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Spontaneous Article

A new species of *Mesolepis* (Actinopterygii) from the Late Carboniferous of Scotland, with especial reference to *Mesolepis wardi* Young

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ABSTRACT: A new species, *Mesolepis arabellae*, is described from material recently recovered from the shales of the Scottish Lower Coal Measure Formation. Up until now, three British species of *Mesolepis* have been named: *Mesolepis scalaris* Young, *Mesolepis wardi* Young, and *Mesolepis micropterus* Traquair. A fourth member of the genus, *Mesolepis pustulosa* Pruvost from the coalfields of Northern France, was named on scale description alone, though the validity of this taxon is uncertain. The new material described here varies from other *Mesolepis* species in its caudal peduncle morphology and overall body shape. Micro-computed tomography of the new species reveals the presence of teeth on the premaxilla and dentary and a splint-like fused prearticular and coronoid element, with implications for a possible feeding behaviour of *Mesolepis*. Additional information on the homogeneous *Mesolepis wardi* is also presented.

KEYWORDS: coalfield, compressed, dentition, Drumgray, *Mesolepis arabellae*, morphology.

1. Introduction

Mesolepis was first established by Young (1866) when he redescribed three specimens previously referred to as '*Platysomi*' and placed the genus in the family Mesolepidae. As with members of Pycnodontidae, he separated *Mesolepis* on account of those genera possessing a ventral fin, whereas members of Platysomidae, Amphicentridae and Eurysomidae lacked one. The Pycnodontidae were differentiated on the basis of their characteristic durophagous dentition, and although the teeth of *Mesolepis* are similar in configuration to those of *Eurynotus,* the genus was separated from Eurysomidae by the absence of a ventral fin. Later, Traquair (1878–80) included *Mesolepis* in the family Platysomidae alongside *Eurynotus, Benedenius, Eurysomus, Wardichthys, Cheirodus* (=*Amphicentrum*) and *Platysomus. Mesolepis* was maintained within the Platysomidae by Moy-Thomas & Miles (1971) based on its apparent lack of durophagous toothplates, but allied more closely with the amphicentrids by Coates (1998). Most recently, when reviewing the anatomy and relationships of deep-bodied Carboniferous actinopterygians, Sallan & Coates (2013) erected the new taxon Eurynotiformes, including within this the styracopterids along with Amphicentridae, *Mesolepis* and *Paramesolepis* to the exclusion of *Platysomus.*

Mesolepis was widely distributed but a relatively uncommon taxa from the Coal Measures of the United Kingdom. *M. wardi* and *M. scalaris* were both originally reported by Young (1866) from North Staffordshire (locality not stated, but almost certainly the Moscovian Knowles Ironstone Shale, Pennine Middle Coal Measures Formation). Additional material of *Mesolepis wardi* was described by Traquair (1878–80) from the Bashkirian Drumgray Coal, Lower Scottish Coal Measures, Lanarkshire, Scotland, who also erected a further species, *M. micropterus*, based on specimens from the Dalemoor Rake Ironstone, Pennine Lower Coal Measures, Derbyshire, England. The animal lived in what is inferred to be a shallow, brackish or freshwater palaeoenvironment. A further species of dubious taxonomic validity was reported from France (Pruvost 1919).

A remarkable feature of *Mesolepis* is the unusual shape of the rostral region of the head and torso (Young 1866; Traquair 1878–80), indicating the animals were exploiting a highly specialised niche in their ecosystem. In a general sense, the body of *Mesolepis* was laterally compressed and dorso-ventrally deep with an arched dorsal region, thus giving the body a rhomboid appearance. The jaws are also distinctive, with a beak-like premaxilla and robust mandibular teeth possessing a characteristic narrow waist and bulbous tip (Traquair 1878–80, plate IV, fig. 8). However, a comprehensive description for this taxon is wanting and details of its endoskeletal structure are entirely unknown, limiting inferences that can be drawn about its ecological role.

Here we describe a near-complete and articulated specimen of *Mesolepis* from Bashkirian shales from Wester Bracco, South Lanarkshire, Scotland. Further geological and stratigraphic information is provided in Elliott (2023) and Elliott *et al.* (2023). Comparison with previously described species highlights differences in caudal peduncle morphology and overall body shape, and we thus establish a new species. We clarify the condition of the dentition and dorsal fin in *Mesolepis*, as well as aspects of the internal anatomy. Wester Bracco represents an important locality for establishing the palaeodiversity of early Pennsylvanian Carboniferous faunas as ray-finned fishes explored new areas of ecological and morphological diversity.

2. Materials and methods

2.1. Methods

Three separate regions of the specimen were CT scanned using a Nikon Metrology XTH 225 ST X-ray tomography instrument at the XTM Facility, Palaeobiology Research Group, University of

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Bristol. The first scan focussed on the anterior region of the part, including the skull and shoulder girdle, and used the following settings: voltage, 106 kV; current, 302 µA; exposure, 1.42 s; projections, 3,141; frames per projection, 1; filter, 0.5 mm copper; effective voxel size, 32.3 µm. The second scan focussed on the anterior region of the counterpart, including the skull, and used the following settings: voltage, 100 kV; current, 220 µA; exposure, 1.42 s; projections, 3,141; frames per projection, 1; filter, 0.25 mm copper; effective voxel size, 22.1 µm. The third scan focussed on the dorsal margin of the body in the counterpart, and used the following settings: voltage, 119 kV; current, 210 µA; exposure, 1.42 s; projections, 3,141; frames per projection, 1; filter, 0.5 mm copper; effective voxel size, 25.6 µm.

The resulting tomographic datasets were segmented in Mimics v.25 (materialise) to create 3D models (.plys). All 3D models were visualised in Blender 2.79 (blender.org).

3. Systematic palaeontology

Osteichthyes Huxley 1880
Actinopterygii Woodward 1891
Eurynotiformes Sallan & Coates 2013
Genus: *Mesolepis* Young 1866

Generic diagnosis: Young 1866.
Body oval, or arched in the anterior dorsal region. Pectoral fin large, rounded. Ventral fin small and narrow, equidistant between pectoral and anal fins. Dorsal fin commencing opposite the ventral and terminating opposite the posterior margin of the anal. Caudal root strong, upper lobe larger than lower lobe. Anterior fin rays the longest, bifurcating only at extremities. Orbit large, well forward. Teeth stalked with a constricted neck and smooth, bluntly conical crown. Scales quadrilateral, those on the flanks higher than broad. Ornament on scales and head bones, tubercles arranged in a linear fashion.

Generic diagnosis: Traquair 1878–80 (emended from Young 1866).

Body deeply fusiform. Maxilla, broad behind, pointed in front. Mandible, short and stout, peculiarly pointed in front. Teeth with bluntly pointed apex, rounded below with a constricted neck. Scales with one or two anterior furrows; ornamented with sinuous, vertical tubercles. Caudal fin heterocercal, deeply cleft, inequilobate. Fin fulcra present.

Type species: *Mesolepis wardi* Young 1866.
Mesolepis arabellae sp. nov.

Diagnosis: Body deep, rhomboid; angle of torso arch acute; tail peduncle short and slender. Large ridge scales along dorsorostral margin of the body arch. Upper and lower jaw teeth stalked with a constricted neck and smooth spherical crown. Posttemporals an inverted cardioid with acuminate caudal margin; medial margin in line and continuous with the slope of the head. Operculum and suboperculum near equal in depth. Scale ornamentation of sinuous ridges traversing the scale at about 45 degrees; tuberculated at rostroventral corner. Scale rostral margin with six or more fine striae running dorso-ventral.

Material:
Holotype: A complete and articulate specimen in visceral view, split into part (GLAHM 163398/1; Fig. 1) and counterpart (GLAHM 163398/2; Fig. 2). Upper Drumgray Coal shale, Wester Bracco, South Lanarkshire.

The specimen measures 110 mm from the most rostral part of the head to the distal tip of the lower caudal fin lobe. The area of the tail peduncle is disturbed and a number of dermal elements of the head are displaced.

Etymology: *Arabellae*, from the shortened form of the Latin word *bella*, meaning beautiful, referring to the quality and appearance of the fossil. Also Arabelle, that which exudes beauty and faith.

Locus typicus: Ardenrigg coal waste tip Wester Bracco, North Lanarkshire (Scottish Lower Coal Measure Formation: Bashkirian).

Additional specimens:
Mesolepis arabellae GLAHM 163395. Scale, lateral view. Calderhead.
Mesolepis arabellae GLAHM 163396. Scale, visceral view. Calderhead.
Mesolepis arabellae GLAHM 163397. Scale, lateral view. Greenrigg.

Further material examined:
Mesolepis sp. GLAHM 163392. Vomerine dentition, Calderhead.
Mesolepis sp. GLAHM 163393. Dentary, Calderhead.

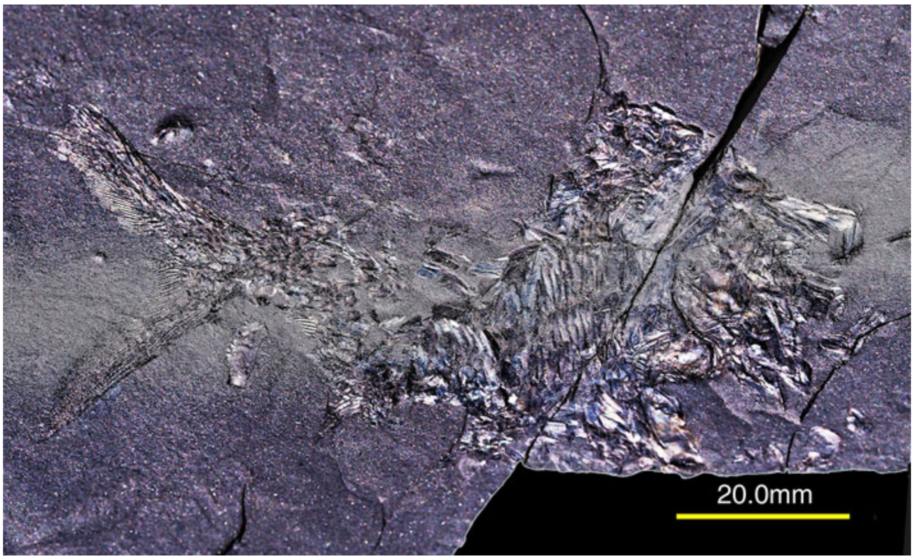

Figure 1 *Mesolepis arabellae sp. nov.* Holotype – part. GLAHM 163398/1. Scale bar 20.0 mm.

Mesolepis sp. GLAHM 163394. Lower jaw, juvenile, Calderhead.
Mesolepis wardi V3226, V3228. Hunterian Museum, Glasgow.
Mesolepis wardi L10930 (type specimen). Manchester Museum, Manchester.
Mesolepis wardi NHMUK PV P1609, NHMUK PV P8042, NHMUK PV P8044, NHMUK PV P9605. Natural History Museum, London.

4. Dermal skull elements

The dermal skull elements are preserved articulated across the holotype part (GLAHM 163398/1; Fig. 1) and counterpart (GLAHM 163398/2; Fig. 2). An interpretive reconstruction of this material is shown in Fig. 3.

The paired posttemporals (pt) in natural articulation have the form of an inverted cardioid exhibiting an acuminate caudal margin. A large median dimple on these elements indicates they have a significant lateral protuberance. Moreover, the posttemporals are found to lie in a continuous line with the slope of the head as in *Platysomus* (Young 1866; Traquair 1878–80; Watson 1928). The parietals (pa) are also paired and trapezoid in form, their connecting suture clearly discernible though possibly fused. A narrow length of material which separates the posttemporals from the parietals is interpreted as the extrascapulars (ext). Rostral to the parietals are paired frontals (fr) that are spatulate in form, wider rostrally and almost four times longer than the parietals (Figs. 3, 4a, c); the supraorbital canal (soc) traverses the length of these bones, the canal adhering close to the lateral margins where it exits into the nasal (na).

The rostral (ro) is displaced some way anterior and dorsal to the rest of the skull (Fig. 3). It exhibits an acuminate caudal margin for articulation with the rostral margins of the frontals; the lateral margins display small rounded embayments regarded as the anterior nostrils (ano). The right nasal bone (na) is preserved anterior to the frontals, but is broken anteriorly (Figs 3, 4e, f). It is of similar length and width as the rostral, with the supraorbital canal traversing the length of the bone near its lateral margin and exiting through the incomplete anterior margin. The lateral margin of the nasal is notched for the posterior nostril. An additional canal-bearing curved bone is preserved between the right nasal and rostral. Although split across the part and counterpart, µCT scans allow it to be reconstructed. It is slender and elongate, with ridges of ornament that run parallel to its lateral margins. These ridges are similar to those present on the bone identified as a right nasal and therefore may represent the left nasal. However, identification is uncertain.

In *M. arabellae* the dermopterotic (dp) is hidden by the overlying operculum (op). The jugal (ju) and dermosphenotic (ds) are not preserved in a condition where a complete description can be given. Nonetheless, these bones, and other elements of the orbital series, are shown in µCT scans of the new species (Fig. 4e, f). The jugal has a concave anterior margin, along which the infraorbital canal (ioc) runs, and a broad posterior expansion, giving it a triradiate appearance. Its ventral extension for the infraorbital canal is long but does not reach the level of the jugal and lacrimal (lac). Two rectangular, canal-bearing bones in alignment with the jugal suggest that additional infraorbitals may be present (?io). The jugal is curved, embracing the posterior margin of the lacrimal, and broadens dorsally. Multiple rami of the infraorbital canal branch towards its posterior margin. The lacrimal is almost ovoid in shape, with concentric ornament following its external margins. Disarticulated elements preserved anterior to the snout region may represent portions of the right infraorbital series.

Ornamentation of the head dermal elements is of low, round and elongated tubercles on the larger bones with a granular sculpture on the smaller facial elements; the granular sculpture is finer and more extensive on the dermal head bones of *M. wardi* (P8042). Ornamentation on the larger bones is directed in linear lines, mostly towards the rostral region. The overall form of most of the facial bones in *M. arabellae* agrees well with that given for *M. scalaris.*

5. The upper and lower jaws

The left upper and lower jaws are preserved in articulation and largely buried within the matrix (Figs 3, 5a–d). The premaxilla (pmx) is approximately oval in form and exhibits a pointed rostral margin at its medial articulation (Fig. 5c, d). The oral margin appears edentulous in lateral view; the lingual surface bears a row of 11 teeth, with one empty socket and two additional small replacement crowns lying in sockets. Each tooth has a spherical crown supported on a conical stalk with a narrow constriction immediately below the crown. There is a small gap between each tooth, and each tooth is located close to the dentary margin of the premaxilla.

The maxilla (mx) is large and plate-like, broader posteriorly with a narrower, angled anterior region as in other species of *Mesolepis* (Figs 3, 4f, 5c, d). Its labial surface is smooth, except for traces of a few growth rings. Teeth are absent from the ventral margin of the maxilla. Two teeth lie flat against the lingual face

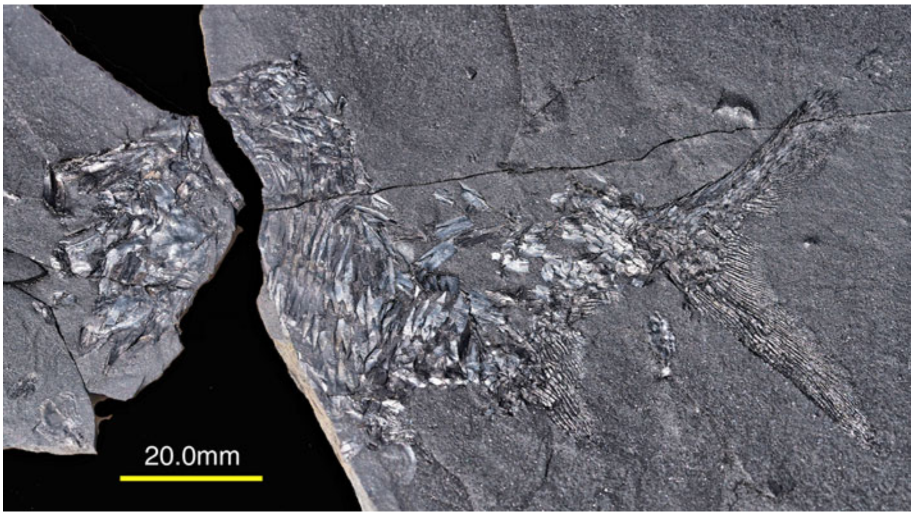

Figure 2 *Mesolepis arabellae sp. nov.* Holotype – counterpart. GLAHM 163398/2. Scale bar 20.0 mm.

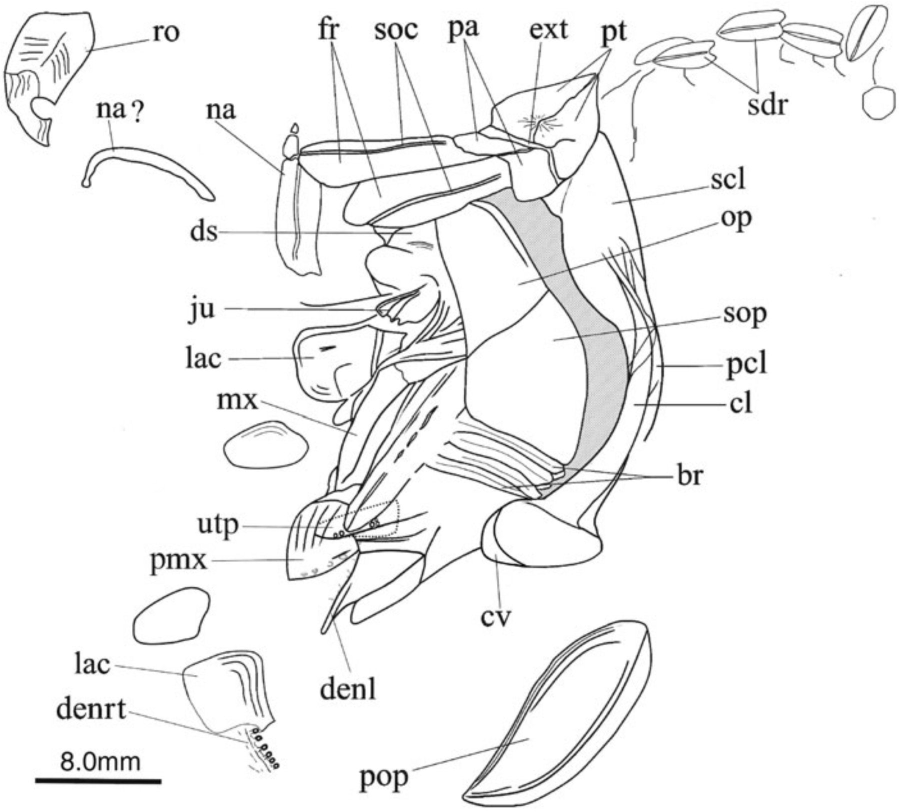

Figure 3 *Mesolepis arabellae sp. nov.* Line drawing of the dermal head bones produced by superimposition of GLAHM 163398/1 and GLAHM s163398/2. Rostral margin is to the left of the figure. Dotted line indicates outline of partly exposed upper jaw tooth plate (utp). Scale bar 8.0 mm. Abbreviations: an = angular; ano = anterior nostril; br = branchiostegal plates; chy = ceratohyal; cl = cleithrum; cor = possible coronoid teeth; cv = clavicle; denl = left dentary; denrt = right dentary tooth row; dhy = dermohyal; dp = dermopterotic; ds = dermosphenotic; ext = extrascapular; fr = frontal; fu = fused lepidotrichium; hmc = hyomandibular canal; hmd = hyomandibula; ioc = infraorbital canal; ?io = possible infraorbitals; ju = jugal; lac = lacrymal; mc = mandibular canal; mx = maxilla; na l = left nasal; na r = right nasal; op = operculum; pa = parietal; pc = prearticular-coronoid plate; pcl = postcleithrum; pmx = premaxilla; pop = preoperculum; popc = preopercular canal; psp = parasphenoid; pt = posttemporal; ptg = propterygium; ro = rostral; san = surangular; scl = supracleithrum; sdr = dorsal ridge scales; soc = supraorbital canal; sop = suboperculum; utp = upper jaw tooth plate.

of the maxilla, but it is unclear whether these emanate from a medial flange of the maxilla, similar to the condition in *Eurynotus* (Friedman *et al*. 2018, fig. 4), or are displaced from another element. Two rows of teeth are borne on one or more upper jaw toothplates (utp) medial to the maxilla (Figs 3, 5c, d). These teeth are similar in overall form to those on the premaxilla, but longer and slightly stouter. Moreover, a few of the more rostrally placed teeth exhibit flat, presumably worn, apical surfaces to the crowns. A line of demarcation between the crown and the pedicel may also be observed in the vomerine dentition of *Mesolepis sp.* from Calderhead (Fig. 6a); this line is interpreted as the lower limit of the acrodin cap. All teeth associated with the upper jaw are directed medially and slightly ventrally.

The lower jaw (Figs 3, 5a–d) is deep, with the rostral margin tapering to a point. The dorsal margin of the dentary (den) in *M. arabellae* has a narrow ledge which supports a row of nine teeth, plus one replacement crown, set into a socket (Fig. 5c, d). These teeth are similar in form to those on the premaxilla (Figs 5c, 6b, c), with a small gap between each tooth, but are directed dorsally and thus visible in lateral aspect. In contrast, the dentary dentition in *M. wardi* is bullet-shaped (Fig. 6d; NHMUK PV P8042, P8044, V3228). The prearticular and coronoids (Fig. 5c, e, f) are fused into a single plate with a peculiar shape. It is closely applied to the inner surface of the dentary and slender, with a bifurcate posterior margin incised with a deep notch. Approximately halfway along the plate, the dorsal margin bears a single, stout tooth. The anterior third of the plate is twisted, and two or three small, conical teeth are present on its anterodorsal margin, presumably representing the coronoid dentition. In addition to the dentary, which makes up the majority of the mandible, a thin angular (an) and surangular (san) both appear to be present (Fig. 5c, d). The posterior margin of the lower jaw, including the articular region and glenoid fossa, is uncertain. A near complete lower jaw of a juvenile (GLAHM 16339), which can only be identified to genus level, is shown in Fig. 6e.

6. Opercular series

The opercular series of *M. arabellae* is similar in form to that found in *M. scalaris*; the only dissimilarity is in the relative dorso-ventral lengths of the operculum (op) and suboperculum (sop) bones. In *M. arabellae* the opercular plates (Figs 3, 4e, f) are about equal in length, whereas in *M. scalaris* the operculum is much smaller than the suboperculum. Moreover, in *M. arabellae* the ventral margin of the suboperculum overlaps a series of four narrow imbricating branchiostegal plates (br) (Figs 3, 4f). The preoperculum (pop) is large and broadly lanceolate (Fig. 3); the preopercular sensory canal (popc) is indiscernible on this bone externally, although a portion of it can be traced in the µCT scan (Fig. 4f).

7. Hyoid arch

The hyoid arch (Fig. 7) is largely obscured by the overlying dermal opercular bones, but can be visualised in the µCT scan. The hyomandibula (hmd) is slightly longer than the suboperculum and almost straight, with only a modest kink between its dorsal and ventral arms (Fig. 7c, d). Although laterally compressed, both its lateral and medial faces bear a robust ridge that is parallel with the anterior margin of the bone. There is no opercular process. Although a foramen is visible, the path of the hyomandibular

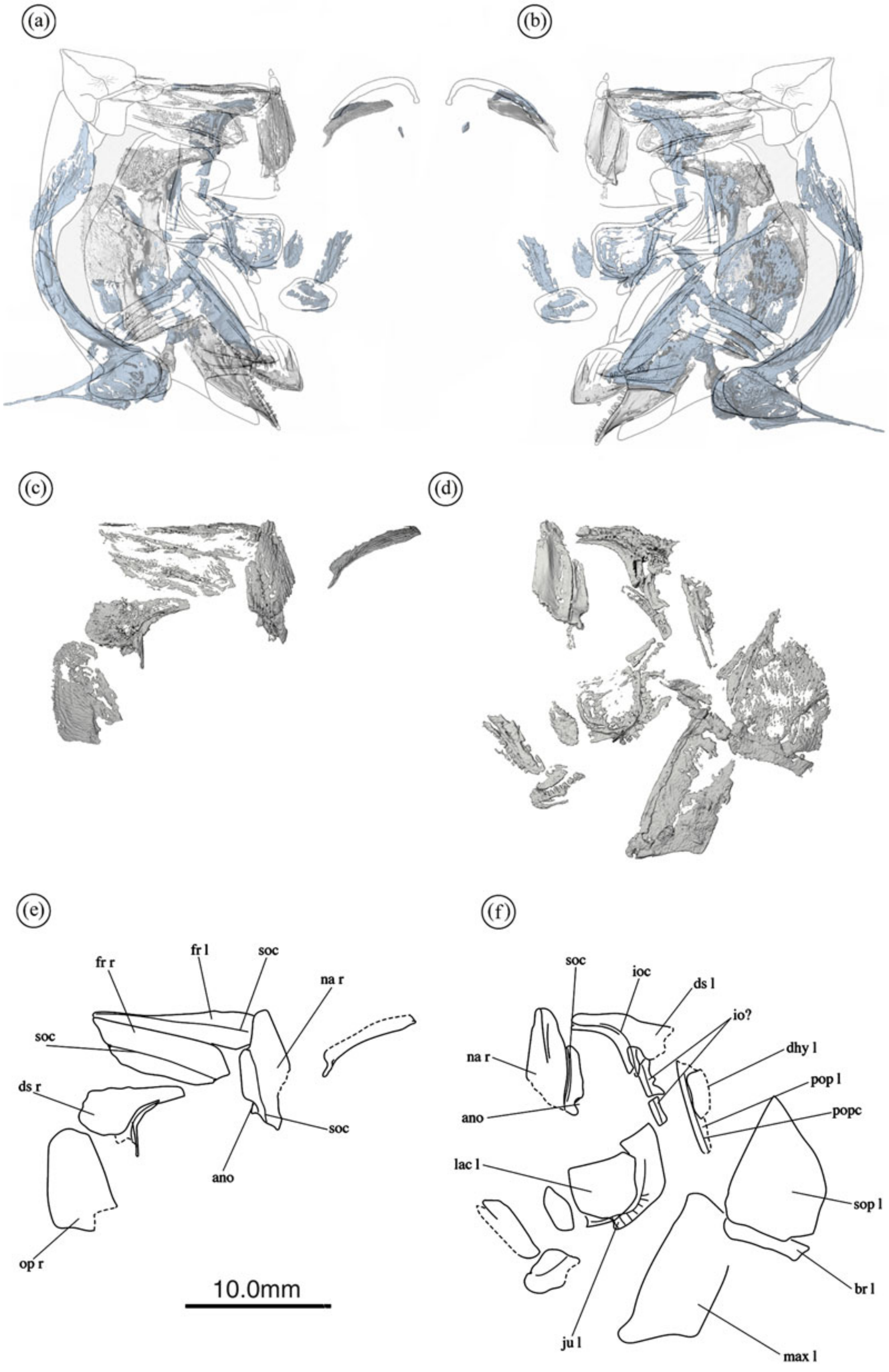

Figure 4 *Mesolepis arabellae sp. nov.* Skull roof and cheek reconstructed from µCT scan. (a) Composite of interpretive line drawing and rearticulated CT scans of part GLAHM 163398/1 (rendered in blue) and counterpart in GLAHM 163398/2 (rendered in grey) right lateral view. (b) Composite of interpretive line drawing and rearticulated CT scans of part GLAHM 163398/1 (rendered in blue) and counterpart in GLAHM 163398/2 (rendered in grey) left lateral view. (c) Render of dermal elements from right side of skull in GLAHM 163398/1 lateral view. (d) Render of dermal elements from left side of skull in GLAHM 163398/2 lateral view. (e) Line drawing of (c). (f) Line drawing of (d). Scale bar 10.0 mm.

canal (hmc) cannot be traced internally. Only a single ceratohyal (chy) can be identified with confidence, and this appears to be associated with the left hyoid arch (Fig. 7c). It is stout and hourglass-shaped, flaring both anteriorly and posteriorly, and with no groove for the afferent hyoid artery. Its short length relative to the elongate jaws suggests that an additional ceratohyal was probably present, although this cannot be identified.

8. Pectoral and pelvic girdles

The bones of the pectoral girdle are very similar in form to those found in *Amphicentrum* = *Chirodus* (Traquair 1875; Bradley Dyne 1939), *Platysomus* and *M. scalaris* (Traquair 1875). As in those taxa, the supracleithrum (scl) and cleithrum (cl) are elongate and almost equal in dorsal-ventral length (Figs. 3,

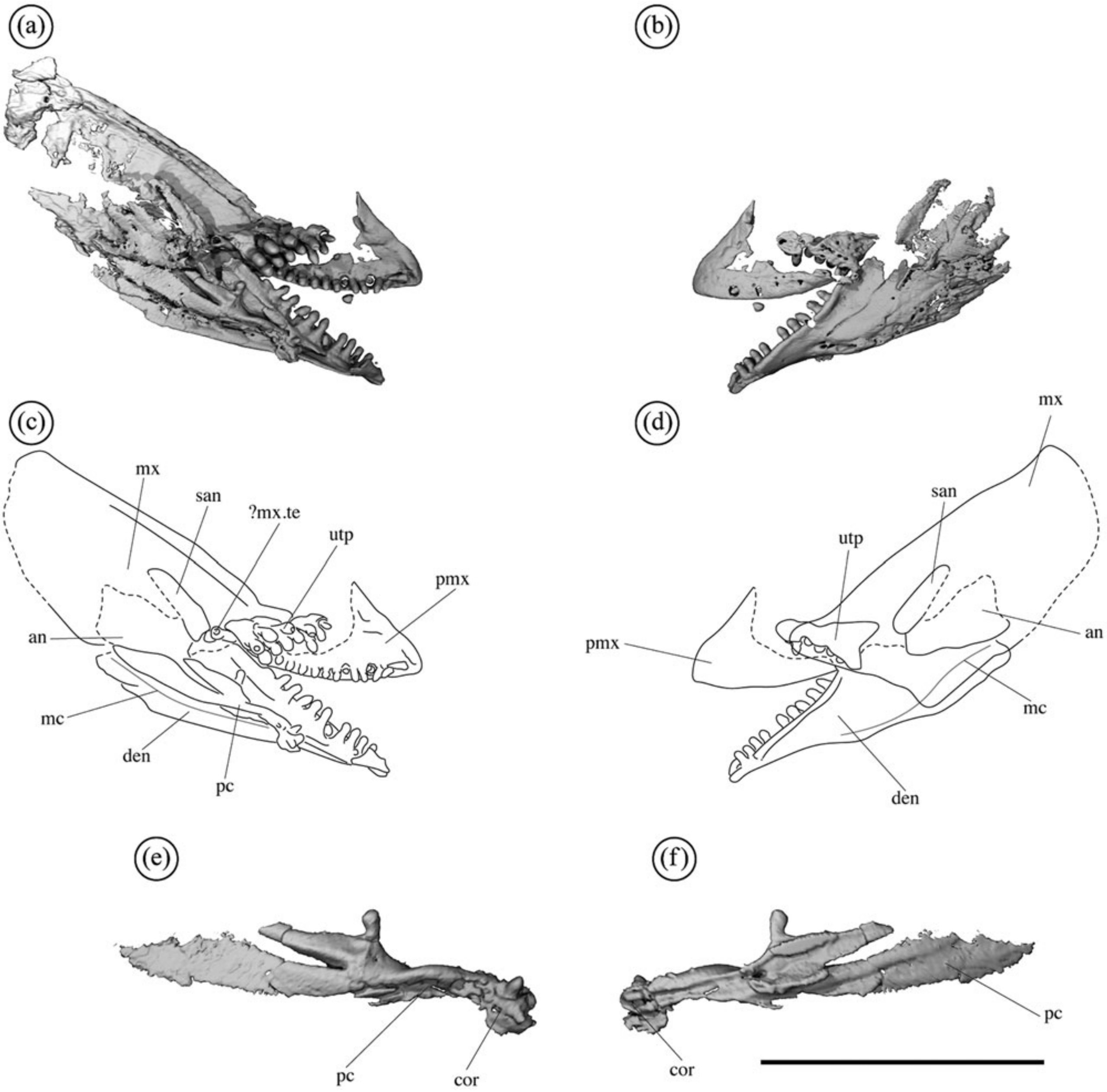

Figure 5 *Mesolepis arabellae sp. nov.* Jaws reconstructed from μCT scan. (a) Render of left jaws in GLAHM 163398/2 visceral view. (b) Render of left jaws in GLAHM 163398/2 lateral view, with maxilla not shown. (c) Line drawing of (a). (d) Line drawing of (b), with outer margins of maxilla drawn. (e) Left prearticular and coronoid plate in GLAHM 163398/2 visceral view. (f) Left prearticular and coronoid plate in GLAHM 163398/2 lateral view. Scale bar 10.0 mm in (a) to (d), 5.0 mm in (e) and (f).

8a–c). However, the cleithrum in *M. arabellae* is more strongly curved in a backwards direction and its broad rostroventral margin is in contact with the complete length of the large, piriform clavicle (cv) (Fig. 8b). A narrow overlap area for the operculum is observed along the rostral margin of the supracleithrum; this continues along the cleithrum as a narrow overlap area for the suboperculum and branchiostegals. The posteroventral margin of the cleithrum is developed into a narrow, elongate process visible in the μCT scan. Possible remains of a postcleithrum (pcl) are observed caudal to the supracleithrum-cleithrum articulation (Figs 3, 8c).

9. Fins

The pelvic, anal and caudal fins are well-preserved in *M. arabellae*. However, a large dorsal fin similar to that found in *M. scalaris* (Traquair 1878–80) is not observed (Figs 1, 2), and there is no evidence of lepidotrichia or endoskeletal support elements externally or in μCT scans. The dorsal fin is also absent from the genotype L.10930 and NHMUK PV P.1609. Amongst specimens referred to *M. wardi*, a well-formed dorsal fin is only observed in NHMUK PV P.9605 (Fig. 9). In this specimen, the dorsal fin is similar in form to that of *M. scalaris* but smaller and of the same size as the anal fin of *M. arabellae*. However, it should be noted that the identification of NHMUK PV P.9605 is somewhat questionable, especially in the scale morphology and in the narrow and slender caudal peduncle. As a consequence of this uncertainty, a dorsal fin has not been included in the line drawing reconstruction of the new species.

The pectoral fin is only partially preserved in *M. arabellae*. The μCT scan shows the propterygium (ptg) to be stout and imperforate (Fig. 8b). It is embraced by several fused lepidotrichia (fu). Other lepidotrichia are preserved in good detail, and additional endoskeletal radials are present but difficult to identify. A complete pectoral fin is preserved in *M. wardi* specimens NHMUK PV P.8042 and in V3226 (Fig. 10a, b). The pectoral

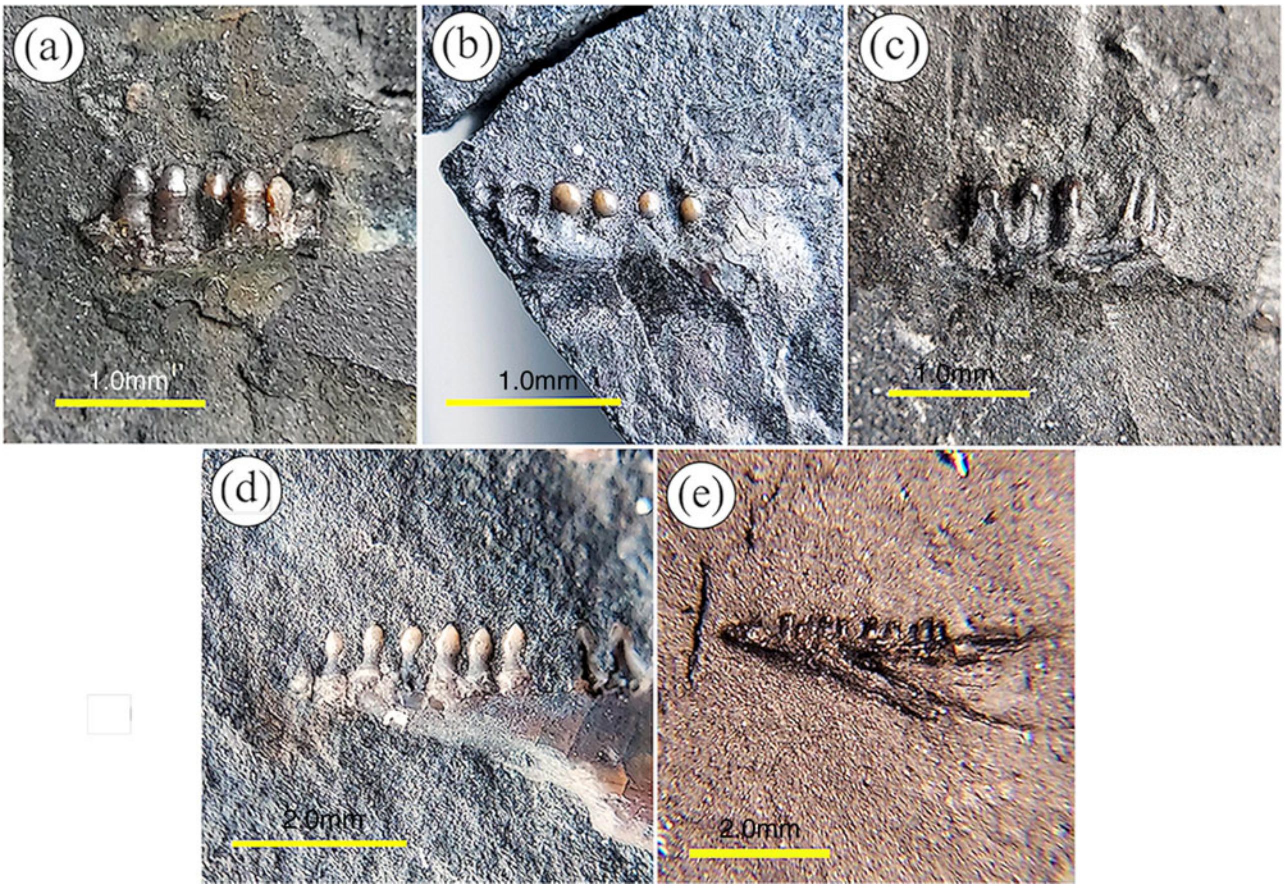

Figure 6 *Mesolepis* dentition. (a) *Mesolepis sp.* GLAHM 163392, vomerine, Calderhead. (b) *Mesolepis arabellae* GLAHM 163398/1 dentary, Wester Bracco. (c) *Mesolepis sp.* GLAHM 163393, dentary, Calderhead. (d) *Mesolepis wardi* V3228, dentary, Castlehill. (e) *Mesolepis sp.* GLAHM 163394, lower jaw, juvenile, Calderhead. Scale bar 1.0 mm in (a) and (c), 2.0 mm in (b), (d) and (e).

fin in these specimens is sub-spatulate in shape and much smaller compared with the pectoral of *M. scalaris.* In V3226 the fin is preserved in an upright position against the body of the fish with the leading-edge fin ray facing the rostral region. As regards to the lepidotrichia, in V3226 the most proximal only show bifurcation; this is similar to the condition shown in *M. arabellae.*

In *M. arabellae* the pelvic fin is wide and triangular; in *M. wardi* (P1609) this fin is decidedly trapezoid (Fig. 10c, d). The pelvic plate is large and shoe-shaped; in V3226 both the proximal and distal radials are observed as small bones and the lepidotrichia is seen to bifurcate for most of their length.

The anal fin of *M. arabellae* (Figs 1, 2) is similar to that found in other *Mesolepis* species; its rostro-caudal axis is long with the first fin rays extended and acuminate, the length of the fin rays decreasing and becoming fringe-like caudally. The heterocercal tail is deeply cleft and inequilobate; the upper lobe being slightly longer than the lower one. The dorsal margin of the upper lobe is furnished with large imbricating V-scales. Additionally, fin fulcra are observed along the leading margins of the anal fin and along the lower lobe of the caudal fin; a few enlarged fulcra also lie close to the base of the ventral margin of the lower lobe.

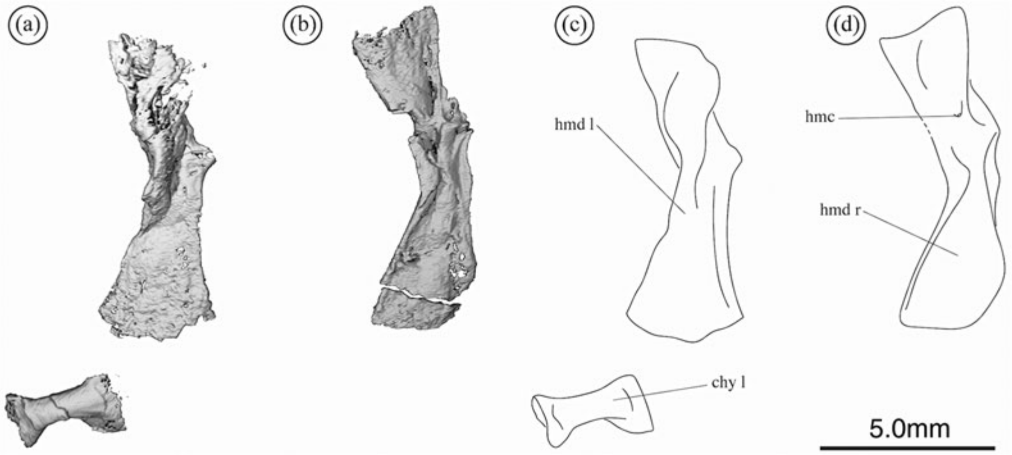

Figure 7 *Mesolepis arabellae sp. nov.* GLAHM 163398/1 and GLAHM 163398/2. Hyoid arch reconstructed from µCT scan. (a) Render of left hyomandibula and ceratohyal in GLAHM 163398/2 lateral view. (b) Render of right hyomandibula elements from left side of skull in GLAHM 163398/2 lateral view. (c) Line drawing of (a). (d) Line drawing of (b). Scale bar 5.0 mm.

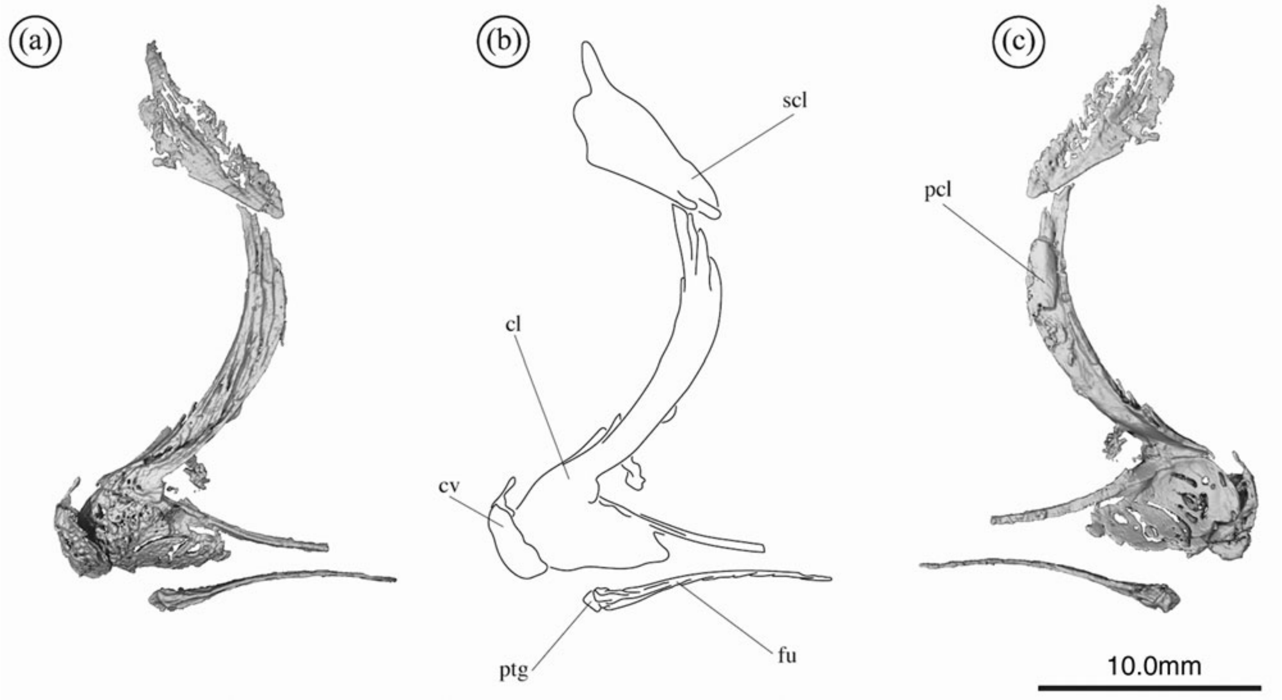

Figure 8 *Mesolepis arabellae sp. nov.* Shoulder girdle and fin elements reconstructed from µCT scan. (a) Render of left shoulder girdle and fin elements in GLAHM 163398/2 lateral view. (b) Line drawing of (b). (c) Render of left shoulder girdle and fin elements in GLAHM 163398/2 visceral view. Scale bar 10.0 mm.

10. Squamation

The squamation of *Mesolepis* has been described to a considerable extent by Traquair 1878–80 (p. 356) and briefly by Young 1866 (p. 313). However, apart from a rather obscure sketch of a scale of *M. scalaris*, there were no figures included with the definitions that adequately illustrate the ornamentation on the lateral surface of the scales of species of *Mesolepis*. For that reason, the following detailed description of a flank scale *M. arabellae* is given and comparisons made to other taxa.

The form of a typical body scale of *Mesolepis* varies from a simple parallelogram or rhombic to trapezoidal (Fig. 11a–f). The height of a flank scale, not including the height of the articular spine, is greater than two and a half times the scale width. The dorsal and ventral margins are normally angled backwards and upwards with the dorsocaudal angle of the scale curving upwards. The rostral and caudal margins may be parallel or they may converge slightly on approaching the ventral border, or the caudal margin may be sinuous in outline. An articular spine normally confined to the rostral portion of the dorsal margin of the scale is about half the height of the scale and triangular in form. A large triangular depression for accommodation of the articular spine of the scale below can be seen on the visceral surface of the scale (Fig. 11b, c). This recess is present in all but the

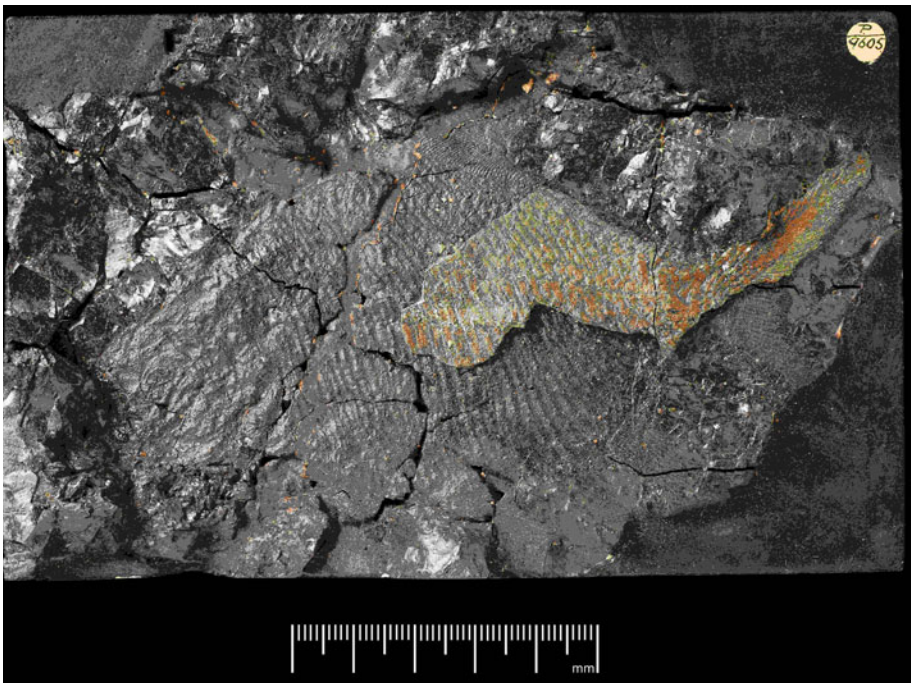

Figure 9 *Mesolepis wardi* P9605. Jarrow Colliery, Kilkenny. Complete specimen in left lateral view; specimen discolouration is a result of mineral decay.

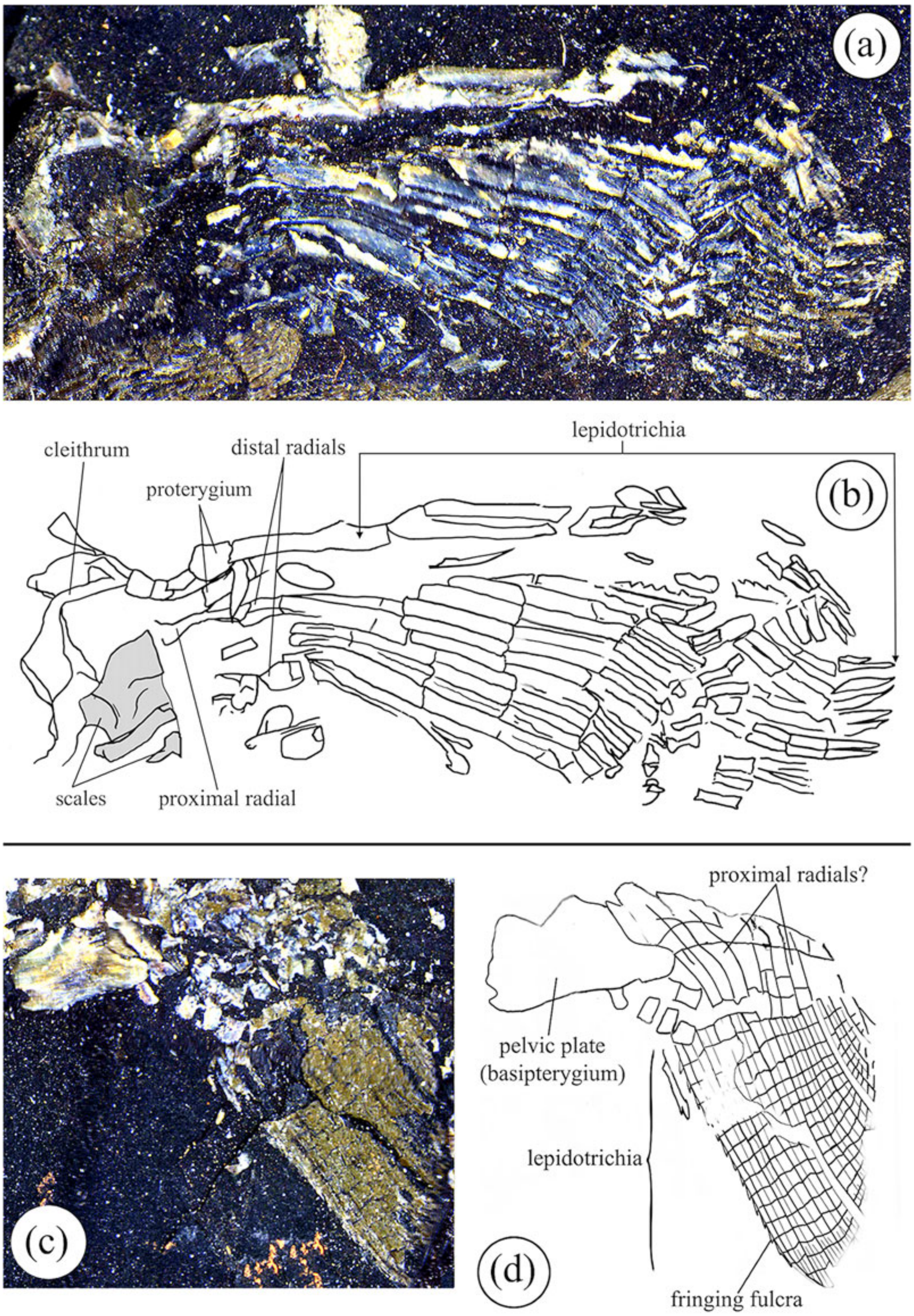

Figure 10 *Mesolepis wardi* V3226. Castlehill. (a) Right pectoral fin. (b) Interpretation of (a). (c) Right pelvic fin. (d) Interpretation of (c).

smallest scales and usually accompanied with a vertical keel which runs parallel with the length of the rostral margin.

Using the diagnoses given by Traquair earlier for comparison, ornamentation of the exposed surface of the scale of *M. scalaris* and *M. wardi* is of sinuous and generally vertical tubercles incorporating one or two furrows along the length of the covered rostral margin. This agrees well with the scale ornamentation in specimens recovered from Castlehill and Fenton sites (Fig. 11e, f). However, in specimens from Wester Bracco, Calderhead and Greenrigg, and including those of *M. arabellae* (Fig 11a–d), the ornamentation of the exposed surface of the scale differs in a number of ways. The sculpture is of flat, occasionally sinuous ridges which traverse the scale forwards and downwards at an angle of about 45 degrees; near the rostroventral corner these ridges coalesce or form elongate or rounded tubercles, similar to those found on the larger dermal head bones. The covered rostral margin of the scale is narrow with six or more fine striae running dorsal-ventral along the margin. The visceral surface of *Mesolepis* scales is generally without ornamentation. However, in specimens from Wester Bracco, Calderhead and Greenrigg sites, the ornamentation on the lateral surface often pervades in a weak fashion through to the visceral surface (Fig 11b, c). This is revealed as a plumate-like sculpture, not only in the large flank scales, but also in the smaller scales of the caudal

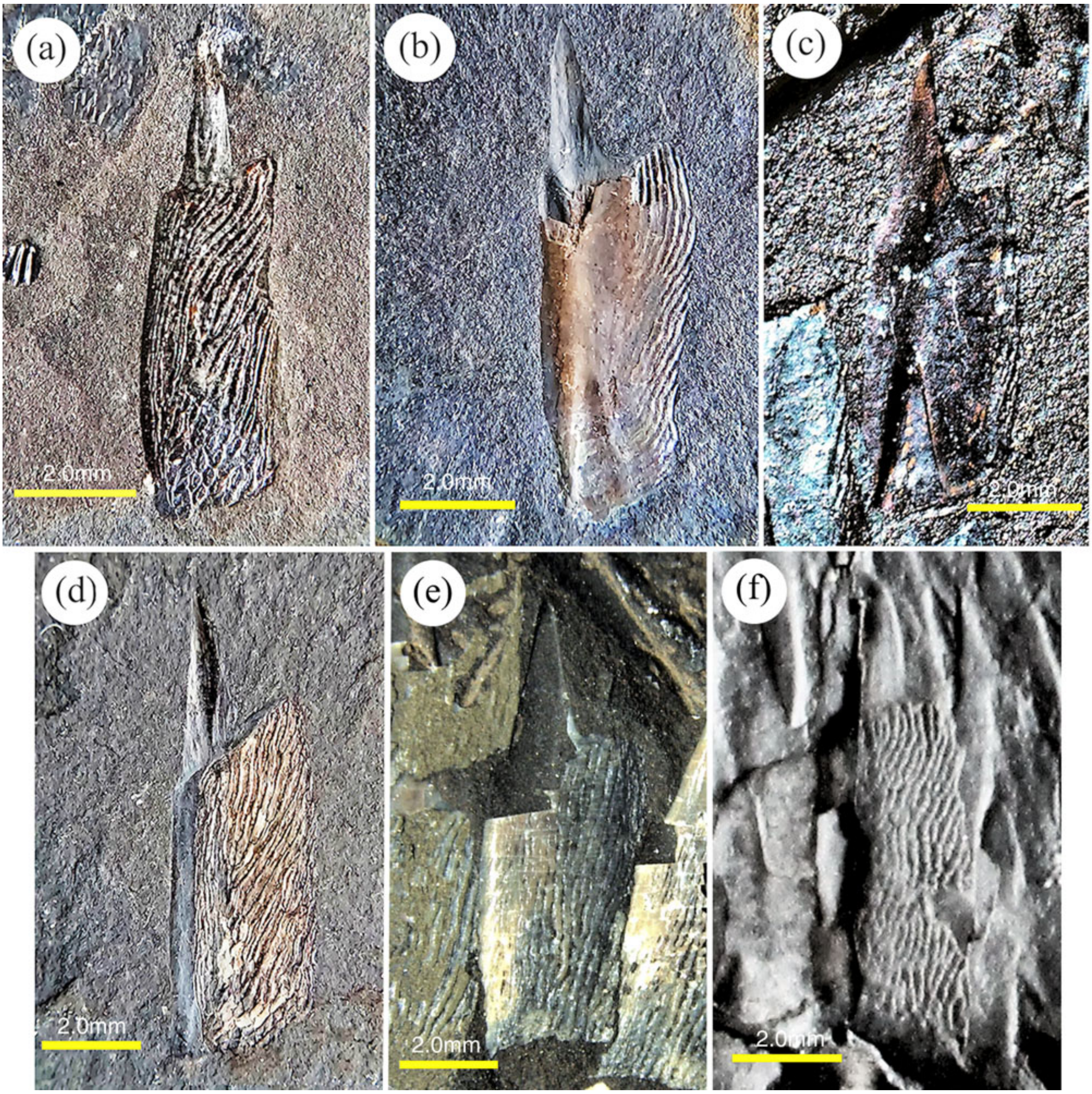

Figure 11 *Mesolepis* scales. (a) *Mesolepis arabellae* GLAHM 163395, lateral view. Calderhead. (b) *Mesolepis arabellae* GLAHM 163396, visceral view. Calderhead. (c) *Mesolepis arabellae* GLAHM 163398/1, visceral view. Wester Bracco. (d) *Mesolepis arabellae* GLAHM 163397, lateral view. Greenrigg. (e) *Mesolepis wardi* V3226, lateral view. Castlehill. (f) *Mesolepis wardi* L10930, lateral view. Fenton. Scale bar 2.0 mm.

peduncle region: a peculiar property that can erroneously be mistaken for fringe-like fin rays. Additionally, the caudal peduncle scale rows of *M. arabellae* exhibit a strong diagonal orientation as found in many primitive actinopterygians, such as *Mesopoma*, *Rhadinichthys* and *Gonatodus.*

A fourth member of the genus, *Mesolepis pustulosa* from the coalfields of Northern France (Pruvost 1919), was named on scale description alone. However, similar scales to those illustrated by Pruvost are a frequent find in shales at Drumgray Coal waste tips. At Wester Bracco and Dewshill, for example, these scales are often associated with the dentition and dermal elements of a yet undescribed species of *Amphicentrum* (=*Cheirodus* McCoy). Pruvost's illustrations do not demonstrate the morphological characteristics shown in *Mesolepis* scales, and are possibly examples of the variation in the scale morphology of *Amphicentrum striatum* (=*Cheirodus striatus*) (Hancock & Atthey 1872) that is also found in the same coalfields. Consequently, until further research is undertaken it appears that the taxonomic position of *M. pustulosa* may be questionable.

11. Discussion

In *M. arabellae,* the body is compressed laterally and deeply arched dorsally, giving the torso a rhomboid appearance (Figs 1–3, 12). Large ridge scales (sdr) are positioned along the dorsorostral margin of the body arch, thus forming a well-defined angle with the dorsocaudal margin at the apex of the arch. These five or six ridge scales extend from the apex to the large posttemporal bones rostrally; similar ridge scales are also found in *M. wardi* (NHMUK PV P.8042, NHMUK PV P.9605), although this condition has not been previously reported. From the apex of the dorsal margin, the head slopes in a rostral direction to the paired frontal bones. The slope changes direction as a result of the forward protrusion of the strongly curved rostral bone. From the rostral bone the slope continues to the snout region formed by the medial coupling of the premaxillary bones. The general arrangement and external morphology of the head dermal elements in *M. arabellae* and *M. wardi* follows essentially that of *M. scalaris* (Traquair 1878–80).

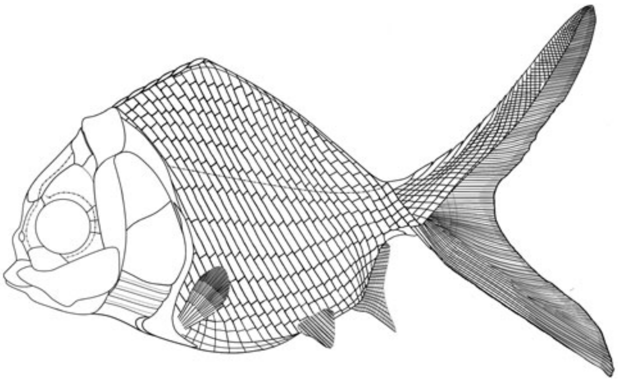

Figure 12 *Mesolepis arabellae sp. nov.* Reconstruction of holotype. Dorsal fin not included in reconstruction due to its absence in GLAHM 163398/1 and in GLAHM 163398/2, and also in the holotype of the type species L.10930.

However, the overall form of the new species indicates a much more slender animal than that given for the homogeneous *Mesolepis wardi* (Fig. 12), and is also deeper than that given for *Mesolepis scalaris* (Young 1866; Traquair 1878–80). The general shape of the body of the new species more closely resembles that of *Paramesolepis* (Moy-Thomas & Dyne 1938). The length of the trunk from the pectoral fin to the root of the tail in *M. arabellae* is estimated to be slightly more than the greatest depth of the trunk; the ratio in *M. wardi* is reported as almost twice the depth (Young 1866). Furthermore, the angle of the torso arch in *M. arabellae* is found to be more acute than in other species of *Mesolepis*. In addition, the tail peduncle of *M. arabellae* is short and slender and of the same condition found in *M. scalaris*; however, the tail peduncle in *M. wardi* is thick and slender (Young 1866). There are also significant differences in scale morphology and in the dentition of the three species of *Mesolepis*.

Differences are also apparent between the dentition of *M. arabellae* and those of other *Mesolepis* species: the teeth of the new species are spherical, and do not exhibit the same bullet-shaped crowns described for *M. scalaris* and *M. wardi* (Traquair 1878–80). In gross morphology, however, the overall tooth design in *Mesolepis* species is similar, resembling that of *Eurysomus* (Traquair 1878–80). In contrast, the dentition of other eurynotiforms such as *Eurynotus* (Friedman *et al*. 2018) and *Amphicentrum* (Bradley Dyne 1939) is coalesced into a toothplate in which the crowns are continuous. The presence of separate tooth crowns throughout the upper and lower jaws of *M. arabellae*, including on the palatal toothplate, supports the argument that *Mesolepis* retains the primitive dental condition relative to more nested members of Eurynotiformes (Friedman *et al.* 2018), although this is yet to be tested in an explicit phylogenetic framework. Certain details of the jaws in *M. arabellae,* such as the presence of teeth on the premaxilla and dentary, violate the taxon diagnosis of Eurynotiformes sensu Sallan & Coates (2013); further μCT-aided study of *Mesolepis* and allied taxa will be needed to determine whether the genus should be removed from Eurynotiformes or the diagnosis revised.

The distinctive form of the head and torso of *M. arabellae,* and indeed of the other species of *Mesolepis*, probably represent ecomorphological modifications that allowed the animal to exploit a specialised niche in its ecosystem. Most occurrences of *Mesolepis* are reported from estuarine or fluvio-deltaic environments. Friedman *et al*. (2020) states that the pelagic realm results in fewer opportunities to interact with a heterogeneous environment and offers fewer ecological niches for diversification. However, demersal and particularly benthic habitats provide considerable physical and biological complexity by presenting opportunities to physically interact with the substrate during both feeding and locomotion, thus potentially driving diversification.

A laterally compressed and deep body, small paired-fins and reduced dorsal fin would have facilitated access to narrow spaces between the flora or rocky fissures; this morphology also allowed for greater manoeuvrability with a reduced turning circle. In these situations, the role of the dorsal fin would be reduced as there would be little or no side currents producing roll; this would result in most of the manoeuvring being carried out by lateral movement of the caudal and anal fins alone. A further and interesting example in the fossil record of this morphology includes some species of the more recent Pycnodontidae (Poyato-Ariza 2005). Amongst living taxa, lateral compression and deepening of the body are often associated with high flexibility in living fishes such as angelfish (Pomacanthidae) and butterflyfish (Chaetodontidae) as the sides of the fish offer a large surface area for braking and rapid changes in direction (Fletcher *et al*. 2014), with a common assumption being that this body shape results in a trade-off for swimming performance. However, Satterfield *et al*. (2022) investigated this hypothesised link and found little correlation between body shape and swimming performance. One potential explanation for this is the variation in swimming mode observed in living taxa, the most common being body and caudal fin undulation and median-paired fin swimming, but these cannot be easily inferred in fossil taxa.

Three methods of prey capture are known in fishes: suction feeding, ram feeding, and manipulation (Liem 1980). In suction feeding, the predator expands the buccal cavity or pharynx by protrusion of the jaw, thus creating a pressure gradient that forces the prey to move towards the gape of the mouth. In ram feeding, the predator ingests free-swimming prey by forward movement of the body and protruding jaws. As the premaxilla and maxilla in *Mesolepis* did not allow for jaw protrusion, and the deep body morphology adapted for high manoeuvrability did not allow for high speed to catch prey, both ram and suction feeding, which are based on speed and jaw protrusion, can be ruled out as a primary feeding strategy. Manipulation, where the jaws are directly applied to the prey and used to extract it from the substratum (Wainwright & Bellwood 2002), was the most likely primary feeding strategy used by *Mesolepis*. Manipulation also allows for a more comprehensive variation in herbaceous material and animal food sources (Poyato-Ariza 2005), which may account for the specialised form of dentition found in *Mesolepis*. Conversely, manipulation is rare in extant ray-finned fishes that tend to use ram and suction as a primary feeding strategy.

μCT scans reveal a distinctive dentition of the upper and lower jaws of the specimen, which suggests a crushing role. However, although the worn surface of some of the vomerine teeth indicate a grinding action, possibly as the result of a durophagous diet, it is likely that the diet of *Mesolepis* was of a more specialised nature.

Although little is known of the musculature of the jaws of *Mesolepis*, the large caudal expansion of the maxilla and the robust mandible that deepens posteriorly suggest they could exert a large force due to the high mechanical advantage exerted by the jaw musculature. These fishes also have relatively small gapes, which give a high mechanical advantage of the adductor muscles (Wainwright & Richard 1995). In pycnodonts, a Triassic–Eocene radiation of actinopterygians that have also converged on a deep-bodied, durophagous morphotype, the crushing performance was carried out by molariform vomerine and prearticular teeth (Poyato-Ariza 2005). These molariform teeth usually present large worn surfaces in adult specimens that are a clear indication of an intense grinding action. However, the rounded vomerine, maxillary and dentary teeth in *M. arabellae* are not molariform and their morphology is therefore not suited for a crushing function, particularly not for hard shells and carapaces. Food considered more appropriate for this dental morphology might be more likely be in the form of small aquatic prey. However, caution must be taken when inferring diet solely on the basis of jaw and tooth morphology (Dean *et al.* 2017): many extant taxa eat a broad range of prey items, despite apparently essentialised tooth morphology. One example is the batoid fish of the genus *Rhynchobatus*, which possesses rounded pebble-like teeth apparently adapted to cracking hard shells, but which eats softer-bodied cartilaginous stingray as well as shellfish and crabs.

With regards to *Mesolepis*, potential prey in the form of invertebrates and other vertebrates could be found throughout the Scottish coal measure deposits. Early chondrichthyans such as *Callopristodus*, *Helodus* and *Pleurodus* formed a composite part of the ecosystem (Elliott 2018); however, here they are considered too large a prey for *Mesolepis.* Nonetheless, also inhabiting the shallow swamp regions were large numbers of small actinopterygians (Elliott 2014, 2018) and immature stages of the coelacanth *Rhabdoderma*, *Strepsodus* and *Rhizodopsis* (Elliott 2023) as well as the small megalichthyid *Megalichthys pygmaeus. M. pygmaeus* was considered abundant at certain horizons, including those where *Mesolepis* material was recovered (Elliott & Challands 2021). At these locations the thick cosmine-covered dermal bones of individual *M. pygmaeus* are occasionally found in small heaps, with many of the bones broken and badly damaged; the damage to the bones was almost certainly the consequence of a crushing action by other animals. Further work is needed on complete, uncrushed specimens of *Mesolepis* in which the articular and quadrate are known in order to establish functional attributes and better infer likely sources of prey.

12. Data availability

Raw data (.TIFF stacks), Mimics files and three-dimensional surface files (PLY files) for each of the three M. arabellae CT scans are deposited in Zenodo (10.5281/zenodo.11046840).

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15. Competing interest

The authors declare no competing interests.

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