caithness. Traquair (1888) considered *A. coriaceus* a synonym of *A. peachi* and erected a new genus *Mesacanthus* for *A. peachi*, *A. pusillus*, and the Lower Devonian *Acanthodes mitchelli*

Egerton, 1861, with the latter species nominated as the type for *Mesacanthus*. Traquair (1888) differentiated *Mesacanthus* from *Acanthodes* based on the former having intermediate (prepelvic) fin spines. In the same work he considered that both *M. pusillus* and *M. peachi* were valid species based on morphological proportions. Traquair (1890) later differentiated *Acanthodes* from *Mesacanthus* by the location of the pelvic fin spines, as Woodward and Sherborn (1890) did not believe there were enough diagnostic characters to validate a new genus. The difficulty in differentiating between *M. pusillus* and *M. peachi* was evident to Paton (1976); in her catalogue of fossil fishes in the National Museum of Scotland she referred all Middle Devonian specimens from the Orcadian Basin to *Mesacanthus* sp. Trewin and Davidson (1999) were the first to publish an opinion that *M. pusillus* and *M. peachi* belonged in the same species, but provided no evidence for that assumption. Baron (2015) showed that there were no proportional morphological differences between *M. pusillus* and *M. peachi* and synonymised the two species, supporting Trewin and Davidson’s (1999) opinion, while also showing statistical differences between the older type species *M. mitchelli* and the Middle Devonian species. The most recent papers concerning *M. pusillus* are the description by Burrow et al. (2020a) of a putative dermal spiracle cover in a specimen from Cromarty, nomination of a lectotype by Baron and Seymour (2021), and description of the jaw cartilage structure by Burrow and den Blaauwen (2021). Up to date, no morphological description of the head or skeletal reconstruction of the species has been published.

The type species for the family and genus, *Mesacanthus mitchelli* from the Lower Devonian (Lochkovian) Midland Valley of Scotland was recently intensively redescribed by Burrow et al. (2022). In order to further test whether the Scottish Middle Devonian mesacanthids should all be assigned to the one species, and indeed whether they should be retained in *Mesacanthus*, we have examined extensive material collected by MJN and JdB over the last decades from all stratigraphic levels, from numerous localities in northern Scotland (Figure 1). The ornament and distribution of dermal elements, relative dimensions and ornament of fin spines, and morphology of endoskeletal structures

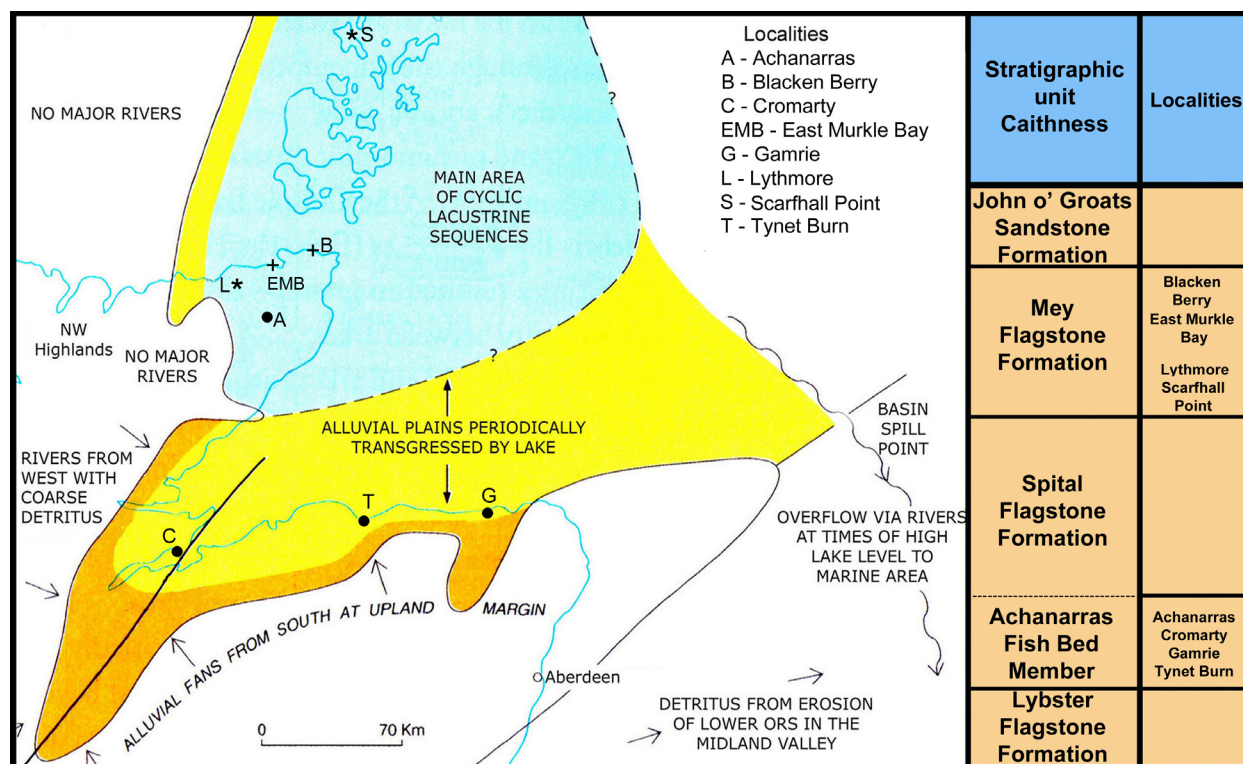


FIGURE 1. Generalized map of the Orcadian Basin (modified from Burrow et al., 2016, fig. 2) with a few key sites indicated and their relative stratigraphical horizon indicated. Circles indicate the Achanarras Fish Bed Member horizon, crosses the upper Mey Flagstone Formation horizon, and stars the lower Mey Flagstone Formation horizon and their equivalents.

are described and compared. Thin sections were made of part or all of the selected specimens to show the histological structure of the spines, scales, and other dermal elements, as well as the endoskeletal jaws, scapulocoracoids, and basal fin cartilages. Scales and other small dermal elements have been imaged using scanning electron microscopy.

GEOLOGICAL AND STRATIGRAPHIC DISTRIBUTION

It has been demonstrated in many previous publications (e.g., Burrow et al., 2020b) that there are five fish-bearing faunal zones in the Middle Devonian Orcadian Basin. These zones equate well to the biostratigraphy of the Baltic region (Newman et al., 2017), Belarus and elsewhere in Laurussia (Plax and Newman, 2021). Here we refer to Caithness stratigraphical units in the Caithness Flagstone Group, but mesacanthid specimens occur at the same biostratigraphical levels across the whole of the Orcadian Basin (see Burrow et al., 2020b:figure 5.1 for an example of these stratigraphical units). The lowest unit, the Lybster

Flagstone Formation, does contain a small acanthodian, which is probably a mesacanthid, but the specimens are for the most part disarticulated and not well preserved. In the highest faunal zone, the John o' Groats Sandstone Formation, no acanthodian remains have been discovered so far. There are thus three faunal zones confirmed to have a mesacanthid in the Orcadian Basin (Figure 1). The lowest stratum with identifiable specimens is the Achanarras Fish Bed Member, which is at the boundary of the Lybster and Spital flagstone formations. Historically, most specimens collected from this level in the Moray Firth area have been assigned to *Mesacanthus pusillus*. There is then a gap in articulated remains until the base of the Mey Flagstone Formation, in fish beds with the tetrapodomorph *Osteolepis panderi* (Pander, 1860). Finally, articulated mesacanthid specimens are found at the top of the Mey Flagstone Formation. Most mesacanthid remains (and possibly small individuals of other acanthodians) from northern Caithness and Orkney have been assigned over the last century to *Mesacanthus peachi*. One mesacanthid species is present in all the strata

from the Lybster Flagstone Formation up to the top of the Mey Flagstone Formation. This stratigraphical distribution is repeated in equivalent strata across the whole of the Orcadian Basin.

For this project, morphology and histology of scales and spines and other dermal elements of mesacanthid specimens from these three different zones have been investigated to determine if there are any diagnostic differences between specimens from different levels.

MATERIAL AND METHODS

Methods

Macrophotographs of NHMUK PV OR 35786, a well-preserved Tynet Burn specimen assigned by Woodward (1891) to *Acanthodes pusillus*, were taken using a Nikon D750. Other macrophotographs of specimens were taken using a Canon EOS 450. Microphotographs of specimens were taken using a DSC-H2 camera on a Nikon Eclipse E400. Thin sections were made by JdB using epoxy resin and carborundum grinding powder down to 4 microns.

Environmental scanning electron microscopy (ESEM) images were made using a Hitachi Table-top TM-1000 at the Queensland Museum.

Remarks. One specimen from Blacken Berry was in the collection of Dr. Paul de Buissonjé (Amsterdam), whose collection was mostly donated in the NMS in 1996. Unfortunately, this specimen was not found when searched for and must be considered lost at present. However, at the time it was in Dr. Buissonjé's collection it was photographed by JdB using a Canon A1 and a negative taken, which is now housed in the NMS under the registration number NMS G.2022.10.686. Other specimens show the same characters of the nasal region, but due to the particular clarity of the nasal region of this specimen the authors have made the decision to use the negative as a proxy specimen.

Material

The Achanarras fish bed member horizon. From the Moray Firth area: **Corbie Den** (British Grid reference (BGR) NJ 791622), NMS G.2019.3.11; **Cromarty** (BGR NH 795672), NMS G.2019.3.10, NMS G.2021.7.125, NMS G.2021.7.126, NMS G.2021.7.135, NMS G.2021.7.136, NMS G.2021.7.303, NMS G.2021.7.94; **Den of Findon** (BGR NJ 795637; most localities referred to Gamrie come from here): NMS G.2021.7.292; **Tynet Burn** (BGR NJ 384121), GLAHM V3573, NHMUK PV OR 35786 (Neotype), NRM P1645. From Caith-

ness: **Achanarras Quarry** (BGR ND 150545): NMS G.2021.7.27, NMS G.2021.7.284, NMS G.2021.7.285, NMS G.2021.7.29, NMS G.2021.7.45, NMS G.2021.7.51.

The lower part of the Mey Flagstone Formation (Osteolepis panderi) horizon. From Caithness: **Cairnfield Quarry** (BGR ND152651): NMS G.2021.7.290, NMS G.2021.7.84, NMS G.2021.7.93, NMS G.2022.10.6, NMS G.2022.10.14; **Cairn of Hattel** (BGR ND 191691): NMS G.2022.10.17; **Castlehill** (BGR ND 200694): NMS G.2022.10.13; **Lythmore** (also known as Overton) (BGR ND 066666): NMS G.2021.7.202, NMS G.2021.7.286, NMS G.2022.10.2, NMS G.2022.10.4, NMS G.2022.10.6; **Ness of Litter** (often referred to as Holborn Head) (BGR ND 080710): NMS G.2021.7.209; **Skinnet** (BGR ND 123618): NMS G.2021.7.238, NMS G.2021.7.241, NMS G.2021.7.251. From Orkney: **Scarfall Point** (Westray) (BGR HY 457488): NMS G.2022.10.15.

The upper part of the Mey Flagstone Formation horizon. From Caithness: **Blacken Berry** (BGR ND 308749): NMS G.2018.28.15, NMS G.2019.3.8, NMS G.2021.7.202, NMS G.2021.7.265, NMS G.2021.7.269, NMS G.2021.7.64, NMS G.2022.10.1, NMS G.2022.10.12; **Button Geo** (Stroma) (BGR ND 345478): NMS G.1975.12.26, NMS G.2022.10.8, NMS G.2022.10.9; **East Mey** (BGR ND 292747): NMS G.2021.7.162; **East Murkle Bay** (EMB) (BGR ND 178692): NMS G.2021.7.158, NMS G.2021.7.165, NMS G.2021.7.166; **Pennyland** (BGR ND 110691): NMS G.1887.35, NMS G.2019.3.9, NMS G.2022.10.5. From Orkney: **Surrigarth** (Westray) (BGR HY 491451): NMS G.2021.7.187.

Horizon uncertain. From Caithness: **Brims Ness** (BGR ND 038713) NMS G.2021.7.78.

Institutional Abbreviations

ELGNM – Elgin Museum, Elgin, United Kingdom. GLAHM – Hunterian Museum, Glasgow, United Kingdom. GSM – British Geological Survey collection, Keyworth, United Kingdom. MB, Museum für Naturkunde, Berlin, Germany. MV – Museum Victoria, Melbourne, Australia. NHMUK – Natural History Museum, London, United Kingdom. NMS – National Museums of Scotland, Edinburgh, United Kingdom. ROM – Royal Ontario Museum, Toronto, Canada.

SYSTEMATIC PALAEOLOGY

Class CHONDRICHTHYES Huxley, 1880
Subclass ACANTHODII Owen, 1846, sensu
Coates et al., 2018

- Order ACANTHODIFORMES Berg, 1937
 Family MESACANTHIDAE Moy-Thomas, 1937
 Genus ORCADACANTHUS n. gen.
zoobank.org/857D5D7F-DA96-481F-B6AD-45803BB25622
- Type and only known species.** *Orcadacanthus pusillus* (Agassiz, 1844) n. comb.
Diagnosis. As for the type species.
Etymology. Orcad-, referring to the Orcadian Basin where the genus is found, and -acanthus, Greek for thorn.
- Orcadacanthus pusillus* (Agassiz, 1844) n. comb.
 Figures 2-20, Supplemental Figure 1
- 1844 *Acanthodes pusillus*; Agassiz, p. 35-36, pl. 28, figures 8-10.
 1859 *Acanthodes pusillus*; Gordon, p. 41.
 1860 *Acanthodes pusillus*; Gregory, p. 145, 147.
 1861a *Acanthodes peachi*; Egerton, p. 57-59, pl. 6, figures 1-2.
 1861a *Acanthodes coriaceus*; Egerton, p. 59-60, pl. 6, figures 3-5.
 1861b *Acanthodes peachi*; Egerton, p. 78.
 1868 *Acanthodes pusillus* Agassiz; Peach, p. 72.
 1868 *Acanthodes pusillus* Hancock and Atthey, p. 364.
 1878 *Acanthodes peachii*, Eg.; Geikie, p. 404, tabs. 1-2.
 1878 *Acanthodes coriaceus*, Eg.; Geikie, tabs. 1-2.
 1878 *Acanthodes pusillus*, Ag.; Geikie, tabs. 1-2.
 1888 *Mesacanthus pusillus*, Ag.; Traquair, p. 512.
 1888 *Mesacanthus peachi*, Egert.; Traquair, p. 512.
 1890 *Acanthodes peachi* (Egerton); Woodward and Sherborn, p. 119.
 1890 *Acanthodes pusillus* (Agassiz); Woodward and Sherborn, p. 119.
 1890 *Mesacanthus pusillus*, Ag.; Traquair, p. 481.
 1890 *A. Peachii*, Eg.; Traquair, p. 481.
 1891 *Acanthodes pusillus*, Agassiz: Woodward, p. 11-12, pl. 1, figures 5-6.
 1891 *Acanthodes peachi*, Egerton; Woodward, p. 12-13.
 1894 *Mesacanthus Peachi* (Egert.); Traquair, p. 285.
 1895 *Mesacanthus pusillus*, Agassiz, 1844; Traquair, p. 245.
 1906 *Acanthodes Pusillus*; Wallace, tab. 1.
 1914 *Mesacanthus Peachi* (Egert.); Crampton and Carruthers, p. 6.
 1935 *Mesacanthus peachi* (Egert.); Wilson, p. 38.
 1948 *Mesacanthus pusillus*; Read, p. 63.
 1948 *Mesacanthus peachi*; Phemister, p. 67.
 1948 *Mesacanthus pusillus*; Phemister, p. 68.
 1964 *Mesacanthus pusillus* Agassiz, 1844; Novitskaya and Obruchev, p. 189.
 1965 *Mesacanthus pusillus*; Waterston, p. 293.
 1968 *Mesacanthus pusillus* (Agassiz); Peacock, Berridge, Harris and May, p. 135.
 1970 *Mesacanthus pusillus* (Agassiz); Miles, p. 362.
 1974 *Mesacanthus peachi*; Donovan, Foster and Westoll, tab. 2.
 1976 *Mesacanthus peachi* Egerton; Mykura, p. 78.
 1979 *M. pusillus* (Agassiz) 1844; Denison, p. 47-48.
 1979 *M. peachi* (Egerton) 1861; Denison, p. 48.
 1979 *M. sp.*; Denison, p. 48.
 1980 *Mesacanthus peachi*; Donovan, p. tab. 3.
 1982 *Mesacanthus pusillus* Ag; Andrews, p. 47, figure 19d-f.
 1986 *M. peachi* (Egerton); Trewin, p. 37.
 1997 *M. peachi*; Young, p. 49.
 1997 *M. pusillus*; Young, p. 49.
 1999 *Mesacanthus pusillus* Agassiz 1844; Trewin and Davidson, p. 543, tab. 3.
 1999 *Mesacanthus peachi* Egerton, 1861: Dineley, p. 174, 181, 212.
 1999 *Mesacanthus pusillus* (Agassiz, 1844); Dineley, p. 198, 212, 215, figure 6.20.
 2005 *Mesacanthus pusillus* (Agassiz); Newman and Dean, p. 2-6.
 2005 *Mesacanthus pusillus* Agassiz 1844; Barclay and Trewin, p. 10.
 2008 *Mesacanthus peachi* (Agassiz, 1844)); Hanke, p. 289.
 2008 *Mesacanthus pusillus* (Egerton, 1861); Hanke, p. 289.
 2010 *Mesacanthus pusillus* (Agassiz, 1844); Newman, p. 13-15, figures 21-23.
 2015 *Mesacanthus pusillus* Agassiz; Baron, p. 2-13, 15, 17-19, figures 6, 8.
 2020 *Mesacanthus pusillus*; Burrow, Newman and den Blaauwen, 1155-6, figure 1g.
 2020 *Mesacanthus pusillus* Agassiz, 1844; Newman, den Blaauwen and Burrow, p. 34.

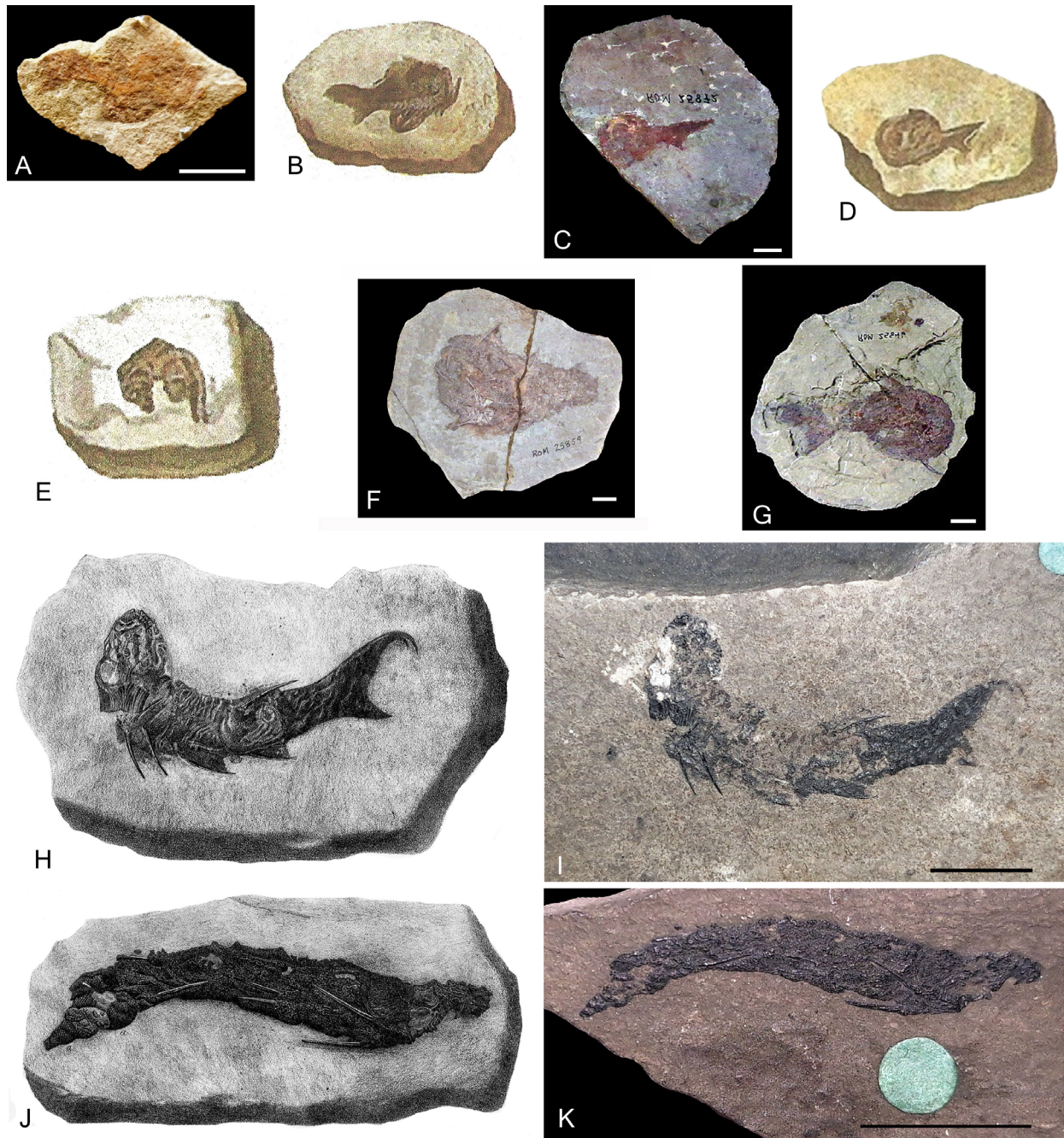


FIGURE 2. *Orcadacanthus pusillus* specimens from Tynet Burn, Scotland and type specimens of junior synonyms *Acanthodes peachi* and *A. coriaceus* from Caithness. **A**, ELGNM.1978.191.1, electronically flipped horizontally to match **B**. **B**, Agassiz type specimen (1844-5, plate 28, figure 8). **C**, ROM 25872 electronically flipped horizontally to match **D**. **D**, Agassiz type specimen (1844-5, plate 28, figure 9). **E**, Agassiz type specimen (1844-5, plate 28, figure 10). **F**, *Diplacanthus crassissimus*, ROM 25859. **G**, *O. pusillus*, ROM 25846 electronically flipped horizontally to match **B**. **H**, **I**, *Acanthodes peachi* GSM 21448 from Barragill (East Mey): **H**, specimen as figured by Egerton (1861, plate 6, figure 2); **I**, current state. **J**, **K**, *Acanthodes coriaceus* GSM 28831 from Gallow's Hill (Pennyland), near Thurso: **J**, specimen as figured by Egerton (1861, plate 6, figure 4); **K**, current state. Scale bars equal 10 mm.

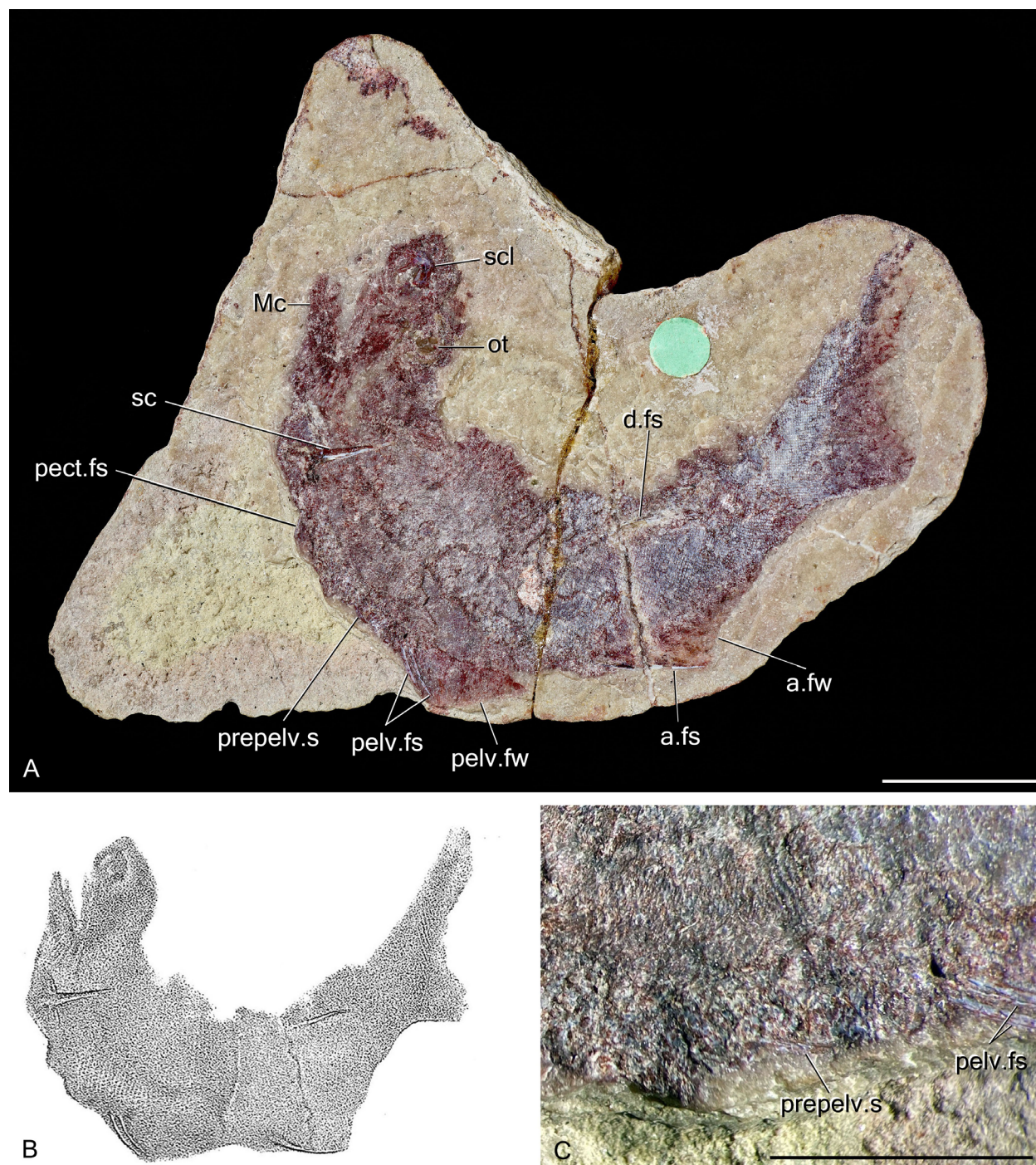


FIGURE 3. *Orcadacanthus pusillus* neotype NMHUK PV OR 35786 from Tynet Burn. **A**, photograph of the specimen. **B**, figure of specimen from Woodward 1891, plate 1, figure 5. **C**, close-up of the prepelvic spine. Abbreviations: a.fs, anal fin spine; a.fw, anal fin web; d.fs, dorsal fin spine; Mc, Meckel's cartilage; pect.fs, pectoral fin spine; pelv.fs, pelvic spine; pelv.fw, pelvic fin web; prepelv.s, prepelvic spine; ot, otic capsule; sc, scapula; scl, sclerotic plate. Scale bar equals 10 mm in A, 5.0 mm in C.

- 2021 *Mesacanthus pusillus*; Baron and Seymour, p. 1-3, figures 1, 2.
 2021 *Mesacanthus pusillus*; Burrow, p. 63, figures 26D, 27C.
 2021 *Mesacanthus pusillus*; Burrow and den Blaauwen, p. 86, 89, figure 7d, e.
 2022 *Mesacanthus pusillus*; Burrow, den Blaauwen, and Newman, p. 4, 12.

DIAGNOSIS AND DESCRIPTION

Revised diagnosis. Mesacanthid acanthodian up to 60 mm long, maximum depth to length ratio about 0.2; rostrum extends about half an orbit length in front of the eye; covering of robust polygonal tesserae extending down to nares anteriorly and down to mouth post-orbitally; c. five large, wide sclerotic plates ornamented with parallel grooves that are oblique across the plates or parallel to the plate edges (autapomorphy); thin denticulated semicircular plates above anterior and posterior nares; anterior end of Meckel's cartilage truncated (autapomorphy); main gill cover subcircular, extending below Meckel's cartilage for about three quarters of its length; branchiostegal rays ornamented with three sharp or rounded longitudinal ridges; dorsal-most branchiostegal rays curved; scapular shaft high and circular in cross section (apomorphy); pelvic spines positioned halfway between pectoral and anal fin spines; very short (apomorphy), straight prepelvic spines just anterior to pelvic spines; pelvic spines strong and straight and at least half the length of the pectoral spines and two-thirds the length of the anal spine; large cartilages at bases of median spines; pelvic and anal fins large with long bases (apomorphy); scales up to 0.2 mm wide with a central pulp cavity that often opens out through the base (autapomorphy); scale crowns can extend more than a base length behind the posterior corner of the scale base (autapomorphy).

Neotype. NHMUK PV OR 35786 (Figures 3, 5H), a complete specimen including the head with lower jaws from Tynet Burn, Moray, Scotland.

Remarks. When referring to *Orcadacanthus pusillus* in this section, we use the genus name that the relevant authors used at the time. Andrews (1982) stated that all of the part specimens from the syntype series were lost, but suggested that ELGNM.1978.191.1 from Tynet Burn (Figure 2A) could be the counterpart of one of Agassiz's specimens (1844-5, plate 28, figure 8) of *Acanthodes pusillus* (Figure 2B). She also suggested that one of the specimens from Tynet Burn purchased by

the Royal Ontario Museum from Portsoy Minerals in 1968, referred to as ROM 87 in her paper (now ROM 25872; Figure 2C), could be the counterpart of another of Agassiz's type specimens (1844-45, plate 28, figure 9; Figure 2D). The final specimen figured by Agassiz (1844-5, plate 28, figure 10; Figure 2E) has never been compared with or referred to any specimen in a collection and the drawing is very poor. Andrews (1982) noted that the back of specimen 'ROM 87' had a label written by George Gordon (1801-1893; see Andrews (1982) for details on Gordon) stating the specimen was a counterpart of one of Agassiz's figured specimens. This label has not been found, and ROM curator Kevin Seymour does not recall ever seeing one (personal commun., 2020). The typed fossil list from Portsoy Minerals held in the Royal Ontario Museum was appended in pencil by Kevin Seymour with the ROM catalogue numbers allocated to the specimens, thus for example # 87 ('ROM 87') was assigned catalogue number ROM 25872. However, also on this list next to specimen # 17 (also from Tynet Burn; now ROM 25859) is the typed comment that it was a reputed counterpart of an Agassiz type specimen. Neither specimen was identified taxonomically on the list. ROM 25859 (Figure 2F) is a good example of *Diplacanthus crassisimus*, but it clearly does not match the morphology of the *Diplacanthus* specimens figured by Agassiz (1844-5, plates 13-14). We can only suggest that the provenance of # 17 and # 87 on the Portsoy list were mixed up, if Andrews (1982) was correct about the label on # 87. However, Andrews (1982) stated that neither of the two *Mesacanthus pusillus* specimens ROM 25872 and ELGNM.1978.191.1 could be unconditionally attributed to any Agassiz's (1844-5) figures, as the drawings were of too poor quality.

Moving forward, Baron (2015) considered the possibility that as well as ROM 25872 and ELGNM 1978.191.1, ROM 25846 (Figure 2G) could possibly be the counterpart of one of Agassiz's type specimens. Baron (2015) also followed Andrews (1982) in concluding that none of Agassiz's (1844-5) figures were clear enough to allow confirmation that any of the specimens mentioned above were the type counterparts.

Baron and Seymour (2021) subsequently addressed the type specimen issue and nominated ROM 25872 as the lectotype of *Mesacanthus pusillus*, as they thought there was enough similarity between it and the Agassiz (1844-5, plate 28, figure 9) specimen. However, there are discrepancies between ROM 25872 and that Agassiz syntype,

and we are not convinced that ROM 25872 is the counterpart of this specimen. We consider that the confusion and uncertainty surrounding the provenance of ROM 25872 and ROM 25859 and the lack of specific diagnostic characters in ROM 25872 mean that under ICZN rules 74.2 and 75.5, it is not acceptable as a type specimen.

Woodward (1891, p. 11) stated that the type specimen of *Acanthodes pusillus*, an 'imperfect fish', was in Forres, Scotland, presumably in the Falconer Museum. Both S.M. Andrews and two of the authors (MJN, JdB) searched this collection for a possible type specimen, but none was found. ELGNM 1978.191.1, the other specimen identified by Andrews (1982) as a possible counterpart of a syntype (Agassiz, 1844-5, plate 28, figure 8), could be the specimen described by Woodward, as it is possible that the Elgin and Falconer museums, just 12 miles apart and closely associated, swapped material in the nineteenth century. The morphology of this specimen is similar to that illustrated by Agassiz, indicating that it might belong to the syntype series. However, it is very poorly preserved and like ROM 25872 preserves no specific diagnostic characters, also making it unsuitable as a type specimen. As *Acanthodes peachi* and *Acanthodes coriaceus* have been regarded as junior synonyms of *Orcadacanthus pusillus*, their type specimens GSM 21448 and GSM 28831, respectively (Figure 2H-K), were also considered as potential candidates for a neotype, but they are from localities in Caithness, not the type locality of Tynet Burn (which is in Moray).

As none of the purported surviving members of the type series precisely match the original (Agassiz, 1844) figures, no definite archival evidence links possible counterpart material to the original syntypes, and after extensive searching, we must concur with previous authors (e.g., Andrews, 1982) that considered them lost. Agassiz's (1844) figures and description are insufficient to distinguish this species from other mesacanthids, necessitating a neotype to stabilize usage of the species name *Acanthodes pusillus*. After Agassiz (1844-5), Woodward (1891) provided the next detailed description of specimens of the species from the type locality of Tynet Burn. Here we designate NHMUK PV OR.35786 (Figure 3A), the best preserved of the specimens described by Woodward (1891, plate 1, figure 5; Figure 3B), as the neotype, as it exhibits the diagnostic characters for the species. Strangely, Woodward (1891) did not mention the prepelvic spines of this specimen, despite one of the spines being clearly identifiable

(Figure 3A, C). Perhaps this was related to the dispute he had with Ramsay Traquair about the appropriateness of erecting the new genus, given that these spines were a defining character for *Mesacanthus*.

Type locality. Several exposures either side of the Tynet Burn, Moray, Scotland. British Grid reference NJ 384121. Specifically, the neotype comes from the upper nodule bed, bottom unit (*Osteolepis* bed) as described by Trewin and Davidson (1999).

Remarks. Agassiz (1844-5) only stated that his specimens of *Acanthodes pusillus* came from Gordon Castle rather than the locality of Tynet Burn. Andrews (1982) stated that the specimens could therefore have come from elsewhere. However, we consider this unlikely as the owner of Gordon Castle (Charles Gordon-Lennox, 5th Duke of Richmond, 1791-1860) was also the owner of Tynet Burn, and Egerton (1861b, p. 58) stated that the species came from Tynet Burn.

Stratigraphic and geographical occurrence. From the Middle Devonian of the Orcadian Basin of Scotland.

Description

General features. Specimens long and slender with a maximum depth to length ratio about 0.2 (Figures 3A, 4A-E). The fish range in length from 15 mm to 60 mm. The smallest individuals are only partially ossified (Figure 4A), with the head being the last region to be mineralised (see discussion). The spine complement comprises paired pectoral, pelvic, and prepelvic spines, a single (posterior) dorsal spine, and an anal spine. All the spines have fin webs except the tiny prepelvic spines. The pelvic fin spines are straight and about half the length of the pectoral fin spines and two-thirds the length of the anal and dorsal fin spines. The dorsal fin spine is slightly curved, and posterior relative to the anal fin spine. Pelvic spines are halfway between the pectoral and anal spines; prepelvic spines are closer to the pelvic fin spines than the pectoral fin spines. The caudal fin has an upper lobe extended into a tapered tip and a short triangular lower lobe. The scapula shaft is relatively slender and about five times the height of the triangular area forming its base; scapula height is always less than the pectoral spine length. The ratio of scapula height to pectoral fin spine length is highly variable, possibly associated with the variable mineralisation of the suprascapular region.

Head and branchial region, morphology. Dermal cover on the head is quite extensive, comprising large polygonal tesserae, extending down to the

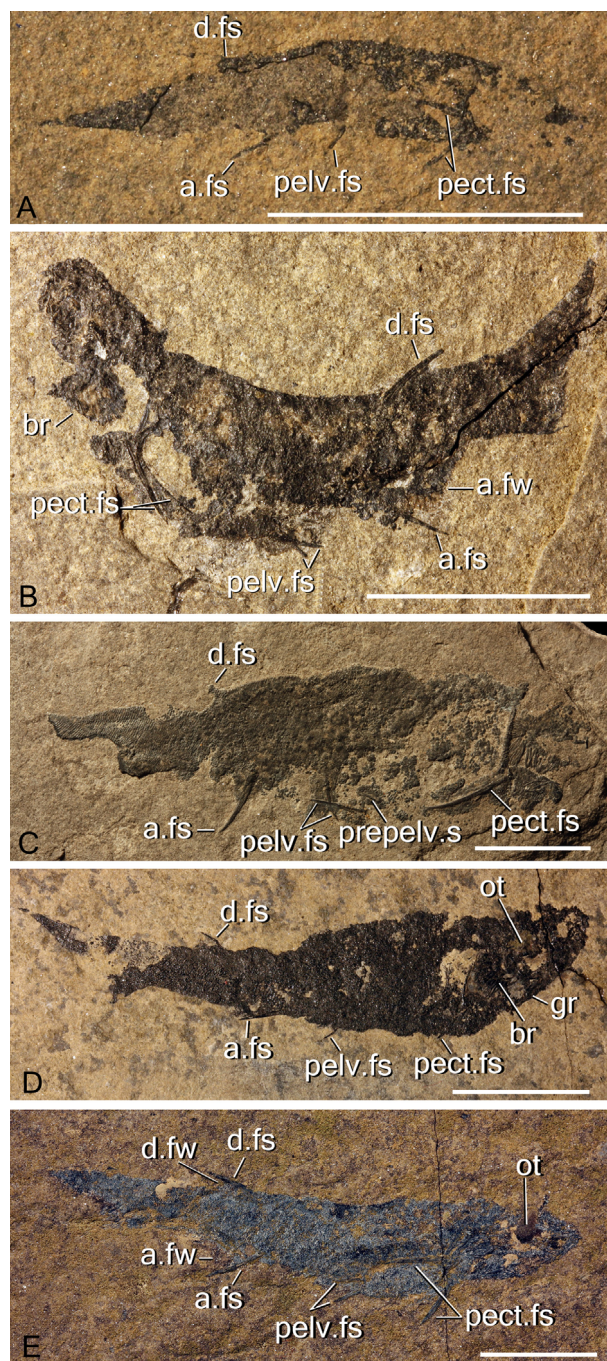


FIGURE 4. *Orcadacanthus pusillus*, complete specimens. **A**, NMS G.2021.7.27 from Achanarras Quarry. **B**, NMS G.2021.7.78 from Brims Ness. **C**, NMS G.1887.35 from Thurso (probably Pennyland). **D**, NMS G.2021.7.269 from Blacken Berry. **E**, NMS G.2022.10.8 from Button Geo, Stroma. Abbreviations: a.fs, anal fin spine; br, branchiostegal rays; d.fs, dorsal fin spine; d.fw, dorsal fin web; gr, gular rays; ot, otic capsule; pect.fs, pectoral fin spines; pelv.fs, pelvic fin spines; prepelv.s, pre-pelvic spines. Scale bars equal 10 mm.

nares anteriorly and down to the mouth post-orbitally (Figure 5A-C). The eye is surrounded by about five (the precise number is difficult to judge precisely due to preservation) wide sclerotic plates ornamented with parallel linear grooves running obliquely (Figure 5B, bottom) or concentrically (Figure 5B, top). These grooves terminate against a narrow smooth area along the inner edge (Figure 5E-F). Two displaced sclerotic plates (Figure 5F) were misidentified as a spiracle cover in Burrow et al. (2020a, figure 1g). Behind the eye, the otic capsule is indicated by a grainy infilling (Figure 5C). This is also the case in some Tynet Burn specimens (Figure 5G), but sometimes the infilling is calcitic (Figure 5H). A preopercular canal runs just dorsal to the palatoquadrate (Figure 5H), but no other sensory lines have been identified. The tesserae covering the head (Figure 5A-C) resemble those of *Mesacanthus mitchelli* and other mesacanthids, being polygonal elements with a flat base, but they form a more extensive cover than in *M. mitchelli*.

The main branchiostegal cover has a clearly defined sub-circular outline and comprises close-set branchiostegal plates (Figure 5I-J) that more or less curve back from the anterior angle, paralleling the dorsal and ventral edges of the cover. The branchiostegal plates extend under the posterior third of the Meckel's cartilage (Figure 5A). The distribution of these plates is perhaps best seen in the only specimen of *Acanthodes peachi* figured by Egerton (1861, plate 5, figure 2; Figure 2H, I), preserved with the ventral surface of the head and branchial region exposed. These plates are ornamented with three longitudinal ridges that can be sharp crested (Figure 5I) or more rounded (Figure 5J). Despite examining hundreds of specimens, we have not identified any subsidiary gill covers above or behind the main cover, which appears to extend over all or most of the branchial region.

The palatoquadrate and Meckel's cartilage are the only mineralised endoskeletal elements that we have identified in the head region. Meckel's cartilage (Figure 5K) is a single element with a truncated anterior end (Figure 5A-B, K). In no specimen is the mandibular joint well preserved. The palatoquadrate (Figure 5L) is a single element, with a short suborbital region and long curved posterodorsal edge supported by an extra-palatoquadrate ridge. The palatobasal articulation to the neurocranium consists of a small notch at the anterodorsal corner of the palatoquadrate.

One of the distinctive characters of the species is the form of the plates surrounding the two

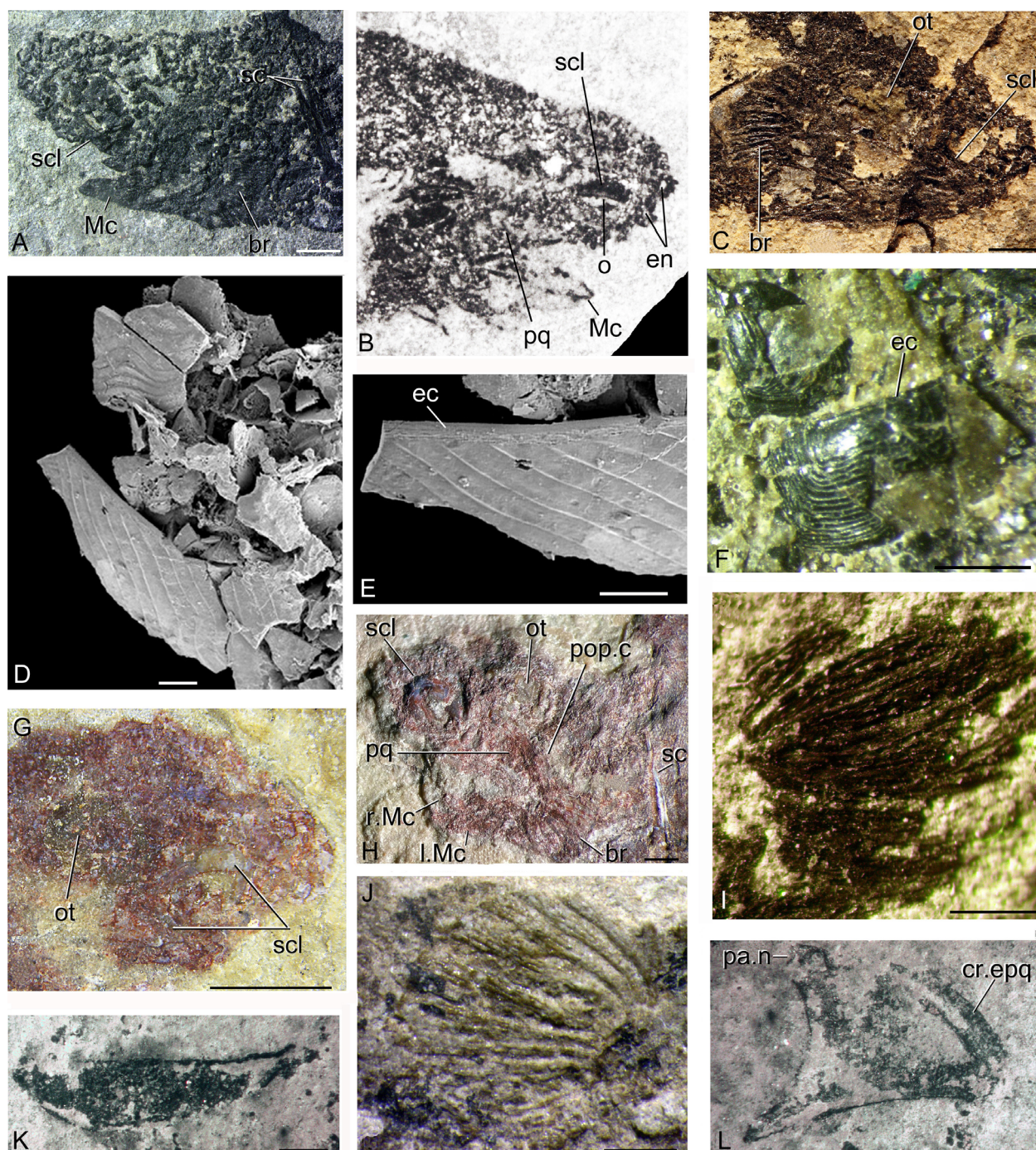


FIGURE 5. *Orcadacanthus pusillus*, details of the head. **A**, NMS G.2021.7.286 from Lythmore. **B**, NMS G.2022.10.686 from Blacken Berry. **C**, NMS G.2021.7.269 from Blacken Berry. **D-E**, NMS G.2021.7.125.5.3 from Cromarty, SEM image of a sclerotic plate. **F**, NMS G.2019.3.10 from Cromarty, detail of two sclerotic plates (modified from Burrow et al., 2020, figure 1g). **G**, GLAHM V3573 from Tynet Burn. **H**, NHMUK PV OR 35786 from Tynet Burn. **I**, NMS G.2022.10.2 from Lythmore, detail of main branchial cover. **J**, NMS G.2021.7.292 from Den of Findon (Garnie), detail of main branchial cover. **K-L**, NMS G.2021.7.285 from Achanarras. **K**, palatoquadrate. **L**, Meckel's cartilage. Abbreviations: br, branchial ray; cr.epq, extra-palatoquadrate ridge; ec, sclerotic plate eyeball contact area; en, external naris; l.Mc, left Meckel's cartilage; nb, nasal bone; o, orbit; ot, otic capsule; pa.n, palatobasal articulation to the neurocranium; pop.c, preopercular canal; pq, palatoquadrate; r.Mc, right Meckel's cartilage; sc, scapula, scl, sclerotic plate. Scale bars equal 2 mm in A-C, G-H; 100 μ m in D-E; 1 mm in F, J-L; 500 μ m in I.

pairs of external nares on the anteriormost rostrum, in front of the orbit (Figure 6A). The nasal plates of the left side are usually slightly separated from those of the right side, but close to the mid-line. The anteriormost nasal openings can be fully enclosed by four or five similar, smooth plates (Figure 6B-C), or alternatively by a robust semicircular plate and smaller plates or tesserae (Figure 6D). These variants do not appear to be related to the size of the fish. Slightly smaller plates surround (at least partially) the posterior nares, which are contiguous with the anterior nares (Figure 6D). At least some of the plates surrounding the anterodorsal nasal opening have denticles on the inner concave edge of the plate (Figure 6D). However, denticles are on the outer convex edge of some of the plates around the posterior nasal opening (Figure 6D-E). Some better preserved and more complete nasal plates (Figure 6F-G) show their complex structure

with the shiny ornament layer and its sharply pointed denticles formed of thin overlapping layers. **Head and branchial region, histology.** Thin sections show that the sclerotic plates are composed of lamellar bone with a thin outer layer forming the parallel ornament strips visible on the surface of the elements. Each strip slightly overlaps the contiguous strip (Figure 7A-B), producing the grooves visible on the surface. Thin sections of the nasal plates show they have internal projections that are presumed to have enclosed canals (Figure 7C-D). At least in some specimens, the bone can be relatively thick and formed of thin lamellae with the paired external plates fused together (Figure 7C). In both the sclerotic and nasal plates, a vascular canal plexus extends through the base of each outer layer, delimiting the 'ornament' from the underlying acellular bone layers. No dentine tubules have been identified in the ornament layer, but this is most likely a preservational feature given

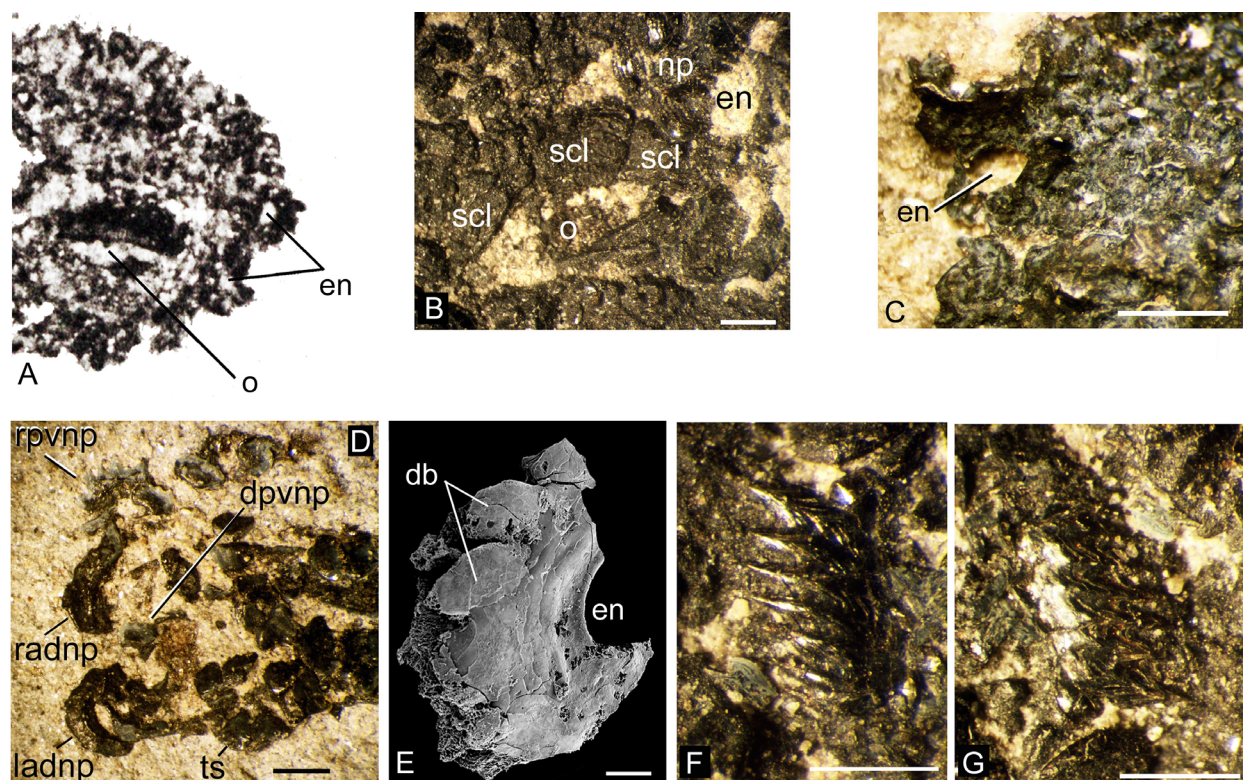


FIGURE 6. *Orcadacanthus pusillus*, details of the nasal area. **A**, NMS G.2022.10.686 from Blacken Berry showing right orbit and rostrum on the laterally flattened head. **B**, NMS G.2021.7.238 from Skinnet, orbit and one or two nasal openings. **C**, NMS G.2021.7.209 from Ness of Litter. **D**, NMS G.2021.7.93 from Cairnfield, dorsoventrally flattened rostrum. **E**, NMS G.2021.7.125.5s from Cromarty, ESEM of detached nasal plate, internal surface. **F-G**, NMS G. 2021.7.238 from Skinnet, displaced nasal plates. Abbreviations: db, denticle base; dpvnp, displaced posteroventral plate; en, external nare; ladnp, right anterodorsal nasal plate; np, nasal plate; o, orbit; radnp, right anterodorsal nasal plate; rpvnp, right posteroventral nasal plate; scl, sclerotic plate; ts, tesserae. Scale bars equal 500 μ m in B-D, F-G; 100 μ m in E.

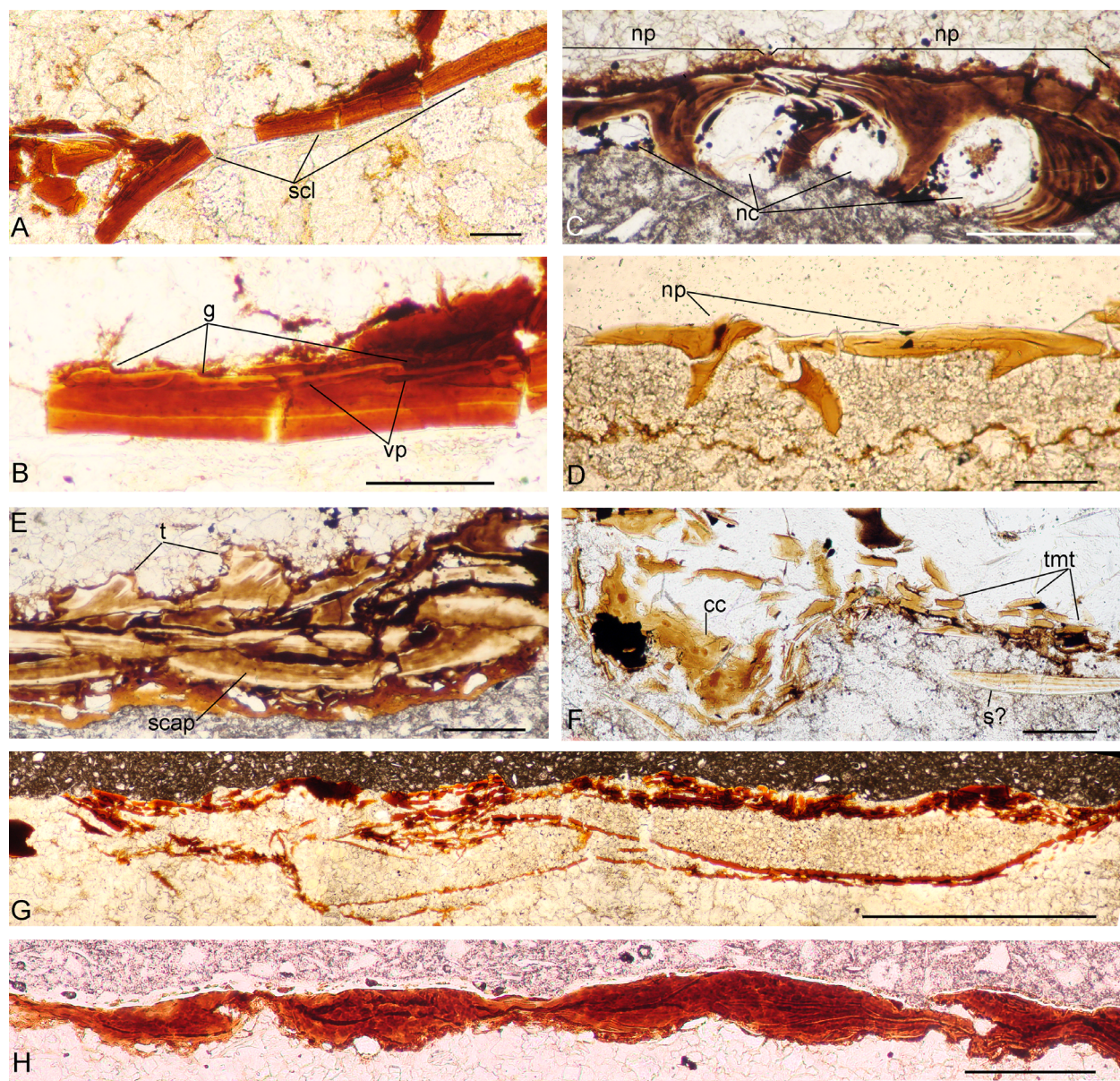


FIGURE 7. *Orcadacanthus pusillus* head and branchial elements, histology. **A-B**, NMS G.2021.7.136 from Cromarty, sclerotic plates, vertical section NMS G.2021.7.136.5, with close-up of one plate in (B). **C**, NMS G.2021.7.265 from Blacken Berry, NMS G.2021.7.265.3, pair of nasal plates. **D-F**, NMS G.2019.3.11 from Corbie Den: **D**, NMS G.2019.3.11.3, pair of nasal plates. **E**, NMS G.2021.7.265 from Blacken Berry, NMS G.2021.7.265.5, vertical section through head tesserae oblique section through scapulocoracoid. **F**, lower jaw transverse section NMS G.2019.3.11.4, ventral edge to left (the presumed transverse section through a posterior scale crown (s?) was mislabelled as a sclerotic plate in Burrow and den Blaauwen, 2021:figure 7E). **G**, NMS G.2021.7.126 from Cromarty, NMS G.2021.7.126.3, transverse section through jaw cartilages. **H**, NMS G.2021.7.162 from East Mey, NMS G.2021.7.162.5, transverse section through branchiostegal plates (ornament layer to bottom). Abbreviations: br, branchiostegal plate; cc, calcified cartilage; g, grooves; nc, nasal canals; np, nasal plates; scap, scapulocoracoid; scl, sclerotic plates; t, tesserae; tmt, tessellate mineralised tesserae; vp, vascular plexus. Scale bars equal 100 µm in A-F, 1.0 mm in G.

they are often not preserved in fin spines or scales either (see below). The thin, clear zones in the outer layers forming these elements (Figure 7C), which give the shiny surface appearance in well-preserved material (Figure 6G-H), probably result from diagenetic alteration of dentine rather than being enameloid.

The Meckel's cartilage is thickened along the lower edge as in *M. mitchelli* (Burrow et al., 2022), and lacks a separate mandibular bone. Burrow and den Blaauwen (2021, figure 7D, E) noted that the hard tissue forming the outer layer of the jaws is composed of layered blocks of amorphous mineralised tissue, and a thickened ventral edge on the Meckel's cartilage encasing a globular calcified cartilage core (Figure 7F, G). The tissue forming the jaw surfaces shows no evidence for rings of Liesegang or bone cells and processes, and is not layered. Burrow and den Blaauwen (2021) referred to the structure as tessellated mineralised tesserae (tmt).

The crown of the dermal tesserae on the antero-dorsal part of the head can have relatively high odontodes (Figure 7E), thus differing from those of *M. mitchelli*, which are relatively flat. Unfortunately, their histological structure was not well preserved in any of the specimens sectioned. Preservation was also poor in sections through the branchiostegal plates (Figure 7H), only showing layering through the plates which had 'melted' together.

Shoulder girdle (Figures 8A, D, E, H, 9A, 10A).

The scapulocoracoid has a long shaft that is circular to oval in cross-section and expands ventrally to a short triangular blade. The shaft length is quite variable relative to the length of the pectoral spine, ranging from being about the same length to half the length, seemingly unrelated to stratigraphic level or the size of the fish. Both scapular shaft and ventral blade are fully perichondrally ossified laterally, but the blade is often only partly ossified medially (Figure 8A). The ventral edge of the element curves around the proximal end of the pectoral fin spine (Figure 8D-E). The spines must have been firmly attached to the scapulocoracoids by ligaments or tendons as well as articulating in the embayment of the scapulocoracoid blade (Figure 9A), as they are commonly preserved in connection both in articulated and disarticulated specimens, sometimes even as isolated complexes with no other remains of the fish. As a result, this region and the head are often skewed so that both right and left pectoral girdles and spines are on the exposed surface. The scapulocoracoid is com-

posed of lamellar perichondral bone surrounding a hollow core presumed to have been filled with uncalcified cartilage (Figures 7E, 9A, 10A), with the bone layers added centripetally.

Fin spines (Figures 8, 9, 10B-N, 11, 12). The pectoral, pelvic, dorsal, and anal spines have two or three weakly developed longitudinal ridges on each side (Figure 8C, F, G, I). In cross-section, these ridges are usually symmetrical and sharp-crested. There is no groove separating the leading edge ridge and the 'shoulders' of the spine, just a concave slope or, rarely, an indentation. The pectoral spines are slightly asymmetric in cross-section, with a subtriangular shape. The leading edge ridge is about a third of the total width of the spine. The dorsal spines are more laterally compressed than the anal spines, with sub-parallel sides, whereas the main body of the anal spine has a more rounded cross-section (Figures 10D-F, 11, 12A-B). Both of these median spine forms are deeper than wide, and the rounded leading edge ridge is about half the maximum width of the spine. The central pulp cavity in anal spines is open at the proximal end of the spines but is enclosed for most of its length (Figures 11C, 12B); in dorsal spines the cavity is marginally open along most of the length (Figures 11B, C, 12A-B); and in the pectoral spines the pulp cavity is open for about the proximal 20% of its length (Figure 11A). In spines of young fish, the pulp cavity is relatively wide with no inner lamellae developed (Figure 9). In older fish this main pulp cavity is gradually reduced by addition of inner layers of dentine, with dentine tubules extending through the layers (Figure 10F, G, J). The cavity is about a third the total width of the spine proximally, with the inner lamellar layers reducing its relative width towards the distal end. All spines have a secondary longitudinal canal above the main pulp cavity, in the base of the leading edge ridge (Figure 10B-K, N), and extending the length of the spine. Smaller calibre longitudinal canals are developed in each 'shoulder' at the proximal end of the spine, but these only extend about two-thirds its length. The main pulp cavity on the tiny (< 2 mm long) pre-pelvic spines (Figures 9B, C, 12C) is open for most of their length, with a very small calibre secondary canal in the base of the relatively high, narrow leading edge ridge. Both dorsal and anal spines have a large, hollow, thin-walled basal plate (here infilled, probably by calcite) extending viscerally from the open base of the inserted end of the spines (Figures 10H, I, 12A). Presumably the plate was filled with uncalcified cartilage in life.

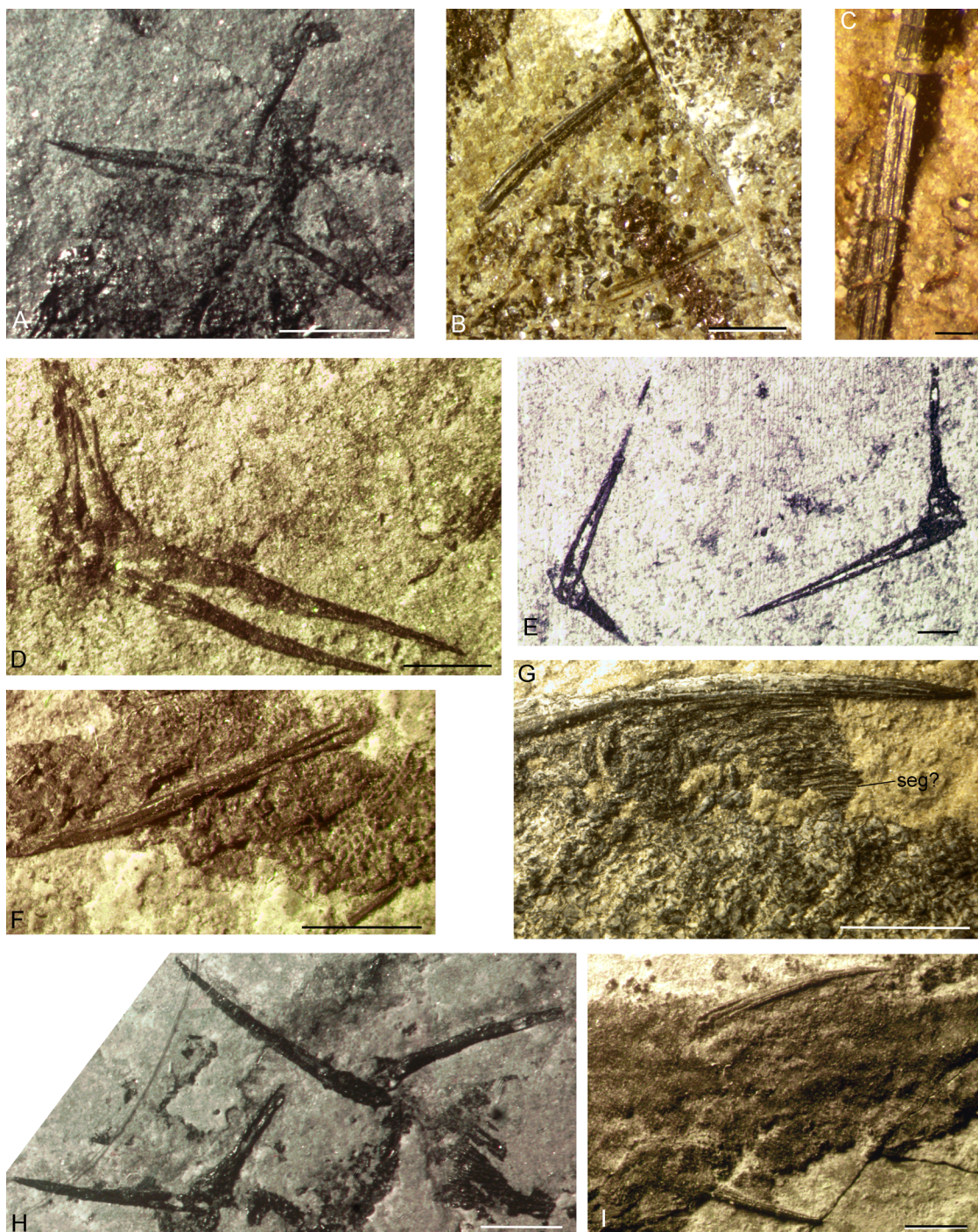


FIGURE 8. *Orcadacanthus pusillus* shoulder girdle, spines morphology. **A**, NMS G.2021.7.45 from Achanarras, articulated pectoral girdles and spines. **B**, NMS G.2019.3.10 from Cromarty, disarticulated pectoral spines and scales. **C**, NMS G.2021.7.135 from Cromarty, disarticulated pectoral spine, mid-spine ornament ridges. **D**, NMS G.2021.7.94 from Cromarty, articulated pectoral girdles and spines. **E**, NMS G.2021.7.290 from Cairnfield, pair of articulated pectoral girdles and spines, sliced by saw thus showing longitudinal sections through the elements. **F**, NMS G.2021.7.165 from East Murkle Bay, possibly the dorsal spine. **G**, NMS G.2021.7.202 from Blacken Berry, dorsal fin spine and fin rays. **H**, NMS G.2021.7.158 from East Murkle Bay, articulated pectoral girdles and spines. **I**, NMS G.2021.7.187 from Surrigarth, articulated fish, dorsal and anal fin spines. A-D, Achanarras Fish Bed Member horizon; E-F, lower part of the Mey Flagstone Formation horizon; G-I, upper part of the Mey Flagstone Formation horizon. Abbreviations: seg?, possible segmented rays. Scale bars equal 2.0 mm.

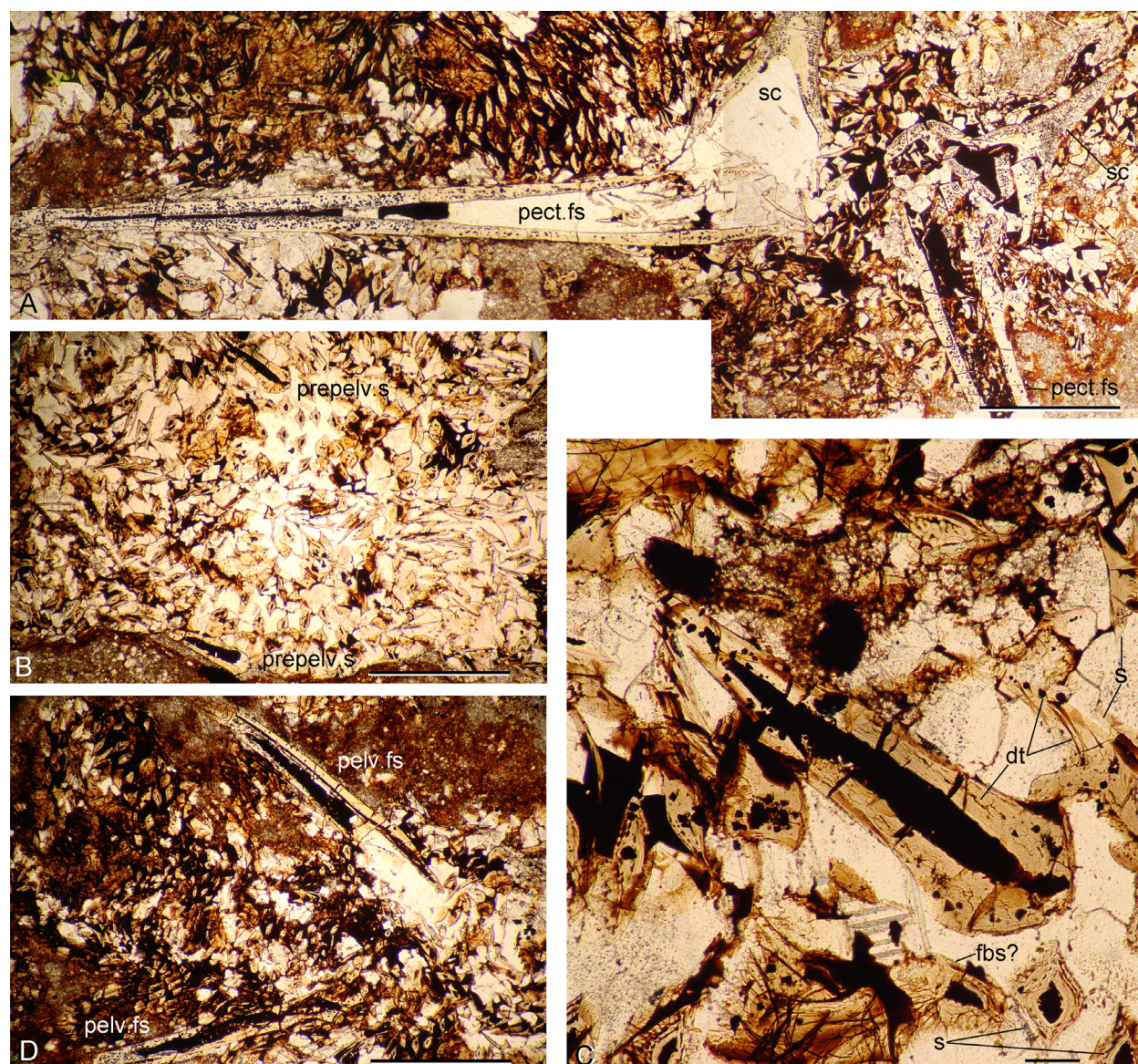


FIGURE 9. *Orcadacanthus pusillus* scapulocoracoid and paired spines histology, horizontal section through headless? articulated specimen NMS G.2022.10.1 from Blacken Berry. **A**, scapulocoracoids and pectoral fin spines, longitudinal sections of spines and oblique sections through scapulocoracoids (composite of three images); **B**, **C**, prepelvic spines; **D**, pelvic fin spines. Abbreviations: dt, dentine tubules/canals; fbs?, possible large scale near fin spine base; pect.fs, pectoral fin spine; pelv.fs, pelvic fin spine; prepelv.s, prepelvic spine; s, scales; sc, scapulocoracoid. Scale bars equal 10 mm in A, B, D, 1.0 mm in C.

In rare cases, ossified fin rays are preserved in the dorsal fin (Figure 8G). These rays are straight rods about 0.5 mm wide, extending back for about half the length of the fin from the spine insertion, and possibly segmented distally (seg?, Figure 8G). The rays are circular to oval in cross-section and are possibly formed by the fusion of two separate rays, as larger rays appear to show a median fusion and some smaller rays appear to be partly fused; growth lines parallel the outer surface (Figure 10L, M). They more or less form two layers

in the fin, and are overlain by very thin, short overlapping elements that might be composed of dentine rather than bone. However, no tubules are visible so their composition cannot be determined, and we are thus uncertain as to whether these are dermal or endoskeletal structures. These short fin elements, unlike the larger fin rays, are typically preserved in all the fins (Figure 10C, G, L, M).

Scales. Squamation and detached scales from all three faunal zones where *Orcadacanthus* occurs were examined to determine any differences. Body

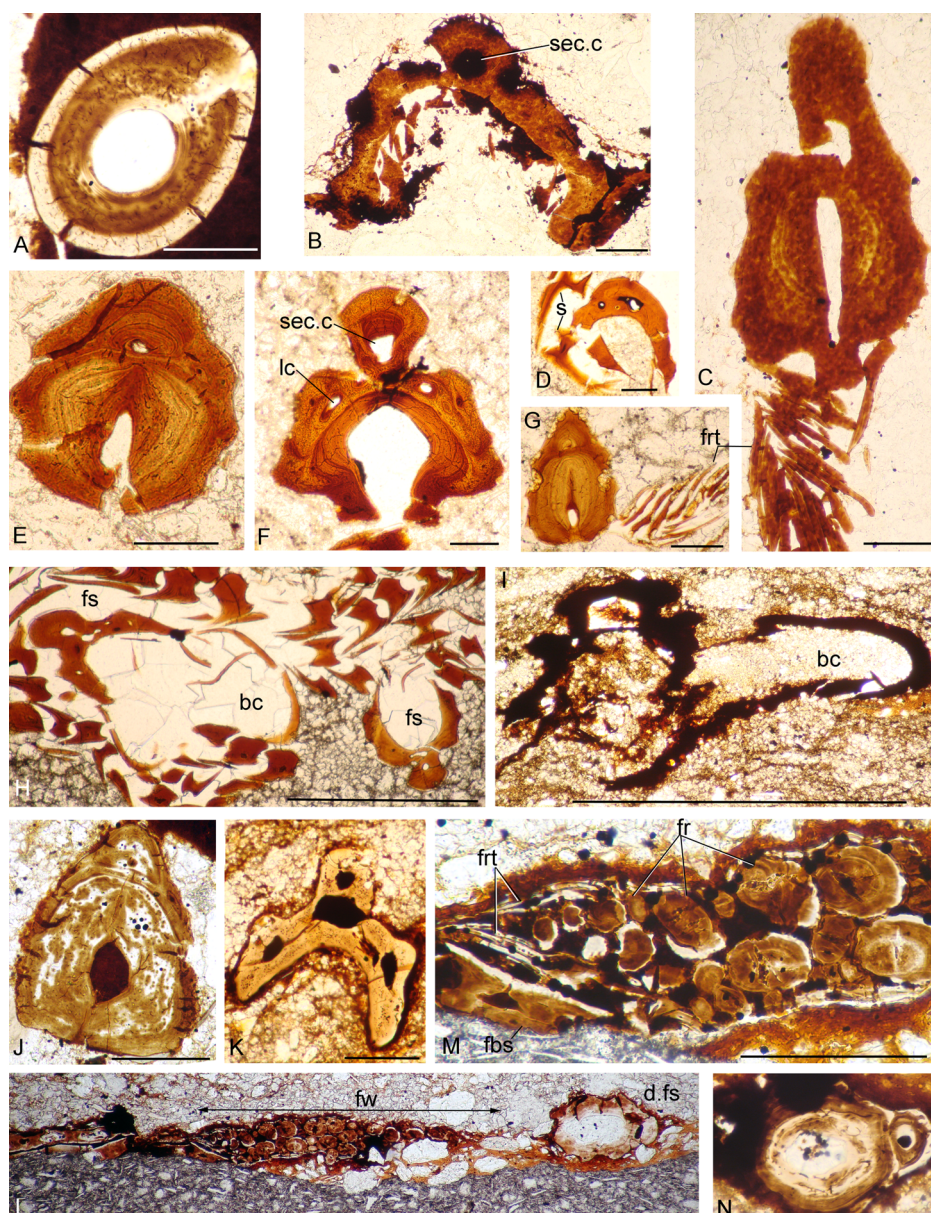


FIGURE 10. *Orcadacanthus pusillus* shoulder girdle, spines histology. **A**, NMS G.2022.10.13 from Castlehill, cross-section of scapulocoracoid shaft. **B-C**, transverse sections of spines from Achanarras: **B**, NMS G.2021.7.284.4, proximal end, possibly of pectoral spine; **C**, NMS G.2021.7.51.2, possible dorsal spine and small fin rays. **D**, NMS G.2019.3.11.7 from Corbie Den, NMS G.2019.3.11.2.7, transverse section, possible anal spine, proximal end. **E**, NMS G.2021.7.303.9 from Cromarty, NMS G.2021.7.303.9, transverse section, possible anal spine. **F**, NMS G.2021.7.136.9 from Cromarty, NMS G.2021.7.136.9, transverse section, possible anal spine. **G-H**, NMS G.2021.7.303 from Cromarty: **G**, NMS G.2021.7.303.6, transverse section, tip of possible dorsal spine and small fin rays; **H**, NMS G.2021.7.303.7, median spines and basal cartilage. **I**, NMS G.2022.10.15 from Scarfhall (Op beds horizon), transverse section, median spine and basal cartilage. **J**, NMS G.2022.10.17, bonebed sample from Cairn of Hattel, NMS G.2022.10.17.4, transverse section of distal end, possible dorsal spine. **K**, NMS G.2022.10.12 from Blacken Berry, proximal end of prepelvic spine. **L-N**, NMS G.2021.7.265 from Blacken Berry: **L-M**, NMS G.2021.7.265.14, dorsal fin and spine cross section: **L**, whole depth of fin plus dorsal spine; **M**, closeup of fin rays, large basal scale, and small outer fin 'rays'; **N**, NMS G.2021.7.265.14, distal end of dorsal spine. A-H, Achanarras Fish Bed Member horizon; I-K, lower part of the Mey Flagstone Formation horizon; L-N, upper part of the Mey Flagstone Formation horizon. Abbreviations: bc, basal cartilage; d.fs, dorsal fin spine; fbs, scale from base of fin; fr, fin ray; frt, fin raylet; fw, fin web; lc, longitudinal canal; s, scale; sec.c, secondary longitudinal canal. Scale bars equal 100 μ m in A-F, 1.0 mm in G, H.

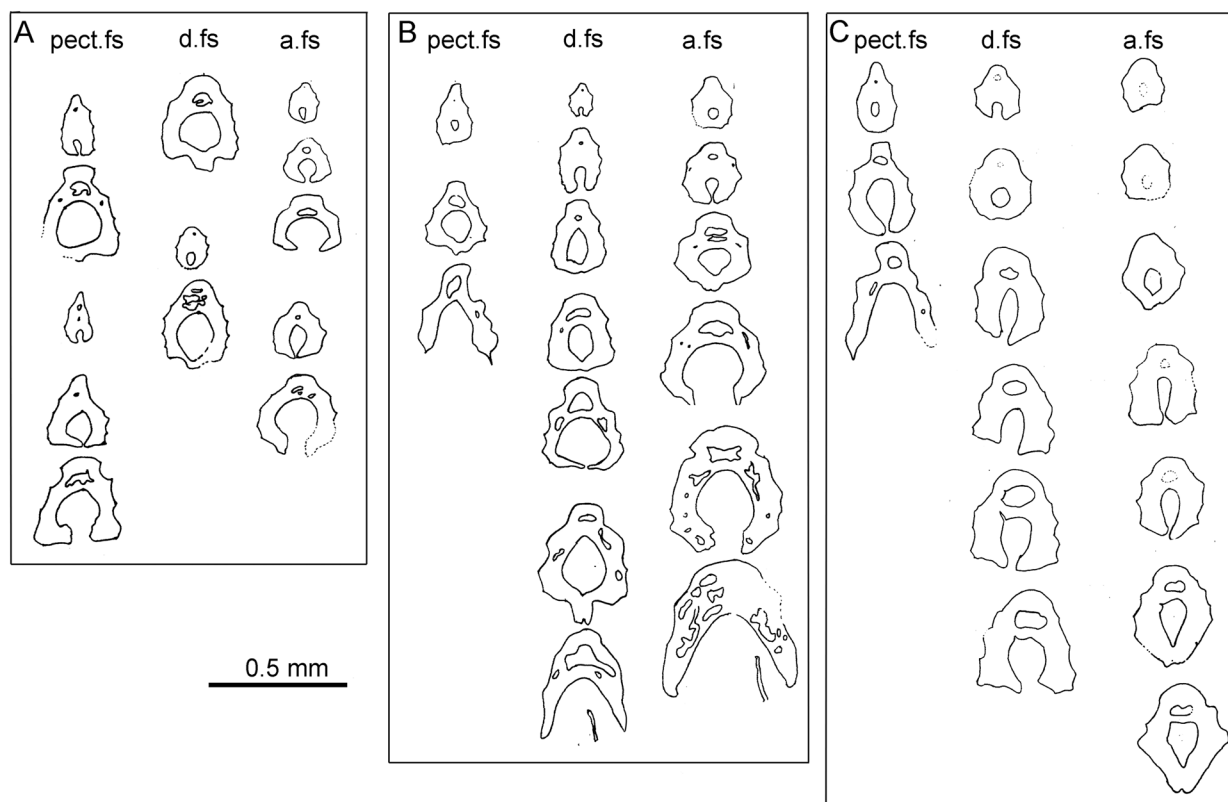


FIGURE 11. *Orcadacanthus pusillus* spines from articulated fish, Sollas serial section drawings. **A**, Achanarras Fish Bed Member horizon: pectoral spine (pect.fs) from Den of Findon, dorsal (d.fs) and anal (a.fs) spines from Tynet Burn. **B**, lower part of the Mey Flagstone Formation: all from west of Cairn of Hattel. **C**, upper part of the Mey Flagstone Formation horizon; pectoral spine from Blacken Berry, dorsal and anal spines from NMS G.2021.7.187, Surrigarth.

scales of fish from Cromarty (Figure 13) in the Achanarras Fish Bed Member horizon were c. 0.2 mm wide with a slightly convex base, marked base-neck rim and deep neck (Figure 13A-E, G). The smooth crown overhangs the base all round and has a sub-hexagonal outline. The anterior edge is slightly downturned, with its two halves meeting at an angle c. 160° at the rounded median corner. The side edges are subparallel to each other, diverging from the anterior edges at c. 130° , and the posterior edges converge at the posterior corner at c. 80° . The crown surface has a low median depression just behind the anterior edge. A scattered specimen from Cromarty (Figure 13F) also yielded this type of scale, plus much larger scales (Figure 13H-J), probably from near the fin spine bases. These scales are over 0.5 mm long, with a crown that extends up to three base lengths behind the posterior corner of the base. The neck and slightly convex base are both low.

We have much more information on the internal structure of scales from all three levels, as the histological preservation is better than that of the

squamation surfaces. Scales from Cromarty (Figure 14A-F) and Achanarras (Figure 14G) show a very similar structure to those of *Mesacanthus mitchelli*, differing mainly in having more crown growth zones, with up to seven observed. The embryonic zone has a variably developed central pulp cavity, being totally filled in most scales (Figure 14A-D). Some scales, however, retain a wide cavity, with the base formed of upwardly convex lamellae presumed to have progressively filled in the pulp canal that formerly opened out through the base (Figure 14E). Ascending canals rise up in each crown growth zone from wider circular canals (Figure 14B). A hypermineralised enameloid layer overlies a thin dentine layer in the upper horizontal area of the outer three or four growth zones (Figure 14A-D). As each hypermineralised layer merges into the underlying dentine layer rather than being clearly separated from it, the tissue is regarded as enameloid rather than enamel. Fin web scales are smaller than the body scales, usually with flatter bases and an elongate crown; short, thin fin rays appear to have formed within the web (Figure 14F).

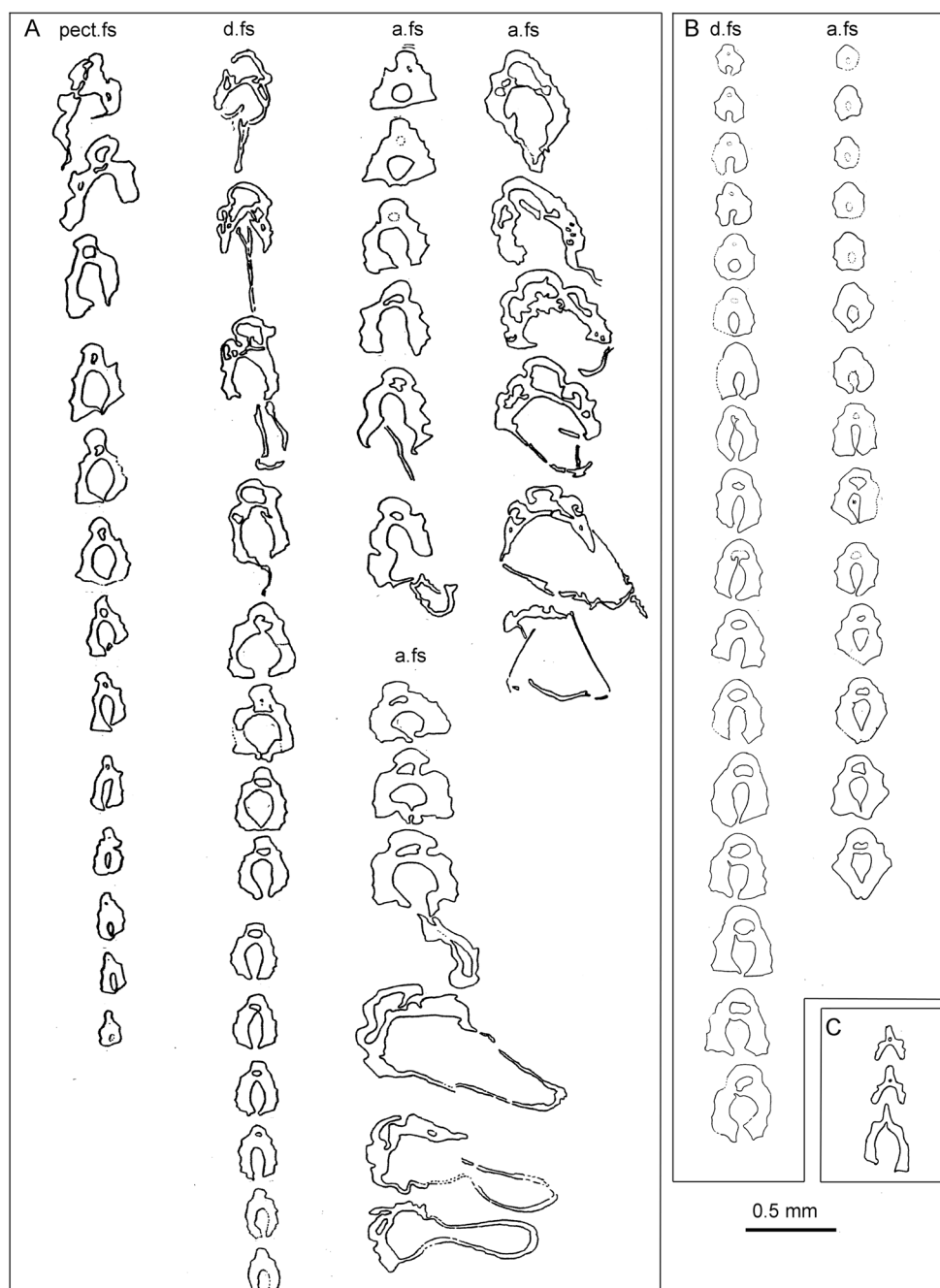


FIGURE 12. *Orcadacanthus pusillus* spines from bonebeds in the Mey Flagstone Formation, Sollas serial section drawings. **A**, pectoral, dorsal and three anal spines from Cairn of Hattel, at the lower part of the Mey Flagstone Formation horizon. **B**, dorsal and anal spines from Surrigarth (Westray), upper part of the Mey Flagstone Formation. **C**, pre-pelvic spines, a single section each of two from Clardon and one from Blacken Berry, upper part of the Mey Flagstone Formation.

Rare scales have a pair of small protruding nodes posteriorly, low on the neck (Figure 14G). Body scales on the specimen from Corbie Den (Figure 14H) appear to have a flatter base and deeper neck.

Scale surface detail is very rarely preserved in squamation on specimens from the lower part of the Mey Flagstone Formation (Figure 15). The scales are tightly packed and overlapping (Figure 15C-D). Scales from this level mostly retain a pulp cavity in the embryonic crown zone (Figure 16A-D,

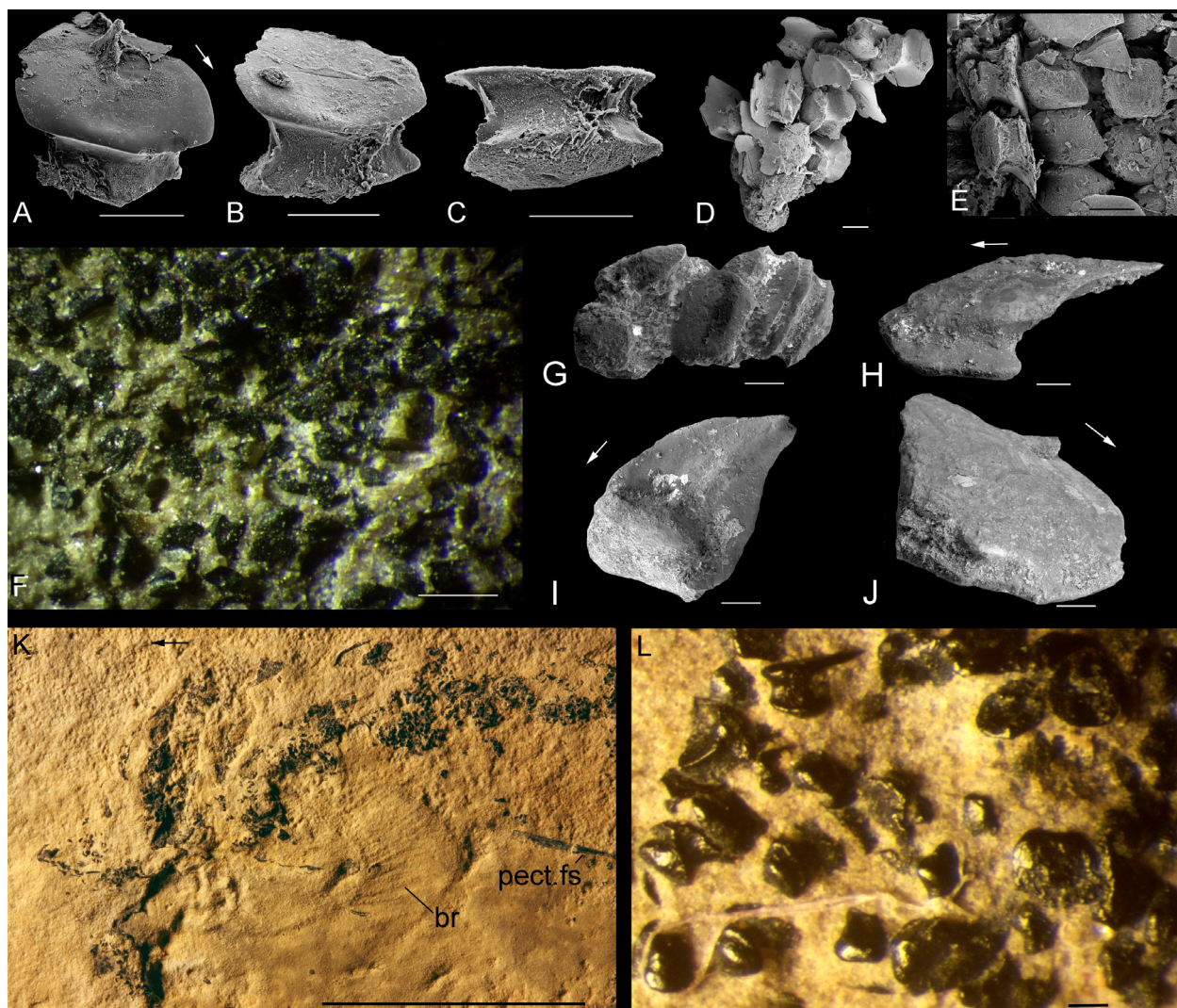


FIGURE 13. Achanarras Fish Bed Member horizon, *Orcadacanthus pusillus* scale morphology. Cromarty specimens, all ESEM images except F, light microscope image. **A-E**, NMS G.2021.7.125, disarticulated fish: **A**, NMS G.2021.7.125.5h, flank? scale, anterocrown view; **B-C**, NMS G.2021.7.125.5r, flank? Scale, anterocrown and anterior views; **D**, NMS G.2021.7.125.5d, clump of scales, showing posterior views; **E**, NMS G.2021.7.125.5l, clump of scales showing lateral and basal views. **F-J**, NMS G.2019.3.10, disarticulated fish: **F**, patch of scales; **G**, NMS G.2019.3.10.4d, clump of five scales; **H**, NMS G.2019.3.10.4e, dorsoventrally compressed scale with long posterior crown, lateral view; **I**, NMS G.2019.3.10.4c, dorsoventrally compressed scale with long posterior crown, basal view; **J**, NMS G.2019.3.10.4a, dorsoventrally compressed scale with long posterior crown, anterocrown view. **K-L**, NMS G.2021.7.284 from Achanarras: **K**, front half of specimen; **L**, disrupted mid-flank squamation showing scales in basal, crown and lateral views. Scale bars 1.0 mm in K, 0.5 mm in F, 0.1 mm in A-E, G-J, L. Arrows indicate anterior direction. br, branchiostegal plate impressions; pect.fs, pectoral fin spine. Scale bars equal 10 mm in K, 500 μ m in F, 100 μ m in A-E, G-J, L.

G-I), with the cavity in small scales often opening out through the base (Figure 16D). Scales often have the dome-shaped lamellae in the base (Figure 16B, F) resulting from the gradual infilling of the open pulp cavity. Flat-based scales often have an elongate posterior crown extending over a base length beyond the posterior edge of the base (Figure 16E). As in the scales from the lower levels, cir-

cular canals extend round the neck region (Figure 16I), with smaller calibre ascending canals extending up from them (Figure 16F, G-I).

Body scales from the upper part of the Mey Flagstone Formation horizon (Figure 17) are either similar to the most common form from the Achanarras horizon, with a convex base (Figure 17A, E) and subhexagonal crown (Figure 17D, H),

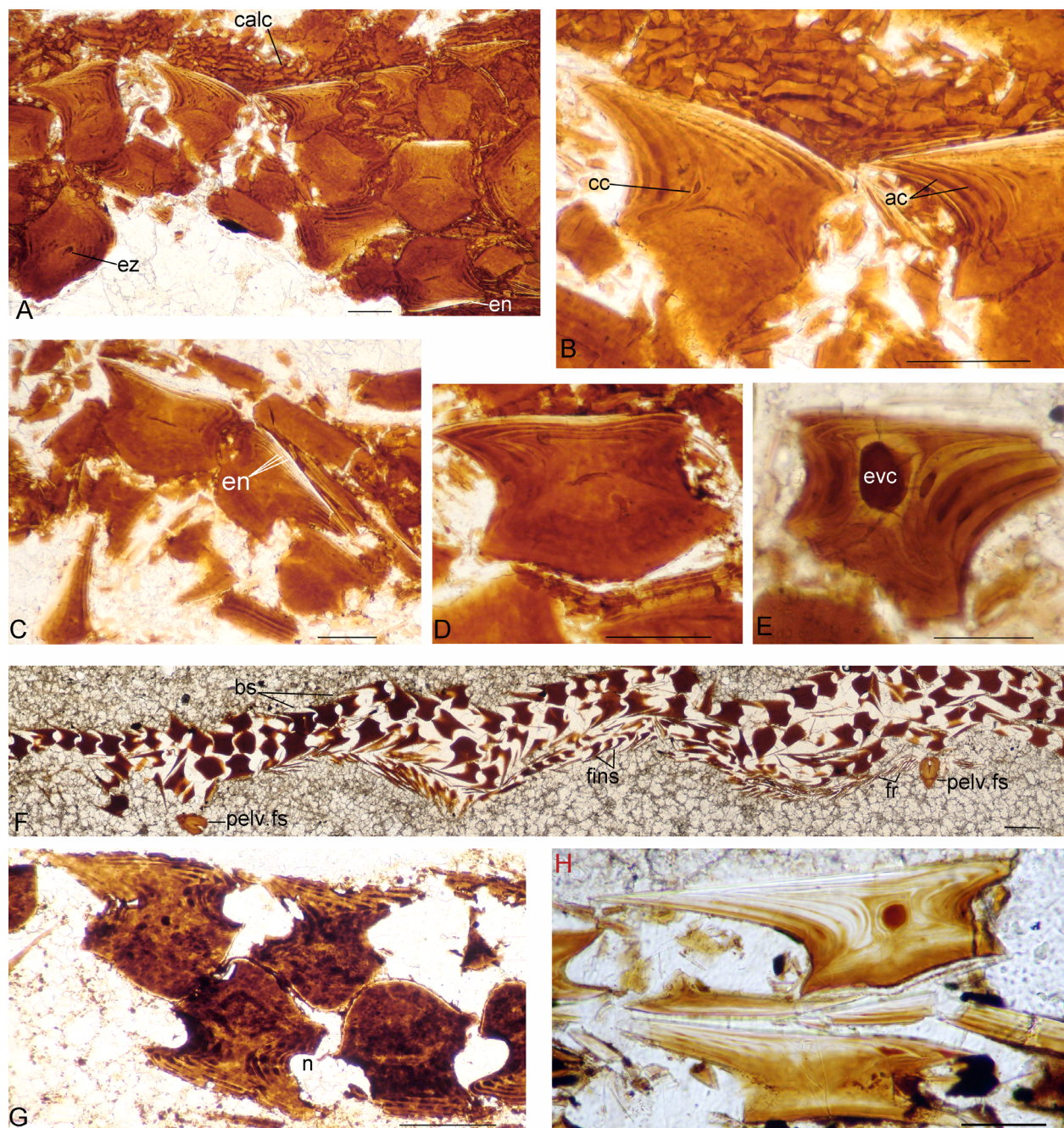


FIGURE 14. Achanarras Fish Bed Member horizon, *Orcadacanthus pusillus* scale histology. **A-F**, Cromarty specimens: **A-E**, NMS G.2021.7.136, disarticulated fish; **A-B**, NMS G.2021.7.136.2, scales and ?jaw cartilage tesserae; **C**, NMS G.2021.7.136.4, scales and cartilage; **D-E**, NMS G.2021.7.136.6, scales without and with a central pulp cavity, latter with radiating canals; **F**, NMS G.2021.7.303, dorsoventrally compressed articulated fish, NMS G.2021.7.303.6, transverse section posterior to ?pelvic spines through the body, tips of the spines and the fins. **G**, Achanarras specimen NMS G.2021.7.284, section NMS G.2021.7.284.3 through scales of two sides, centre of body trunk. **H**, Corbie Den specimen NMS G.2019.3.11, vertical longitudinal sections in NMS G.2019.3.11.4, centre of body trunk. ac, ascending canal; bs, body scales; calc, calcified cartilage blocks; cc, circular canal; en, enameloid; evc, embryonic crown zone vascular cavity; fins, finweb scales; fr, fin rays; n, node-like neck protuberance; pelv.fs, pelvic fin spine. Scale bars equal 100 µm.

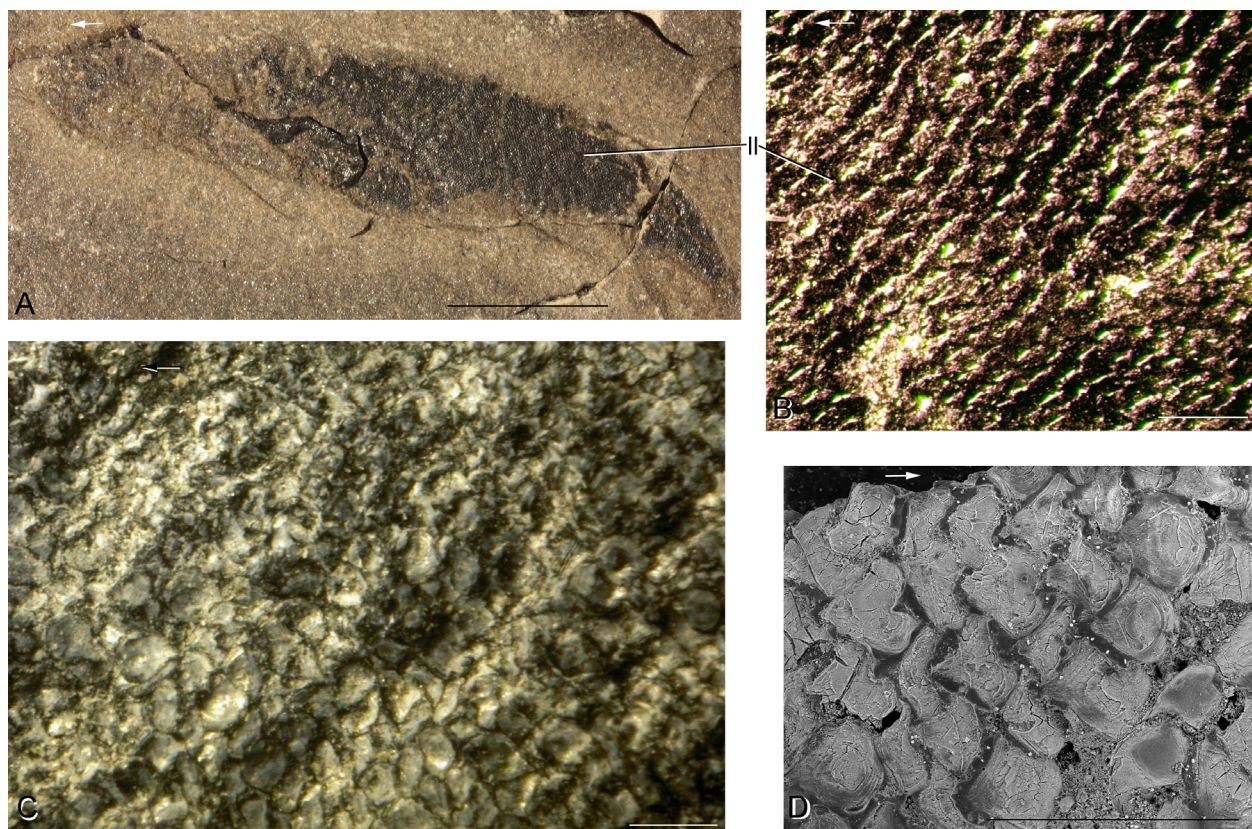


FIGURE 15. Lower part of the Mey Flagstone Formation, *Orcadacanthus pusillus* scale morphology. Light microscope images except D, ESEM. **A-B**, NMS G.2021.7.241 from Skinnet. **A**, whole specimen lacking head, left side squamation exposed. **B**, midflank squamation with lateral line. **C**, NMS G.2021.7.202 from Lythmore, eroded squamation on the left side below the dorsal fin. **D**, NMS G.2022.10.6 from Cairnfield squamation patch NMS G.2022.10.6.2b. Abbreviation: ll, lateral line. Scale bars equal 10 mm in A, 500 μ m in B-D.

or, more commonly, with a deep neck (Figure 17C, F, H-J) and flat base pierced by a large pulp canal (Figure 17C, G, J). Many of the larger scales have a very short base with an elongate crown that extends well beyond the posterior edge of the base (Figure 17B, C, F). Based on our observations of scale morphology, there is no clear distinction between scales from the three horizons, other than an apparent increase in the higher levels of the proportion of flat-based scales with a pulp cavity opening out through the base. In the lowest horizon, this type of structure only seems to occur in scales from the smaller fish, presumably juveniles.

The tendency to retain the embryonic pulp cavity is even more common in the scales of fish from the upper part of the Mey Flagstone Formation horizon (Figures 9, 18A-H). Small juvenile *Orcadacanthus pusillus* are relatively common at this level, with squamation comprising scales with just a single growth zone and a wide open pulp canal through the flat base (Figure 18E-G). We have not identified any dentine tubules or vascular

canals in these scale sections. Larger scales (with the usual complement of vascular canals, dentine tubules in the multiple superposed crown growth zones) also have a relatively flat base, with just a small central convexity (Figures 9, 18B, D, H). The embryonic zone in these scales remains devoid of dentine, with the outer three or four crown growth zones having regularly spaced tubules running back from the circular and ascending canals in the posterior part of the crown (Figure 18H).

DISCUSSION

Orcadacanthus pusillus has been placed in the genus *Mesacanthus* for many years based on the overall similar body proportions to the type species *Mesacanthus mitchelli*. Other valid species recognised are *Mesacanthus grandis* Gagnier and Goujet 1997 from the Lochkovian of Spitsbergen, based on one articulated specimen, and *Mesacanthus semistriatus* Woodward (1892) from the Emsian of New Brunswick, based on one articu-

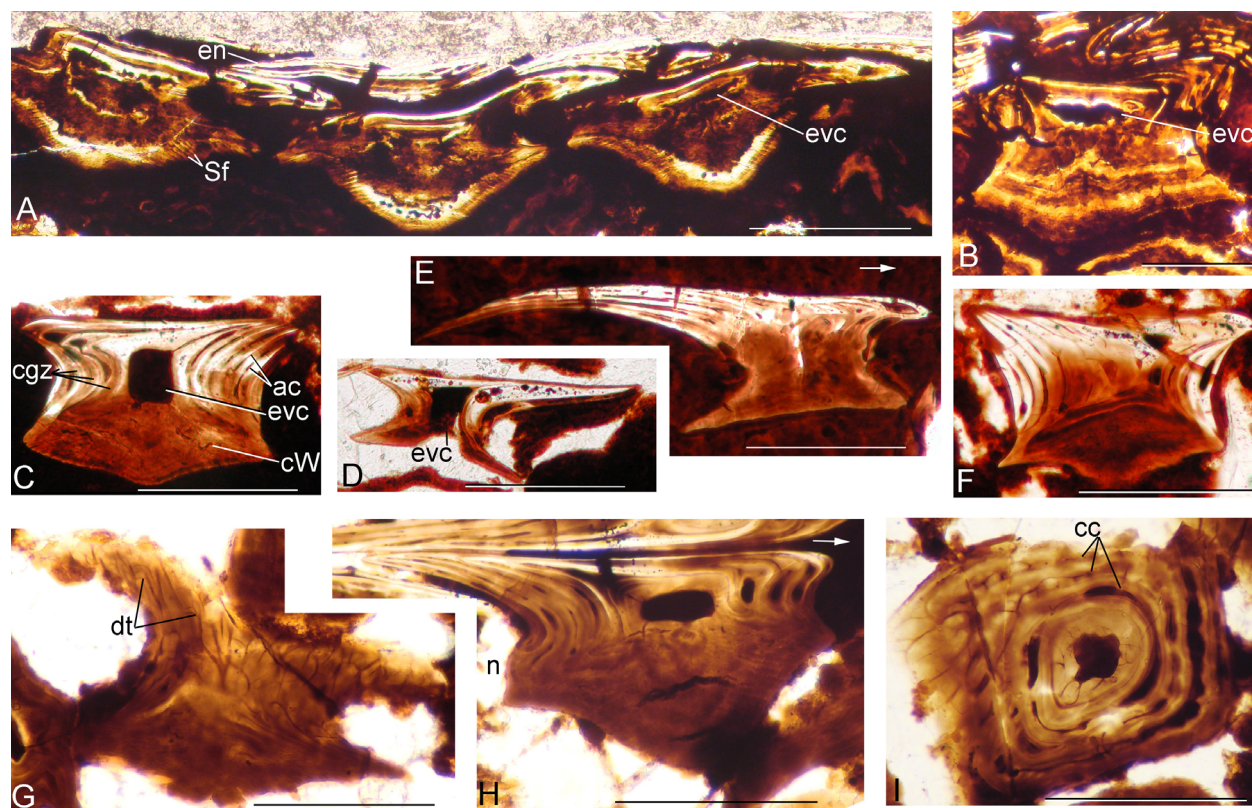


FIGURE 16. Lower part of the Mey Flagstone Formation (*Osteolepis panderi* horizon), *Orcadacanthus pusillus* scale histology. **A**, NMS G.2021.7.84 from Cairnfield, vertical section NMS G.2021.7.84.3 through squamation. **B**, NMS G.2021.7.251 from Skinnet, vertical section NMS G.2021.7.251.3. **C-F**, NMS G.2022.10.17 from Cairn of Hattel bonebed. **C**, NMS G.2022.10.17.3, oblique vertical section of convex based scale through large embryonic zone vascular cavity. **D**, NMS G.2022.10.17.4, vertical longitudinal section of small scale with vascular cavity opening out through the base. **E**, NMS G.2022.10.17.2, vertical longitudinal section of scale with long posterior crown and flat base. **F**, NMS G.2022.10.17.1, off-centre vertical transverse section of convex-based scale. **G-I**, bonebed section NMS G.2022.10.13 from Castlehill. **G**, vertical longitudinal section of scale with central vascular cavity. **H**, vertical transverse section of convex-based scale showing ascending canals. **I**, horizontal section through the crowns of two adjacent scales. Abbreviations: ac, ascending canal; cc, circular canal; cgz, crown growth zones; cW, canals of Williamson; dt, dentine canals/tubules; en, enameloid?; evc, embryonic crown zone vascular cavity; n, node-like protuberance; Sf, Sharpey's fibres. Arrows indicate anterior direction. Scale bars equal 500 µm in A, F, G, 100 µm in B-E, H-I.

lated specimen and isolated fin spines; both are poorly known. The main characters used to assign *M. grandis* to the genus are the presence of a single dorsal spine (an acanthodiform character), the spine being shallowly inserted (interpreted as a mesacanthid character), and smooth crowned scales (a mesacanthid and acanthodid character). *Mesacanthus semistriatus* was reassigned from *Acanthodes* to *Mesacanthus* by Whiteaves (1907), but the main characters recognised for the species – a single dorsal spine and smooth crowned scales – are similarly shared by mesacanthids and acanthodids. Prepelvic spines – the main character used by Traquair (1892) to distinguish the genus

from *Acanthodes* – have not been reported for either of these two species.

The two Scottish species *Mesacanthus mitchelli* and *Orcadacanthus pusillus* do share the character of prepelvic spines (as do other mesacanthids *Promesacanthus*, *Lodeacanthus*, and *Triazeugacanthus*) but are otherwise quite different from one another. Both species are known from many articulated specimens so we feel confident in erecting a new genus for *O. pusillus*. They differ from each other principally by the shape of the anterior part of the head (Figure 5A-C), with *M. mitchelli* being more snub-nosed with the eyes closer to the rostrum (Burrow et al., 2022, figure 12) and having a less extensive polygonal tesseral

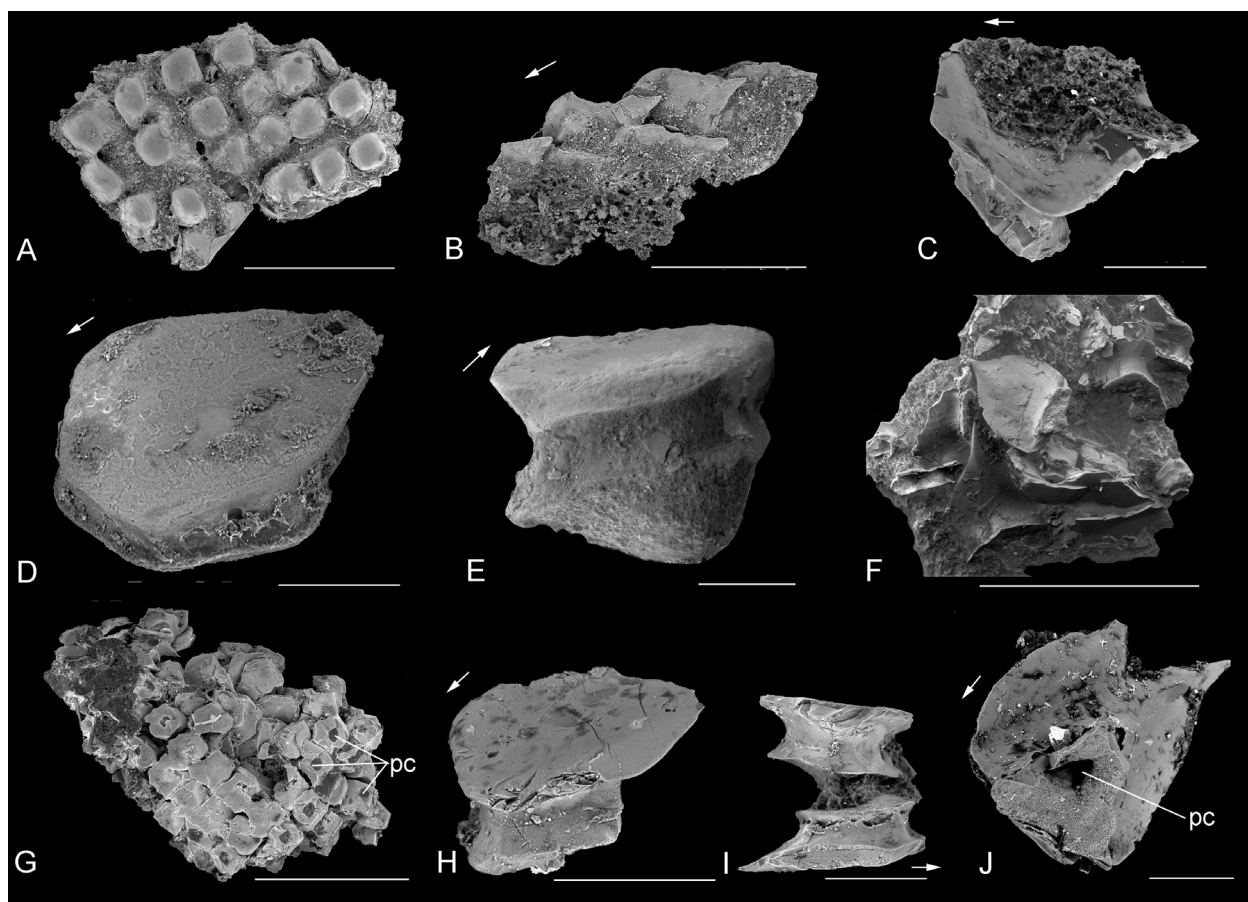


FIGURE 17. Upper part of the Mey Flagstone Formation *Orcadacanthus pusillus* scale morphology. **A-C**, Pennyland specimen NMS G.2022.10.5: **A**, NMS G.2022.10.5.2c, squamation patch, basal view; **B**, NMS G.2022.10.5.2b, encrusted articulated scales in crown view; **C**, NMS G.2022.10.5.2g, encrusted scale, crown view; **D-J**, Blacken Berry specimens. **D-F**, NMS G.2018.28.15: **D**, NMS G.2018.28.15.2a.9, crown view; **E**, NMS G.2018.28.15.2a.4, posterolateral view; **F**, NMS G.2018.28.15.2a.2, disarticulated scale clump, basal views; **G-J**, NMS G.2021.7.64: **G**, NMS G.2021.7.64.2e, squamation patch, basal view; **H**, scale NMS G.2021.7.64.2b, anterocrown view; **I**, NMS G.2021.7.64.2g, two scales from either side of the fish fused together, in lateral view; **J**, NMS G.2021.7.64.2a, scale with bifurcate posterior crown, in basal view showing open pulp cavity. Arrows indicate anterior direction. Abbreviation: pc, pulp canal. Scale bars equal 100 µm.

cover on the head. The lower jaw also differs, being narrower at the anterior end in *M. mitchelli* and truncated in *O. pusillus* (Figure 5A-B, K). Another difference is the sclerotic plate ornament, comprising low broad vermiculate ridges in *M. mitchelli* (Burrow et al., 2011, figure 1E; Burrow et al., 2022, figure 4a) and concentric or oblique flat overlapping layers in *O. pusillus* (Figure 5D-F). The scapular shaft in *M. mitchelli* is relatively short and broad with a semicircular cross-section, whereas in *O. pusillus* it is relatively longer and slender with a circular cross-section. Figure 19 shows reconstructions of the head and branchial region of *O. pusillus* and *M. mitchelli*. Spines of the two species (other than the prepelvic spines) do not differ greatly, with the main difference being the deeper

groove between the leading edge ridge and lateral faces on the spines of *M. mitchelli*. The pelvic spines of *O. pusillus* are much smaller than those of *M. mitchelli*. Body scales of *M. mitchelli* are all very small, up to 0.1 mm wide with a convex base, and show little variation over the body, whereas those of *O. pusillus* show more variation. Typically, the crown of *O. pusillus* scales extends much further past the posterior corner of the base than in *M. mitchelli* scales. The majority of scales on fish from the higher levels have a flat base, often with a central pulp cavity opening out through the base. These scales thus appear to show extreme paedomorphism, as they are found on fish through the whole size range for the species, not just on the smaller specimens. If the scales with only a single

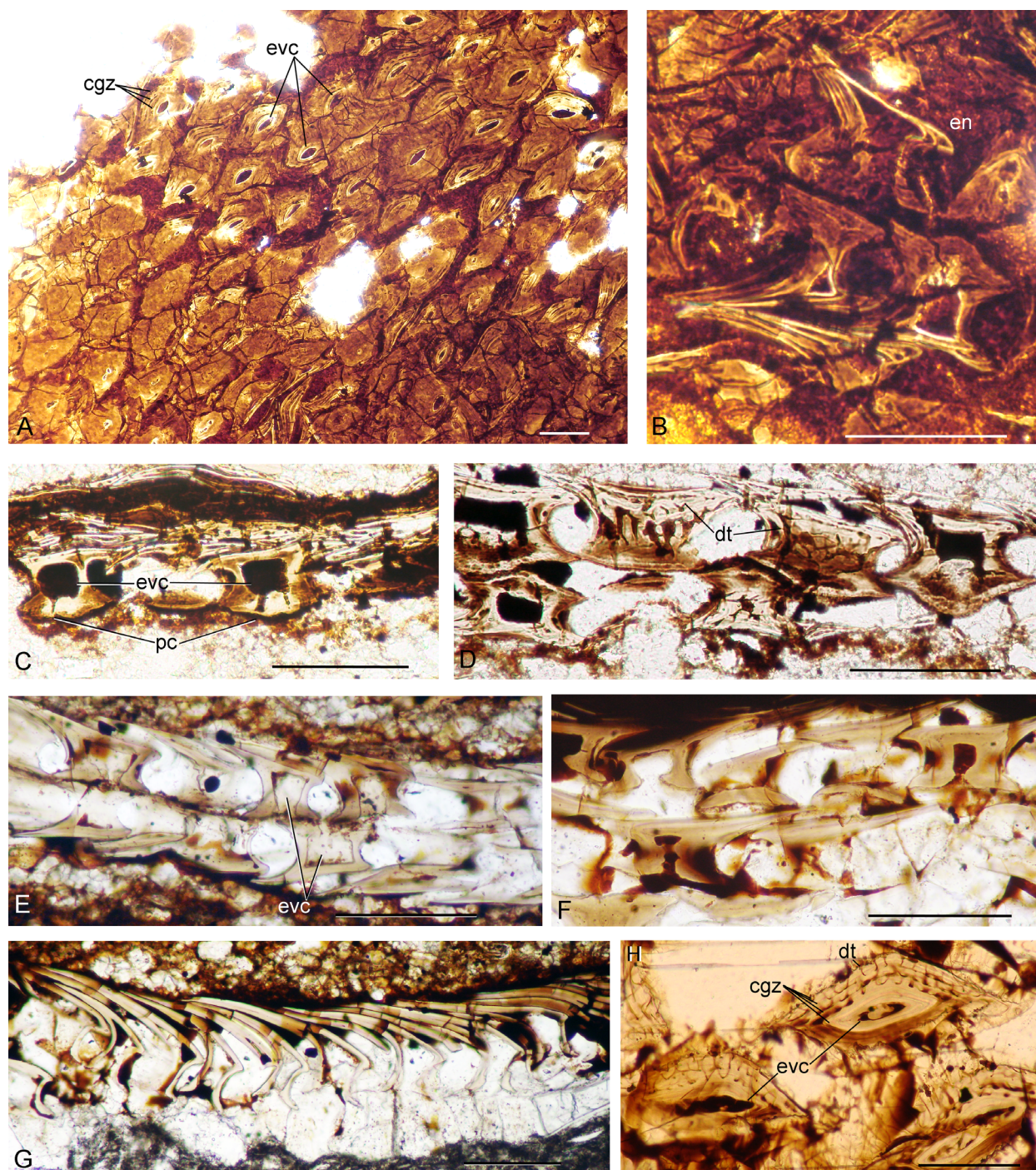


FIGURE 18. Upper part of the Mey Flagstone Formation *Orcadacanthus pusillus* scale histology. **A-B**, Pennyland specimen NMS G.2019.3.9, section NMS G.2019.3.9.2 through squamation patch. **A**, horizontal sections mid-scale; **B**, vertical longitudinal sections of scales from both sides of the fish, bases pressed together. **C-H**, Blacken Berry specimens. **C-D**, NMS G.2019.3.8, scales with two or three crown growth zones. **C**, NMS G.2019.3.8.9 showing wide central pulp cavities and canals extending down to base; **D**, NMS G.2019.3.8.11 showing ascending canals and dentine overlain by enameloid in the central levels of crown growth zones; **E-G**, NMS G.2018.28.15, juvenile fish, scales with only one growth zone; **E-F**, NMS G.2018.28.15.4, scales with open basal pulp canal, both sides of fish squashed together; **G**, NMS G.2018.28.15.5, one layer of scales with strongly overlapping posterior crowns, possibly from a fin. **H**, NMS G.2022.10.1, section NMS G.2022.10.1.2, horizontal section through scales with four crown growth zones. Abbreviations: cgz, crown growth zones; dt, dentine canals/tubules; en, enameloid; evc, embryonic crown zone vascular cavity; pc, pulp canal. Scale bars equal 100 μ m.

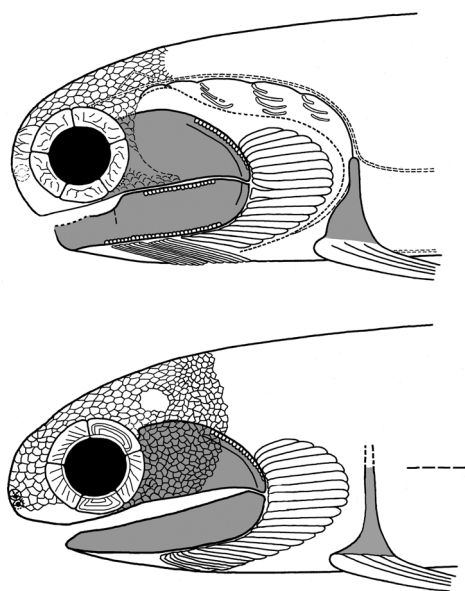


FIGURE 19. *Mesacanthus mitchelli* (upper) compared with *Orcadacanthus pusillus* (lower).

crown growth zone from juvenile *O. pusillus* (Figure 18E-G) were recovered as isolated scales, they would probably be described as chondrichthyan placoid scales, or possibly even thelodont scales! Dearden et al. (2024, p. 24) noted a similar comparison in relation to the polyodontode scales of *Vernicomacanthus* and monodontode scales of *Lupopsyrus*. the two animals are similar in gross anatomy in some respects, but *Lupopsyrus* is much smaller and its monodontode scales look a lot like the central odontode of scales of *Vernicomacanthus*.

The genus with which *Orcadacanthus* shares most features is probably *Triazeugacanthus affinis* (Whiteaves, 1887) from the Frasnian Escuminac Formation, Miguasha, Canada. The latter differs in having pectoral, dorsal, and anal spines that are all about the same length, pelvic spines closer to the anal than the pectoral spines, branchiostegal plates that only extend back over half the branchial region, different ornament of irregular small pits on the sclerotic and nasal plates, and most specimens having a large median plate above the anterior nasal openings (Miles, 1966). Miles (1966:185, figure 18) noted that the large nasal plate is basically two semicircular halves fused in the middle, above the nasal openings, with the dorsal margin of the bone being strongly jagged. Gagnier (1996) described fin rays in all the fins on *Triazeugacanthus*, including the caudal fin, and noted that there are two pairs of nasal openings.

One of the notable aspects of *Orcadacanthus pusillus* specimens is the variation in preservation (Figure 20). Specimens from the Moray Firth are usually preserved in nodules. Whilst these are mostly solitary specimens, sometimes there can be multiple fish in one nodule (Figure 20A). Elsewhere the specimens are preserved on flagstone, often in large numbers. Egerton (1861, p. 58) erected the junior synonym *Mesacanthus peachi* for fish from Barragill (East Mey) flagstones, which he considered differed from *O. pusillus* in being “thicker and less elegant”, having proportionately longer pelvic spines, and dorsal and anal spines opposite each other. However, Baron (2015) demonstrated that any differences in spine and body dimensions within the two species are not statistically significant. When looking at large numbers of articulated specimens, it becomes clear that many specimens have suffered a high degree of rigor mortis, especially when compared to its sister taxon *Mesacanthus mitchelli*. This is particularly true for the nodule specimens from near the Orcadian Basin margin at Tynet Burn and other localities in the Moray Firth (Figure 20B), where fish beds resulted from rapid flooding at the lake edge by rising waters (Trewin and Davidson, 1999). The specimens here can often be doubled up on themselves. In contrast, fish in the flagstone sequences at Achanarras Quarry (Figure 4A) and other localities in Caithness and Orkney, which formed in the deeper waters in the basin centre, while often being arched back, mostly show less distortion – although there are exceptions (Figure 20C). This highly contorted preservation is also seen in higher strata (Figure 20D) and probably reflects a lack of robustness in the body of *O. pusillus* and the hypersalinity in the shallower lake edges mentioned by Trewin (1986).

One feature that is only seen in rare specimens from the upper part of the Mey Flagstone Formation horizon is mineralisation of the fin rays in the dorsal, and possibly anal, fins. Fin rays have previously been reported in all the fins on *Triazeugacanthus* (as noted earlier), unidentified fins on *Homalacanthus concinnus* (Whiteaves, 1887), the anterior dorsal fin of *Diplacanthus crassissimus*, the pelvic fin of *Cheiracanthus latus* Egerton, 1861, and the pectoral fins of *Acanthodes* (Coates, 1994, figure 3A) and *Ischnacanthus gracilis* (Egerton, 1861a) (Miles, 1970, figure 8), with the latter specimen showing the rays possibly becoming segmented distally. Presumably fin rays could have been present in the paired and median fins of other acanthodians but were usually unmineralised and

so not fossilised. Goodrich (1909) and Watson (1909) described acanthodians other than *Orcadacanthus pusillus*

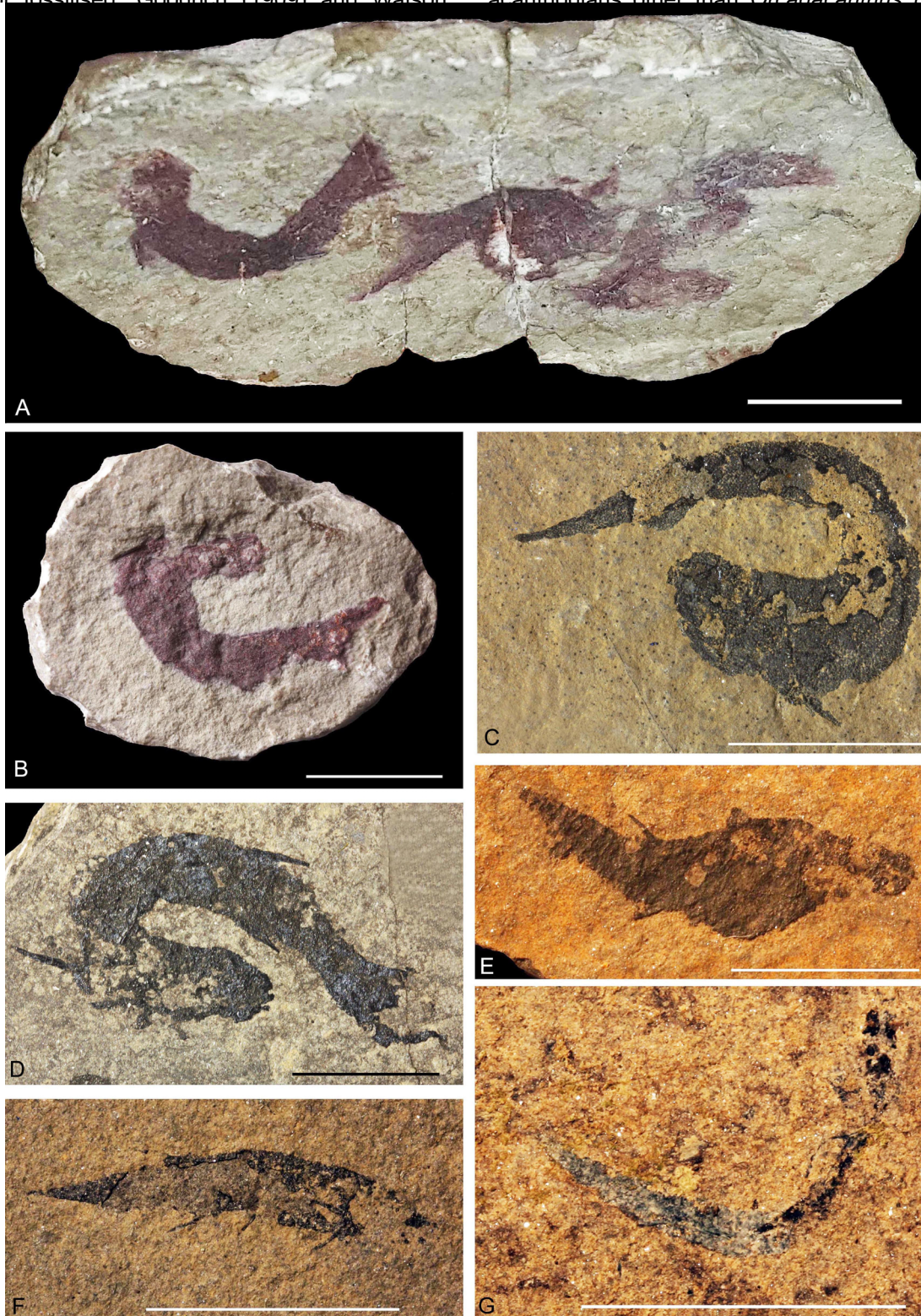


FIGURE 20. *Orcadacanthus pusillus*, preservation of specimens. **A**, GLAHM V3573 from Tynet Burn. **B**, NRM P1645 from Tynet Burn. **C**, NMS G.2021.7.29 from Achanarras. **D**, NMS G.2021.7.166 from East Murkle Bay. **E**, NMS G.1975.12.26 from Stroma (specific locality not recorded, but almost certainly Button Geo). **F**, NMS G.2021.7.27 from Achanarras. **G**, NMS G.2022.10.9 from Button Geo, Stroma. Scale bars equal 10 mm.

alised dermal and endoskeletal elements (Figure 20G). This pattern corresponds to that shown for *Triazeugacanthus affinis* as demonstrated by Chevrinais et al. (2015, 2016, 2017).

CONCLUSIONS

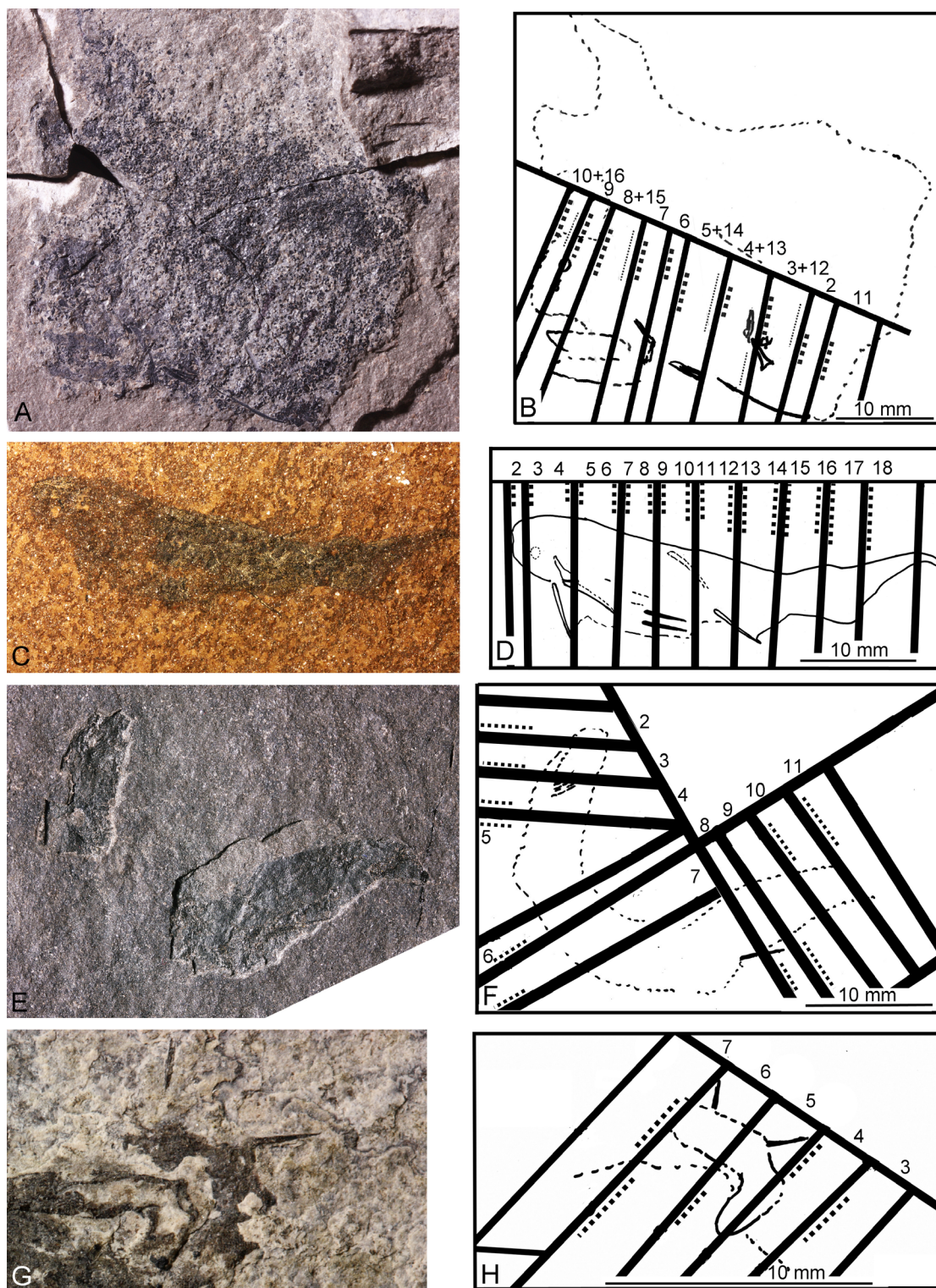
Orcadacanthus pusillus was for a long time poorly known and considered a rather uninteresting and unimportant little fish. This study has discovered many new characteristics that clearly differentiate it from the type species of *Mesacanthus*, *Mesacanthus mitchelli*, and warrant the erection of a new genus. Particularly interesting characteristics include the nasal plates, where we show their internal structure for the first time, the histological structure of acanthodian fin rays, and the apparently paedomorphic development of the body scales. The mesacanthid showing closest similarity to *Orcadacanthus* is *Triazeugacanthus* from the Frasnian of Miguasha, Canada, which also has very small prepelvic spines, fin spines with c. three longitudinal ridges on each side, a tall slender scapular shaft, and denticulated nasal plates.

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SUPPLEMENTAL FIGURE 1. Original images and maps of cuts for articulated specimens of *Orcadacanthus pusillus* sacrificed for serial sectioning; block lines indicate the sides that sections are glued to, and cut-off sections are glued to sides indicated by dotted lines. **A-B**, NMS G.2019.3.4 from Cromarty, slightly scattered specimen, labels 2-16 correspond to sections NMS G.2019.3.4.2-16. **C-D**, NMS G.2021.7.265 from Blacken Berry; labels 2-18 correspond to sections NMS G.2021.7.265.2-18. **E-F**, NMS G.2019.3.8 from Blacken Berry; labels 2-11 correspond to sections NMS G.2019.3.8.2-11. **G-H**, NMS G.2018.28.15 from Blacken Berry, small *Orcadacanthus pusillus* specimen above the head of *Markacanthus costulatus*; labels 3-7 correspond to sections NMS G.2018.28.15.3-7.

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