



Styracopterid (Actinopterygii) ontogeny and the multiple origins of post-Hangenberg deep-bodied fishes

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Received 4 March 2013; revised 29 April 2013; accepted for publication 2 May 2013

The Carboniferous fish family Styracopteridae (Actinopterygii) originated as part of the initial radiation of ray-finned fishes following the end-Devonian Hangenberg extinction. Specimens of *Styracopterus fulcratus* (Traquair, 1890) have been collected from post-extinction Tournaisian and Visean Scottish sediments for over 100 years, including sites containing some of the earliest ‘Romer’s Gap’ tetrapods. Re-examination of this supposedly long-lived, static species has revealed two genera, *Styracopterus* and *Fouldenia* White, 1927, divergent from each other and previous descriptions. Here, we show that styracopterids are among the earliest actinopterygians with durophagous dentition and toothplates, the latter likely to have derived from the ectopterygoids and coronoids. On the basis of this and other traits, such as the presence of an enameloid ‘beak’, the fusiform styracopterids are linked to some, but not all, the deep-bodied actinopterygians previously placed in the suborder Platysomoidei. A new plesion, Eurynotiformes, is erected to contain the styracopterids, the deeply fusiform *Eurynotus* and the widespread *Amphicentrum*, among other laterally compressed fishes. This implies that platysomoids are polyphyletic: deep-bodied and/or durophagous fishes evolved multiple times following the Hangenberg event. Reconstructed styracopterid growth series show that trunk depth increased during maturation, mirroring the shape variation observed among the Eurynotiformes. Other ontogenetic changes involve fin-ray differentiation, jaw form, dermal bone ornamentation, and scale morphology; all of these are widely used as actinopterygian diagnostic characters. Further investigation of Eurynotiformes should reveal the extent of evolutionary and ontogenetic change within the earliest actinopterygian radiation, and are likely to rewrite their phylogeny.

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doi: 10.1111/zoj.12054

ADDITIONAL KEYWORDS: Carboniferous – diversification – durophagy – end-Devonian mass extinction – ichthyology – Mississippian – ray-finned fishes – reef fishes – Romer’s Gap – Tournaisian.

INTRODUCTION

Styracopterus fulcratus (Traquair, 1881) was previously the only ray-finned fish species (Actinopterygii) found at two well-documented Mississippian Scottish Lagerstätten (359–323 Mya; Gradstein *et al.*, 2012):

the Tournaisian Foulden fauna, a euryhaline environment bearing ‘Romer’s Gap’ tetrapods (347 Mya; Wood & Rolfe, 1985; Smithson *et al.*, 2012); and the Visean Glencartholm fauna (338 Mya; Schram, 1983; Smithson *et al.*, 2012), a nearshore marine system. This fusiform actinopterygian is the type species for the family Styracopteridae (Moy-Thomas, 1937; Gardiner, 1985), which also contains the genus *Benedenius* (Van Beneden, 1878) from the early Visean

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of Belgium (Traquair, 1877–1914, 1890; Moy-Thomas, 1937; Mottequin, 2008). *Benedenius* was considered a platysomoid (Palaeozoic deep-bodied fishes; Traquair, 1878, 1879) before this relationship was hypothesized (Fraipont, 1890; Traquair, 1890; Boulenger, 1899, 1902).

Styracopterus has been the subject of taxonomic uncertainty. The species *S. fulcratus* was originally named from just a handful of incomplete Visean fishes placed in the genus *Holurus* (Traquair, 1881). Subsequently attributed specimens have been variously assigned to two genera and three species (Traquair, 1881, 1890; Moy-Thomas, 1937; Moy-Thomas & Bradley Dyne, 1938; Gardiner, 1985). The first of these synonymized taxa was *Styracopterus ischipterus* (Traquair, 1881), represented by a few small fish (< 6 cm) recovered from the Tournaisian Coldstream locality in 1870 (Traquair, 1881, 1890; Smithson *et al.*, 2012), and placed into synonymy with *S. fulcratus* by Moy-Thomas (1937) decades later. The second was *Fouldenia ottadinica* White, 1927, one of the original Foulden fauna fishes described by White in 1927, which was made a species of *Styracopterus* by Moy-Thomas (1937) and folded into *S. fulcratus* by Gardiner (1985).

In the Mississippian aftermath of the end-Devonian vertebrate mass extinction, actinopterygians radiated into a variety of new lineages and niches (Hurley *et al.*, 2007; Sallan & Coates, 2010; Sallan & Friedman, 2012). This involved the appearance of novel ecomorphologies, including the first recorded actinopterygian durophages, deep-bodied fishes, and eel-shaped forms (Sallan & Coates, 2010; Sallan *et al.*, 2011; Friedman & Sallan, 2012; Sallan, 2012; Sallan & Friedman, 2012). The increase in actinopterygian diversity and abundance is readily apparent through comparison of the Foulden and Glencartholm faunas (Dineley & Metcalfe, 1999; Sallan & Coates, 2010; Friedman & Sallan, 2012; Sallan & Friedman, 2012). Despite the wealth of catalogued material from these proximate localities, the resident actinopterygians have never received more than brief descriptions; *S. fulcratus* is no exception (Traquair, 1881, 1890; White, 1927; Moy-Thomas, 1937, 1938; Moy-Thomas & Bradley Dyne, 1938; Gardiner, 1985). In addition, and as a result, *Styracopterus* and most co-occurring taxa are grouped into poorly defined, highly persistent suborders, probably obscuring patterns of diversification. Thus, a reinvestigation of the apparently long-lived species *S. fulcratus*, found at localities dated 10 Myr apart which featured different environmental conditions and salinities, and previously broken into three taxa, might provide essential information for understanding actinopterygian diversity during their initial radiation.

The re-examination undertaken in the present work, involving all catalogued material of *Styracopterus* in the UK, has revealed far more anatomical detail than previously realized. Many traits support the existence of two monospecific genera: a Tournaisian *Fouldenia ischiptera* (Traquair, 1881) and a Visean *S. fulcratus*. Thus, from the outset, it is likely that Gardiner's (1985) description combining these disparate taxa into a single reconstruction is inaccurate. In addition, *Fouldenia* is shown to be the earliest known actinopterygian with a durophagous dentition. The styracopterids exhibit a series of likely synapomorphies with 'platysomoid' fishes, notably those with toothplates: members of the family Amphicentridae (*Eurynotus*, *Cheirodopsis*, and *Amphicentrum*; Traquair, 1879; Bradley Dyne, 1939; Moy-Thomas & Miles, 1971; Coates, 1988). Here, a new actinopterygian plesion, termed the Eurynotiformes after the first named genus *Eurynotus* (Agassiz, 1833–1844), is erected to contain styracopterids and the family Amphicentridae, as well as *Mesolepis* and *Paramesolepis*. The argument in support of erecting this new plesion is laid out below.

Moy-Thomas (1937) was the first to hypothesize ontogenetic change in styracopterids, noting size-related differences in skull roof ornamentation of *Styracopterus* and suggesting that specimens of '*S. ischipterus*' from late Tournaisian Coldstream (Traquair, 1881, 1890; Smithson *et al.*, 2012) might be juveniles. The latter are identical to near-contemporary small individuals of *Fouldenia* recovered in subsequent decades. Scottish styracopterid specimens exhibit a large range of body sizes (3–12 cm total lengths for *F. ischiptera* and 8–16 cm total lengths for *S. fulcratus*), thereby allowing documentation of ontogenetic data not readily available for most early actinopterygians. Size-related differences in ornamentation, scale structure, fin form, body depth, jaw morphology, and other traits are described below, representing the oldest described actinopterygian growth series.

MATERIAL AND METHODS

All catalogued specimens of *Styracopterus* and *Fouldenia* in the collections of the National Museums of Scotland, Edinburgh (NMS), the Natural History Museum, London (NHM), the British Geological Survey, Edinburgh (GSE), and the Hunterian Museum, Glasgow (GLAHM) were examined. The photographs of Glasgow Museums (GM) specimen 1902.85md were provided by Alastair Gunning, Curator of Geology at the Kelvingrove Art Gallery and Museum. Specimens of other Carboniferous actinopterygians, particularly Eurynotiformes, in the collections of the NHM, GSE, GLAHM, and NMS

were examined for comparison (Appendix S1). In addition, specimens of *Benedenius* housed in University of Liege, the Royal Belgian Institute of Natural Sciences, and the Abbaye de Maredsous were studied, and high-resolution pictures of the same specimens were provided by Paul van Genabeek, director of the Centre Grégoire Fournier (Appendix S1).

ANATOMICAL ABBREVIATIONS

ab, anal basal fulcra; ac, acrodin cap; afr, anal fin rays; an, angular; asq, axial squamation; axb, axial basal fulcra; axf, axial fringing fulcra; axl, axial lobe; br, branchiostegal rays; cb, caudal basal fulcra; cl, cleithrum; cp, caudal peduncle; cv, clavicle; db, dorsal basal fulcra; dcr, dorsal caudal lobe fin rays; dfr, dorsal fin rays; dh, dermohyal; dn, dentary; dp, dermopterotic; dr; dorsal ridge scales ds, dermosphenotic; dsq, dorsal squamation; ec, epichordal fin; ex, extrascapular; ff, fringing fulcra; fr, frontal; hl, hinge line; hm, hyomandibular; ju, jugal; la, lachrymal; ldt, lower jaw denticles; lg, lateral gular; ll, lateral line; mg, median gular; mn, mandible; mnc, mandibular canal; mx, maxilla; na, nasal; op, opercular; pa, parietal; pc, postcleithrum; pcr, pectoral fin rays; pg, peg; pm, premaxilla; po, preoperculum; ps, parasphenoid; pt, post-temporal; pvb, pelvic basal fulcra; pvr; pelvic fin rays; ro, rostral; qj, quadratojugal; ra, radial; sc, supra-cleithrum; sg, shoulder girdle; so; suborbital; soc, supraorbital canal; sq, squamation; th, teeth; udt, upper jaw denticles; vcr, ventral caudal lobe fin rays; vr, ventral ridge scales; vsq, ventral squamation.

SYSTEMATIC PALAEOONTOLOGY

OSTEICHTHYES HUXLEY, 1880

ACTINOPTERYGII COPE, 1881

EURYNOTIFORMES (NOV.)

Type genus: Eurynotus Agassiz, 1833–1844.

Included genera: Eurynotus Agassiz, 1833–1844, *Styracopterus* Traquair, 1890, *Fouldenia* White, 1927, *Benedenius* Traquair, 1878, *Amphicentrum* Young, 1866, *Cheirodopsis* Traquair, 1881, *Paramesolepis* Moy-Thomas & Bradley Dyne, 1938, *Wardichthys* Traquair, 1875, *Proteurynotus* Moy-Thomas & Bradley Dyne, 1938, *Mesolepis* Young, 1866.

Diagnosis: Actinopterygians with tall rectangular trunk scales bearing central pointed pegs at least 50% height of scale; jaw margins covered with thick ganoine and without visible teeth; premaxilla edentulous; dentary edentulous; maxillary dentition mesial to jaw margin and obscured laterally by dermal bone; palatal and mandibular tooth plates

with denticles; maxilla with triangular posterior expanded portion and thick anterior ramus; mandible robust with acute symphysis in lateral aspect; snout blunt in lateral profile; preoperculum tall with horizontal pit line; suboperculum with anteroventral process; dorsal ridge scales prominent and acuminate, running from skull to dorsal fin origin; basal fulcra erect and pointed; median fins with longest fin ray more than fourth in position from leading edge; primary median fin lepidotrichia spine-like and without clear segments; fringing fulcra prominent, pointed, and overlapped distally on all fins. Sympleiomorphies: antorbitals absent; single median rostral; single nasal in contact with frontal and dermosphenotic; frontals longer than parietals; dermopterotic present; uninterrupted contact between preopercular and infraorbitals; supraorbitals absent; dermohyal present; single postcleithrum; axial lobe extending beyond caudal fin and axial fulcra with micromeric elliptical scales; epichordal fin present and distinct from caudal fin.

STYRACOPTERIDAE MOY-THOMAS, 1937

Type genus: Styracopterus Traquair, 1890.

Included genera: Styracopterus Traquair, 1890, *Fouldenia* White, 1927, *Benedenius* Traquair, 1878.

Diagnosis (emended from Gardiner, 1985): Eurynotiform fishes with bands of smooth ganoine ornament on maxilla and dentary, parallel with jaw margins; contact between frontals and parietals v-shaped; nasal expanded ventrally, in contact with lachrymal; dermosphenotic mediolaterally broad with curved anterior process; cleithrum scythe-shaped with wide dorsal process; anal fin height greater than base length; pelvic fins with enlarged basal fulcra; axial lobe with distinct curvature; epichordal fin present; scales on axial lobe elliptical with longitudinal ganoine bands; axial basal fulcra with needle-shaped apex bearing paired dorsal ridges; lepidotrichia jointed regularly throughout length with short, plate-like segments; fringing fulcra paired on anterior margins of paired fins; fringing fulcra on distal portions of anal fin and caudal fin heavily overlapped and elliptical; sensory canals obscured by ornament in skull roof.

STYRACOPTERUS TRAQUAIR, 1890

Type and only species: Styracopterus fulcratus (Traquair, 1881).

Diagnosis (emended from Gardiner, 1985): Styracopterid eurynotiform fish with two smooth ganoine bands on jaw margins of maxilla and dentary; maxilla

with right-triangle-shaped posterior expansion and pointed anterior ramus; dentary shallow with angled anterior margin; mandibular canal pores large; maxillary teeth large and fang-like with a visible collar marking acrodin caps; palatal tooth-plate denticles large, stout, and rounded; mandibular tooth plate denticles small and rectangular; premaxilla fused to rostral; frontals with sigmoidal lateral margin; parietals triangular with sigmoidal lateral margin; dermopterotic curved laterally; post-temporal broad; suspensorium near vertical; preoperculum vertical with straight margins; opercular rectangular; subopercular taller than opercular with straight posterior margin; broad patches and bands of smooth ganoin over pointed anterior ramus; flank scales tall with ornament of nested ridges dorsally and horizontal ridges ventrally; dorsal ridge scales with thick horizontal ornament; ventral ridge scales near skull; pectoral fin long and scythe-shaped with broad leading lepidotrichia bearing rectangular segments; pelvic fin small and triangular with single preceding basal fulcrum; anal fin subtriangular with straight posterior margin.

Occurrence: Early Visean of Scotland.

STYRACOPTERUS FULCRATUS (TRAQUAIR, 1881)

Holurus fulcratus Traquair, 1881

Styracopterus fulcratus Moy-Thomas, 1937

Styracopterus fulcratus Moy-Thomas and Bradley Dyne, 1938

Styracopterus fulcratus Gardiner, 1985

Holotype: GSE 5673 (M146e) and counterpart GSE 5672 (M147e), British Geological Survey, Edinburgh, Scotland, UK, incomplete articulated fish in part and counterpart showing the dorsal portion of the trunk, scales, dorsal fin, and shoulder series (estimated body length, EBL: 12 cm).

Additional material: NHM P1663, incomplete articulated fish in part with trunk, skull, paired and median fins (EBL: 8 cm); GSE 8731, incomplete articulated fish in part showing anterior two-thirds of animal, including skull (EBL: 8 cm); GSE 2136, incomplete articulated fish in part showing anterior third of animal, including skull (EBL: 16 cm); GSE 5663 (part) and GSE 5664 (counterpart), nearly complete articulated fish (EBL: 16 cm); NMS 1891.53.49, National Museums of Scotland, Edinburgh, Scotland, UK, incomplete articulated fish in part showing anterior half of animal (EBL: 11+ cm); NMS 1891.53.50 (part) and NMS 1891.53.51 (counterpart), incomplete articulated fish showing anterior

half of animal (EBL: 11+ cm), GM 1902.85.md (part), Kelvingrove Art Gallery and Museums, Glasgow Museums, Glasgow, Scotland, UK, incomplete articulated fish showing anterior half of trunk and dermal jaws (EBL: 9 cm).

Type locality and horizon: Tarras Waterfoot (Traquair, 1881), River Esk, Eskdale, Dumfriesshire, Scotland, UK. Calciferous Sandstone Series, Cementstone Group, Holkerian regional substage (339–337.5 Mya), early Visean Stage, Mississippian Subsystem, Early Carboniferous.

Other localities and horizons: Glencartholm Volcanic Beds, Dumfriesshire, Scotland, UK. Calciferous Sandstone Series, Cementstone Group, Holkerian regional substage (339–337.5 Mya), early Visean Stage, Mississippian Subsystem, Early Carboniferous (Gardiner, 1985; Dineley & Metcalfe, 1999).

Diagnosis (emended from Gardiner, 1985): As for genus.

Remarks: Moy-Thomas (1937) placed species within the genus *Fouldenia* into the synonymy of the older taxon *Styracopterus* in his redescription of the latter genus. Gardiner (1985) subsequently lumped all designated *Styracopterus* species into *Styracopterus fulcratus*. However, a re-examination of specimens has shown that the characters used by Moy-Thomas (1937) and Gardiner (1985) are diagnostic of many genera within a more inclusive clade: the Eurynotiformes, as diagnosed above. There are in fact two distinct taxa, one being a Visean *S. fulcratus* and the other representing Tournaisian fish (see diagnoses and discussion). Thus, the original genus *Fouldenia* is resurrected, encompassing all specimens assigned to this taxon by White (1927) and subsequent workers, as well as individuals previously attributed to *S. fulcratus* originating from the sediments at the Foulden Fish Bed (Gardiner, 1985) and other Tournaisian-age localities around Northern England and Scotland (Traquair, 1881, 1890; Moy-Thomas, 1937; Gardiner, 1985). The emended diagnosis and description of *Styracopterus* are thus based only on the remaining catalogued specimens of *S. fulcratus*, all from from the Visean of Scotland.

Among all the ray-finned fishes known from the Visean of Scotland, only *Styracopterus* and *Rhadinichthys laevis* Traquair, 1890 are said to reside at Tarras Waterfoot (Moy-Thomas, 1937), a locality not known to contain any other vertebrate or invertebrate remains (Lumsden *et al.*, 1967). The type material of *Tarrasius*, the namesake fish and the only other taxon ever attributed to those deposits, was actually taken from misidentified Glencartholm sediments

(Moy-Thomas, 1933, 1934). Lumsden *et al.* (1967: 116) suggested that the same was true for the remaining taxa; they did not locate any evidence of a shared fauna or previous fossiliferous locality at Tarras Waterfoot. This assertion was subsequently supported by Dineley & Metcalfe (1999) in a survey of vertebrate material. This distinction might be important: recent work has suggested Tarras Waterfoot sediments may be Tournaisian in age (S.P. Wood, pers. comm.). It is notable that the type specimen of *Styracopterus* does not differ from Glencartholm material in either matrix or preservational mode, whereas fishes from proximate Tournaisian localities (e.g. *Fouldenia*), which have different faunal compositions from Glencartholm, are distinct in taphonomy (L.C.S. pers. observ.; Appendix S1).

DESCRIPTION

Skull

The general structure of the skull in *Styracopterus* is largely as depicted by Moy-Thomas (1937) and Gardiner (1985). However, there are inaccuracies in those previous reconstructions, caused in part by the combination of differently sized individuals and the inclusion of *Fouldenia* among the source material. The snout of *Styracopterus* is capped by a subrectangular rostral with a rounded ventral margin above the level of the infraorbitals, contrary to the reconstruction by Gardiner (1985). The division between the rostral and the premaxilla is indistinguishable in the largest individuals, such as GSE 2136 (Fig. 1F), where it is obscured by a field of thick ganoine. This is punctured by large round openings that probably mark the sensory canal, as also found in *Amphicentrum crassum* (Traquair, 1890) (Bradley Dyne, 1939; Coates, 1988), *Cheirodopsis* (NMS 1885.54.34; L.C.S. pers. observ.), *Eurynotus* (NMS 1876.28.2, NMS 1957.1.5686; L.C.S. pers. observ.), and *Paramesolepis* (NMS 1891.53.25; L.C.S. pers. observ.; Appendix S1). The dorsal limit of the rostral in NMS 1891.53.50–51 and GSE 5663 (Fig. 10D, G) is marked by a patch of U-shaped ornament raised well above the bone and contacting both frontals.

The ventral portion of the nasal in *Styracopterus* expands to a blunt margin in contact with the lachrymal and premaxilla. The dorsal half of the nasal curves almost horizontally to contact the frontal and dermosphenotic. Contrary to the reconstruction of Gardiner (1985), there are no obvious lateral indentations for the nares. Ornamentation varies with size: there is little apparent ganoine in GSE 8731 (Fig. 1A), whereas a vertical stripe is found in NMS 1891.53.49 (Fig. 1B). This is joined posteriorly by additional patches of smooth enameloid in GSE 2136 (Fig. 1F). Similar ornamentation is found on the nasals in *Eurynotus*

(NMS 1876.28.2; L.C.S. pers. observ.) and *Benedenius* (L.C.S. pers. observ.; Appendix S1).

The skull roof in *Styracopterus* is similar in composition to previous reconstructions by Moy-Thomas (1937) and Gardiner (1985), but the shapes of the bones differ. The frontals are longer than the parietals, extending from the level of the preoperculum to the midpoint of the lachrymal in the 8-cm fish GSE 8731 (Figs 1A, 4A), and to the level of its anterior margin in larger specimens such as GSE 2136 (Figs 1G, 4C). The frontals narrow anteriorly to form a V-shaped contact with the snout series (Fig. 1). The widest portion of the frontal is marked by a rounded point in front of the dermosphenotic in GSE 5663 (Figs 1G, 4). A posterolateral process that grows larger with size forms a convex (GSE 8731; Fig. 1G) or V-shaped (NMS 1891.53.49, NMS 1891.53.50–51, GSE 5663, GSE 2136; Fig. 1) contact with the parietals. This is contrary to the simple linear suture illustrated by Moy-Thomas (1937) and the convex suture reconstructed by Gardiner (1985), but is similar to *Benedenius* (Traquair, 1878; Fraipont, 1890; L.C.S. pers. observ.; Appendix S1).

As originally described by Moy-Thomas (1937), the ornamentation of the frontal in *Styracopterus* varies by size. The frontal in the small fish GSE 8731 (Fig. 1A) is covered by intercalating ganoine ridges, which largely mirror the lateral margins. Similar ornament is found in the mid-sized NMS 1891.53.50 (Fig. 1D), but the striations are broken and joined by small dots medial to the impression of the supraorbital canal. In the equivalently sized NMS 1891.53.49 (Fig. 10B), more posterior ornament is covered by a large stripe of smooth ganoine. In the largest specimen of *Styracopterus*, GSE 5663 (Fig. 1G), this is joined by two bands running along the lateral margins, which are similar to the frontal ornamentation in *Benedenius* (Fraipont, 1890; L.C.S. pers. observ.; Appendix S1). Yet, in the equivalently sized individual GSE 2136 (Fig. 4F), finer ornament is exposed in the same areas (Fig. 1F). Moy-Thomas (1937) suggested that the large ganoine fields grew directly over the older, smaller ornament, and that appears to be the best explanation for the differences observed within size classes. Similar overgrowth has been observed on the dermal bones of some specimens of *Eurynotus*, where small striations emerge from under blotched enameloid cover (NMS 1876.28.2; L.C.S. pers. observ.; Appendix S1). Likewise, Dietze (1999) reported a similar phenomenon in *Paramblypterus*, where smooth ganoine increased in extent with body size to obscure or replace previous structures.

The parietals in *Styracopterus* are rhomboidal or even right triangular in appearance, not rectangular as reconstructed previously (Moy-Thomas, 1937; Gardiner, 1985). The lateral margin is rounded in

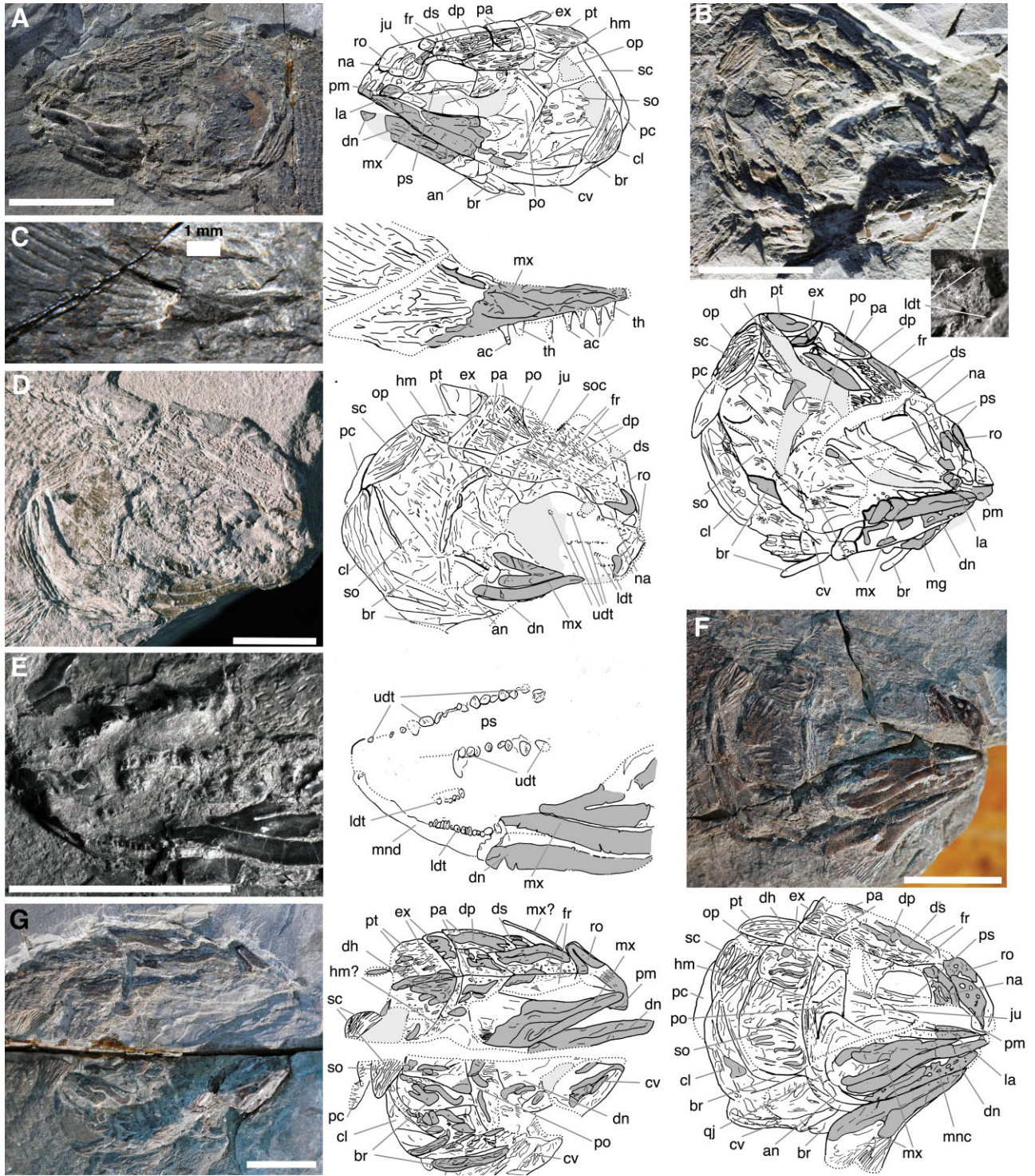


Figure 1. *Styracopterus* cranial material. Unlabelled scale bars equal 1 cm. Medium-grey infill indicates the extent of thick ganoine bands covering other ornament. Light-grey infill indicates unidentified skull material. A, GSE 8731; B, NMS 1891.53.49. C, GM 1902.85md maxilla; D, NMS 1891.53.50; E, NMS 1891.53.51 denticles and jaws; F, GSE 2136; G, GSE 5663.

small and midrange specimens, and is sigmoidal in GSE 5663 (Fig. 1), extending past the lateral limit of the frontal. The posterior margin contacts the extrascapular at a suture line that appears straight in GSE 8731 (Fig. 1), and slightly inclined towards the midline in the larger GSE 5663 and GSE 2136 (Fig. 1F, G). The fine linear ornament found in GSE 8731 (Fig. 1A), NMS 1891.53.50 (Fig. 1D), and GSE 2136 (Fig. 1F) radiates posterolaterally, disrupted at the midpoint by a curved vertical ridge described by Gardiner (1985). An elongated band of smooth ganoine covers this ornament in midsize specimen NMS 1891.53.49 (Fig. 1B). In the 16-cm GSE 5663 (Fig. 1G), this is displaced from the midline by smaller dotted ornamentation, and is joined laterally by two or three seed-shaped ganoine splotches. NMS 1891.53.50 (Fig. 1D) shows a deep furrow for the supraorbital canal along the lateral midline, which curves towards the posterior margin.

The dermopterotic gives the superficial impression of a thick, shallow arc stretching back from the lateral frontal (Fig. 4), as has been reconstructed for *Strepheoschema* (Gardiner, 1985) as well as *Cheirodopsis* and *Canobius elegantulus* Traquair, 1881 (Moy-Thomas & Bradley Dyne, 1938). The dermopterotic stretches from a tapered anterior limit, sitting at the midpoint of the frontal in GSE 8731 (Fig. 1A), and positioned behind the posterolateral process in GSE 5663 (Fig. 1G), to a diagonal posterior contact with the extrascapular. A fine ornament of short lateral ridges, exposed in GSE 8731 (Fig. 1A) and GSE 2136 (Fig. 1F), is almost completely covered by a wide ganoine field running along the midline in 11-cm NMS 1891.53.49 (Fig. 1B) and 16-cm GSE 5663 (Fig. 1G).

Styracopterus possesses one pair of extrascapulars that are rectangular in GSE 8721 (Fig. 10A), but are laterally expanded, with a curved, 'back swept' appearance in NMS 1891.53.49 (Fig. 10B) and GSE 5663 (Fig. 1G), matching the morphology in *Phanerosteon ovensi* (White, 1927; Appendix S1; Fig. 18D) and *Eurynotus* (NMS 1957.1.5686, L.C.S., pers. observ.). Short, striated ornamentation in NMS 1891.53.50 (Fig. 1D) is covered by distinct midline and lateral ganoine splotches in NMS 1891.53.49 (Fig. 1B). In GSE 5663 (Fig. 1G), these fields are fused into a single patch of smooth ornament with four posterior extensions, covering the lateral half of the bone.

The general morphology of the post-temporal in *Styracopterus*, similar to that described by Moy-Thomas (1937) and Gardiner (1985) in *Fouldenia*, the remaining Foulden fishes, and in many other early actinopterygians (Gardiner & Schaeffer, 1989; L.C.S., pers. observ.; Appendix S1), is rhomboid in form (Fig. 1A, D, F). The posterolateral angle is more pointed, and medial margin short, in the small-

est specimen (GSE 8731; Fig. 1A) relative to the largest (GSE 2136, Fig. 1G). A primary ornament of thin, posterolaterally diagonal ridges, as shown in GSE 8731 and GSE 2136 (Fig. 1A, F), is obscured by a half-oval patch of smooth ganoine along the midline NMS 1891.52.49 (Fig. 1B). In GSE 5663 (Fig. 1G), this field covers the entire anteromedial portion of the bone, and bears multiple posterior branches. Additional smaller bands and patches of enameloid are found on the posterior half of those post-temporals.

The orbit in *Styracopterus* is bounded by the dermosphenotic, nasal, lachrymal, and jugal, but not the premaxilla, as inferred by Gardiner (1985). The dermosphenotic is unfortunately broken in all known specimens, but may be reconstructed from fragments (Fig. 4). In GSE 8731 (Fig. 1A), the posterior portion is wide with a ventral margin that curves posterodorsally. The thick process abuts the dermopterotic, and ends on the frontal in GSE 8731, NMS 1891.53.50, and GSE 5663 (Fig. 1A, D, G). Overall, the morphology matches that in *Fouldenia*, and likewise lacks the posterior process that would give the dermosphenotic a T-shaped form (*contra* Gardiner & Schaeffer, 1989). Ornamental ridges are diagonal on the posterior portion in GSE 8731 (Fig. 1A), and are horizontal on the anterior portion in NMS 1891.53.49 (Fig. 1B). In GSE 5663, this latter ornament is covered by a drop-shaped splotch of smooth ganoine, just as in *Eurynotus crenatus* Agassiz, 1833–1844 and *Benedenius* (NMS 1876.28.2, NMS 1957.28.2; Liège *Benedenius*, L.C.S. pers. observ.; Fraipont, 1890).

The jugal is not well preserved in any specimen of *Styracopterus*, but unornamented sections appear in GSE 8731, NMS 1891.53.50, and GSE 2136 (Fig. 1A, D, F), where it abuts the preoperculum and extends to the ventral midline of the orbit. The lachrymal is not much better preserved, limited to anterior sections ending near the premaxillae in GSE 8731, NMS 1891.53.49, and GSE 2136 (Fig. 1A, B, F). These appear rectangular and tall, with some evidence for an ornament of circular ganoine fields in NMS 1891.53.49 (Fig. 1B). There is no sign of an infraorbital canal.

Jaws and dentition

The only endoskeletal element known in *Styracopterus* is the parasphenoid. The dorsal aspect visible in NMS 1891.53.49 (Fig. 1B) is anteriorly narrow with thin lateral ridges that may mark the parbasal canals, and thus matches the morphology in *Fouldenia*. The parasphenoid is interrupted near its midline, obscuring the likely position of the bucco-hypophysial canal. However, another posteriorly expanded portion reveals a central ridge and paired triangular indentations, as in the parasphenoids of other early

actinopterygians (e.g. *Mimipiscis*, Choo, 2011; *Moythomasia*, Gardiner, 1984; *Platysomus superbus* Traquair, 1881, L.C.S., pers. observ.; Appendix S1). This is again disrupted by an impression of the hyomandibula obscuring the posterior extent of the bone. The parasphenoid is visible in lateral view in the lower part of orbit in GSE 8731 (Fig. 1A), where it is inclined anteroventrally and appears quite robust, thickening towards the snout.

The maxilla in *Styracopterus* is largely as described by Moy-Thomas (1937) and Gardiner (1985). The triangular posterior expansion exhibits a rounded peak near the vertical posterior margin of the bone in GSE 2136 (Fig. 1F), where both maxillae are exposed as mirror images. The dorsal margin slopes into a thick, pointed anterior ramus gradually in GSE 8731 and GM 1905.82md (Fig. 1A, B). The transition is steeper and more curved in GSE 2136 (Fig. 1F), reflecting the deeper posterior expansion in larger individuals (Fig. 4). The jaw margin is sigmoidal in GSE 8731, NMS 1891.53.50-1, and GSE 2136 (Fig. 1A, D, E, F), and overlaps the mandible throughout its length. The margin of the maxilla curves upwards diagonally posterior to the dentary. The general form of the maxilla in *Styracopterus* is not far from the taller maxillae of *Amphicentrum* and *Cheirodopsis* (Moy-Thomas & Bradley Dyne, 1938; Bradley Dyne, 1939; Coates, 1988; L.C.S., pers. observ.; Appendix S1).

The ventral edge of the maxilla in *Styracopterus* is lined by a wide band of smooth ganoine that covers the entire lateral surface of the anterior ramus (Fig. 1). A second band begins at the level of the anterior edge of the orbit, separated from the first by a deep furrow, and splits into a V-shape posteriorly. The ventral arm runs laterally, whereas the dorsal band moves upwards along the dorsal edge of the maxilla, with both ending at the level of the back of the orbit in smaller specimens: GSE 8731, GM 1902.85md, and NMS 1891.53.50-1 (Fig. 1A, C, D, E). In the ~16-cm specimens GSE 5663 and GSE 2136 (Fig. 1F, G), these two bands continue horizontally past the midline of the posterior expansion, with the more ventral member meeting the posterior margin. Smaller blotches of enameloid are found around this ornament (Figs 1, 4). As in the skull roof, the portions of smooth ganoine farther away from the jaw margin, or only present in larger individuals, cover a finer ornamentation, exposed in GM 1902.85md, NMS 1980.53.49, and GSE 2136 (Fig. 1B, C, F). This consists of fine, long diagonal ridges radiating posterodorsally onto the posterior expansion of the maxilla from the anterior ramus. Fields of thick ganoine are similarly present on the ventral and anterior maxillae of the eurynotiforms *Amphicentrum*, *Cheirodopsis*, *Paramesolepis*,

Wardichthys, *Eurynotus*, and *Benedenius*, and in all genera except the last, fine ornament is visible on the posterior expansion (Fraipont, 1890; Coates, 1988; L.C.S., pers. observ.; Appendix S1).

The dentary of *Styracopterus* extends nearly the entire length of the lower jaw and appears gracile in comparison with the maxilla. The anteriormost portion forms a narrow 'beak' in GSE 8731 and GSE 5663 (Fig. 1A, F), as the symphysis curves to form an acute point with the edentulous jaw margin. As in *Fouldenia* and *Benedenius* (Van Beneden, 1871; Fraipont, 1890; L.C.S., pers. observ.; Appendix S1), the dentary in *Styracopterus* is covered laterally by two thick, ganoine bands that are only partially distinct (Fig. 1). The lateral midline is punctuated by a line of large, regularly spaced circular openings for the mandibular canal in GSE 2136 (Fig. 1F), which resemble the canal pits in the snout ornament. Such openings are also found in the smooth ganoine covering the mandibles of *Eurynotus* (NMS 1957.1.5686; L.C.S., pers. observ.) and *Amphicentrum* (Coates, 1988; Appendix S1). As reconstructed by Gardiner (1985), the angular in *Styracopterus* is a narrow, half-crescent in GSE 8731, NMS 1891.53.51, and GSE 2136 (Fig. 1A, D, F), and is similar in general morphology to those in *Cheirodopsis* and *Paramesolepis* (Moy-Thomas & Bradley Dyne, 1938; Appendix S1).

Moy-Thomas (1937) and Gardiner (1985) noted, but did not illustrate, 'eight cylindrical blunt teeth' found on the maxilla of *Styracopterus* specimen GM 1902.85md (Fig. 1C). In this individual, the anterior process of the maxilla bears a homogeneous set of large, triangular teeth with acrodin caps, tapered crowns, and robust bases. The morphology and preservation are superficially similar to a robust set of teeth along the margin of an isolated jaw of *Mesolepis wardi* Young, 1866 (NHM P8044; L.C.S., pers. observ.), and a maxillary tooth visible on the anterior portion of the maxilla in a specimen of *Paramesolepis tuberculata* (Traquair, 1890) (NMS 1891.53.25; L.C.S., pers. observ.). Likewise, the *Eurynotus crenatus* specimen NMS 1859.33.F515 (L.C.S., pers. observ.) shows the impression of such an acrodin-caped fang well forward of and distinct from the denticulated tooth plates, and specimen NHM P11679 has a full row of pointed teeth on the mesial surface of the maxilla above the jaw margin (Traquair, 1879; L.C.S., pers. observ.).

Evidence of marginal dentition remains confined to GM 1902.85md (Fig. 10C); all other individuals exhibit a seemingly edentulous gape covered in ganoine ornament. The marginal dentition of other *Styracopterus* specimens might be obscured by a 'beak' of dermal bone and/or ganoine plate, as the maxilla significantly overlaps the mandible in articu-

lated jaws. Unfortunately, the mesial surface of the maxilla is not observed, preventing confirmation. However, *Amphicentrum*, another superficially edentulous fish, has a field of apparent tooth cusps on the mesial maxilla, well dorsal to the sharpened edge of the gape (Bradley Dyne, 1939; Coates, 1988; NMS 1894.73.472; L.C.S., pers. observ.; Appendix S1). Likewise, the maxillary teeth in *Eurynotus* sit in an internal position, hidden from lateral view, and are thus not visible in most specimens (Traquair, 1879; NMS 1859.33.F515; L.C.S., pers. observ.; Appendix S1). Within the Glencartholm fauna, *Cheirodopsis* has a set of six or more incisor-shaped teeth rooted on the mesial side of the maxilla, covered laterally by ganoine-ornamented bones (NMS 1957.1.5781; L.C.S., pers. observ.). Farther afield temporally and geographically, a similar, but reversed, arrangement is found *Aeduella*, where a 'flange' of the maxilla covers the lingual aspect of tooth bases (Gottfried, 1987).

In NMS 1891.53.50–51 (Fig. 1D, E), an individual in which the dermal cheek bones are missing, two near-parallel rows of denticles lacking acrodin caps are situated medial to, and separate from, the remnants of the dentary, but show some alignment with the lower jaw. The crowns of these anteriorly ovoid and posteriorly rectangular denticles are pointed outwards from the matrix. The rows are separated by an area in line with the width of the frontals in the same individual and/or the parasphenoid in the similarly sized specimen NMS 1891.53.49 (Fig. 1B), which also possesses outwardly oriented denticles alongside the anterior limit of the palate. The denticles are probably associated with lower tooth plates, as in *Fouldenia* (see below), *Mesolepis wardi* (NHM P8042; L.C.S., pers. observ.), and *Eurynotus crenatus* (NMS 1859.33.F515; L.C.S., pers. observ.), which have highly similar denticle morphologies. These plates would probably have been constructed from the fused coronoids or other mesial mandibular elements, as described for similarly positioned elements in *Amphicentrum granulosum* Young, 1866, *Cheirodopsis*, and *Eurynotus* (Bradley Dyne, 1939; Traquair, 1879; Coates, 1988; L.C.S., pers. observ.; Appendix S1).

Specimen NMS 1891.53.50–51 also shows a second pair of denticle rows situated around the midline of the disarticulated skull (Fig. 1D, E), again with crowns pointed outwards. These denticles are conical with blunted apices, the largest featuring a narrow, 'lophodont' edge perpendicular to the row, and showing signs of wear-related loss at their crowns. The denticles are heterogeneous in both spacing and size: many of the more posterior members are an order of magnitude larger than the mandibular denticles, whereas more anterior elements are

smaller and more broadly spaced. This is similar to the arrangement of the primary, ventrally pointed row of denticles on the upper toothplates of *Eurynotus* and *Mesolepis* (Traquair, 1879; Watson, 1928; NMS 1874.3A; L.C.S., pers. observ.; Appendix S1).

As with the mandibular set, the space between the upper rows of denticles in NMS 1891.53.50–51 matches the width of the parasphenoid at the same points in NMS 1891.53.49, narrowing anteriorly (Fig. 1B, D, E). In NHM P1663, where a badly preserved skull is observed in nearly ventral view, small, closely packed denticle crowns distinguishable from the maxillary teeth are pushed through a gap just ventral to the mandible and away from the maxilla. The orientation of the denticles in NMS 1891.53.50–51 (Fig. 1D, E) and NHM P1663 suggests the existence of paired palatal tooth plates with ventrally pointed denticles, perhaps derived from the ectopterygoids, as in *Amphicentrum* and *Cheirodopsis* (Traquair, 1879; Moy-Thomas & Bradley Dyne, 1938; Bradley Dyne, 1939; Coates, 1988; L.C.S., pers. observ.; Appendix S1).

Suspensorium

As previously described, the suspensorium in *Styracopterus* is nearly vertical (Moy-Thomas, 1937; Gardiner, 1985). This is supported by the impression of a superficially narrow and cylindrical hyomandibula in NMS 1891.53.50 (Fig. 1D), in which a knob-like opercular process marks the transition from the erect ventral portion to a slightly inclined dorsal half. The true and relative sizes of these parts may be obscured by overprinting of the dermal bones. The head of the hyomandibula is expanded and robust in NMS 1891.53.50, GSE 8731, and possibly GSE 5663 (Fig. 1A, C, G). The head is covered by a triangular dermohyal with fine, linear ornament and a drop-shaped ganoine patch, as noted in GSE 2136 and GSE 5663 (Fig. 1A, G).

The hyomandibula is bounded anteriorly by a very erect preopercular, fully preserved in *Styracopterus* specimen GSE 2136 (Fig. 1F; Gardiner, 1985), which is positioned so that the vertical anterior margin aligns with the rear of the gape. The posterior margin is bounded by a cylindrical ridge and tracks the angle of the hyomandibular, bending diagonally at the level of the horizontal pitline in GSE 2136 to form the narrow, rounded apex (Fig. 1F). The preopercular thus resembles those in *Amphicentrum* (Coates, 1988), *Eurynotus* (Gardiner & Schaeffer, 1989), *Cheirodopsis*, and *Paramesolepis* (Moy-Thomas & Bradley Dyne, 1938; L.C.S., pers. observ.; Appendix S1). The ornament above the premaxilla consists of fine striations radiating from the midline, whereas a ventral process connecting with the quadratojugal is covered in smooth ganoine (Fig. 1F, G).

Opercular series

The operculum is small and rectangular in the specimen of *Styracopterus* with the best-preserved example: the large fish GSE 5663 (Fig. 1G). In line with Moy-Thomas' (1937) reconstruction, The suboperculum is taller and is almost identical to that in *Benedenius* (Traquair, 1878; Fraipont, 1890; L.C.S., pers. observ.; Appendix S1; Fig. 15C). It exhibits a pointed anteroventral process angled towards the jaw joint by a diagonal ventral margin, as in *Benedenius* and *Fouldenia* (L.C.S., pers. observ.; Appendix S1; Fig. 15). This process might be considered diagnostic for Styracopteridae, were similar structures not present in *Tarrasius*, *Strephoschema*, *Holurus*, *Phanerosteon*, *Paramesolepis*, *Amphicentrum*, *Eurynotus*, and *Cheirodopsis* (Moy-Thomas & Bradley Dyne, 1938; Gardiner, 1985; Coates, 1988; Gardiner & Schaeffer, 1989; Sallan, 2012; L.C.S., pers. observ.; Appendix S1). There are differences in the relative sizes and orientation of opercular series bones between *Styracopterus* size classes. In 8-cm GSE 8731 (Fig. 1A), the operculum is inclined forwards at an almost 45° angle, and is nearly equal in length to a curved suboperculum (Fig. 4A). In 11-cm specimens NMS 1891.53.49 and NMS 1891.53.50–51 (Fig. 1B, D), the operculum is still tilted slightly anteriorly and ends just above the curved preopercular, giving way to a taller suboperculum (Fig. 4B).

In GSE 2136 (Fig. 1F), a posteroventrally diagonal line bisects the operculum ornament into an anterior field of curved lateral ridges and a posterior field of concentric lines. This is obscured in larger individuals such as NMS 1891.53.49 (Fig. 1B), in which a broken plate of ganoine is found near the anteroventral corner. The ornament of the suboperculum is also double layered in larger specimens of *Styracopterus*. Thick, wavy lines radiate posteriorly from a primary vertical stripe of ganoine in GSE 2136 (Fig. 1F). In contrast, the anteroventral process is covered by diagonal ridges in GSE 5663 (Fig. 1G); although this is obscured by smooth ganoine distally. In that same specimen, elongate enameloid bands are found on the ventral half of the suboperculum. Similar ornament is found on an articulated suboperculum from the late Tournaisian deposits of Symond's Yat, Herefordshire, England, previously attributed to *Styracopterus* sp. (NHM P62956; L.C.S., pers. observ.; Appendix S1, see below), as well as the more extensive smooth ganoine of the Liege specimen of *Benedenius* (Fraipont, 1890; L.C.S., pers. observ.; Appendix S1).

Gulars and branchiostegals

The branchiostegal rays are not completely preserved in *Styracopterus*, although individual rays are found in several specimens. The primary ray is the tallest and most distally expanded in GSE 5663 (Fig. 1G),

and bears an ornament of two intercalated and wavy bands (Figs 1G, 4C). The second ray is thinner but likewise ornamented, but further members of series are covered with one or two longitudinal enameloid bands and/or fine linear ornament (Figs 1G, 4C). Whereas rectangular branchiostegals directly under the opercular bones are elongate, those originating ventral to jaws in GSE 8731 and NMS 1891.53.49 (Fig. 1A, B) are shorter and more pointed, but remain nearly horizontal in orientation. This is similar to the general orientation and form of the series in *Benedenius* (Fraipont, 1890) and most other eurynotiforms (e.g. *Amphicentrum*, *Cheirodopsis*, *Eurynotus*; Traquair, 1879; Moy-Thomas & Bradley Dyne, 1938; Coates, 1988; L.C.S., pers. observ.; Appendix S1), in which the ventralmost branchiostegals are relatively short and barely visible in lateral view (Fig. 15).

The only evidence of the gular series consists of a badly preserved, displaced lateral gular originating just posterior to the front of the dentary in NMS 1891.53.49 (Fig. 1B) and similar in form to the branchiostegals. Unlike the branchiostegals, the gular is completely covered in ganoine (Fig. 1B). The arrangement of the preserved parts leaves space for a short median gular, as in *Fouldenia*, but it is not clear whether more anterior skeletal material represents this bone. Gular material in other specimens might be hidden by the mandible, as appears to have been the case in *Benedenius*, *Amphicentrum*, *Eurynotus*, *Cheirodopsis*, *Paramesolepis* and other early fishes (Traquair, 1879; Fraipont, 1890; Moy-Thomas & Bradley Dyne, 1938; Coates, 1988; L.C.S., pers. observ.; Appendix S1; Figs 15–19).

Shoulder series

The dermal shoulder series in *Styracopterus* is relatively well preserved and matches the composition described by Moy-Thomas (1937). Unfortunately, the same cannot be said for the endoskeletal girdle, which is not visible in any specimen. The leaf-shaped supracleithrum extends to the midpoint of the suboperculum (Figs 1, 4). The ornament consists of prominent, densely packed, intercalating ganoine ridges running along the vertical axis and fusing towards the midline. The supracleithrum changes from a thin gracile bone with a definite ventral point in the 8-cm specimen GSE 8731 (Fig. 1A) to a wide, rounded form in the 16-cm individuals GSE 5663 and GSE 2136 (Fig. 1F, G).

The rectangular postcleithrum in *Styracopterus* is wide and elongate, but would have been obscured in life by the supracleithrum, except for a rounded posteroventral corner abutting the cleithrum, as shown in GSE 8731 (Fig. 1A). Exposed postcleithra in other specimens resemble the same bone in *Amphicentrum*

(Coates, 1988). The ornament preserved in GSE 5663 (Fig. 1G) consists of thick diagonal striations.

The cleithrum in *Styracopterus* is very tall and erect, with a wide crescent-shaped dorsal process and a tall ventral body with a rounded posterior extension (Figs 1, 4). Thus, it resembles the cleithra of other eurynotiforms, particularly *Fouldenia* and *Eurynotus* (Traquair, 1879; Gardiner & Schaeffer, 1989; L.C.S., pers. observ.; Appendix S1; Fig. 15). The half-ovoid dorsal process of the cleithrum runs to the midpoint of the suboperculum in GSE 8731, NMS 1891.53.50, and GSE 5663 (Fig. 1A, D, G). The ornament in *Styracopterus* specimen GSE 8731 (Fig. 1A) is similar to *Fouldenia*, and other Foulden taxa (L.C.S., pers. observ.; Appendix S1), in that it consists of robust, nearly vertical lines running from apex to base (Fig. 13A). This ornament is covered by wider bands of smooth ganoine in the larger specimens NMS 1891.50.49 and GSE 2136 (Fig. 1B, F). The ventral part of the cleithrum is tall in GSE 2136, and features an ornament of short horizontal ridges covered by smooth enameloid. Like *Fouldenia*, there is a short posterior extension near the ventral surface of the cleithrum.

The cleithrum contacts the clavicle at a concave anterior margin situated beneath the opercular series and jaw joint in NMS 1891.50.49 (Fig. 1B). The clavicle in *Styracopterus* runs along nearly the entire ventral length of the skull, as exposed in GSE 8731, NMS 1891.50.49, GSE 2136, and GSE 5663 (Fig. 1A, B, F, G), curving anteriorly to a rounded point. The clavicle of *Styracopterus* is shallow relative to that of *Fouldenia*, and is completely covered by the mandible in life (Figs 1, 4). The bone is covered with short, wavy bands in NMS 1891.53.49 and GSE 5663 (Fig. 1B, G), an ornament obscured by smooth ganoine patches in the latter.

Paired fins

The pectoral fins in *Styracopterus* originate ventrolaterally, although the endoskeletal attachment is not visible in any specimen. However, GSE 8731 and GSE 5663–4 (Fig. 2A, E, F) show a gap in squamation between the cleithrum and the angled bases of the lepidotrichia, which suggests a naked lobe over the missing radials. The fins in GSE 8731 (Fig. 2A) are elongate and curved, with pointed distal margins and short bases. This results in a scythe-shaped fin similar to those in *Eurynotus*, *Benedenius*, and *Mesolepis* (Agassiz, 1833–1844; Traquair, 1879; Boulenger, 1899; Traquair, 1907; L.C.S., pers. observ.; Appendix S1; Fig. 15). In this individual and others (GSE 5663–4, NMS 1891.53–50; Fig. 2C, E, F), lepidotrichia are thin and tightly packed with enlarged ovoid bases, similar to the median fin rays in *Fouldenia*. Segments are rectangular, with a ridge along the

anterior edge. The rays become thinner distally but there is no evidence for bifurcation. Rays supporting the anterior margin in the 16-cm specimen GSE 5663–4 (Fig. 2E, F) are more robust than, and may be twice as wide as, the other lepidotrichia, with an abrupt transition. However, the absolute size of the fin is invariant between specimens despite a doubling of body length, rendering it relatively larger in smaller specimens.

Traquair (1881) noted impressions of robust pectoral fringing fulcra in the holotype of *Styracopterus* (GSE 5672–3; Fig. 2D), and these served as a basis for the species and eventually genus names (Traquair, 1890). Elongate, blade-like fulcra strongly resemble their likewise paired counterparts in *Eurynotus* (NHM P11679, NHM P11676; L.C.S., pers. observ.; Appendix S1), and those of *Benedenius* in lateral view (Traquair, 1879; Fraipont, 1890; Appendix S1). Each fulcral scale possesses a tapered distal margin and is covered by thick ganoine. More distal pairs are progressively shorter and thinner. In the smallest specimen, GSE 8731 (Fig. 2A), six pairs of fulcral scales sit along the primary lepidotrich, each overlapping a third of the length of their neighbour. The number of fulcra is unchanged in larger specimens NMS 1891.53.50–51 (Fig. 2B, C) and GSE 5663–4 (Fig. 2E, F), yet more distal scales appear lozenge-shaped rather than elliptical. These contact each other at nearly straight margins oriented at a 45° angle relative to the fin axis.

The pelvic fins of *Styracopterus* sit very low on the body, separated by a distance of just two or three median ventral scales in NHM P1663 (Fig. 2G). The fins appear small and triangular, but may be truncated by the better-preserved anal fin. The lepidotrichia in NHM P1663 and GSE 8731 (Fig. 2G, H) are thin and densely packed, divided into elongate segments with no evidence of bifurcation, thus resembling the pectoral rays of *Fouldenia*. The similarly sized individual GSE 8731 (Fig. 2H) possesses fringing fulcra that are slimmer versions of their pectoral counterparts. These are similar to the proximal fringing fulcra on the pelvic fins in a very small specimen of *Eurynotus* (NMS 1874.3A; L.C.S., pers. observ.; Appendix S1). A furrow on the anterior midline of each fulcral scale originates from a wider groove holding the apex of its more proximal neighbour. Three semi-articulated pelvic fulcra are observed in lateral view in the larger specimen GSE 5663–4 (Fig. 11I), and appear relatively thicker and wider. A large, ovoid basal fulcral scale overlaps the pelvic fin in both NHM P1663 and GSE 5663–4 (Fig. 2G, I). This is ornamented with three thick longitudinal bands of ganoine that fuse near the apex of each scale. Unfortunately, the endoskeletal components of the pelvic complex are not visible in any specimen.

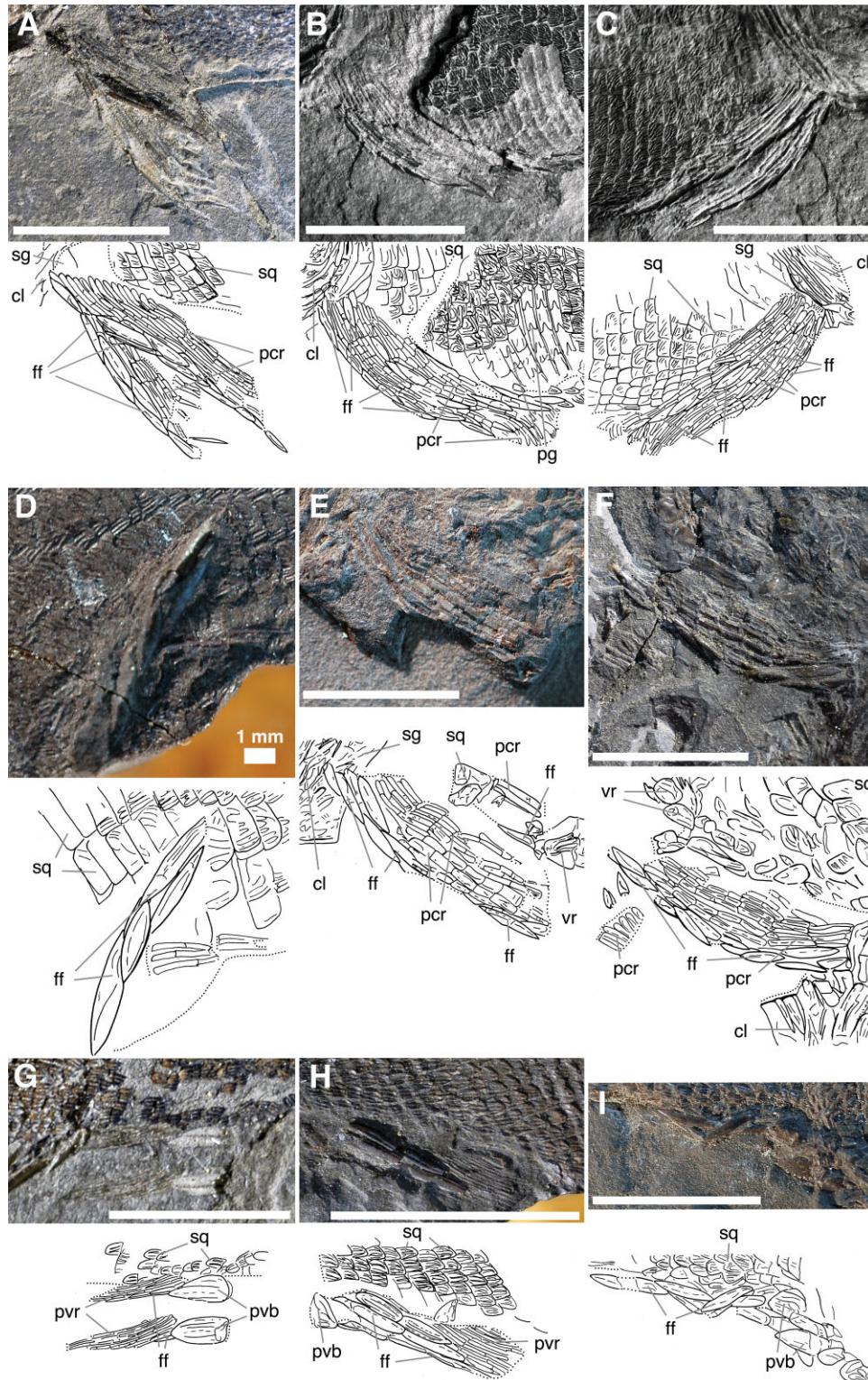


Figure 2. *Styracopterus* paired fins. Unlabelled scale bars equal 1 cm. A, GSE 8731 pectoral; B, NMS 1891.53.50 pectoral; C, NMS 1891.53.51; D, GSE 5672 pectoral; E, GSE 5664 pectoral; F, GSE 5663 pectoral; G, NHM P1663 pelvic; H, GSE 8731 pelvic; I, GSE 5663 pelvic.

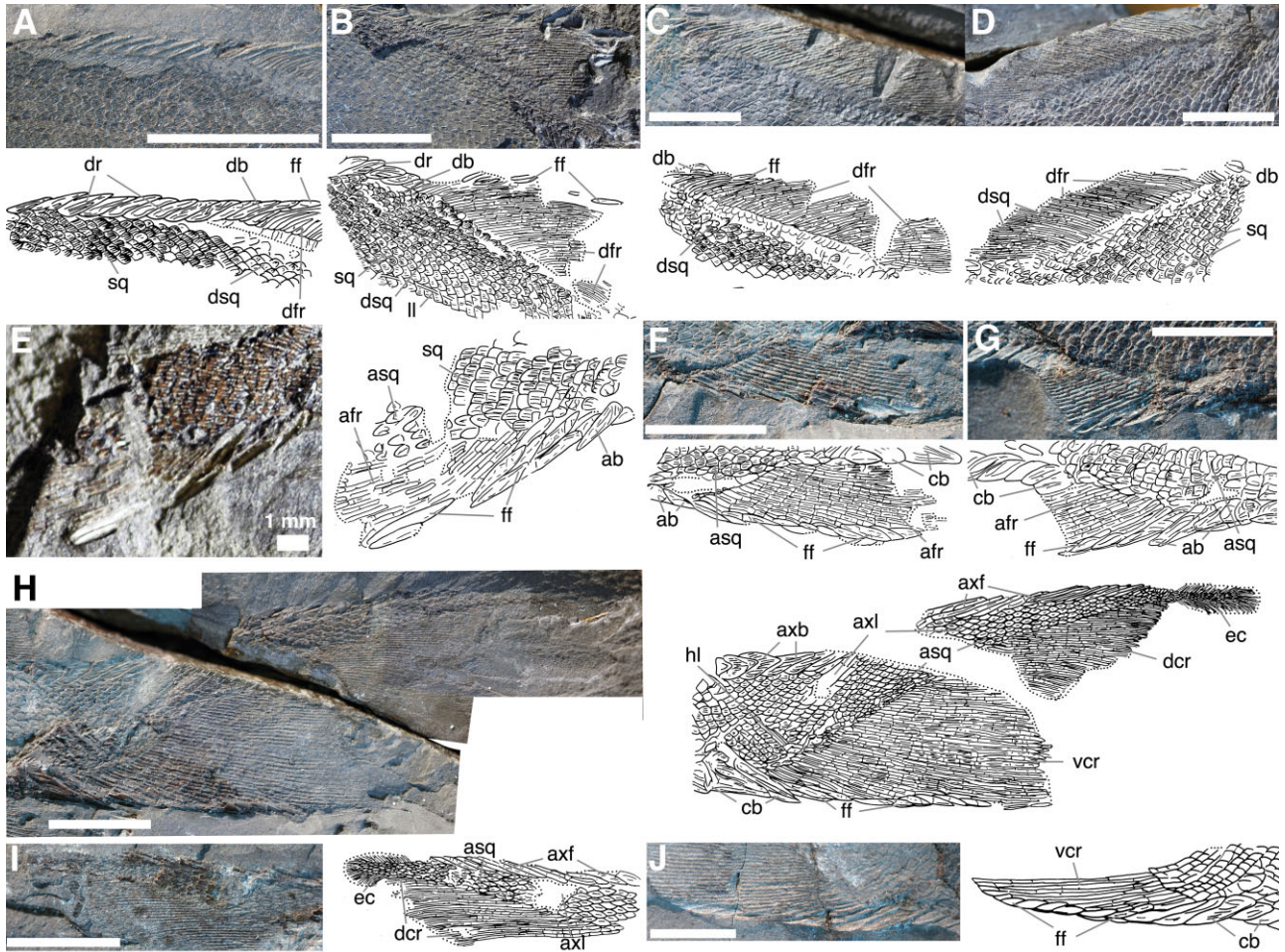


Figure 3. *Styracopterus* median fins and caudal material. Unlabelled scale bars equal 1 cm. A, GSE 8731 dorsal; B, GSE 5672 dorsal; C, GSE 5664 dorsal; D, GSE 5663 dorsal; E, NHM P1663 anal; F, GSE 5664 anal; G, GSE 5663 anal; H, GSE 5664 tail; I, GSE 5663 axial lobe; J, GSE 5663 ventral caudal fin.

Median fins

An exact reconstruction of the dorsal fin in *Styracopterus* was not possible because of incomplete preservation. However, GSE 8731 (Fig. 3A) suggests a long yet sloped anterior margin, whereas GSE 5663–4 (Fig. 3C, D) shows the posterior portion is quite short and rounded. The fin base sits along the diagonally oriented dorsal margin of the body, originating near the point of maximum depth in larger specimens GSE 5672–3 and GSE 5663–4 (Fig. 3B, C, D). In GSE 8731, GSE 5672–3, and GSE 5663–4 (Fig. 3A, B, C, D), the primary lepidotrichia are unjointed, have ovoid bases, and are fused to fringing fulcra like those of the paired fins, just as the leading fin rays of the dorsal fins in *Fouldenia*, *Amphicentrum*, *Cheirodopsis*, *Eurynotus* (NMS 1876.28.2 and NHM P11676), *Paramesolepis*, and *Wardichthys*, among other eurynotiforms (L.C.S., pers. observ.; Appendix S1). These have been referred to elsewhere as ‘horns’ (Weems &

Windolph, 1986). Other lepidotrichia supporting the anterior margin of the dorsal fin in GSE 5672 and GSE 5663–4 (Fig. 3B, C, D) are proximally double the width of those in the posterior half of the fin, which is another commonality with the Eurynotiformes mentioned above (L.C.S., pers. observ.; Appendix S1). Although rays in the anterior portion of the dorsal fin taper to a point, bifurcation is observed in more posterior lepidotrichia, with extent increasing towards the posterior. This biased distribution of dichotomization is also found in *Amphicentrum*, *Eurynotus*, and *Aesopichthys* (Coates, 1988; Poplin & Lund, 2000; L.C.S., pers. observ.; Appendix S1). It seems to allow more posterior flexibility, as indicated by the non-uniform orientations in which these lepidotrichia are preserved in *Styracopterus*. The angle of fin-ray origination decreases gradually along the dorsal fin. This is aligned with a loss in height following a peak in the anterior half of the fin. Other

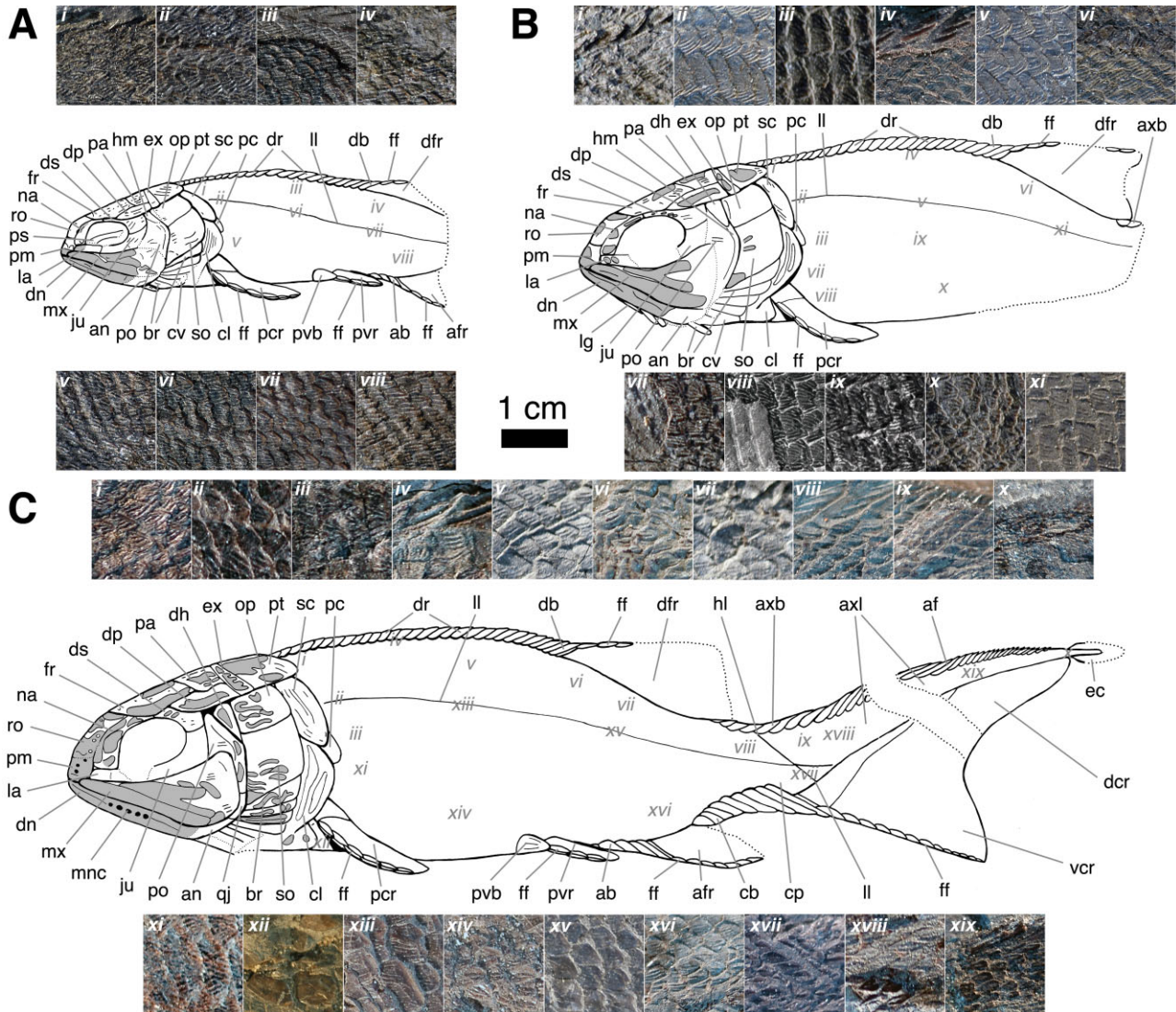


Figure 4. *Styraopterus* reconstructions and squamation. Reconstruction drawings of various size classes are based on all available specimens around each length, and are near actual size at full resolution. Squamation photographs are shown at three times the size, at the scale of reconstructions. Roman numerals on the reconstructions indicate the position of scales with matching labels. Medium-grey infill indicates the documented extent of thick ganioine plates covering other ornament. A, 8-cm, scales from GSE 8731; B, 12 cm, scales from GSE 5672–3; NHM 1891.53.49 and NHM 1891.53.49–50; C, 16 cm, scales from GSE 2136 and GSE 5663–4.

styracopterid and eurynotiform fishes also have such posteriorized peaks relative to *Platysomus*, *Aesopichthys*, and other deep-bodied ray-finned fishes (L.C.S., pers. observ.; Appendix S1). Lozenge-shaped, paired fringing fulcra on the dorsal fins of *Styraopterus* resemble the distalmost fulcra on the pectoral fins (Fig. 3A, B, C). *Eurynotus* also features paired scales on its dorsal fin (NMS 1876.28.2; L.C.S., pers. observ.; Appendix S1), yet fringing fulcra are usually singular on the median fins of other early actinopterygians (e.g. *Platysomus* and *Aesopichthys*; L.C.S., pers. observ.; Appendix S1).

The anal fin is exhibited in lateroventral view in NHM P1663, and the larger specimen GSE 5663–4 (Fig. 3E, F, G) displays a nearly complete fin in part and counterpart. The anal fin of *Styraopterus* is an acute triangle with slightly curved margins rather than the sickle shape of *Fouldenia* (Figs 4, 13). The anal fin in *Styraopterus* has a short base originating in the posterior third of the trunk. It bears lepidotrichia resembling those of the dorsal fin in terms of morphology, as well as changes in dichotomization and height along the fin. Likewise, there is an increase in the relative thickness of the primary anal

lepidotrichia with body size in *Styracopterus*, such that fewer rays appear to make up the anterior margin in GSE 5663 than NHM P1663 (Fig. 3E, F). In GSE 5663–4 (Fig. 3F, G), these lepidotrichia appear to bifurcate into curved terminal segments, conforming to the fringing fulcra. It is not clear whether this is a preservational artifact, a trait specific to the anal fin, or a general characteristic of *Styracopterus* obscured in other fins. In this same individual, proximal fulcral scales are like their pectoral fin equivalents, but more distal fulcra are squat and trowel-shaped, with much greater overlap between successive pairs. These approximate the fringing fulcra morphology in *Cheirodopsis* and *Eurynotus* (NMS 1874.3A, P42077, NMS 1876.28.2, NMS 1893.20; Moy-Thomas & Bradley Dyne, 1938; L.C.S., pers. observ.; Appendix S1). In *Eurynotus*, the fulcra form a thick and almost solid anterior margin for the anal fin, just as in *Styracopterus* (L.C.S., pers. observ.; Appendix S1).

In NHM P1663 and GSE 5663–4 (Fig. 3E, F, G), erect basal fulcra precede the anal fin, with the last two doubling the height of their anterior neighbours to overlap the fringing fulcra. An expanded base supports an elongated distal process, superficially divided into two rami. The proximal portions also resemble the successively taller, spine-like anal basals found in *Amphicentrum*, *Cheirodopsis*, and *Eurynotus* (L.C.S., pers. observ.; Appendix S1).

Tail and caudal fin

The posteriormost portion of *Styracopterus* is only preserved in GSE 5663–4 (Figs 3H, I, 12J), which possesses a nearly complete tail and caudal fin. *Styracopterus* has an epichordal fin, which appears to be diamond-shaped and lacks fulcra (Fig. 3H, I, B). It originates dorsally and ventrally after a two- or three-scale-wide gap following the posterior margin of the caudal fin and the apex of the last axial fulcral scale. The fine, well-separated lepidotrichia emerge diagonal to the body wall, have short segments, and taper distally without bifurcation. Although epichordal fins and lobes are ancestral for osteichthyans, and possibly gnathostomes, the loss of this fin was once thought to define the actinopteran crown (see discussion in Patterson 1982 and Gardiner & Schaeffer, 1989). This was because such a fin was associated primarily with the Devonian stem-taxon *Cheirolepis* among Palaeozoic fishes, and with *Polypterus* among living forms (Pearson, 1982; Long, 1988; Arratia & Cloutier, 1996). However, Watson (1925) found the same structure in the Permian taxon *Palaeoniscum*, whereas Patterson (1982) noted a wider but incomplete distribution, involving derived taxa such as *Bourbonnella* (Gardiner & Schaeffer, 1989). In fact, *Fouldenia* (Figs 11, 12) and other Eurynotiformes

such as *Paramesolepis* (NHM P20425–6; L.C.S., pers. observ.) and *Cheirodopsis* (NHM P20222; L.C.S., pers. observ.) also bear distinct epichordal fins, as do most examined Palaeozoic actinopterygians with elongate axial lobes and completely preserved tails (L.C.S., pers. observ.; Appendix S1). This suggests the presence of an epichordal fin could be the base state for all Palaeozoic actinopterygians, and will require further investigation.

Whereas the tail of *Styracopterus* is superficially inequilateral in GSE 5663–4 (Fig. 3H), the caudal fin itself is nearly homocercal, with a shallow median cleft. The ventral lobe is large and rounded. Lepidotrichia are similar in segment morphology to those of the median fins, and start tapering at around three-quarters of their length. While the majority of lepidotrichia are missing their tips, those in the ventral lobe tend to end in a pointed segment, whereas more dorsal fin rays bifurcate with no apparent regularity. Bifurcation is also observed in lepidotrichia underlying the fringing fulcra and ventral/anterior margin (Fig. 3H, J), as in the anal fin. Although the lepidotrichia in the dorsal lobe are finer than those near the anterior margin, the transition is not as abrupt as in the median and paired fins.

Caudal basal fulcra form a continuous series between the anal and caudal fins (Fig. 3G, H, J). The basals resemble the anal set: more anterior basals are squat with rounded apices and linear ornament oriented parallel with the body axis (Fig. 3G). They transition into tall, erect scales with wide bases and long posterior processes that expand distally, giving them a slightly sigmoid appearance. These abut the primary caudal lepidotrichia. The distal processes consist of two triangular rami joined at the midline around a central groove and furrow. These have a deltoid shape in lateral view. Fringing fulcra are prominent along the ventral margin of the caudal fin (Figs 3H, J, 4), and resemble the set on the anal fin of the same individual and in *Eurynotus* (L.C.S., pers. observ.; Appendix S1). The first caudal lepidotrich in *Styracopterus* has very thick, almost fulcra-like proximal segments, and appears to blend into this set.

Squamation

GSE 5663–4 (Fig. 4C), the largest and most complete specimen of *Styracopterus*, possesses 74 sigmoidal trunk scale rows. These rows curve such that the dorsalmost scales have their posterior margins directed near vertically. The laterally compressed GSE 5663–4 (Fig. 4C) has 25 scales per row over most of the flank, despite posterior decreases in body depth. The smaller, more roundly fusiform GSE 8731 (Fig. 4A) has just 18 scales per row at maximum depth, indicating that scale counts increase during ontogeny yet scale height is ultimately related to body

depth. A prominent 'hinge line' is found on the caudal peduncle of GSE 5663–4 (Figs 3H, 4C), marking the start of ~61 additional caudal scale rows along the peduncle and axial lobe.

Scales on the lateral trunk are tall and largely rhomboid, with smooth margins and rounded posteroventral corners. Imprints of the mesial side of these scales in NMS 1891.53.51 (Figs 2B, 4A) show tall, robust pointed pegs originating from the middle of the dorsal margin and sitting within a similarly shaped central divot on the next member of the row. Fraipont (1890) and Boulenger (1899) illustrated nearly identical flank scales in *Benedenius*, and the same general morphology and articulation is found in *Amphicentrum*, *Eurynotus*, *Cheirodopsis*, and other eurynotiforms (Agassiz, 1833–1844; Traquair, 1879; Bradley Dyne, 1939; Coates, 1988; L.C.S., pers. observ.; Appendix S1). Lateral line scales in *Styracopterus* are marked by a horizontal, cylindrical ridge running along the horizontal midline. These scales otherwise match their neighbours in size and ornamentation.

The ornament, shape, and relative heights of flank scales vary between size classes and positions on the trunk. In the ~8-cm, largely fusiform individuals GSE 8731 and NHM P1663 (Fig. 4A), the tallest, most rectangular scales are found ventral to the lateral line on the anterior flank. These bear up to six lateral bands of ganoine. The top three of these are dorsoventrally directed and form a leaf-shaped, nested pattern similar to the scale ornament in *Fouldenia*. The bottom three bands are more horizontal, tapering and fusing posteriorly. Shorter scales near the midpoint of the body have truncated versions of the same ornament, with the reduction in height successively eliminating more ventral stripes. Even shorter scales near the dorsal and ventral margins in the anterior half of the body, and all scales on the posterior half, are simply ornamented with four horizontal, rectangular bands that fuse posteriorly (Fig. 4A). Such scales have a greater anterodorsal slope and a more prominent posterodorsal margin than their counterparts along the anterior flank, giving them a leaf-like form similar to the trunk squamation of smaller specimens of *Fouldenia* (Fig. 13). This also describes nearly the entire flank squamation in the smallest two *Styracopterus* specimens, GSE 8731 and NHM P1663 (Fig. 4A), which is far more homogeneous than large individuals. In the midsize individuals GSE 5672–3, NMS 1891.53.50–51, and NMS 1891.53.49 (Fig. 4B), the nested ornament increases in size to contain up to seven concentric bands, resembling the anterior flank scales of the largest specimens of *Fouldenia* (Fig. 13D). Scales near the ventral margins of the anterior half of the body in midsize *Styracopterus* are ornamented entirely by nested ridges, rather than the simple

striations found in the smaller GSE 8731 (Fig. 4A, B). Scales on the dorsal surface and posterior half of midsize fish are taller than their counterparts in GSE 8731 (Fig. 4A, B), and bear an additional horizontal ganoine band. A distinct field of ovoid scales is found near the dorsal fin in midsize *Styracopterus*, such as GSE 5672–3 (Fig. 3B), with posterior margins oriented towards the lepidotrichial bases. These are covered with three or four flat ganoine lines that fuse at the apex, resembling the ornament of the pelvic basal fulcra in miniature.

In the largest individuals, GSE 5663–4 and GSE 2136 (Fig. 4C), anterior flank scales are elongate and rectangular, with an ornament of nine or ten diagonal striations over three horizontal bands. The nested pattern is broken; most of the ridges run off the posterior edge or fuse with a marginal line of ganoine. The more dorsal and ventral scales remain rhomboid, adding yet another horizontal line of ganoine to bring the total to six per scale (Fig. 4C). Scales on or near the caudal peduncle in GSE 5663–4 do not differ greatly from the posterior flank scales of smaller specimens, and become shorter and more elongately rhomboid near the caudal fin base (Figs 3H, J, 4A, C).

There is no evidence of a distinct field of squamation along the anteroventral surface of the trunk in *Styracopterus*, unlike *Fouldenia* (see below). Nor is there a trace of ventral ridge scales in the smallest specimen NHM P1663 (Fig. 4A). However, two slightly enlarged, deltoid scales are visible on the ventral margin around the trunk midline in the midsize fish NMS 1891.53.49 (Fig. 4B). These bear an ornament of fine longitudinal bands. In the largest specimen, GSE 5663–4 (Figs 2E, F, 4C), a series of four squat, trapezoidal scales is preserved in medial view at the ventral margin of the body, just anterior to the pelvic basal fulcra. These ventral ridge scales cover a third of the distance between the shoulder girdle and pelvic fins. However, anterior members of the series could be obscured by the intact pectoral fins. The ridge scales are not much larger than the adjacent trunk squamation, and thus their overall state is similar to that in *Benedenius* (Traquair, 1878; Fraipont, 1890; Boulenger, 1899; L.C.S., pers. observ.; Appendix S1).

Prominent ridge scales cover the entire dorsal midline from nape to fin in *Styracopterus*, as originally illustrated for the holotype by Traquair (1881, 1890; Moy-Thomas, 1937; Gardiner, 1985). Scales in the anterior half of the series are smaller, more rounded, and horizontally oriented than the erect ridge scales near the dorsal fin (Figs 3, 4); however, ontogenetic differences are apparent. In the 8-cm fishes GSE 8731 and NHM P1663 (Figs 3A, 4A), horizontal ridge scales along the anteriormost dorsum

have rounded margins but are otherwise indistinguishable from the proximate trunk squamation, in contrast to the more erect, spine-like members in the posterior half of the series. These ridge scales have a rounded proximal portion joined to a curved, pointed apex, and an ornament of thick vertical striations. In the midsize fish NMS 1891.53.50–51, NMS 1891.53.49, and GSE 5672–3 (Fig. 4B), the dorsal ridge scales are enlarged and the anteriormost members are distinguishable by their acuminate shape and central grooves. The longitudinal ornament found in smaller fish is replaced by thick horizontal bands in more posterior ridge scales (Fig. 4B). Although the posterior half of the dorsal ridge series is unknown in the largest specimens (GSE 5663–4, GSE 2136; Fig. 4C), the anteriormost ridge scales have the same morphology as the most posterior scales of the smallest specimens (Fig. 4C). Pointed ridge scales overlap each other at 45° angles and bear a diagonal banded ornament.

Caudal squamation is only observed in GSE5663–4, but exhibits considerable variation along the length of the peduncle and axial lobe (Figs 3H, J, 4C). Peduncle squamation above the hinge line consists of rhomboid scales with rounded margins and thick ganoine cover; however, scales situated along the lepidotrichial bases are small and seed shaped, with no discernable ornament pattern. Elongate, diamond-shaped scales cover the base of the axial lobe and feature a single furrow in their otherwise solid ornament. These transition to smaller, seed-shaped scales at the horizontal midpoint of the axial lobe, yet the ornament pattern is retained (Fig. 4C). Smaller versions of these scales are found in the portion bearing the epichordal fin.

The basal and fringing fulcra on the peduncle and axial lobe are very similar in morphology to those in *Fouldenia* and *Benedenius* (Traquair, 1878; Fraipont, 1890; L.C.S., pers. observ.; Appendix S1; Figs 3H, 4B, C, 12A, B, 13). The scales in *Styracopterus* decrease in size and length posteriorly, so that the last few resemble the paired fulcra of the median fins (Fig. 3H, I). As in *Fouldenia* and *Benedenius* (Fraipont, 1890; L.C.S., pers. observ.; Appendix S1), The distalmost fulcral pair in *Styracopterus* occurs at the level of the last caudal fin ray base (Fig. 3H, I).

FOULDENIA WHITE, 1927

Type and only species: Fouldenia ischiptera (Traquair, 1881).

Diagnosis (emended from Moy-Thomas, 1937): Styracopterid euryotiform fish with three longitudinal ganoine bands sitting parallel with and alongside jaw margins on maxilla and dentary; maxillary teeth small, blunt, and rounded; mandibular tooth plate

denticles with constricted base and blunt crown; dentary deep with blunt anterior margin; maxilla with blunt anterior ramus and rounded triangular posterior expansion; rostral bearing horizontal bands of ganoine; frontal with straight lateral margin; parietal with straight lateral margin; suspensorium 45° off vertical; preopercular with concave anterior and convex dorsoposterior margins; opercular half-ovoid and equal in length to subopercular; long axis of branchiostegals long and held away from ventral margin of dentary; paired fin lepidotrichia cylindrical and thin; flank scales ornamented with nested lines of ganoine in adult; distinct anteroventral squamation with juvenile scales in adult; pelvic fin preceded by two enlarged basal fulcra; anal fin with strongly concave posterior margin.

Occurrence: Late Tournaisian of Scotland and England.

FOULDENIA ISCHIPTERA (TRAQUAIR, 1881)

Holurus ischipterus Traquair, 1881

Styracopterus ischipterus Traquair, 1890

Fouldenia ottadinica White, 1927

Styracopterus ottadinica Moy-Thomas, 1937

Styracopterus ischipterus Moy-Thomas, 1937

Styracopterus fulcratus Gardiner, 1985

Holotype: GSE 2187 (M1122b, holotype of '*Styracopterus ischipterus*'), British Geological Survey, Edinburgh, UK, nearly complete articulated individual in part (EBL: 6 cm).

Paratypes: NHM P13178 (holotype of '*Fouldenia ottadinica*'), Natural History Museum, London, UK, nearly complete, flattened articulated individual showing dorsal aspect in part (EBL: 9 cm); NHM P13179, impression of complete articulated skull in part (EBL: 8 cm); NHM P13187 (part) and NHM P13188 (counterpart), nearly complete articulated individual (EBL: 5 cm); NHM P13180 (part) and NHM P14560 (counterpart), incomplete articulated anterior half of individual (EBL: 8 cm); NHM P13182 (part) and NHM P13183 (counterpart), incomplete articulated anterior half of individual (EBL: 8.5 cm); NHM P13186, articulated posterior half of individual in part (EBL: 10 cm); NHM P13186, articulated caudal portion of individual in part (EBL: 10 cm).

Additional material: GSE 2143, articulated anterior portion of individual, including skull (EBL: 3 cm); NHM P14562, incomplete articulated individual in part (EBL: 6 cm); NHM P14564, nearly complete articulated individual in part (EBL: 9 cm); NHM P61546, incomplete articulated individual in

part with trunk squamation and skull (EBL: 8 cm); NHM P61549, complete articulated individual in part (EBL: 10 cm); NHM P61002, incomplete articulated individual in part with trunk squamation, paired fins, and posterior skull (EBL: 10.5 cm); NHM P13181 (part) and NHM P14561 (counterpart), incomplete articulated anterior third of individual (EBL: 12 cm); NHM P61548, nearly complete articulated individual in part and counterpart (EBL: 12 cm); NMS 1980.40.30, National Museums of Scotland, Edinburgh, Scotland, UK, articulated postcranium of individual in part and counterpart (EBL: 4 cm); NMS 1965.4.2, nearly complete articulated individual in part (EBL: 5 cm); NMS 1965.4.2, articulated postcranium of individual in part (EBL: 5.5 cm); NMS 1980.40.27, articulated postcranium of individual in part and counterpart (EBL: 6.5 cm); NMS 1965.4.3, nearly complete articulated individual in part and counterpart (EBL: 7 cm); NMS 1956.5.1, incomplete articulated individual in part and counterpart (EBL: 7.5 cm); NMS 1984.67.61, nearly complete articulated individual in part (EBL: 7.5 cm); NMS 1984.67.63, nearly complete articulated individual in part and counterpart (EBL: 9 cm); NMS 1980.40.31, nearly complete articulated individual in part (EBL: 9.5 cm); NMS 1984.67.65, nearly complete articulated individual in part and counterpart (EBL: 9.5 cm); NMS 1984.67.64, incomplete anterior two-thirds of individual in part (EBL: 11 cm); NMS 1984.67.62, nearly complete articulated individual in part, lacking axial lobe (EBL: 11.5 cm); GLAHM V8327, Hunterian Museum, Glasgow, Scotland, UK, nearly complete articulated postcranium of individual in part (EBL: 8 cm).

Type localities and horizon: River Tweed below Coldstream, Berwickshire, Scotland, UK. Calciferous Sandstone Series, Cementstone Group, Schopfites claviger-Auroraspor macra (CM) miospore biozone (348–347 Mya; Smithson *et al.*, 2012), Tournasian 3 (TN3) zone, Ivorian regional substage, Dinantian regional stage, late Tournasian stage, Mississippian subsystem, Carboniferous system (Traquair, 1881; Gardiner, 1985; Smithson *et al.*, 2012).

Other localities and horizons: Foulden Fish Bed, Foulden Burn, Berwickshire, Scotland, UK. Calciferous Sandstone Series, Cementstone Group, CM biozone, TN3 zone, Courceyan regional substage, Dinantian regional stage, late Tournasian stage, Mississippian subsystem, Carboniferous system (White, 1927; Gardiner, 1985; Wood & Rolfe, 1985; Dineley & Metcalfe, 1999; Smithson *et al.*, 2012); Coomsden Burn, Redewater, Northumberland, England, Cementstone Group, Dinantian regional stage, late Tournasian stage, Mississippian subsystem, Carboniferous

system (White, 1927; Moy-Thomas, 1938; Gardiner, 1985).

Diagnosis (emended from Traquair, 1881): As for genus.

Remarks: The genus *Fouldenia* includes all specimens from Foulden previously assigned to *Styracopterus* (Moy-Thomas, 1937; Gardiner, 1985), as well as specimens from the Calciferous Sandstones at Coldstream originally attributed to *Holurus ischipterus*, subsequently to *S. ischipterus* (or 'ischipterus'), and finally to *S. fulcratus* (Traquair, 1881, 1890; Moy-Thomas, 1937; Gardiner, 1985). The Coldstream specimens are here found to be indistinguishable from juveniles of *Fouldenia*, as originally predicted by Moy-Thomas (1937), and are thus reassigned to the latter taxon. The older name for the single known species within *Fouldenia* is therefore *ischipterus* (Traquair, 1881), not *ottadinica*. This has been corrected to *ischiptera* to agree with the gender of the genus. Likewise, the appropriate holotype for *Fouldenia* is GSE 2187, as designated for *Holurus ischipterus* by Traquair (1881), rather than NHM P13178 as proposed for *Fouldenia* by White (1927).

DESCRIPTION

Skull

The construction of the skull of *Fouldenia* is largely as illustrated by White (1927) and Gardiner (1985), but there are several discrepancies. Starting at the anterior end, *Fouldenia* bears an elongate, nearly erect median rostral, featuring sigmoidal lateral margins (Figs 5–7, 13). The rostral exhibits a slight curve in smaller specimens, but is significantly inclined halfway along its length in larger individuals, where it is ornamented with wide, horizontal ganoine bands (Figs 7B, 13D). The elongate, curved nasals of *Fouldenia* are bounded by the premaxilla and lachrymal ventrally, and frontal and dermosphenotic dorsally (Figs 5C, D, F, G, 6C, 7C, D, E). The nasal widens towards the gape and does not exhibit marginal indentations for the nostrils, contrary to Gardiner's (1985) reconstruction.

In the smallest specimens of *Fouldenia* (e.g. NHM P14562; Fig. 5B), the frontals and parietals are relatively wide and nearly equal in size, but in larger fish (e.g. NHM P13181; Fig. 7D) the frontals appear longer and narrower. These are joined at a diagonal suture line formed by the posterolateral processes on the frontals. The supraorbital canal runs through the lateral midline of these bones, and the mesial surface of the canal is apparent in the holotype NHM P13178 (Fig. 6B) and NHM P61549 (Fig. 6H). Frontal ornament consists primarily of horizontal striations,

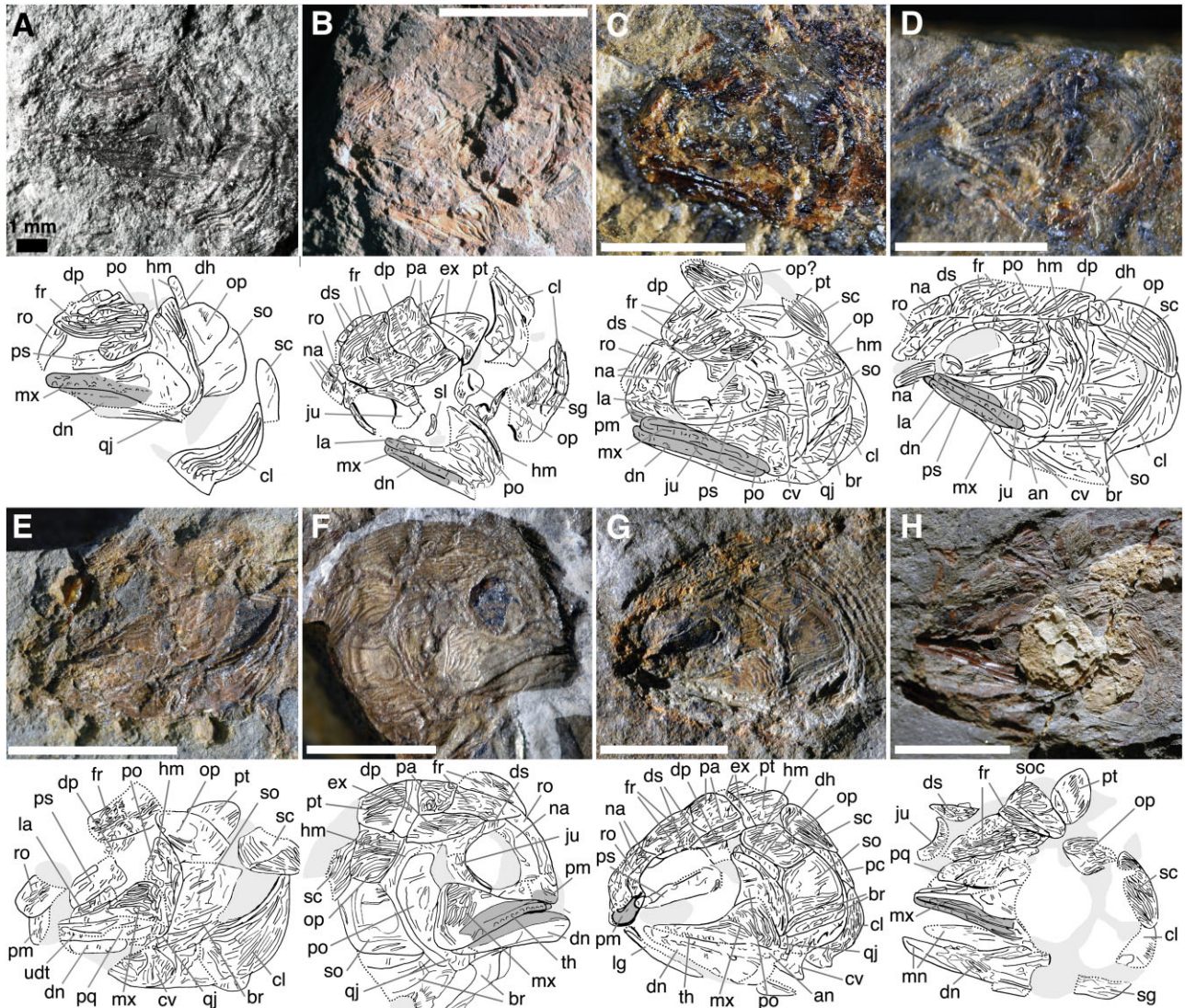


Figure 5. *Fouldenia* cranial material I. Photographs and interpretative drawings for specimens of 4–8 cm in total length. Unlabelled scale bars equal 1 cm. Medium-grey infill indicates the extent of thick ganoine ornament. Light-grey infill indicates unidentified skull material. A, NMS 1980.40.30; B, NHM P14562; C, NMS 1965.4.3; D, NMS 1956.5.1; E, NMS 1984.67.61; F, NHM P13179; G, NHM P13180; H, NHM P61546.

although a curved ridge at the midpoint marks a granulated or wavy posteromedial ornament field in both NHM P14562 (Fig. 5B) and NHM P13181 (Fig. 7D). The parietal ornament consists of intercalating wavy ridges laterally and more longitudinal bands dorsally, as is apparent in NHM P13179, NHM P13180, and NHM P13181 (Figs 5F, G, 7D). The dermopterotic is more like that described by White (1927) than Gardiner's (1985) reconstruction; the posterior portion is wide and the margins are smooth (Figs 5–7). The lateral margin curves to form an anterior point. This margin sits at the level of the curved ridge on the frontal in NHM P14562 (Fig. 5B)

and NHM P13181 (Fig. 7D), whereas the straight posterior margin contacts the extrascapular. This spatial relationship appears fixed in individuals of all sizes. *Fouldenia* possesses one pair of rectangular extrascapulars (Figs 5B, F, D, 6A, C, F, B, 7D) that sit at the level of the anterior margin of the opercular series, ornamented with short horizontal striations. The post-temporal is wide with a diagonal posterior margin. Although the general form is blunt and rounded in smaller fish (e.g. NHM P14562, NHM P13179, NHM P13180; Fig. 5B, F, G), it tapers to a rounded lateral point in larger specimens (e.g. NMS 1984.67.64, NHM P61002, NHM P61548;

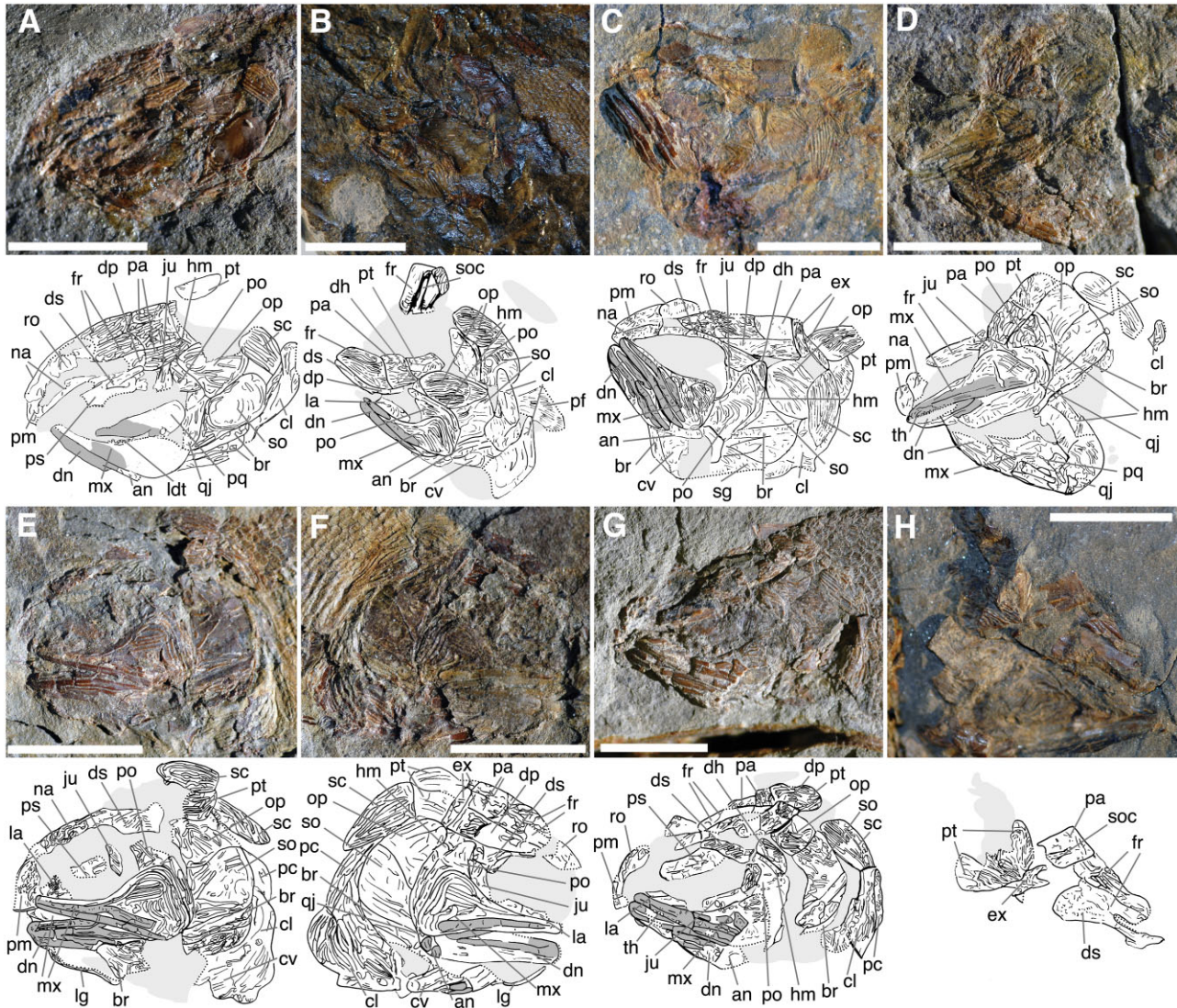


Figure 6. *Fouldenia* cranial material II. Photographs and interpretative drawings for specimens of 8.5–10 cm in total length. Unlabelled scale bars equal 1 cm. Medium-grey infill indicates the extent of thick ganoine plates covering other ornament. Light-grey infill indicates unidentified skull material. A, NHM P13183; B, NHM P13178; C, NHM P14564; D, NMS 1980.40.31; E, NMS 1984.67.65 (part); F, NMS 1984.67.65 (counterpart); G, NHM P61549 (part); H, NHM P61549 (counterpart).

Fig. 7A, B, D). The post-temporal is also long, extending past the opercular series.

The orbit in *Fouldenia* is bounded by the nasal, the dermosphenotic, and two infraorbitals (the lachrymal and jugal), but not by the premaxilla as described by Gardiner (1985). The dermosphenotic is ornamented with horizontal ridges (Fig. 6C) and stretches from the nasal to the preoperculum, leaving little room for any unobserved supraorbitals or suborbitals. In specimens under 7 cm in total length (e.g. NHM P14562 and NMS 1965.4.3; Fig. 5B, C), the dermosphenotic is a homogenous, thick crescent, whereas in larger specimens (e.g. NHM P14564 and NMS 1984.67.64;

Figs 6C, 7C) it features a distinct rectangular ventral portion and an elongated anterior process. Contrary to the previous description by Gardiner (1985) and coding for a t-shaped dermosphenotic by Gardiner & Schaeffer (1989), there is no evidence for a distinct posterior process (NHM P14562, NMS 1965.4.3, NMS 1956.5.1, and NHM P14564; Figs 5B, C, D, 6C).

The jugal is unfortunately incomplete in specimens of *Fouldenia*, but largely conforms to that described by Gardiner (1985). It forms a thick arch extending from the dermosphenotic to the midpoint of the orbit in NMS 1984.67.65 and NHM P13179 (Figs 5F, 6F), and widens with size (NHM P61548 and

symphyseal margin is diagonal and the jaw margin is prominent. In smaller specimens (Fig. 5), a more gracile, blunt dentary is almost entirely overlapped by the maxilla. The crescent-shaped angular in *Fouldenia* (Figs 5D, G, 6A, F, G) is obscured by the maxilla in smaller specimens, as described by White (1927) and Gardiner (1985). However, it extends posteriorly in larger fish (e.g. NHM P13185, NHM P14562, and NMS 1984.67.65; Figs 6B, C, 7B), with its juncture with the quadratojugal exposed.

Bands of smooth ganoine sit parallel with the jaw margins in all specimens, and the prominence of these is apparent in NHM P14564 (Fig. 6C), NHM 1984.67.65 (Fig. 6E), NHM P61549 (Fig. 6G), NHM 1984.67.64 (Fig. 7B), and NHM P61548 (Fig. 7E). The smallest specimens (e.g. NMS 1980.40.30 and NHM P14562; Fig. 5A, B) have a single rectangular tract on each side of the gape. This increases to two maxillary and three mandibular bands in mid-sized individuals, such as NHM P13179 (Fig. 5F), with an additional tract added along the anterodorsal margin of the maxilla in larger individuals like NMS 1984.67.65 (Fig. 6E). In the largest specimens of *Fouldenia* (e.g. NMS 1984.67.64; Fig. 7B), the bands are fused and intercalated, joined by shorter segments of ornament, forming a solid enameloid 'beak'. Similar ganoine cover is found in *Styracopterus* (see above) and the Visean styracopterid *Benedenius* (Van Beneden, 1871; Traquair, 1877–1914, 1878; De Koninck, 1878; Moy-Thomas, 1937; L.C.S., pers. observ.; Appendix S1), as well as the *Cheirodopsis*, *Amphicentrum*, *Paramesolepis*, and *Eurynotus*, albeit without distinct bands (L.C.S., pers. observ.; Appendix S1; Fig. 15). A line of tiny holes in the dentary ornament marks the mandibular canal in NMS 1984.67.64 (Fig. 7B), as do similar openings in *Eurynotus* (NMS 1957.1.5686; L.C.S., pers. observ.), *Amphicentrum* (Coates, 1988), and *Styracopterus* (L.C.S., pers. observ.). The rest of the maxilla is ornamented with concentric ridges at the margins (as in NMS 1984.67.65; Fig. 6E) and a distinct field of lateralized wavy ridges at the centre of the posterior portion. The angular in *Fouldenia* is almost completely covered by enameloid patches in fish over 9 cm in total length, such as NMS 1984.67.65, NHM P61002, and NMS 1985.67.64 (Figs 6F, 7A, B, 13C, D), yet is naked in smaller individuals.

The gape in all specimens of *Fouldenia* appears edentulous in lateral aspect. White (1927) described and illustrated small, blunt teeth from the posterior portion of the dermal mandible in NHM P13183 (Fig. 6A). These possess flat, bulbous crowns and thin waists (Fig. 14), resembling the pediculate dentition of the Palaeozoic actinopterygians *Mesolepis* (Traquair, 1879; Boulenger, 1902; Coates, 1988; L.C.S., pers. observ.; Appendix S1), *Eurysomus*, as

illustrated by Traquair (1879: pl. IV; fig. 6.5), and *Benedenius*, as described by Boulenger (1902). Given the position of these 'teeth' in the *Fouldenia* specimen NHM P13182–3 (Fig. 6A), away from the dentary and just ventral to the palatoquadrate, they are likely associated with coronoid-derived mandibular tooth plates like those found in *Styracopterus* and other eurynotiform fishes (Moy-Thomas & Miles, 1971; Coates, 1988; L.C.S., pers. observ.; Appendix S1; Fig. 14).

There is also evidence for an upper jaw dentition obscured from lateral view. In NHM P61549 (Fig. 6G), a homogeneous set of closely situated, small round elements is exposed by a gap in the anterior ramus of the maxilla. In NMS 1984.67.61 (Fig. 5E), tall cylindrical teeth with expanded crowns are found in the same area, with roots attached to what is either the mesial surface of the maxilla or reinforced palatal bones. NMS 1980.40.31 (Fig. 6D) has imprints of tooth or denticle bases overlying an impression of the maxilla and remnants of ganoine ornamentation. These teeth are positioned similarly to the maxillary dentition found in *Amphicentrum* and *Styracopterus*, but may also be associated with ectopterygoid-derived tooth plates, as in the same taxa (Bradley Dyne, 1939; Coates, 1988; L.C.S., pers. observ.; Appendix S1). In light of the mandibular tooth plate denticles in NHM P13183, it is probable that *Fouldenia* possesses both maxillary teeth and palatal tooth plates (Fig. 14), but the fossil evidence and/or morphological similarity prevents definite differentiation.

The jaws of *Fouldenia* are supported by a nearly vertical suspensorium, as reconstructed by Gardiner (1985). The hyomandibula is exposed in a number of individuals of different sizes, including NMS 1980.40.30, NHM P14562, NHM P14564, and NMS 1985.67.64 (Figs 5A, B, 6C, 7B). The thick hyomandibula features an expanded dorsal head located near the dermopterotic, as in *Amphicentrum* (Bradley Dyne, 1939), and covered laterally by a teardrop-shaped dermothyal with an ornament of vertical ridges (Figs 6G, 7B). Whereas the hyomandibula is nearly straight in smaller specimens (e.g. NMS 1980.40.30; Fig. 1A), it exhibits a high degree of curvature in the large individuals listed above.

The preoperculum in *Fouldenia*, best preserved in NMS 1980.40.30, NHM P13180, NHM P14564, and NHM P61002 (Figs 5A, G, 6C, 7A), is tall with an indistinct dorsal arm ending near the skull roof and a thick posteroventral process to the quadratojugal. The anterior margin is shallowly curved, whereas the posterior margin mirrors the hyomandibula and is lined by a wide ridge. A horizontal pit line is visible just above the maxilla in many specimens (e.g. NHM P61002, NHM P13180, NHM P13179, NMS 1956.5.1, and NMS 1985.67.64; Figs 5D, F, G,

7A, B), and bisects the ornament into a ventral field of vertical ridges and a dorsal field of horizontal and inclined lines (see NHM P14564 and NHM P61002; Figs 6C, 7A).

Opercular series

The operculum of *Fouldenia* is similar to that reconstructed by White (1927), in that it is slightly inclined with a rounded apex just under the extrascapular and a sigmoidal ventral margin at the level of the horizontal pitline (see NMS 1984.67.64, NHM P13179, NMS 1980.40.30; Figs 5A, F, 7B). The bone is wider and much less tapered in individuals over 8 cm (Figs 6, 7), so that it appears more plate-like than ovoid. The ornamentation consists of intercalated diagonal ridges running posteroventrally, as seen in NHM P61002 (Fig. 7A).

The suboperculum of *Fouldenia* is largely rectangular in NHM P61002 (Fig. 7A). It extends ventrally to the quadratojugal and posteriorly to the level of the post-temporal. The posterior margin is slightly rounded, whereas the ventral margin is sigmoidal, bearing an anteroventral process reaching towards the jaw joint, as originally illustrated by White (1927; Figs 6E, 7A, 13) and also found in other styraconterids, euryotiforms, and the Palaeozoic taxa listed in the description of *Styraconterus* (L.C.S., pers. observ.; Appendix S1). Like the other styraconterids (L.C.S., pers. observ.; Appendix S1), the ornamentation of the suboperculum in NHM P13180 (Fig. 5G) and NHM P61002 (Fig. 7A) is divided: the ganoine ridges on the process and near the ventral margin are posteroventrally diagonal, whereas the ornamentation elsewhere radiates horizontally or dorsally from the anterior margin of the bone.

Gulars and branchiostegals

Fouldenia has small leaf-shaped median gular with ventral ornament of concentric bands mirroring the same shape, as revealed by the displaced bones of NMS 1984.67.64 and NHM P61548 (Fig. 7B, E). The morphology of rectangular lateral gulars in NHM P13180, NMS 1984.67.65, and NMS 1984.67.64 (Figs 5G, 6E, 7B) is difficult to distinguish from the branchiostegals. The largest individuals of *Fouldenia* may have up to 12 rectangular branchiostegal rays with rounded distal margins, although no specimen has a complete set (Fig. 7). The rays increase in length posteriorly and are held at an almost 45° angle to their origin in 10–12-cm fish, as shown by NMS 1984.67.64 (Fig. 7B). This ‘flaring’ is unusual as the branchiostegals are directed inwards towards the ventral midline in most early actinopterygians (Gardiner, 1984). It might be caused by diagenetic crushing or other taphonomic processes, as all Foulden actinopterygians share this trait (White,

1927; Moy-Thomas, 1938; Gardiner, 1985; Fig. 17). However, the open positioning of the branchiostegals in these fishes may be induced by a robust clavicle and shoulder girdle, forcing the branchiostegal bases above the ventral body margin (Gardiner, 1985; L.C.S., pers. observ.; Appendix S1; Figs 5E, B, 7C, E, 13C, D). It is notable that individuals of *Fouldenia* under 8 cm in length do not exhibit such flaring, and likewise have more ventrally positioned gapes (Figs 5C, D, 13A, B).

Shoulder girdle

The inclined, rounded supracleithrum in *Fouldenia* extends to a pointed margin near the midline of the suboperculum (Fig. 7B). There is no evidence of the course of the posterior lateral line, as it is likely to be obscured by the dense, vertical ganoine ridges spread out around the midline in NHM P61548 (Fig. 7B). Neither White (1927) nor Gardiner (1985) described postcleithra in *Fouldenia*, but a single postcleithrum is preserved in NMS 1984.67.62, NMS 1984.67.65, NHM P61549, and NHM P13180 (Figs 5C, G, 6E, G). This is similar to the postcleithra in *Paramesolepis* (Moy-Thomas & Bradley Dyne, 1938), *Amphicentrum* (Coates, 1988), and *Styraconterus* (L.C.S., pers. observ.; Appendix S1), in that it is long with rounded margins and ends around the first branchiostegal.

The cleithrum in *Fouldenia* is inclined posteriorly, and bears a broadly crescentic dorsal process with a pointed dorsal limit and a rounded posterior process underlying the pectoral fin insertion. (Figs 5A, B, E, 6B, 7A), as in other Foulden actinopterygians (White, 1927; Moy-Thomas, 1938; Gardiner, 1985; L.C.S., pers. observ.; Appendix S1). The cleithrum is ornamented with vertical stripes of ganoine that mirror the curved posterior margin. A process of the endoskeletal shoulder girdle is exposed where the cleithrum curves around the point of pectoral fin insertion in NHM P14562 (Fig. 5B) and NHM P61546 (Fig. 5H), and is covered with longitudinal ridges distinct from any nearby dermal ornament. The cleithrum joins with the laterally convex posterior margin of the clavicle at the level of the opercular series in NMS 1984.67.62 (Fig. 7C) and NMS 1984.67.65 (Fig. 6F). The morphology of the clavicle is largely obscured, but it appears very thick (as discussed above) and somewhat triangular in the lateral dimension in NMS 1984.67.61, NHM 1984.67.65, NHM P61002, and NHM P14564 (Figs 5E, 6C, F, 7A).

Paired fins

The pectoral fin is situated near the ventral body margin and has a nearly vertical insertion into the shoulder. The fin is supported by at least six radials: posterior/ventral radials preserved in NHM P61002 (Fig. 8J) and NMS 1984.65.61 (Fig. 8C) are elongate,

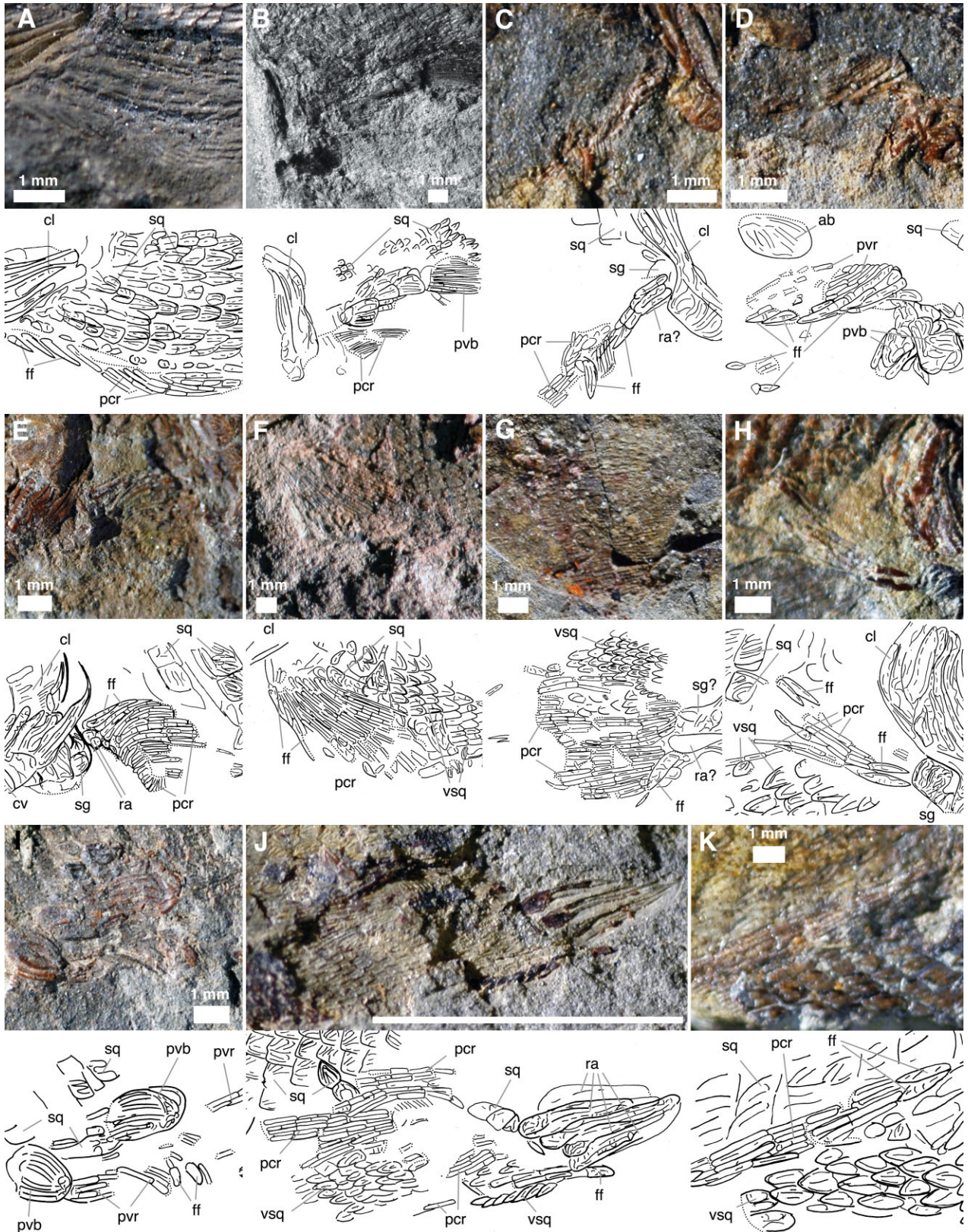


Figure 8. *Fouldenia* paired fins. Unlabelled scale bars equal 1 cm. A, GSE 2143 pectoral; B, 1980.40.30 pectoral; C, 1984.67.61 pectoral; D, NMS 1984.67.61 pelvic; E, GLAHM V8327 pectoral; F, NHM P13183 pectoral; G, NHM P14564 pectoral; H, NMS 1984.67.65 pectoral; I, NHM 1984.67.65 pelvic; J, NHM P61002 pectoral; K, NMS 1984.67.64 pectoral.

with narrow, somewhat overlapped proximal ends and rounded distal portions. The middle of each radial in NHM P61002 (Fig. 8J) consists of a narrow cylindrical body with a thin ventral flange. GLAHM V8327 (Fig. 8E) shows the squat anterior/dorsalmost radials, which sit in a shorter space between the primary fin rays and the dermal shoulder. The presumptive propterygium is surrounded by fin rays, as is diagnostic for actinopterygians (Coates, 1999; Gardiner *et al.*, 2005). The difference in length between the anterior and posterior radials matches the diagonal orientation of lepidotrichial bases in NHM P13183, GLAHM V8327, and NHM P14564 (Fig. 8F, G), an arrangement found in other early actinopterygians such as *Mimipiscis* (Choo, 2011) and *Styracopterus* (L.C.S., pers. observ.; Appendix S1).

As noted by White (1927), no specimen of *Fouldenia* exhibits a complete pectoral fin, obscuring its exact shape. The proximal fins in GSE 2143, GLAHM V8327, NHM P13183, and NHM P14564 (Fig. 8A, E, F, G) suggest that it was wide-based with a slightly curved anterior margin lined by fringing fulcra that are barely distinguishable from lepidotrichial terminals. The lepidotrichia are thin, cylindrical, and densely packed, with long segments throughout their length. Thus, the pectoral fin more closely resembles that of *Phanerosteon oveni* (White, 1927; L.C.S., pers. observ.; Appendix S1) and the Visean *Tarrasius* (Sallan, 2012), than *Styracopterus*.

Only a handful of specimens have incomplete pelvic fins. The curved anterior edge is preserved in NMS 1984.67.61 (Fig. 8D), with an unsegmented primary fin ray and further lepidotrichia similar to those of the pectoral fin. Large, leaf-shaped fringing fulcra are differentiated from lepidotrichial terminals by linear central furrows. Two large, ovoid basal fulcra overlap the leading edge of the pelvic fin in NMS 1984.67.65 (Fig. 8I). These are ornamented with concentric, longitudinal striations that fuse at the posterior margin. The size of the fin base is restricted by the short distance between the pelvic and anal basal fulcra in all fish, even though the position of the pelvic fin changes with size (Fig. 13). In the 4-cm individual NMS 1980.40.30, the pelvic fin is situated near the distal pectoral fin, whereas in larger specimens, such as NMS 1984.67.65, it originates posterior to the body midline (Fig. 8).

Median fins

The dorsal fins in the largest specimens of *Fouldenia* are as described by White (1927): tall and superficially triangular, with the peak in the posterior half of the fin. In these individuals (e.g. NHM P61548 and NHM P61549; Fig. 9E, F), the anterior margin of the dorsal fin and leading lepidotrichia are straight, and the fin originates in the posterior portion of the

body (Fig. 13C, D). In the smaller specimens NMS 1980.40.30, NMS 1980.40.27, and NMS 1965.4.3 (Fig. 9A, B, C), the dorsal fin is rounded with curved lepidotrichia held nearly parallel with the body axis, and originates at the midpoint of the trunk, opposite the pelvics and well before the anal fin (Fig. 13A, B). Robust, erect basal fulcra sit against the dorsal lepidotrichia. Disarticulated fulcra in NMS 1980.40.31 (Fig. 9D) exhibit needle-like distal processes with paired cylindrical ridges separated by a deep furrow, bounded ventrally by rounded plates with concentric ornament. The primary dorsal lepidotrichia are thick and unsegmented, presenting a spine-like form when combined with the elliptical fringing fulcra (Fig. 9). The remaining lepidotrichia have rounded bases and short plate-like segments with cylindrical anterior ridges.

The anal fin in *Fouldenia* is very similar to the dorsal fin, with the first few lepidotrichia likewise consolidated into 'spines', a feature readily apparent in NMS 1965.4.3 (Fig. 10C, D). Anal basal fulcra in NMS 1984.67.62 and NHM P61548 (Fig. 10I, J) are evocative of their dorsal equivalents and those of *Styracopterus* (see above). However, more anterior basal fulcra in this series of four or five are thick and rounded like the dorsal ridge scales. The anal fin base extends to the base of the caudal peduncle. Like the dorsal fin, the anal fin is rounded in smaller specimens such as GSE 2187 (Fig. 10B) and NHM P13183. The anterior margin remains curved in the largest fishes, whereas the posterior margin is deeply concave (e.g. NHM P13183), resulting in a superficially half-crescent form in NHM P61548 (Fig. 10J).

Tail and caudal fin

The caudal region of *Fouldenia* comprises over a third of the total body length in the smallest specimens (e.g. NMS 1980.40.30; Figs 11A, 13A) and a quarter in the largest (e.g. NHM P61549; Figs 12D, 13D). As described by White (1927), the tail consists of a thick caudal peduncle, a deep yet shallowly cleft caudal fin, and a very long, tapering axial lobe extending beyond the fin. The dorsal surfaces of the peduncle and axial lobe are covered by enlarged basal fulcra that, as preserved in NHM P13183 and holotype NHM P13178 (Fig. 12A, B), are identical to the dorsal fin basal fulcra in NMS 1980.40.31 (Fig. 9D). The posteriormost basal fulcra on the ventral surface of the peduncle in NMS P13183 (Fig. 12A), originally illustrated by White (1927), are nearly mirror images, except that the paired rami separate to form distinct points distally (Fig. 12A), and are thus narrower versions of the same scales in *Styracopterus*. More posterior basal fulcra on both the peduncle and axial lobe are progressively shorter and have pointed apices,

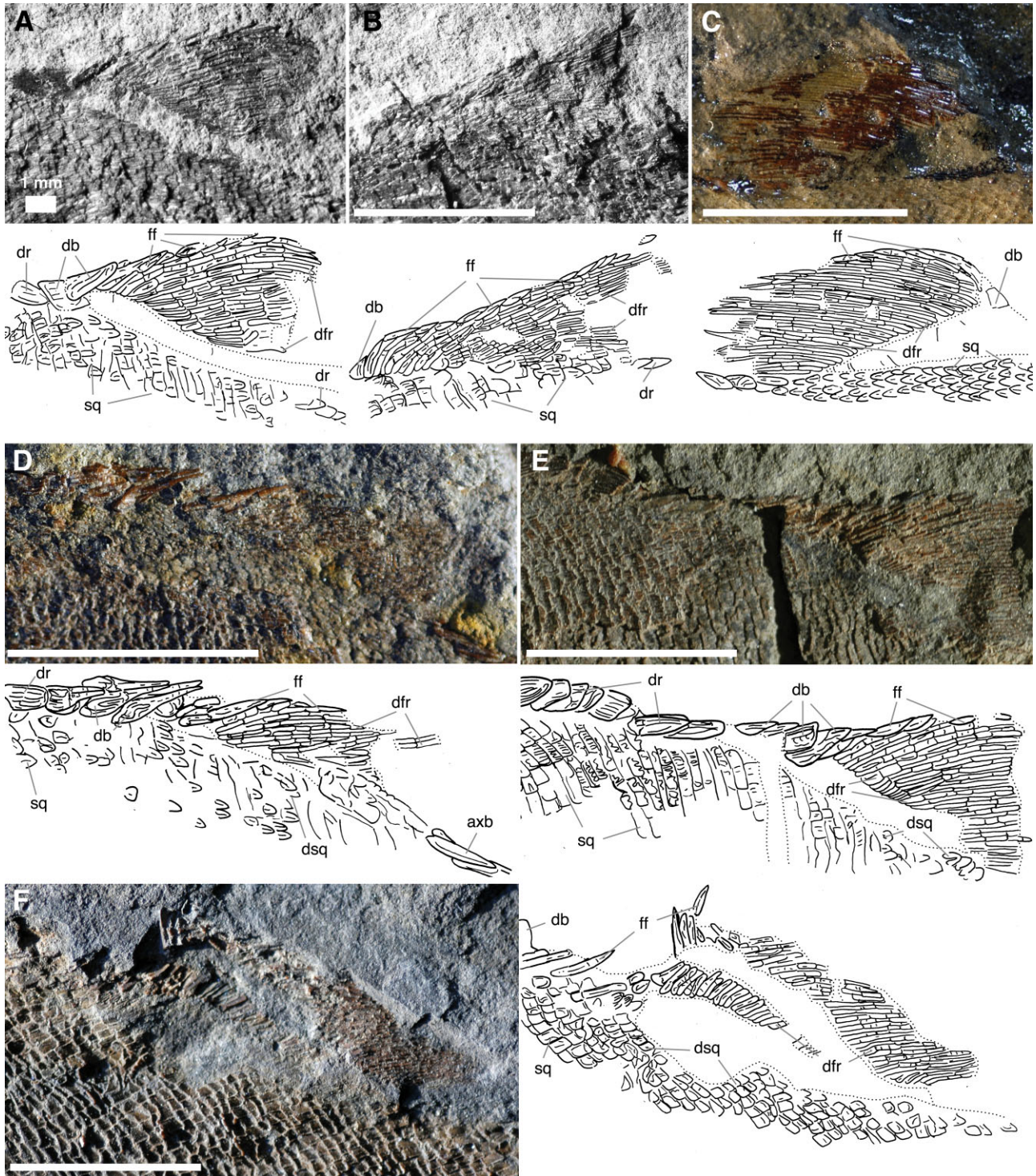


Figure 9. *Fouldenia* dorsal fins. Unlabelled scale bars equal 1 cm. A, NMS 1980.40.30; B, NMS 1980.40.27; C, NMS 1965.4.3; D, NMS 1980.40.31; E, NHM P61548; F, NHM P61549.

providing a highly overlapped, elliptical appearance in lateral view (Figs 11, 12).

Prominent fringing fulcra line the entire ventral margin of the caudal fin in NMS 1965.4.2,

NMS 1965.4.3, NMS 1980.40.31, and NHM P13185 (Figs 11A, F, 12C, E). These are also elliptical, slightly overlapped, and sit perpendicular to the lepidotrichia. Fulcra appear as narrow spines with longitudinal

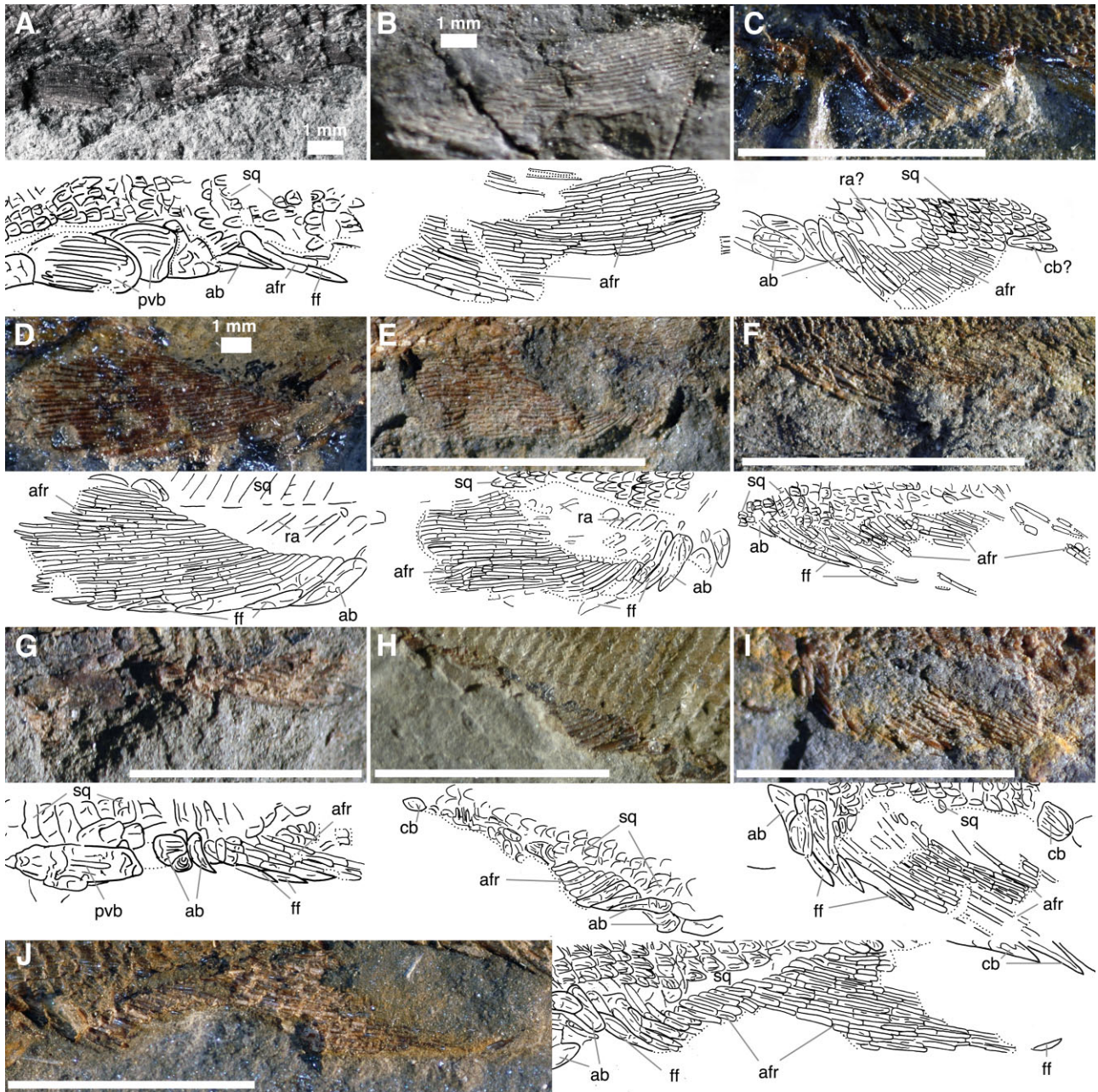


Figure 10. *Fouldenia* anal fins. Unlabelled scale bars equal 1 cm. A, NMS 1980.40.30; B, GSE 2187; C, NMS 1965.4.3 (part); D, NMS 1965.4.3 (counterpart); E, NMS 1984.67.61; F, NMS 1980.40.31; G, NMS P61549; H, NHM P61002; I, NMS 1984.67.62; J, NHM P61548.

furrows on the base of the axial lobes in NHM P13183 and NMS 1965.4.2 (Figs 11C, 12A), becoming smaller and more inclined distally in GSE 2187, NMS 1965.4.3, and NHM P13185 (Figs 11C, F, 12E). Fulcra in the second half of the series are paired in larger specimens (Fig. 12), a trait previously reported only in *Cheirolepis* (Gardiner, 1984), but also found along the distalmost tails of *Styracopterus*, *Aesopichthys*, and other Foulden fishes (L.C.S., pers. observ.;

Appendix S1). In fact, all the axial lobe fulcra are paired in smaller, probably juvenile individuals with relatively shorter axial lobes, such as NHM P13187, NMS 1965.4.2, and NMS 1980.40.27 (Fig. 11B, C, E), suggesting fusion during ontogeny in *Fouldenia* and perhaps other actinopterygians. The large specimens NMS 1980.40.31 and NHM P13185 (Fig. 12C, E) are the only individuals with complete axial lobes, which lack fulcra distal to the caudal fin. This arrangement

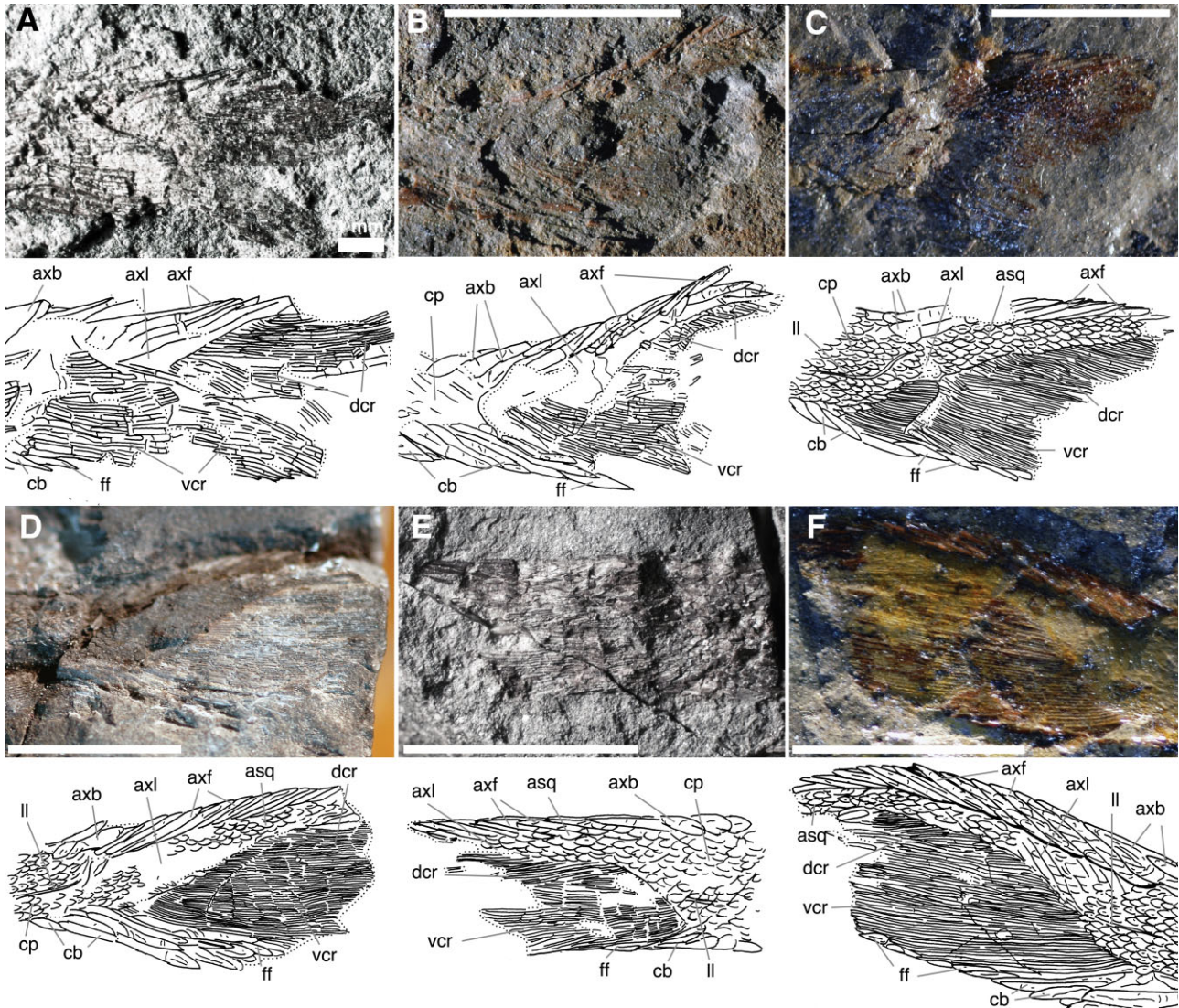


Figure 11. *Fouldenia* tails and caudal fins I. Photographs and interpretative drawings for specimens of 4–7 cm in total length. Unlabelled scale bars equal 1 cm. A, NMS 1980.40.30; B, NHM P13187; C, NMS 1965.4.2; D, GSE 2187; E, NMS 1980.40.27; F, NMS 1965.4.3.

is similar to that of the elongated axial lobe in the deep-bodied Serpukhovian genus *Aesopichthys* (Poplin & Lund, 2000; L.C.S., pers. observ.; Appendix S1), as well as other styracopterids and *Eurynotus* (e.g. NMS 1878.18.12; Traquair, 1879; L.C.S., pers. observ.; Appendix S1).

Both NMS 1980.40.31 and NHM P13185 (Fig. 12C, E) bear remnants of a distinct epichordal fin around the distalmost tail. Lepidotrichia found along the ventral surface of the posteriormost axial lobe differ from the caudal lepidotrichia in their tapering morphology, and originate after a considerable gap.

The first few lepidotrichia of the caudal fin are consolidated and bear elongated fringing fulcra like their equivalents in the median fins (Figs 11, 12).

Likewise, the remaining rays in the ventral lobe have plate-like segments with anterior ridges and taper to a point (Figs 11, 12). The bases of ventral lobe lepidotrichia are distinctly thick and wide in NHM P61548 (Fig. 12), giving the appearance of an extended peduncle. Lepidotrichia in the dorsal lobe originate from the axial lobe in NHM P13185, NHM P61549, and NMS 1980.40.31, and are similar to the paired fin rays in their thin, cylindrical morphology. These apparently lack bifurcation, although most are truncated at their distal extremities.

The overall appearance of the tail and caudal fin varies between size classes. Small individuals have long peduncles that exhibit a gradual, not well marked, transition into a thin axial lobe (Figs 11, 12,

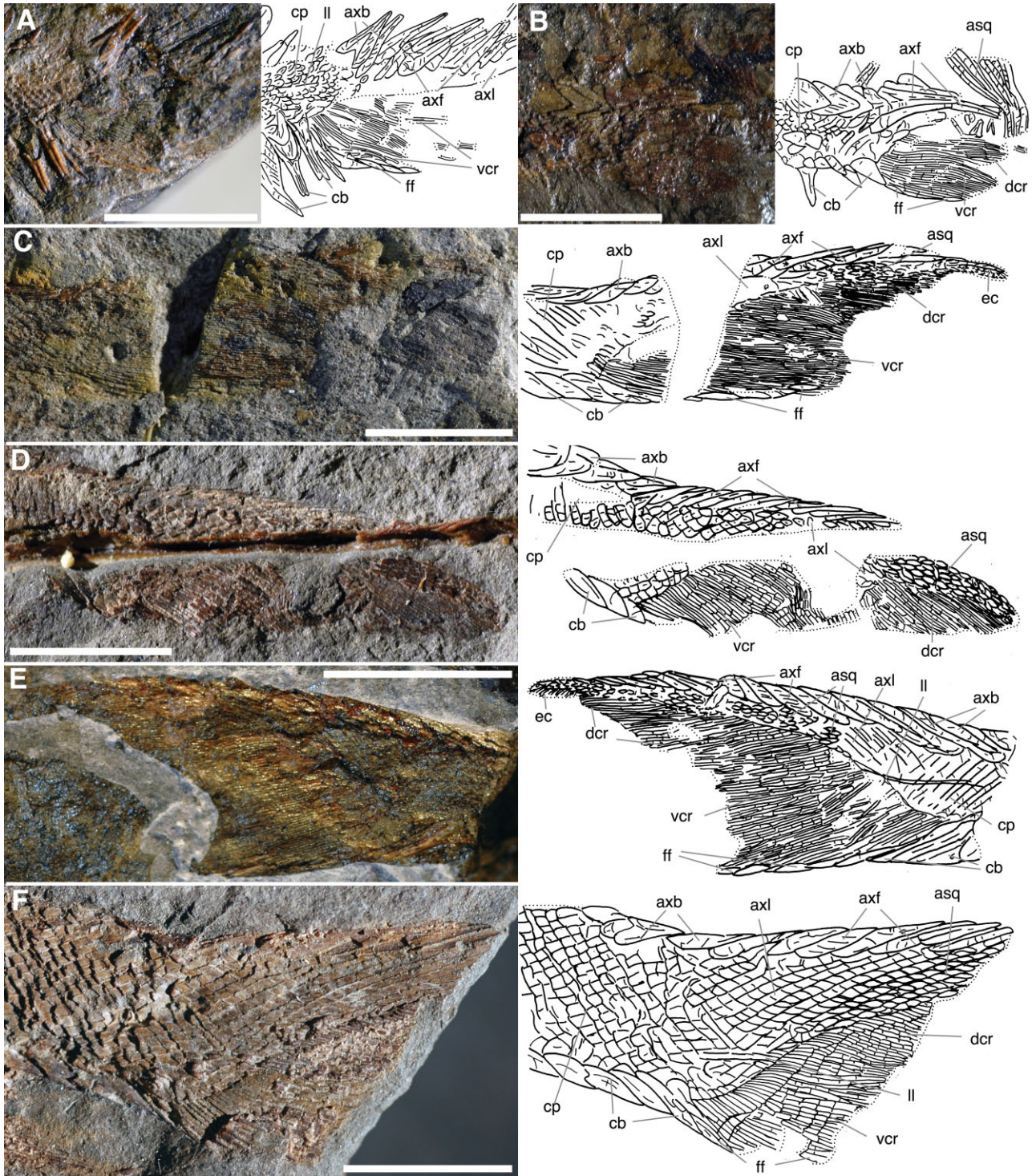


Figure 12. *Fouldenia* tails and caudal fins II. Photographs and interpretative drawings for specimens of 8–12 cm in total length. Unlabelled scale bars equal 1 cm. A, NHM P13183; B, NHM P13178; C, NMS 1980.40.31; D, NHM P61549; E, NHM P13185; F, NHM P61548.

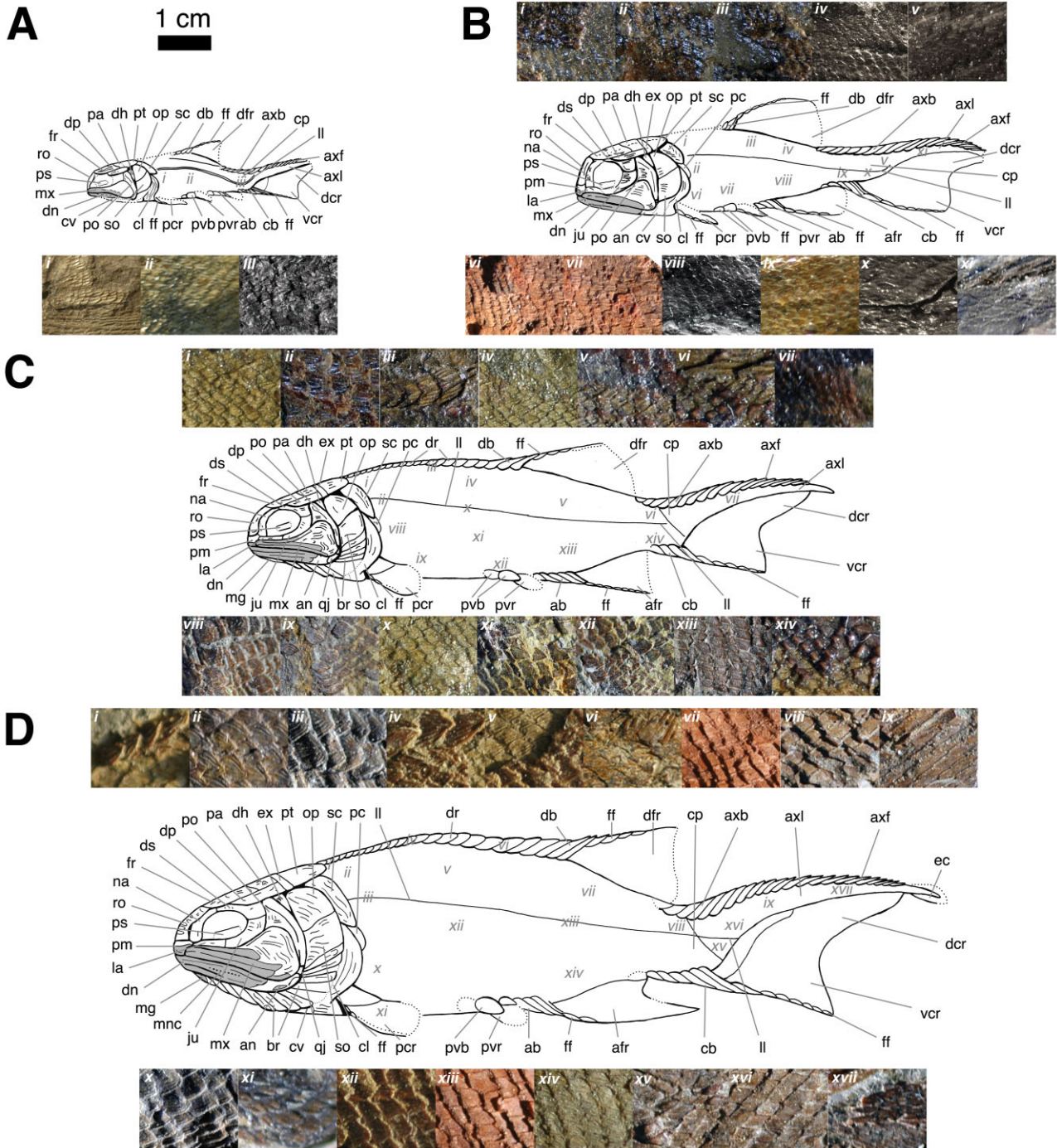


Figure 13. *Fouldenia* reconstructions and squamation. Reconstruction drawings of various size classes are based on all available specimens within each class. Squamation photographs are shown at three times the size, at the scale of reconstructions. Roman numerals on the reconstructions indicate the position of scales with matching labels. Medium-grey infill indicates the documented extent of thick ganoine plates covering other ornament. A, 3–4 cm, scales from GSE 2143; NHM 1965.4.2 and NHM 1980.40.30; B, 6–7 cm, scales from NMS 1965.4.3, NMS 1965.4.6, NHM P14562, and GSE 2187; C, 8–9 cm, scales from NHM P13183, NHM P61546, NHM P13178, and GLAHM V8327; D, 11–12 cm, scales from NHM P61002, NHM P61548, and NMS 1984.67.64.

13A, B). Their long caudal fins exhibit shallow clefts and small, narrow fringing fulcra. In contrast, the largest individuals, such as NHM P61548 and NHM P13183 (Fig. 12E, F), have tall peduncles with nearly vertical posterior margins and a marked transition into a wide-based, distally tapering axial lobe. Caudal fins have deep clefts and are equilobate, and feature robust fringing fulcra. The terminus of the lateral line changes along with the morphology. In the 5-cm individual NMS 1965.4.2 (Fig. 11C), the lateral line curves parallel with the posterior margin of the caudal peduncle as it approaches the end of the body, turning onto the midline of the axial lobe. In the 12-cm fishes NHM P13185 and NHM P61548 (Fig. 12E, F), the lateral line is largely horizontal, and appears to end on the caudal fin just ventral to the base of the axial lobe, but may continue at the caudal fin base.

Squamation

The largest individual of *Fouldenia*, NHM P61548 (~12 cm EBL), has 51 sigmoidal scale rows from the skull to the peduncle, with up to 34 scales from the dorsal ridge to the anal midline. However, individuals under 6 cm in length have significantly fewer scales: NMS 1965.4.2 (5 cm EBL) has approximately 34 rows of up to 25 scales. The slightly longer NMS 1965.4.6 (5.5 cm EBL) has around 40 rows, whereas NMS 1980.40.27 (6.5 cm EBL) had almost the maximum number of rows, although the number of scales per row remains at 25. The larger NMS 1984.67.61 (7.5 cm EBL) has 30 scales per row at maximum body depth. Fish of 8–9 cm in total length, such as NHM P61002 and NMS 1984.67.63, have approximately the same counts as the largest specimen. Thus, scale counts increase with body size primarily through the generation of rows up to the midpoint of the observed growth series, at which point addition at the margins and increases in scale height cover changes in body area.

In smaller specimens of *Fouldenia*, such as GSE 2143 (3 cm EBL), NMS 1980.40.30 (4 cm EBL), NMS 1965.4.6 (5.5 cm EBL), NHM P14562 (6 cm EBL), and GSE 2187 (6 cm EBL), all scales are small and acuminate, with smooth margins (Fig. 14A, B), and bear two longitudinal bands of smooth ganoine. These are identical to the scales found on the smallest specimens of the co-occurring *Aetheretmon* (NHM P61006; L.C.S., pers. observ.). Like *Aetheretmon*, the smallest *Fouldenia* individuals, such as NMS 1980.40.30 (Fig. 9A), lack scales around the bases of their median fins. This suggests that squamation first developed around the lateral line in these fishes, just as it does in living teleosts (Koumoundoros, Divanach & Kentouri, 2001).

Juvenile scales develop near the dorsal and ventral midlines and are retained on the posterior

half of specimens NMS 1965.4.3, NMS 1984.65.61, and NMS 1956.5.1, which range from 7 to 7.5 cm in estimated body length, and have greater body depths anteriorly (Fig. 13C). In individuals over 8 cm in length [e.g. NHM P13178 (9 cm EBL), NMS 1984.67.65 (9.5 cm EBL), NHM P61502 (10 cm EBL), NMS 1984.67.65 (11 cm EBL), and NMS 1984.67.65 (11 cm EBL); White 1927; Fig. 13C], 'juvenile' scales are limited to an anterior ventral field around the pectoral fins and clavicle. The largely scaleless actinopterygian *Phanerosteon* (e.g. NMS 1970.26.27; L.C.S., pers. observ.; Appendix S1), found at both Foulden and Glencartholm, exhibits rows of small scales in the same area (White, 1927; Gardiner, 1985). Scale rows in this region in *Amphicentrum* and *Benedenius* have a different orientation from those on the rest of the flank (Traquair, 1878, 1879; L.C.S., pers. observ.; Appendix S1). This anterior ventral field (or pectoral peduncle; Sire & Arnulf, 1990) might represent a distinct region of scale development in some early actinopterygians, just as it does in some living teleosts (Koumoundoros *et al.*, 2001).

In individuals larger than 8 cm in length, such as NMS 1984.65.61 and NHM P13182 (Fig. 13C, D), rhomboid scales on the anterolateral flank have smooth margins and exhibit four or more posteroventrally diagonal bands of ganoine. The scales in larger fish (e.g. NHM P61546) are taller and feature a more complex ornament of diagonal ganoine bands that fuse in nested fashion towards the posteroventral corner and a stripe lining the posterior margin. This ornamentation is repeated vertically on the taller, more rectangular anterior flank scales of the larger specimens. A small notch on the posterior margin marks the transition between ornamentation fields, giving the bilobate appearance described by White (1927) and the impression of scale fusion.

Scales on the posterior flank of fish over 8 cm (e.g. GLAHM V8327 and NHM P13182) are shorter and horizontally elongated (Fig. 13C, D), yet exhibit a rhomboid shape and ornamentation similar to the more anterior squamation. In specimens over 10 cm in total length, these scales have the same relative height and morphology as anterior flank scales in 8-cm fish (Fig. 13C, D). In large specimens of *Fouldenia*, the lateral line scales are taller than other members of the same row, but are otherwise indistinguishable apart from a raised cylindrical bump that bisects the ornament horizontally (Fig. 13C, D). The lateral line runs from the level of the supracleithrum to the midline of the caudal peduncle in the largest specimens (Figs 12F, 13D). The diverse flank scales in *Fouldenia* are similar in shape and ornament to various iterations in the Permian taxon *Acrolepis sedgwicki* Agassiz, 1833–1844, as first illustrated by Agassiz (1833–1844; NHM P553; L.C.S., pers. observ.;

Appendix S1), which is a large marine fusiform actinopterygian that diverges from *Fouldenia* in most other non-plesiomorphic traits.

All specimens over 8 cm in length possess a distinct 'hinge line' in the peduncle squamation, marking the transition between scales with vertically directed pegs and those with posteriorly directed pegs, a trait found in many other early actinopterygians (Patterson, 1982; Gardiner & Schaeffer, 1989; Coates, 1998, 1999; Figs 12F, 13C, D). Peduncle rows on both sides of the hinge line contain small rhomboid scales fully covered in ganoine and featuring an anterior ridge (Figs 12D, 13C, D). These resemble the micro-squamation present on the entire tail surface of *Tarrasius* (Sallan, 2012; L.C.S., pers. observ.; Appendix S1). Scales on the proximal axial lobe and along the base of the caudal fin are diamond shaped, whereas the more distal squamation consists of very small elliptical scales resembling the 'juvenile' flank scales (Figs 12D, 13).

Fouldenia specimens over 8 cm in length possess prominent dorsal ridge scales that run from the nape to the dorsal fin basal fulcra (White, 1927; Fig. 13C, D). They are highly overlapped: each has a triangular furrow on the anterodorsal surface to hold the distal end of their neighbour. The anteriormost ridge scales are squat with rounded margins and slightly pointed apices, and feature longitudinal striations. Ridge scales in the posterior half of the series are longer, wider, and vertically oriented, and exhibit more robust ornamentation. The last few ridge scales are thinner and have distal processes like the dorsal basal fulcra, and are similarly erect and overlapped. Thick ganoine ridges on these scales run parallel with the body axis. Thus, the transition between the last two dorsal ridge scales, the basal fulcra, and the primary lepidotrichia appears gradual (Fig. 13C, D).

DISCUSSION

THE INTERRELATIONSHIPS OF THE STYRACOPTERIDAE

Comparisons among the Styraopteridae

Fouldenia and *Styraopterus* were previously consolidated into a single genus and species: *S. fulcratus* (Gardiner, 1985). However, although they are both styraopterids, based on the diagnostic traits given above, *Fouldenia* is readily distinguishable from *Styraopterus* at all sizes by skeletal morphology, ornamentation, and dentition.

An articulated mandible, suboperculum, and primary brachioistegal ray from the late Tournaisian of Symond's Yat, Herefordshire, England, in the collections of the NHM (NHM P62956), has been attributed to *Styraopterus* sp. (Appendix S1) on the basis of ganoine bands covering the dentary. The suboper-

culum is similar to that of *Styraopterus* specimen GSE 5663–4 (L.C.S., pers. observ.), as well as *Benedenius* from the early Visean of Belgium (Fraipont, 1890; L.C.S., pers. observ.; Appendix S1), in that wavy ganoine stripes radiate from the anterior margin and the prominent anteroventral process bears a distinct linear ornament. However, this material is not diagnostic for any known taxon, is considerably older than the first appearance of *Styraopterus*, and is much larger than any contemporary specimen of *Fouldenia*. Thus, although NHM P62956 is likely to be a styraopterid, it cannot be further attributed.

Traquair (1890) first noted the connection between *Styraopterus* and *Benedenius*, a 'platysomoid' from the Visean of Belgium (Traquair, 1878, 1879) which was subsequently moved the 'paleoniscoid' group on the basis of this relationship (Fraipont, 1890; Boulenger, 1899, 1902; Moy-Thomas & Miles, 1971). Moy-Thomas (1937) asserted that *Benedenius* was little more than a deeper-bodied, much larger (~30 cm EBL; Boulenger, 1899) version of the Glencartholm taxon in all aspects. He established the family Styraopteridae to hold these genera (including *Fouldenia*). However, Gardiner (1985) split this relationship on the basis of perceived differences in dentition and jaw shape in published reconstructions.

Although a re-description of *Benedenius* is long overdue, it can be shown from previous reports and re-examination of known specimens that the genus shares all the diagnostic traits of the Styraopteridae (L.C.S., pers. observ.; Appendix S1; Fig. 15C). The edentulous jaw margins and dermal bones of *Benedenius* are fully covered by plates of smooth ganoine (Fraipont, 1890; Fig. 15C), with ornamentation on some bones (such as the frontal and suboperculum) nearly identical to that in *Styraopterus* (Fraipont, 1890; L.C.S., pers. observ.; Appendix S1). Boulenger (1902) described the 'teeth' along the lower jaw of *Benedenius*, which are notably hidden from lateral view and placed mesially to the jaw margin (L. C. S. pers. obs; Appendix S1), as 'intermediate in shape between those of *Mesolepis* and *Eurysomus* (Boulenger, 1902: 52). In this, they resemble the mandibular denticles in *Fouldenia* (White, 1927; Figs 6, 14). Boulenger (1902) described the fringing fulcra and scythe-like pectoral fins of *Benedenius* as generally matching the forms in *Eurynotus* (Agassiz, 1833–1844; Traquair, 1879; Coates, 1994; L.C.S., pers. observ.; Appendix S1; Fig. 15), which likewise describes the morphology in *Styraopterus*. In addition, the trunk and ridge scale morphology illustrated by Fraipont (1890) and Boulenger (1899) is highly similar to their counterparts in *Styraopterus*, including the ornament of the rhomboid scales of the dorsal trunk, the erect, pointed scales of the dorsal ridge,

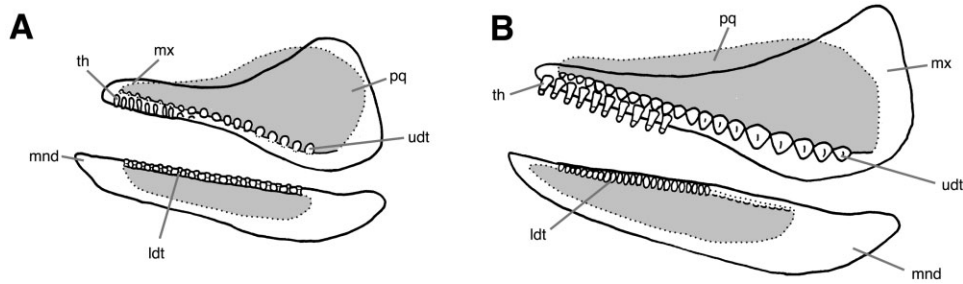


Figure 14. Reconstructions of styraopterid dentitions: A, *Fouldenia*; B, *Styraopterus*.

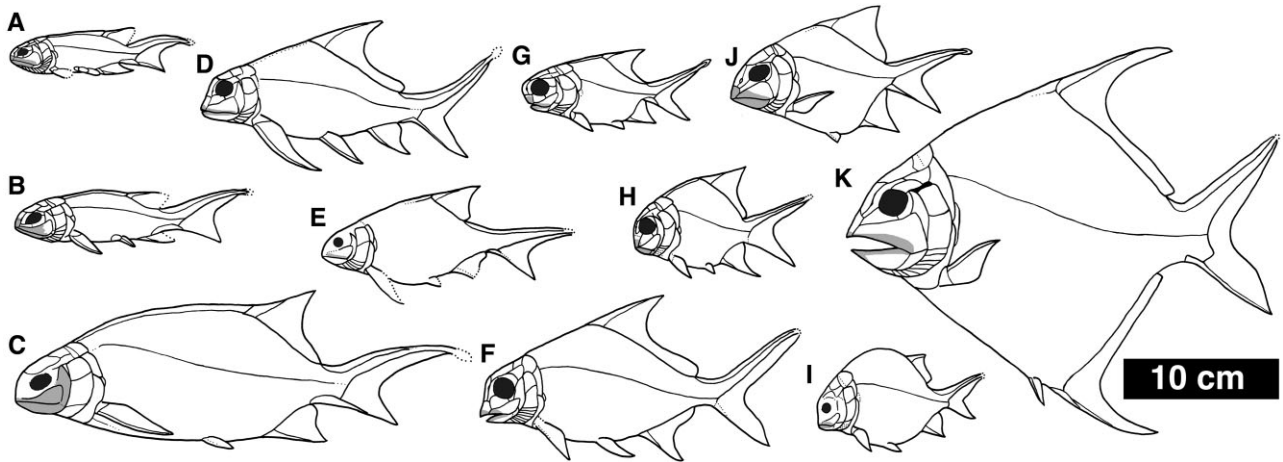


Figure 15. Styraopteridae and other Eurynotiform taxa from North America and Europe. Medium-grey infill represents the extent of the thick ganioine plates along the jaws based on specimens listed in the Appendix S1, lines along leading edges of fins represent depth of fringing fulcra and consolidated fin spines. A, *Fouldenia* from the late Tournaisian of Scotland. Lines on the median fins represent the extent of consolidated, spine-like lepidotrichia. Lines on the pectoral fins represent fringing fulcra depth. B, *Styraopterus* from the early Visean of Scotland. C, *Benedenius* from the early Visean of Belgium (based on Traquair, 1878, Fraipont, 1890, and the specimens listed in Appendix S1). D, *Eurynotus* from the Visean–Permian of Euramerica and Russia (based on Traquair, 1879 and the specimens listed in Appendix S1). E, *Proteurynotus* from the early Visean of Scotland (based on Moy-Thomas & Bradley Dyne, 1938). F, *Mesolepis* from the Serpukhovian–Pennsylvanian of Europe (based on Traquair, 1907 and the specimens listed in Appendix S1). G, *Paramesolepis tuberculata* from the early Visean of Scotland (based on Moy-Thomas & Bradley Dyne, 1938 and the specimens listed in Appendix S1). H, *Paramesolepis rhombus* from the early Visean of Scotland (based on Moy-Thomas & Bradley Dyne, 1938). I, *Wardichthys* from the late Visean and Serpukhovian of Scotland (based on Traquair, 1907 and the specimens listed in Appendix S1). J, *Cheirodopsis* from the early Visean of Scotland (based on Moy-Thomas & Bradley Dyne, 1938 and the specimens listed in Appendix S1). K, *Amphicentrum* from the late Visean–Permian of Euramerica (based on Coates, 1988 and the specimens listed in Appendix S1).

and the rectangular lateral flank scales bearing tall, centrally positioned pegs (see Figs 2, 4). There are, of course, differences between *Benedenius* and *Styraopterus*, including more complex suture lines between the skull roof bones, as well as deeper jaws in *Benedenius* (Fraipont, 1890; L.C.S., pers. observ.; Appendix S1; Fig. 15C). These might be ramifications of differences in body and skull dimensions as well as different ontogenetic trajectories (see below). However, full accounting of the divergent traits will have to await a more detailed description of *Benedenius*.

Comparisons with previous allies

Traquair (1881) originally assigned *S. fulcratus* and some specimens now belonging to *Fouldenia* to the Glencartholm genus *Holurus*, now represented by a single species *Holurus parki* Traquair, 1881 (Fig. 16A). White (1927) noted similarities between the median fins of *Fouldenia* and *Holurus*, whereas Moy-Thomas & Bradley Dyne (1938) mentioned only a ‘superficial’ likeness. Despite this history, there does not appear to be a close relationship between *Holurus* and the styraopterids, based on a lack of styraopterid

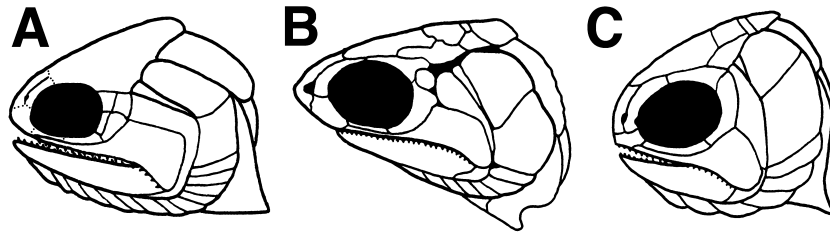


Figure 16. Comparison of early actinopterygian skulls I. A, *Holurus* (based on Moy-Thomas & Miles, 1971). B, *Mesopoma* (after Coates, 1999). C, *Canobius* (after Moy-Thomas & Bradley Dyne, 1938).

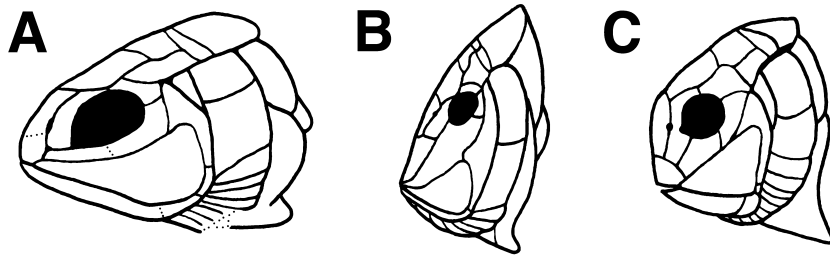


Figure 17. Comparison of early actinopterygian skulls II. A, *Styraopterus*. B, *Platysomus superbus* (after Moy-Thomas & Bradley Dyne, 1938). C, *Adroichthys* (after Gardiner, 1969).

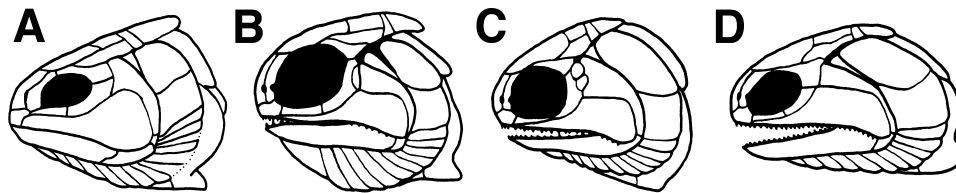


Figure 18. Comparison of early actinopterygian skulls III. A, *Fouldenia*. B, *Strepheoschema* (after Gardiner, 1985). C, *Aetheretmon* (after Gardiner, 1985). D, *Phaneroosteon* (after Gardiner, 1985).

and/or eurynotiform traits in the former. In addition, *Holurus* differs in a greater retention of traits primitive for actinopterygians, such as a lack of fringing fulcra in the *Holurus* holotype GSE 5688 (Moy-Thomas & Bradley Dyne, 1938; L.C.S., pers. observ.; Appendix S1). *Holurus* shares with the fusi-form Foulden fish *Phaneroosteon* a preopercular pitline that runs diagonally onto the maxilla (White, 1927; Moy-Thomas & Bradley Dyne, 1938; L.C.S., pers. observ.; Appendix S1), in contrast to the horizontal orientation in styracopterids (Figs 9, 13). The jaw apparatus of *Holurus* is more similar to Devonian actinopterygians such as *Stegotrachelus* (Swartz, 2009) than those of Eurynotiformes, with an oblique suspensorium, angular preoperculum, and a maxilla with a rectangular posterior expansion (Moy-Thomas & Bradley Dyne, 1938). These primitive traits are unexpectedly combined with derived features such as additional infraorbitals and distinct suborbitals (Moy-Thomas & Bradley Dyne, 1938; Fig. 16B), bones

that are absent in styracopterids (Figs 17A, 18A), *Phaneroosteon* (Fig. 18D), and many other Mississippian actinopterygians (Gardiner & Schaeffer, 1989).

White (1927) asserted that *Fouldenia* most closely resembled the Visean Glencartholm actinopterygian *Canobius ramsayi* Traquair, 1881 (Fig. 16C) in having a triangular maxilla and enlarged suboperculum, despite other differences. These homoplastic shape traits are found in a number of other fishes, including platysomids, and are not phylogenetically informative (Sallan & Friedman, 2012). However, a relationship between the ‘canobiids’ and styracopterids has been hypothesized elsewhere. Traquair (1881) noted unspecified similarities between the suspensorium and opercular series of the ‘palaeoniscid’ *Canobius* (then containing *Mesopoma*) and those of the ‘platysomid’ *Eurynotus*, presenting this as a challenge to the accepted divisions of early actinopterygians. Gardiner & Schaeffer (1989) placed *Styraopterus* (then containing *Fouldenia*) *a priori* alongside *Canobius* in the

Mesopoma group for their cladistic analysis of exemplars; however, most of the states used for this assignment are symplesiomorphic or miscoded in Styraopterids. The dermosphenotic of *Fouldenia* and *Styracopterus* lacks the posterior process (Figs 16B, C, 17A, 18A) necessary for the 't-shaped' descriptor applied to *Mesopoma* by Gardiner & Schaeffer (1989). In *Mesopoma* and *Canobius* (Fig. 16B, C), this shape is facilitated by a half-oval area containing one or more suborbitals, a feature found in the Foulden fish *Strephoschema* (Fig. 18B) but absent in Eurynotiformes. All remaining traits shared by *Mesopoma*, *Canobius*, and the styraopterids are symplesiomorphic: a fused dermopterotic, consolidated premaxilla on the gape, single pair of extrascapulars, contact between the frontals and dermosphenotics, fringing fulcra, ridge scales, elongate frontals, and a lateral line ending on the axial lobes (Patterson, 1982; Gardiner & Schaeffer, 1989; Coates, 1999; Figs 16B, C, 17A, 18A). In contrast, the canobiids lack all the diagnostic traits for either Styraopteridae or Eurynotiformes (L.C.S., pers. observ.; Appendix S1).

Comparisons with deep-bodied taxa and the membership of the Eurynotiformes

The assignment of *Benedenius* to the Styraopteridae raises the possibility of a connection between this family and various deep-bodied platysomoid fishes. Before *Styracopterus* was discovered, *Benedenius* was included in Traquair's (1879) family Platysomidae alongside the Carboniferous actinopterygians *Amphicentrum* (Fig. 15K), *Eurynotus* (Fig. 15D), *Mesolepis* (Fig. 15F), *Wardichthys* (Fig. 15I), *Platysomus* (Fig. 17B), and *Eurysomus* (= *Platysomus*). This taxonomy combined a few of the deep-bodied actinopterygian families proposed earlier by Young (1866), including a Platysomidae containing the nominal genus *Platysomus* and defined by pointed teeth, a monogeneric Amphicentridae defined by denticulated tooth plates and edentulous jaw margins (as in Styraopteridae), and a Mesolepidae comprised of *Eurynotus* and *Mesolepis*, defined by 'Eurysomus'-like teeth with restricted necks (as in *Fouldenia*). All of these were included alongside pycnodont teleosts in Young's (1866) suborder 'Lepidopleuridae', erected on the basis of deep body shapes and 'strong pegs' on the scales.

In Traquair's (1879) formulation of a distinctly Palaeozoic 'Platysomidae' excluding teleosts, *Benedenius* was noted as similar to *Eurynotus* in form, although commonalities with other taxa, excluding *Platysomus*, were also described. After the discovery of *Styracopterus* (Traquair, 1881), Fraipont (1890) and Traquair (1890) moved *Benedenius* back into the 'Palaeoniscidae' with all other non-platysomid Palaeozoic actinopterygians, partly on the basis of its close rela-

tionship with the new fusiform taxon. However, Boulenger (1899) disputed this reassignment, asserting that there were few differences between *Benedenius* and *Eurynotus* (as noted above; Fig. 15C, D), and that it should continue to be allied with *Mesolepis* and *Wardichthys*.

Moy-Thomas (1937) placed his new family Styraopteridae apart from the platysomids; however, he pointed out that the relationship between the deep-bodied *Benedenius* and his fusiform reconstruction of *Styracopterus* challenged assumptions of common ancestry for the other deep-bodied taxa (despite the fact that the gibbose *Eurynotus* was already included in Platysomidae; Moy-Thomas, 1937). Yet, Moy-Thomas and Bradley Dyne's (1938) later description of the deep-bodied, tooth-plated Glencartholm fish *Cheirodopsis* (Fig. 15J) found both similarities to *Amphicentrum* (Fig. 15K) in osteology and dentition, and the styraopterids in jaw ornament (meaning the smooth ganoine fields) and fringing fulcra morphology. Nevertheless, Moy-Thomas & Miles (1971) split Berg's (1940) deep-bodied suborder Platysomoidea into just two families: a Chirodontidae (= Amphicentridae) containing the durophagous tooth-plated *Eurynotus*, *Proteurynotus*, *Amphicentrum*, *Cheirodopsis* (Fig. 15), and *Adroichthys* (Fig. 17C), and a Platysomidae, comprising taxa thought to lack such dentition (*Platysomus* and *Mesolepis*; Figs 15F, 17B). Coates (1988) retained the basic split within the Platysomoidea, but moved *Mesolepis* to the amphicentrid side of the equation. This taxon was based on diagnostic dentition (including tooth plates), scales with strong central pegs, and a triangular maxilla, all of which are possessed by the styraopterids. *Paramesolepis* (Fig. 15G, H), another deep-bodied Glencartholm taxon previously synonymous with *Mesolepis* (Traquair, 1890; Moy-Thomas & Bradley Dyne, 1938), was excluded from the Platysomoidea entirely (Coates, 1988).

In the first published cladistic analysis of early actinopterygians that included deep-bodied taxa, Gardiner & Schaeffer (1989) ignored the internal split within the platysomoids and their dentition, placing all the aforementioned genera within a single deep-bodied *Platysomus* group based on a triangular maxilla, and elongated premaxilla and a compact or *Cheirodopsis*-like 'c'-shaped dermosphenotic, the latter approximating the form of the bone in *Styracopterus* (Figs 4C, 19A). In that analysis, *Styracopterus* was placed *a priori* in the *Mesopoma* (Fig. 16B) group on the basis of several incorrect character states (see above) and several homoplastic, possibly symplesiomorphic traits also found in the *Platysomus* group and elsewhere (a vertical suspensorium, a reduction in the relative size of the preoperculum, and a subopercular equal to or larger in size than the

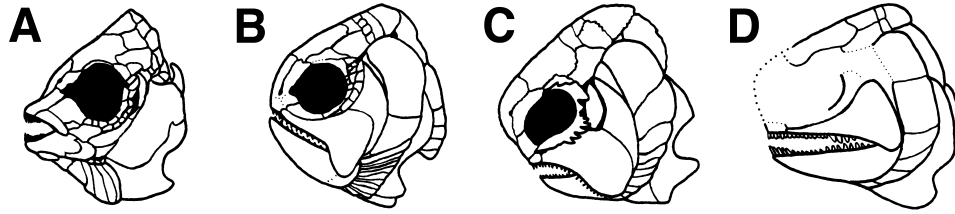


Figure 19. Comparison of early actinopterygian skulls IV. A, *Discoserra* (after Hurley *et al.*, 2007). B, *Proceramala* (after Poplin & Lund, 2000). C, *Aesopichthys* (after Poplin & Lund, 2000). D, *Frederichthys* (after Coates, 1993).

opercular). Thus, a relationship could not be recovered. However, both groups fell on the neopterygian stem, a placement earlier asserted by Gardiner (1985) for the Styracopteridae.

Here, we have placed Styracopteridae with Coates' (1988) definition of Amphicentridae, excluding *Adroichthys* (Fig. 17D) for the reasons explained below, within the new plesion Eurynotiformes. This was done on the basis of many diagnostic traits that were previously used to define single families or taxa, but which are in fact shared widely. This group includes *Paramesolepis* (Fig. 15G, H), which was cladistically recovered within the platysomids by Mickle, Lund & Grogan (2009; see below), albeit apart from the amphicentrids. Whereas tooth plates and durophagous tooth forms are widespread in actinopterygians and gnathostomes (Traquair, 1879; Moy-Thomas & Miles, 1971; Coates, 1993; Sallan *et al.*, 2011; Friedman & Sallan, 2012), several aspects of the dentition in these taxa seem to be diagnostic. One of these is the mesial position of the maxillary tooth row, hidden laterally by the dermal bone itself. This trait was first noted for *Eurynotus* by Traquair (1879), and has since been recovered in *Styracopterus* (Moy-Thomas, 1937), *Amphicentrum* (Coates, 1988), *Cheirodopsis*, *Mesolepis*, *Paramesolepis*, and *Fouldenia*, as noted above (L.C.S., pers. observ.; Appendix S1). Another is the complete absence of marginal dentition on the dentary and premaxilla (Figs 14, 15). Finally, all the contained taxa possess denticulated, enameloid-covered tooth plates along the mandible and the palatoquadrate, as described and/or observed in *Wardichthys*, *Eurynotus*, *Mesolepis*, *Cheirodopsis*, *Amphicentrum*, *Benedenius*, and now *Styracopterus* and *Fouldenia* (Traquair, 1879, 1881; Boulenger, 1902; Moy-Thomas & Bradley Dyne, 1938; Bradley Dyne, 1939; Coates, 1988, 1994; L.C.S., pers. observ.; Appendix S1). Furthermore, blunt denticles with restricted bases found along the lower tooth plate in *Fouldenia* (White, 1927; see above) are highly similar to the same in *Mesolepis* (Traquair, 1879; L.C.S., pers. observ.; Appendix S1) and *Benedenius* (Boulenger, 1902), whereas the upper denticles in *Styracopterus* resemble those in *Eurynotus* and *Amphicentrum* (Traquair, 1879; Watson,

1928; Coates, 1988; L.C.S., pers. observ.; Appendix S1). In contrast, the various platysomids have conical, pointed teeth along the margins of their dermal jaws, whereas durophagous members of the group add denticles to the parasphenoid rather than specialized surfaces (Traquair, 1879; Moy-Thomas & Miles, 1971; Mickle & Bader, 2009; L.C.S., pers. observ.; Appendix S1).

The dentaries, maxillae, and premaxillae of the Eurynotiformes bear fields of smooth ganoine, forming wide bands around the jaw margins in *Amphicentrum* (Coates, 1988; L.C.S., pers. observ.; Appendix S1), *Cheirodopsis* (Moy-Thomas & Bradley Dyne, 1938; L.C.S., pers. observ.; Appendix S1), *Fouldenia*, *Styracopterus*, and *Benedenius* (Boulenger, 1902; L.C.S., pers. observ.; Appendix S1), and *Paramesolepis* (Moy-Thomas & Bradley Dyne, 1938; L.C.S., pers. observ.; Appendix S1; Fig. 15). The same phenomenon is seen to a lesser extent in *Eurynotus*, *Mesolepis*, and *Wardichthys* (L.C.S., pers. observ.; Appendix S1; Fig. 15). In contrast, the dermal jaw bones of platysomids have fine linear ornamentation resembling that in *Wendyichthys*, *Frederichthys*, *Mesopoma*, and other fusiform taxa (Gardiner, 1984; Coates, 1993, 1999; Lund & Poplin, 1997; Mickle & Bader, 2009; L.C.S., pers. observ.; Appendix S1). Another diagnostic feature of Eurynotiformes concerns scale morphology: all included taxa have rectangular flank scales with smooth posterior margins and tall pointed central pegs. Such scales have been illustrated previously for *Eurynotus* (Agassiz, 1833–1844; Traquair, 1879), *Benedenius* (Fraipont, 1890; Boulenger, 1899), and *Amphicentrum* (Bradley Dyne, 1939; Coates, 1988), and are now noted for *Styracopterus* and *Cheirodopsis* (L.C.S., pers. observ.; Appendix S1). A similar peg in *Platysomus* (Traquair, 1879; L.C.S., pers. observ.; Appendix S1) sits along the leading edge of a rhomboid trunk scale with a prominent anterodorsal corner, more closely approximating the primitive condition for actinopterygians (Gardiner, 1984; Coates, 1999; Friedman & Brazeau, 2010; L.C.S., pers. observ.; Appendix S1). Eurynotiform scales and dermal bones tend to have a heterogeneous ornament of imbricated, fused, and intercalated bands, ridges, and/or dots, with greater

complexity in younger and larger forms (Traquair, 1879, 1881, 1890; Moy-Thomas & Bradley Dyne, 1938; Coates, 1988; L.C.S., pers. observ.; Appendix S1). The described ornamentation can be obscured by fields of smooth ganoine, as observed in *Styracopterus* (see above). In contrast, all species of *Platysomus* have an ornament of thin, vertical striations on both the scales and the opercular series (Traquair, 1879; Moy-Thomas & Bradley Dyne, 1938; L.C.S., pers. observ.; Appendix S1), which approximates the anterior portion of the scale ornament in *Mesopoma* (Coates, 1993) and Devonian taxa (Gardiner, 1984).

Fringing fulcra morphology is diagnostic for Eurynotiformes. These scales provide a stout margin for the leading edge of fins, with definite hydrodynamic consequences. The fulcral scales are enlarged, elongated, and pointed, with heavy ganoine cover. Overlap increases distally on the fins in *Styracopterus*, *Eurynotus*, and *Amphicentrum* (L.C.S., pers. observ.; Appendix S1). More proximal fulcra are paired in the first two taxa and perhaps others, but this needs more investigation. In the median fins, the fulcra can be difficult to distinguish from the terminals of the many lepidotrichia falling anterior to the level of peak fin height. In contrast, the fringing fulcra in platysomids tend to be minute, and the majority of fulcra on the median and caudal fins line a single long lepidotrich (often the fourth) which makes up most of the anterior margin (L.C.S., pers. observ.; Appendix S1). This is similar to the condition in *Mesopoma* (Coates, 1993, 1999) and crown neopterygians such as various fossil holosteans (Grande, 2010).

The suboperculum in various eurynotiforms tends to be longer than the operculum, with a definite anteroventral process (L.C.S., pers. observ.; Appendix S1; Fig. 15), whereas the operculum is the taller bone in most species of *Platysomus* (Traquair, 1879; Moy-Thomas & Bradley Dyne, 1938; Moy-Thomas & Miles, 1971; Mickle & Bader, 2009; Fig. 17C), as well as Devonian actinopterygians (Gardiner, 1984; Arratia & Cloutier, 1996) and bobasatranids (Campbell & Phuoc, 1983). In Eurynotiformes, the maxilla bears a thick anterior ramus that transitions into, and can be indistinguishable from, the triangular posterior expansion, whereas in *Platysomus superbis* the small ramus is distinct and curved (Moy-Thomas & Bradley Dyne, 1938; Mickle & Bader, 2009; L.C.S., pers. observ.; Appendix S1), as in *Cheirolepis*, *Rhadinichthys*, and various less derived, fusiform taxa from Glencartholm (e.g. *Rhadinichthys*; Arratia & Cloutier, 1996; Moy-Thomas & Bradley Dyne, 1938; L.C.S., pers. observ.; Appendix S1). Furthermore, all eurynotiforms have at most one pair of extrascapulars, whereas many species of platysomid have two or more (Mickle & Bader, 2009; Figs 15,

17B), as in *Mesopoma* and many other actinopterygians (Coates, 1993; Fig. 16B). There are many other traits and character combinations that unite the Eurynotiformes to the exclusion of the platysomids, and these are laid out in detail in the diagnosis and the emended descriptions of the styracopterids above.

In light of the distribution of diagnostic tooth plates and scales among the Eurynotiformes and the specific traits of that clade, it could be fruitful to reconsider the identities of the large volume of ichthyolith material previously attributed to these taxa, particularly for *Eurynotus*. Most relevant here is the type and only catalogued specimen (GSE 5699) of the species *Eurynotus* (?) *apron* Traquair, 1881 from the Calciferous Sandstone series of Tweeden Burn. This is a slab containing scales and dermal material only provisionally assigned to that genus. A re-examination of this material revealed marked similarities to *Styracopterus* from identically aged deposits (L.C.S., pers. observ.), showing Eurynotiform traits such as central pegs and heavy smooth ganoine ornament. Traquair (1881) noted the presence of similar flank scales elsewhere in Scotland and Ireland: these could also be styracopterid, but are not particularly diagnostic among Eurynotiformes from that vague description alone.

Based on the distribution of characters listed above, platysomoids are not likely to be more closely related to the Eurynotiformes than other groups of Scottish Carboniferous actinopterygians. Although a phylogenetic analysis is necessary to discount a sister-group relationship, the styracopterids share enough character states with 'paleoniscoid' taxa that a simple, dual-lineage platysomid clade seems unlikely. Indeed, there are many similarities between *Fouldenia* and the other fusiform fishes from Foulden (*Strephoschema*, *Phanerosteon ovensi*, *Aetheretmon*; Fig. 18), none of which appears to be a close relative of *Platysomus* (Fig. 17C). For example, all the Foulden fishes share several probable skull synapomorphies or symplesiomorphies: a long frontal with a rounded anterior margin, a single pair of extrascapulars, tall rostrals, a rhomboid post-temporal, thin infraorbitals, a dermohyal, and an ovoid supracleithrum (Gardiner, 1985; Fig. 17). None of these states are found in *Platysomus* (Mickle & Bader, 2009; Fig. 17B). In addition, *Phanerosteon ovensi*, *Fouldenia*, and additional eurynotiforms exhibit nasals that contact the dermosphotic, and lack both supraorbitals and suborbitals (Gardiner, 1985; L.C.S., pers. observ.; Appendix S1; Fig. 17A, D), symplesiomorphies shared with many stem-actinopterygians and/or stem-neopterygians, but not *Platysomus* (Gardiner & Schaeffer, 1989; Mickle & Bader, 2009; Fig. 17B).

Although there are differences in anamestic bones and dentition, shared traits within the Foulden actinopterygians (Fig. 18) might suggest endemic

diversification in Tournaisian Scotland, with lineages continuing into the Visean Glencartholm assemblage (Dineley & Metcalfe, 1999). Alternatively, considering the symplesiomorphic nature of many of these traits, they could reflect the starting conditions of a large portion of the post-Hangenberg actinopterygian radiation (Sallan & Coates, 2010; Sallan & Friedman, 2012). Better descriptions of Foulden taxa and new phylogenetic analyses, involving additional data from recently discovered Foulden fauna localities (Smithson *et al.*, 2012), will be needed to determine which is the case. For now, the relationship between the fusiform, Tournaisian actinopterygian *Fouldenia*, and some but not all of the deep-bodied fishes previously assigned to Platysomoidea supports a hypothesis that deep-bodied forms arose multiple times during the Palaeozoic diversification of actinopterygians (Coates, 1988, 1993; Sallan & Friedman, 2012).

The multiple origins of deep-bodied actinopterygians

Concerning the number of deep-bodied clades present within the Mississippian actinopterygian fauna, it should be noted that *Adroichthys*, an actinopterygian from the early Visean of South Africa (Fig. 17C), is here excluded from the Eurynotiformes despite previous assignment to the Amphicentridae (Gardiner, 1969; Moy-Thomas & Miles, 1971; Coates, 1988). *Adroichthys* is gibbose, has a triangular maxilla, and possesses both mandibular and palatal tooth plates, with the latter modified from the ectopterygoid as in *Amphicentrum* (Bradley Dyne, 1939; Gardiner, 1969; Coates, 1988). However, *Adroichthys* diverges from the Eurynotiformes in that its jaws are tuberculated (Gardiner, 1969) and lack smooth ganoine cover. The premaxilla and dentary of *Adroichthys* exhibit the primitive set of marginal teeth, whereas the maxilla is edentulous (Gardiner, 1969), a pattern exactly opposite that of the eurynotiform dentition. The rhomboid flank scales in *Adroichthys* possess primitively small and slanted pegs (Gardiner, 1969), like those found in the Devonian taxa *Moythomasia* (Gardiner, 1984) and *Mimipiscis* (Choo, 2011), rather than the tall, pointed eurynotiform version. The longest lepidotrichia in the median fins of *Adroichthys*, the sixth, comprises most of the leading edge and bears all the minute fringing fulcra (Gardiner, 1969). Although the exact fin ray differs, this trait is shared with *Platysomus*, *Discoserra*, and most early actinopterygians (L.C.S., pers. observ.; Appendix S1), but is entirely divergent from the condition of the anterior margins of the fins in Eurynotiformes. Finally, *Adroichthys* lacks basal fulcra in all fins, a postcleithrum, an anteroventral process on the suboperculum, and an anterior ramus on the maxilla.

Most of the morphologies shared by *Adroichthys* and the Eurynotiformes, such as a dermopterotic and a

dermothyal, are symplesiomorphic (defining a wide array of early actinopterygians, such as *Phanerosteon* and *Mesopoma*; Figs 16B, 18D), as are the majority of traits shared with *Platysomus* (e.g. the lack of basal fulcra; Moy-Thomas & Bradley Dyne, 1938; Mickle & Bader, 2009). *Platysomus* differs from *Adroichthys* in many phylogenetically relevant ways: it lacks dorsal ridge scales, has a premaxilla excluded from the gape, and possesses both a postcleithrum and a second pair of extrascapulars (Patterson, 1982; Gardiner & Schaeffer, 1989; Fig. 17B, C). On the basis of these observations, it is hypothesized here that the suborder Platysomoidea can be split into at least three distinct lineages, with confirmation pending new descriptive and phylogenetic work (cf. Mickle & Bader, 2009).

Independent origins for Palaeozoic deep-bodied actinopterygian lineages have been hypothesized previously (Coates, 1988, 1993; Lund, 2000; Poplin & Lund, 2000; Mickle & Bader, 2009). Indeed, not one of the five gibbose and deep-bodied genera named subsequent to Gardiner & Schaeffer's (1989) study was definitively assigned to the Platysomoidea or synonymous clades. Coates (1993) found that the gibbose *Frederichthys* from the Serpukhovian of Bearsden, Scotland, features three of the character states used to designate the *Platysomus* group by Gardiner & Schaeffer (1989): a laterally compressed body, a triangular maxilla, and a deep mandible – all shared with styraopterids. However, it was suggested that these shared traits could result from independent modification of actinopteran traits through differential growth (Coates, 1993; see below), a hypothesis previously raised by Moy-Thomas (1937) for the origins of various platysomids. Coates (1993) also noted the possibility of a sister-group relationship between *Frederichthys* and the here-designated eurynotiform *Paramesolepis*, the 'least derived member' of the *Platysomus* group (Coates, 1993: 143), on the basis of a reduced number of enlarged branchiostegals and the presence of fang-like teeth at the anterior end of the mandible. However, the branchiostegals in *Paramesolepis* and other Eurynotiformes are much thinner than in *Frederichthys* (L.C.S., pers. observ.; Appendix S1; Figs 15G, H, 19D), and branchiostegals may be hidden beneath the mandible in taxa with deep jaws (e.g. *Fouldenia* versus *Styraopterus*). A re-examination of the holotype of *Paramesolepis tuberculata* (NMS 1885.54.38) showed that the 'teeth' described by Moy-Thomas & Bradley Dyne (1938) are artifacts of ganoine on the broken and warped dentary, indistinguishable in composition from the rest of the ornament (L.C.S., pers. observ.). The jaw margins in other specimens are edentulous; the only evidence of dentition is a single thick denticle, lacking an acrodin cap, found mesial to the jaw impression in NHM P20425 (L.C.S., pers. observ.; Appendix S1).

The marginal teeth of *Frederichthys*, as well as a set of mesial denticles, were described as resembling the dentition in *Mesolepis*, and therefore *Fouldenia*, in their 'constricted bases' (Coates, 1993: 136). However, putting aside homology, the crowns of the latter two taxa are short and flat, and/or bulbous, rather than long and 'banana-shaped' (Traquair, 1879; Coates, 1993; L.C.S., pers. observ.; Appendix S1). In addition to mandibular teeth, the sole specimen of *Frederichthys* also possesses a palatal dentition (Coates, 1993), but this is attached to the parasphenoid, as in platysomids (Mickle & Bader, 2009; L.C.S., pers. observ.; Appendix S1), rather than ectopterygid-derived tooth plates associated with the palatoquadrate, as in Eurynotiformes (Traquair, 1879; Bradley Dyne, 1939; Coates, 1988; L.C.S., pers. observ.; Appendix S1).

In addition to dental distinctions, *Frederichthys* differs from *Mesolepis*, *Paramesolepis*, and other Eurynotiformes in the absence of most other diagnostic and phylogenetically relevant traits. First, *Frederichthys* possess two pairs of extrascapulars, as in *Platysomus* and *Mesopoma*, rather than one, as in the Eurynotiformes (Moy-Thomas & Bradley Dyne, 1938; Coates, 1993, 1999; Figs 15, 16B, 17C, 19D). The flank scales of *Frederichthys* are primitive in form and fringing fulcra are absent (Coates, 1993, 1999), putting this taxon more in line with potential stem actinopterygians such as *Phanerosteon* and *Tarrasius* (Sallan, 2012). Thus, *Frederichthys* probably represents a further independent lineage of gibbose taxa.

Four other Mississippian actinopterygian genera were used to erect new deep-bodied clades outside the Platysomoidei: the Guildayichthyiformes (*Discoserra* and *Guildayichthys*; Fig. 19A) and the Aesopichthyidae (*Aesopichthys* and *Proceramala*; Lund, 2000; Poplin & Lund, 2000; Fig. 19B, C). These have been included alongside *Platysomus* in various cladistic analyses, all of which indicated paraphyly and polyphyly for Palaeozoic deep-bodied actinopterygians. Trees published alongside the original descriptions of these taxa (Lund, 2000; Poplin & Lund, 2000) show the Platysomoidei as sister to a clade containing the new family of interest and a fusiform group: Guildayichthyiformes and crown Actinopterygii, and Aesopichthyidae and a 'Rhadinichthyidae' group, the latter including the fusiform Bear Gulch taxa *Wendyichthys*. These results suggest that the deep-body shape is a reversible trait, as such a silhouette would be ancestral for both clades. These topologies also render Platysomoidei paraphyletic with respect to many other actinopterygians (Lund, 2000; Poplin & Lund, 2000); however, Lund (2000) found *Platysomus* to be the closest relative of the eurynotiform *Amphicentrum*, albeit a paraphyletic one.

A further analysis by Cloutier & Arratia (2004), using many of the same characters, excluded platysomoids but recovered the same guildayichthyiform–crown actinopterygian and aesopichthyid–rhadinichthyid clades. These were separated by nearly all other included Mississippian and Devonian taxa, thus indicating at least two origins for deep-bodied Palaeozoic fishes (Cloutier & Arratia, 2004). Mickle *et al.* (2009), using many of the same characters, recovered at least three origins for deep-bodied Palaeozoic actinopterygians, as the Guildayichthyiformes (Lund, 2000; Hurley *et al.*, 2007; Fig. 19A) and the aesopichthyids (Poplin & Lund, 2000; Fig. 19B, C) were separated from each other, and the included 'platysomoids,' by both fusiform Bear Gulch taxa and major divisions of living actinopterygians. However, the study did not find a simple split between the Eurynotiformes and platysomoids, as the recovered 'Platysomiformes' clade showed *Platysomus* (Fig. 17C) to be paraphyletic relative to its amphicentrid sister taxa (*Amphicentrum* and *Cheirodopsis*; Fig. 16J, K). Synapomorphies subtending and within this platysomiform clade consist of previously diagnostic traits dating back to Traquair (1879). Many of these were noted by other authors to be homoplastic or symplesiomorphic (e.g. Gardiner & Schaeffer, 1989; Coates, 1993), such as a 'beak'-like snout, edentulous jaw margins (not correct for *Platysomus*), a tall subopercular, and a maxilla with a triangular posterior expansion, the complete absence of suborbitals, contact between the lachrymal and nasal, a complete line of dorsal ridge scales, 'phyllodont' teeth, and a single rostral (the latter two characters for the amphicentrid clade alone; Mickle *et al.*, 2009).

A cladistic study by Hurley *et al.* (2007), using a distinct set of characters but only a restricted set of Mississippian fish, recovered independent origins for all the deep-bodied lineages included. *Amphicentrum* was separated by a number of fusiform Palaeozoic taxa from the near-neopterygian Guildayichthyiformes and the deep-bodied Triassic bobasatraniform *Ebanaqua* (Campbell & Phuoc, 1983; Long, 1991). Whereas Bobasatraniformes have been separated from platysomoids by several authorities, including Gardiner & Schaeffer (1989) and Moy-Thomas & Miles (1971), other workers have noted strong similarities between them, specifically in regards to *Ebanaqua* (Campbell & Phuoc, 1983; Weems & Windolph, 1986; Long, 1991; Coates, 1993; Mickle & Bader, 2009). In the Hurley *et al.* (2007) analysis, *Amphicentrum* (Fig. 15K) is defined by many apomorphic and symplesiomorphic character states shared by the styracopterids, including a fixed maxilla approximating a right triangle (shared with *Styracopterus*; Fig. 18A) and a preoperculum with a broad dorsal margin.

These studies and the trait distributions discussed above suggest that additional cladistic analyses involving all six potentially independent Palaeozoic deep-bodied lineages (Eurynotiformes, Platysomidae–Bobasatraniformes, Guildayichthyiformes, Aesopichthyidae, *Frederichthys*, and *Adroichthys*), alongside other fusiform actinopterygians, are likely to support distinct origins for most of these clades. The traits once used to unite the Platysomoidei, including durophagous dentitions and lateral compression, are likely to be highly homoplastic within the Palaeozoic actinopterygian radiation.

ONTOGENETIC CHANGE IN STYRACOPTERIDS AND EARLY ACTINOPTERYGIANS

Ontogenetic changes were largely ignored by previous descriptions of *Styracopterus* and *Fouldenia*; however, the alterations are to such a degree that size classes could be treated as distinct taxa if viewed in isolation. This was the case for the *Fouldenia* juveniles constituting the defunct species '*Styracopterus ischipterus*'. Splitting on the basis of incomplete growth series has occurred elsewhere: several, size-restricted species of *Elonichthys* from the Pennsylvanian of Mazon Creek, Illinois, were synonymized into the growth series of a single taxon by Schultze & Bardack (1987). Ontogenetic trait changes have been noted among other fishes (Cloutier, 2010), many of which involve dermal bone shape and ornament (see Dietze, 1999), as commonly used in diagnoses (see Traquair, 1877–1914; Newberry, 1889; Gardiner & Schaeffer, 1989). This situation is highly problematic.

If a high degree of ontogenetic variation is common among early actinopterygians, a non-trivial portion of named taxa might represent different growth stages. It is troubling that many Carboniferous ray-finned fishes are known either mostly or wholly from very large (e.g. *Acrolepis hopkinsi* McCoy, 1848, *Nematoptychius greenocki* Woodward, 1891, and *Amphicentrum crassum*; Bradley Dyne, 1939; Dineley & Metcalfe, 1999; L.C.S., pers. observ.), very small (e.g. *Cornuboniscus*, White, 1939; *Melanecta*, already hypothesized to be a juvenile, Coates, 1998; L.C.S., pers. observ.), or otherwise homogeneously sized individuals, and/or described from few similarly sized exemplars (e.g. the original description of *Fouldenia*; White, 1927). It is even possible that widespread genera with body lengths under 10 cm, such as *Canoibius*, might be the morphologically conserved young of a more inclusive clade with diverse adult forms, much like the leptocephalus larvae of modern elopomorph teleosts (Nelson, 2006). Schools of juvenile fishes now attributed to *Kalops* are known from the Serpukhovichian of Bear Gulch, Montana (Lund, Greenfield-Allen & Grogan, 2012; L.C.S., pers. observ.). Yet, despite

the common preservation of small animals and the general abundance of materials at that locality, most of the dozens of resident actinopterygian species have no known juvenile specimens.

The availability of early actinopterygian juvenile material, and their ontogenetic trajectories, is obscured by lack of appropriate descriptions. Even previous descriptions of Foulden fishes were based on aggregates of a few individuals without regard to size differences, despite a large range of specimen body lengths and abundant juveniles (Dineley & Metcalfe, 1999; L.C.S., pers. observ.; Appendix S1). Future descriptions should take the possibility of preserved juveniles into account. The ontogenetic changes described for *Fouldenia* and *Styracopterus*, involving alterations in scale shape, body depth, fin position, and other traits widely used in phylogenetic studies, could provide a guideline for detecting the preserved ontogenies of other ray-finned fishes.

If the ontogenetic trajectories observed here operated within other eurynotiform lineages, they may provide a source for variation within the group. If body size and depth are linked ontogenetically, then continued growth of a *Styracopterus*-like fish would result in the observed morphology of *Benedenius*, as originally hypothesized by Moy-Thomas (1937). *Benedenius* is only known from large adults, and is distinguished from other styracopterids by a greater area of smooth ganoine cover on its dermal bones, increased complexity of the skull roof suture lines, and relatively taller subopercular (Traquair, 1878; Fraipont, 1890; L.C.S., pers. observ.; Fig. 15B, C). These are all differences that could be produced by scaling of ontogenetic trends in *Styracopterus* (Fig. 13). Looking to more distantly related Eurynotiformes, many are also characterized by such traits: greater relative body depth, shortened skulls with blunted snouts, taller preoperculars, suboperculars, and other dermal bones, as well as more robust dentaries (Figs 5–16). Another widespread characteristic is long-based dorsal fins, as on the posterior halves of the bodies of *Cheirodopsis*, *Eurynotus*, and *Amphicentrum* (Traquair, 1879; Moy-Thomas & Bradley Dyne, 1938; Coates, 1988; L.C.S., pers. observ.; Fig. 15). The movement of the dorsal fin in *Fouldenia*, which covers the entire posterior half of the trunk in the smallest fishes, suggests that allometric scaling might explain the possibly homoplastic origins of this feature. Finally, there is the equilobate tail in *Amphicentrum*, *Cheirodopsis*, *Paramesolepis*, and other deep-bodied taxa, which feature a short, straight axial lobe, and a vertical or even concave peduncle margin (Fig. 15). The relative length and angle of the axial lobe and the angle of the peduncle change during styracopterid ontogeny, as does the caudal fin form, and thus change in the trajectories of these traits may produce such morphologies.

CONCLUSION

As redescribed here, the previously widespread and long-lived Scottish Carboniferous actinopterygian *S. fulcratus* is split into two monospecific genera in two faunas. One of these, the fusiform *Fouldenia ischiptera* from the late Tournaisian Foulden Fish Fauna, is the earliest known member of a division of mostly deep-bodied actinopterygians, the Eurynotiformes. The close relationship between the styracopterids and many eurynotiform taxa formerly included in the shape-based subclass Platysomoidea (e.g. *Amphicentrum*) suggests at least two large radiations of euryhaline, deep-bodied, and at least partially durophagous actinopterygians that originated in Euramerica in the aftermath of the end-Devonian extinction (Sallan & Coates, 2010; Sallan & Friedman, 2012). These clades were widespread, involving many co-occurring taxa in well-sampled actinopterygian faunas. Eurynotiformes are found in Mississippian-age sediments in Scotland and the rest of Euramerica, and survived into the late Permian in at least Russia (Gardiner, 1993; Coates, 1994; Appendix S1). Platysomoids, particularly the genus *Platysomus* and the Bobasatraniformes, if included, crossed the Permian–Triassic boundary and the recent equator, appearing in Gondwanan localities by the Mesozoic (Weems & Windolph, 1986; Long, 1991; Gardiner, 1993; Mickle & Bader, 2009; Appendix S1).

Like younger, deeper-bodied Eurynotiformes, *Fouldenia* possessed a crushing maxillary dentition and denticulated tooth plates modified from the ectopterygoid and coronoids, an almost vertical suspensorium, and robust, ganoine-covered jaws (Figs 14, 15). *Fouldenia* is thus the earliest recorded durophagous actinopterygian, appearing in line with an increasing number of shell-crushing predators in the late Tournaisian and Visean (Sallan *et al.*, 2011). Yet, in adults of *Fouldenia*, the specialized feeding apparatus is attached to a skull of middling depth with a moderate gape, a fusiform, generalist body, and fins much like those of other Foulden fishes with different diets (Breder, 1926; White, 1927; Moy-Thomas, 1938; Webb, 1982; Gardiner, 1985; Sallan & Friedman, 2012; Figs 13, 15). The larger Visean taxon *S. fulcratus* has a similar dentition (Fig. 14), but the suspensorium is more erect, the denticles are more stout, the jaw margins are sharper, the reinforcement of the snout and skull through both suturing of dermal bones and thick ganoine cover is increased, and the morphology of the maxilla is more derived (Fig. 18A). The skull of *Styracopterus* is attached to a deeper, more laterally compressed body with scythe-shaped pectoral fins (Fig. 4). This approximates the body forms of the much larger *Benedenius* and the widespread *Eurynotus* (Fig. 15). These postcranial shapes

might have better facilitated a marine and/or durophagous lifestyle, as in many living fishes within the marine teleost family Carangidae (jacks), which the Eurynotiformes may approximate in form and ecological breadth (Webb, 1982; Nelson, 2006; Fig. 15).

As discussed above, eurynotiform morphological diversity might relate to a large number of ontogenetic changes, as experienced by *Fouldenia* and *Styracopterus*. Many of the documented differences between juvenile and adult styracopterids, such as their relative body depth, scale height, lateral compression, jaw thickness, skull profile, and fin position, mirror the diagnostic distinctions between eurynotiform lineages. In his description of *Styracopterus*, Moy-Thomas (1937) hypothesized that differential growth rates could have resulted in multiple appearances of deep-body shapes among Palaeozoic actinopterygians. For Eurynotiformes, this holds true not only for body aspect, but many other traits. Further information on the ontogenetic trajectories of early actinopterygians might reveal that taxa with more derived body forms, and clades with greater disparity, experience greater ontogenetic change relative to those with ‘primitive’ or more fusiform aspects. Ontogeny could turn out to be a major factor driving the path of early actinopterygian diversification.

ACKNOWLEDGEMENTS

This article is dedicated to the memory of the late Stan Wood, a tireless hunter of Scottish Palaeozoic fishes and discoverer of new localities, who immeasurably increased our knowledge of early vertebrate life. He collected many of the specimens examined here, particularly the important juveniles, after uncovering new outcrops for both Foulden and Glencaitholm. We thank J. Liston for facilitating our examination of the GLAHM Foulden specimens in Edinburgh and A. Gunning of the Kelvingrove Museums for providing photographs of the *Styracopterus* maxillary dentition. We thank B. Mottequin and E. Poty (Université de Liège), and especially P. Van Genabeek (Centre Gregoire Fournier) for arranging a visit to the Abbey de Maredsous to examine the type specimens of *Benedenius*. S. Wild, M. Dean, M. Howe, and L. Albornoz-Parra (BGS Edinburgh), S. Walsh (NMS), Z. Johanson and M. Richter (NHM), and A. Henrici (Carnegie Museum of Natural History) helpfully facilitated access to their various collections, and L. Smith, M. LaBarbera, M. Hale, M. Webster, M. Foote, and K. Boyce offered useful comments. Finally, we thank S. Stamberg and J. Long for their helpful reviews of a previous draft of this article. L.C.S. was supported by the National Science Foundation (DEB DDIG 1011002), the Evolving Earth

Foundation, the Paleontological Association, the Paleontological Society, the American Society of Ichthyologists and Herpetologists, the University of Michigan, and the Michigan Society of Fellows. M.I.C. was supported by the National Science Foundation (DEB 0917922) and the University of Chicago.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Examined specimens.