SPANISH JOURNAL OF PALAEONTOLOGY

RESEARCH PAPER

Non-tetrapod sarcopterygians from the Valentia Slate Formation (Givetian, Devonian) of the Iveragh Peninsula, south-western Ireland: systematic reappraisal and palaeobiogeographic implications

Sarcopterigios no-tetrápodos de la Formación Pizarras de Valentia (Givetiense, Devónico; Península de Iveragh, suroeste de Irlanda): reevaluación sistemática e implicaciones paleobiogeográficas

Vincent DUPRET[iD], Hannah BYRNE[iD], TOM CHALLANDS[iD], Øyvind HAMMER[iD], Kenneth HIGGS[iD], John LONG[iD], Grzegorz NIEDŹWIEDZKI[iD], Martin QVARNSTRÖM[iD], Iwan STÖSSEL[iD] & Per Erik AHLBERG[iD]

Abstract: The Middle Devonian (Givetian) Valentia Slate Formation in the Iveragh Peninsula, southwest Ireland, is more renowned for the second oldest record of tetrapod trackways in the world than for its heavily metamorphosed bone remains. The present study focuses on new discoveries of non-tetrapod sarcopterygian fish fossils from the Valentia Slate Formation. Micro-CT scanning technology allows a re-interpretation of a previously published acanthodian fin spine as a fanged coronoid of a probable Rhizodontida and the identification of a Dipnoi tooth plate and bone. In addition, a scale of *Holoptychius* is described. The presence of rhizodontids suggests Gondwanan ties, and a first northward dispersal wave of these vertebrates into Euramerica as early as middle Givetian. This hypothesis is supported by the common occurrence of the placoderm *Bothriolepis* in the Valentia Slate Formation.

Resumen: La Formación de Pizarras de Valentia del Devónico Medio (Givetiense), en el suroeste de la península de Iveragh, Irlanda, es más conocida por el segundo registro más antiguo del mundo de huellas de tetrápodos, que por sus restos de huesos fuertemente metamórfizados. El presente estudio se centra en los nuevos descubrimientos de fósiles de peces sarcopterigios no tetrápodos de dicha formación. El uso de técnicas de escaneo con Micro-CT permite una reinterpretación de lo que fue publicado previamente como una espina de acantodio en un coronoides con dentículos de un probable rizodontido, así como la identificación de huesos y una placa dental de Dipnoi. Además, se describe una escama de *Holoptychius*. La presencia de rizodontidos sugiere cierta conexión con Gondwana, así como una primera ola de dispersión de estos vertebrados hacia el norte (Euramérica) ya durante en el Givetiense medio. Esta hipótesis está respaldada por la presencia común del placodermo *Bothriolepis* en la Formación de Pizarras de Valentia.

INTRODUCTION AND GEOLOGICAL SETTING

The Valentia Slate Formation is the oldest division of the Devonian Old Red Sandstone succession in the Iveragh Peninsula of southwest Ireland. It is extensively exposed on Valentia Island and along the Atlantic coastal section from Dromgour to St Finan's Bay (Fig. 1). The Formation is mainly composed of purple and purple-grey siltstones with lesser amounts of purple and green sandstones and pebble conglomerates. These fluvial and floodplain sediments were deposited in the large extensional Munster Basin in late Middle Devonian times (Capewell, 1975; Graham *et al*., 1992; Pracht, 1996; Russell, 1984; Stössel *et al*., 2016; Williams *et al*., 1989). The formation also contains a variety of dolerite-gabbro intrusions and volcanoclastic deposits (Graham *et al*., 1995), that include the Enagh

Tuff Bed in Valentia Harbour and the Keel Tuff Bed in St. Finan's Bay; both have yielded Middle Devonian (Givetian) ages of 384.9 ± 0.7 My and 385.0 ± 2.9 My respectively (Williams *et al*., 1997, 2000). This makes the Valentia Slate Formation slightly older than the Givetian–Frasnian boundary, which is currently dated at 382.7 ± 1.6 My (see Cohen *et al*., 2013). In late Carboniferous time, the Valentia Slate Formation rocks were deformed by the Variscan orogeny (Cooper *et al*., 1986) corresponding to low-grade green schist facies metamorphism (Arndt, 2011; Meere, 1995; Stössel *et al*., 2016). This deformation produced significant crustal shortening and a strong tectonic cleavage in the rocks, which has had a pronounced effect on the preservation of the fossil material. The metamorphism
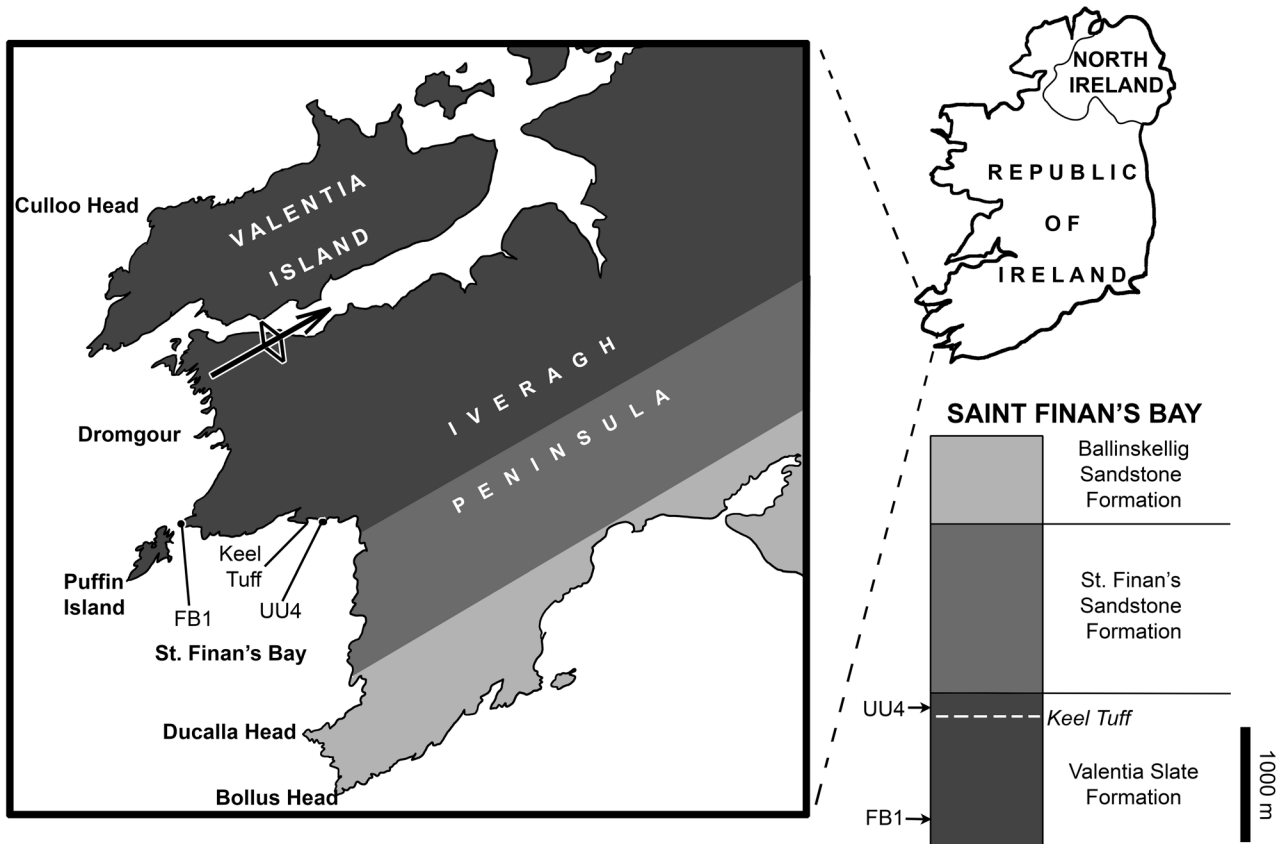
Figure 1. Simplified geological map of south-western Ireland (modified after Russell, 1978). Abbreviations: **FB1,** locality "Fish Bed 1" in Russell (1978, fig. 2); **UU,** locality "Uppsala University field work" in Dupret *et al.* (2023, fig. 1).

has led to zones of mineralization around the bones, as well as elemental exchange between bone and matrix (Dupret *et al.*, 2023) of the fossil material.

The Valentia Slate Formation on Valentia Island is of great palaeontological importance as it contains the second oldest record of tetrapod trackways in the world (Clack, 1997; Stössel, 1995; Stössel *et al.*, 2016). The Formation also contains a fauna of disarticulated non-tetrapod vertebrate remains (Dupret *et al.*, 2023; Russell, 1978). Russell recorded five vertebrate fossil horizons (FB1–FB5) in the Valentia Slate Formation at St Finan's Bay. He attributed the skeletal material to two taxa: the antiarch placoderm *Bothriolepis* sp. (by far the most abundant material) and an acanthodian, represented by a single fin-spine (herein reinterpreted as a fanged anterior coronoid of rhizodont; see further). In addition to this, Sarcopterygian scales attributed to the genus *Sauripterus* were also reported from the overlying Frasnian St. Finan's Sandstone Formation. However, this latter identification has now been discounted, with the material now being re-interpreted as indeterminate holoptychiid material of little stratigraphic value (see Bray, 1990 and Holland & Sanders, 2009, p. 202–203).

Russell (1978, p. 159) believed the occurrence of *Bothriolepis* in the Valentia Slate Formation "would imply a maximum age of either uppermost Givetian or basal Frasnian". This age assignment has been significantly refined by the Isotopic dating of the Keel Tuff, that stratigraphically occurs 800 m above the main *Bothriolepis* fauna (FB1) in St Finan's Bay. The Keel Tuff has yielded an isotopic age of 385 My (Williams, 2000) which unequivocally demonstrates that Valentia Slate Formation is Givetian in age, and makes the *Bothriolepis* material the earliest record of the genus in Laurussia (Dupret *et al.*, 2023).

The present study is primarily based on the re-examination of material originally described by Russell (1978) and stored in the fossil vertebrate collections of the Natural History Museum of London. In particular, a CT-scan of the specimen (NHMUK PV P 59686) originally described as an acanthodian fin spine has been carried out to determine more precisely its taxonomic attribution. The analysis of the CT-data reveals that this specimen is not an acanthodian fin spine but rather a fanged coronoid of a sarcopterygian, probably a rhizodont. During the CT-scan, a hidden dipnoan tooth plate was detected within the matrix of the same block containing the fanged coronoid. In addition, a dermal scale (NMING:F35232) obtained from the Valentia Slate Formation at St Finan's Bay (location UU4 in Fig.1) during recent field work is assigned to the porolepiform genus *Holoptychius*. The current article describes this new sarcopterygian material and draws systematic and palaeobiogeographic considerations.

MATERIAL AND METHODS

The material consist of two specimens. NHMUK PV P 59686, one rhizodont coronoid with fang and marginal teeth, one facial bone, and one lungfish toothplate. Two *Bothriolepis* (Placodermi, Antiarchi) remains are also present in the slab but were not analysed in this study. NMING:F35232, one isolated *Holoptychius* sp. dermal scale.

The specimen NHMUK PV P 59686 was scanned at the Natural History Museum, London, UK, using a Nikon HMX ST 225 system (Nikon Metrology, Leuven, Belgium) with a tungsten reflection target. The X-ray beam typically generated a voltage of 180 kV filtered with 1.5 mm of copper. Given the positive correlation between the beam spot size and the power of the source, the intensity was adjusted to avoid geometric blurring which occurs when the spot size is larger than the recorded pixel size. The µCT acquisitions consisted of 2699 projections, with an exposure time of 708 ms. Voxel size is 33.47 µm. Tomographic reconstructions were done using the Nikon CT-pro 3D and CT-agent software (Nikon Metrology GmbH, Alzenau, Germany), generating a 16-bit volumetric raw file.

The specimen NMING:F35232 was scanned at the Oslo Museum of Natural History, Norway, using a Nikon Metrology XT H 225 ST microfocus CT instrument, at 220 kV, 245 µA, 4444 projections, 2 frames per projection,1 mm tin filter, Fast CT protocol (not minimising ring artefacts) and a voxel size of 23.9 µm.

Scans were studied using Drishti Import (v. 2.6.4) and Drishti (v. 2.6.4; Limaye, 2006, 2012), and Materialise Mimics (v. 23). In Mimics, each structure corresponds to a mask used to generate a high quality 3D object, itself transformed into a .stl file. Each .stl file was then imported into Materialise 3-matic (v. 15.0) and Blender (v. 2.82). In 3-matic, the following operations were applied to each .stl file to increase manageability while preserving accuracy: reduce number of triangles (geometrical error 0.1, preservation of surface contours) and smoothing (factor 0.1). The stls were then saved as 3D pdf files (see Supplementary Material).

RESULTS

Rhizodontida

The material that may be provisionally attributable to Rhizodontida comprises a right anterior coronoid, partly exposed in lateral view on the surface of the block, and an unidentified facial or ethmoid bone buried in the matrix (**cor**, **indet**, Figs. 2–3).

The coronoid fang lies in the cleavage plane of the matrix (**co.fa,** Fig. 3A–3I). It is slightly asymmetrical, the labial side being flattened because of weathering, but the left/lingual side is more cylindrical in section. The longitudinal striation visible externally that Russell (1978) identified as acanthodian fin spine ridges are in fact internal plicidentinous folds (**pl**, Fig. 3J). The fang
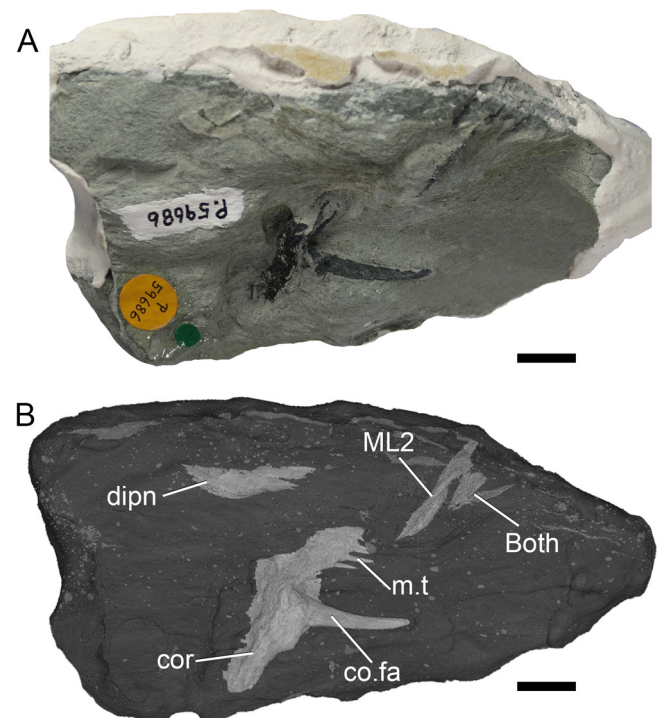

Figure 2. Specimen NHMUK PV P 59686. **A,** Photograph of the specimen revealing part of the coronoid and fang (mistaken for an acanthodian spine by Russell, 1978); **B,** digital rendering showing the inclusions with matrix semi-transparent. Abbreviations**: Both.,** indeterminate *Bothriolepis* plate; **co.fa,** coronoid fang; **cor,** coronoid; **dipn,** dipnoan **toothplate**; **m.t,** marginal teeth; **ML2,** lateral marginal plate 2 (*Bothriolepis* sp. nov.); scale bar = 10 mm.

is slender and posteriorly recurved, measures 17.3 mm from its base (indicated by a resorption area) to the tip, and 4.7 mm in diameter at its base (anteroposterior measurement). The fang is preceded anteriomesially by a 5.3 mm long replacement socket (**r.s**, Fig. 3B, 3D) and followed by a 6.7 mm long and 4.8 mm deep diastema separating the fang from a series of 5 smaller marginal teeth (**m.t**, Fig. 3), the latter being distributed longitudinally over a 7.3 mm length. The lateral side of the replacement socket is higher than its mesial lamina, and is aligned with the line at the base of the fang demarcating the resorption area mentioned above, more obvious mesially than laterally (**r.a**, Fig. 3B–3D). Marginal teeth 3 and 4 are closer to each other than to the other ones; the highest marginal tooth is the second one, the smallest is the fifth. When observed in anterior or posterior views, the marginal teeth appear aligned in a slightly more mesial plane than the fang. A slightly sinuous contact surface for the dentary is observed on the lateral side of the coronoid, and an elongated anteroposterior slit anteriorly corresponds to the anterior suture with the dentary (**de.oa, de.s**, Fig. 3C, 3E, 3H). An oblique contact face for the middle coronoid is observed posteriorly (**m.cor.cf**, Fig. 3B). The anteromesiolateral edges of the coronoid outline the edge of the precoronoid fossa (**p.cor.f**, Fig. 3D–3G). The digital removal of the other bone allows the observation of the articular facet for the prearticular (**p.art.cf**,
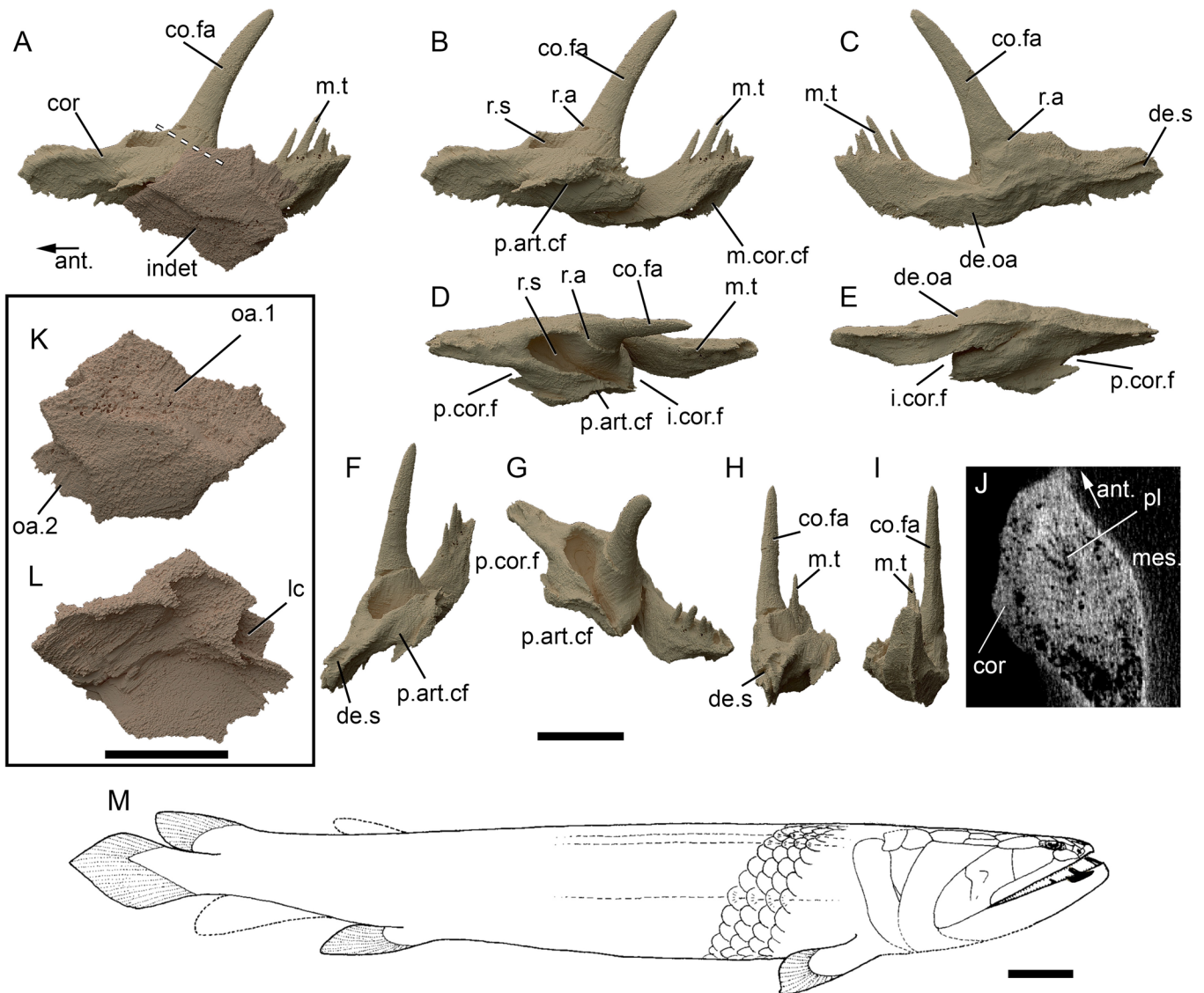
Figure 3. Digital renderings of probable rhizodont coronoid found in NHMUK PV P 59686. **A–I,** Complete specimen with coronoid and teeth; and **K, L,** indeterminate facial bone; Isolated coronoid in **B,** mesial; **C,** lateral; **D,** dorsal; **E,** ventral; **F,** oblique anterodorsal; **G,** oblique posterodorsal; **H,** anterior and **I,** posterior views; **J,** transverse tomogram at the base of the coronoid fang, as indicated by dashed line in **A**; **K–L,** indeterminate facial or skull roof bone in: **K,** external and; **L,** internal views; **M,** outline of the rhizodont *Gooloogongia* in right lateral view (Frasnian, Australia; slighty modified from Johanson and Ahlberg, 2001, fig. 18a; reprinted with permission), with coronoid NHMP 59686 blackened. Abbreviations**: ant.,** anteriorward; **co.fa,** coronoid fang; **cor,** coronoid; **de.oa,** contact surface with dentary; **de.s,** anterior suture for the dentary; **i.cor.f,** intercoronoid fossa; **indet.,** indeterminate facial bone; **lc,** canal for sensory line; **mes.,** mesial side; **m.t,** marginal teeth; **oa.1,** overlap area 1 on the indeterminate facial bone; **oa.2,** overlap area 2 on the indeterminate facial bone; **p.art.cf,** articular facet for the articular; **p.cor.f,** precoronoid fossa; **pl,** plicidentine; **r.a,** resorption area; **r.s,** replacement socket; scale bars = 10 mm (A–I, K, L), or 10 cm (M).

Fig. 3B, 3D, 3F–3G), which lies ventromesially from the base of the coronoid fang. The intercoronoid fossa lies mesially from the lamina with diastema and marginal teeth (**i.cor.f**, Fig. 3D). The tomograms reveal that the fang is made of plicidentine (**pl**, Fig. 3J).

The other unidentified bone is shaped like an asymmetrical pentagon (indet, Fig. 3A, 3K–3L). The external side shows a short and sharply outlined overlapping area and possibly a large one with a smoother transition (**oa1, oa2**, Fig. 3K–3L). The inner side (that faces the mesial side of the coronoid) reveals the path of a canal of the lateral line system (**lc**, Fig. 3L). It is uncertain whether this bone and the coronoid belong to the

same individual or even the same taxon. It could be one of the lateral skull bones, like the tabular of the postparietal shield, or the intertemporal in the ethmosphenoid skull roof, as both these bones have a linear sensory line canal passing through them. Both are of similar shape to these bones in rhizodontids like *Gooloogongia* (Johanson & Ahlberg, 2001).

Holoptychius sp.

Osteichthyan scales are extremely rare in the Valentia Slate Formation, but we have recovered one example of a round scale exposed in internal view

(NMING:F35232). Just over half the scale is preserved; the remaining part consists of an imprint of a smooth external surface. The scan model of the complete external side reveals a posterior ornamented area composed of diverging ridges and a smoother anterior overlap area for surrounding scales (Fig. 4). The character of the ornament is diagnostic for the porolepiform genus *Holoptychius*.

Dipnoi

A left lower jaw tooth plate from a lungfish is entirely enclosed in the matrix of the same block that contains the sarcopterygian coronoid (NHMUK PV P 59686) and therefore can only be observed digitally (Fig. 5). It carries 11 radiating tooth rows, merging into an undivided ensemble lingually. The heel on the lingual side is slightly involuted. The basal view reveals a flat and anteroposteriorly elongated area of bone which appears to represent an eroded prearticular, underlying the denticulated area but also extending posteriorly as a slender blade.

All identifiable teeth are conical, except the longest and most labial ones which are slightly curved antero-occlusally. Each tooth row is composed of 3 (posteriorly) to 5 (anteriorly) identifiable teeth; lingually they are fused into a field, probably a combined effect of basal growth and surface wear. No inter-row teeth or denticles, nor evidence for resorption, nor overgrowth are visible. The angle between first and last tooth rows is moderate (65°). The lingual heel is rounded, and no lingual callus can be identified.

DISCUSSION

Rhizodontida

It is noteworthy that marginal teeth are cylindrical in section and well preserved, indicating that the specimen did not suffer from extensive deformation: observed shapes and sizes of the bones can be considered accurate.

The attribution of the fanged anterior coronoid to a rhizodont rests on its unusual morphology, which is very different to those of other sarcopterygian groups such as porolepiforms (Ahlberg, 1991) and elpistosteg-ids (Ahlberg & Clack, 1998) in particular the narrow and anteroposteriorly elongated body of the bone, the tooth-less dorsal margin anterior to the fang pair, the slender recumbent fang shape. Additionally, the diastema separating the fangs from a posterior raised region that carries marginal teeth is similar to the condition observed in *Gooloogongia* (Johanson & Ahlberg, 2001, fig. 5). We conclude that the coronoid most probably derives from a primitive *Goologongia*-like rhizodont. Its Givetian occurrence would make it by far the earliest rhizodont from Euramerica, where all other known representatives are Famennian or Carboniferous (Davis *et al.*, 2001, 2004). By contrast, the Gondwana record is older, extending down into the Aztec Siltstone of Antarctica which may span the period from the Eifelian to the Givetian (Long *et al.*, 2021). This coronoid is thus, like the presence of *Bothriolepis*, a possible indicator of Gondwanan faunal affinities for the Valentia Slate Formation.

Dipnoi

The lungfish tooth plate appears unusually derived for a Givetian taxon. The number of tooth rows and moderately high tooth ridge angle is more typical of Famennian lungfishes (Smithson *et al.*, 2016). Whereas *Dipterus valenciennesi* from the Eifelian of Scotland can possess the same number of tooth rows, this is seen only in the palatal tooth plates (see Blaauwen *et al.*, 2006; White, 1965). The pterygoid tooth plates of *Dipterus*, however, may possess a similar tooth ridge angle to the specimen described here but lack a rounded heel and the first tooth row is always straight along the lingual margin in *Dipterus*.

The solid, worn field in the lingual region of the tooth plate is a further difference to *Dipterus* which, despite also turning ventrally in this region, does not wear down
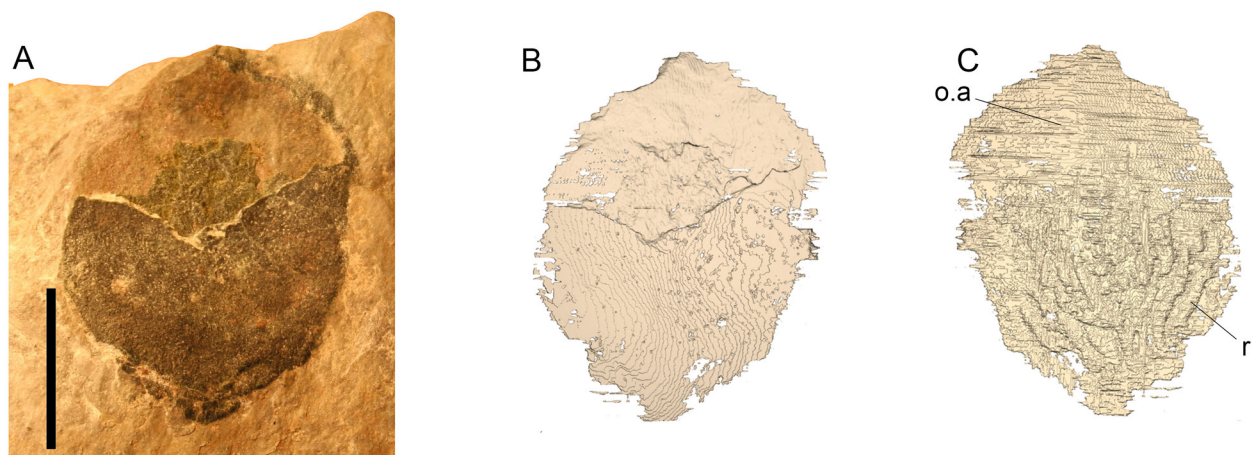

Figure 4. Isolated scale of *Holoptychius* sp. Specimen NMING:F35232. **A,** Photograph, internal view; **B–C,** digital rendering showing the **B,** internal and **C,** external sides of the scale; **o.a,** overlap area for anterior scales; **r,** ridge; scale bars = 10 mm.
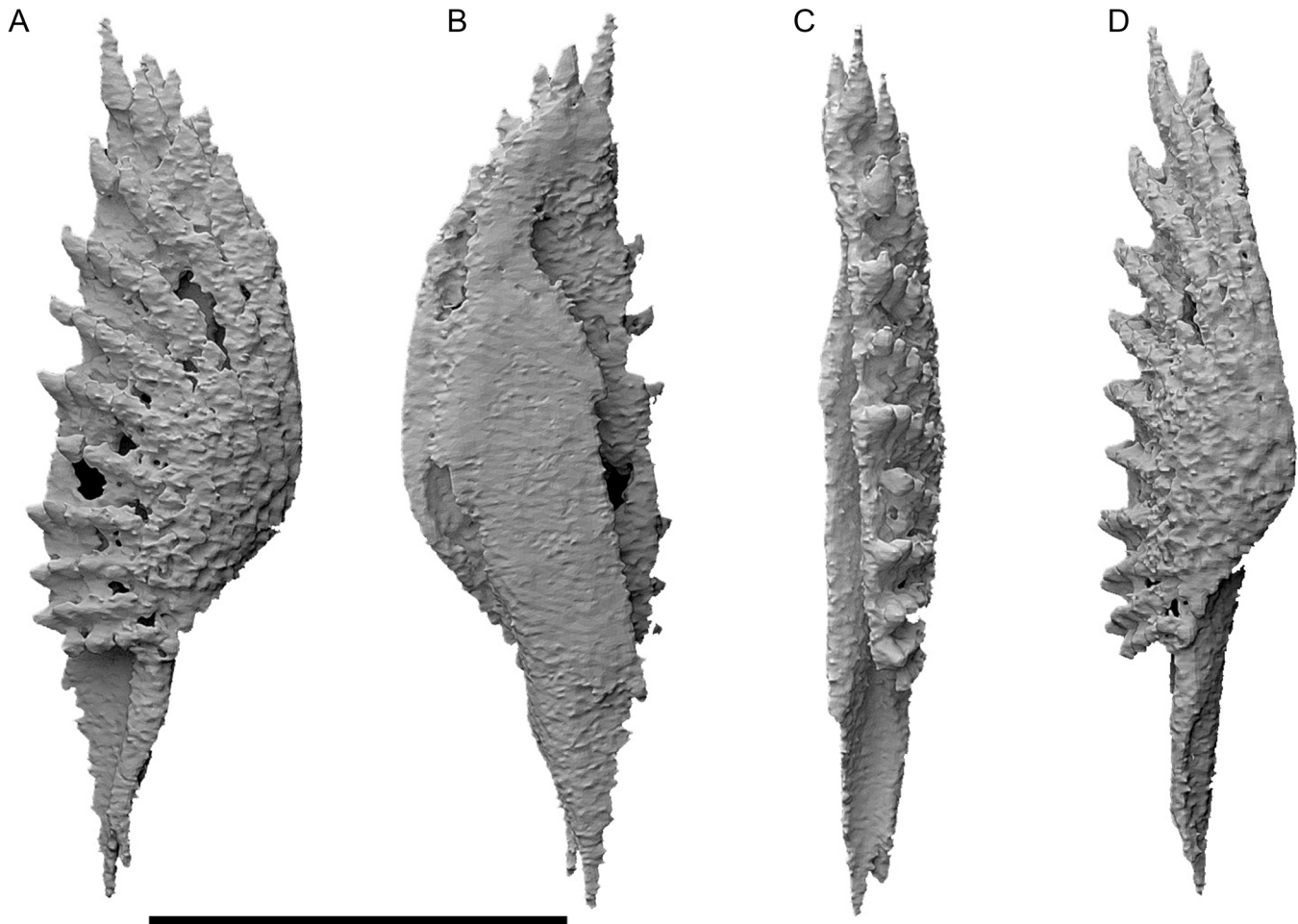
Figure 5. Indeterminate Dipnoi left lower jaw toothplate preserved in the matrix of NHMUK PV P 59686 in **A,** occlusal; **B,** basal; **C,** labial and **D,** lingual views; scale bar = 10 mm.

due to a lack of occlusion with the palatal tooth plates (Blaauwen *et al*., 2006). Unlike *Dipterus,* and many other fossil dipnoans, the curvature of the anterior teeth is a feature observed in early development stages of the Recent *Neoceratodus* (Smith *et al*., 2002, fig. 1). Similar anteriorly protruding teeth are also observed in hatchlings and juveniles of *Andreyevichthys epitomus* from the late Famennian of Tula Region, Russia (see Krupina, 1987; Krupina & Reisz, 1999, fig. 2B; Smith *et al*., 2002, fig. 6f–6h) and from indeterminate lungfish tooth plates from the Famennian of Greenland (Clack *et al*., 2019, figs. 5, 7), but have not been recorded from any Givetian taxa. Our specimen cannot however be attributed to any of these taxa because they all bear fewer tooth rows.

The protruding teeth of our Irish dipnoan tooth plate recall strongly those of a specimen from the Upper Devonian of Zaab Valley, Turkey, that had then been attributed to "*Dipterus* sp." by Smith (although with 6 tooth rows only; Smith, 1986, fig. 3; Smith & Krupina, 2001, fig. 1A; see also Janvier *et al*., 1984). Turkey belonged to the northern margin of Gondwana during the Devonian, again suggesting a Gondwanan affinity for this faunal component.

Holoptychius sp.

The *Holoptychius* scale represents one of the earliest known records of this genus. It is typically Late Devonian, extending up to the end of the Famennian, but has been recorded from the Sietiņi Member of the Gauja Formation of Estonia and Latvia (Mark-Kurik, 2000, tab. 2B), and in the Lan' stage of Belarus (Mark-Kurik, 2000, tab. 3), both of which are late Givetian. A supposed record in the early Givetian of the Orcadian Lake in Scotland (Sallan & Coates, 2010, referring to Dineley & Metcalf, 1999; Traquair, 1890; Woodward & Sherborn, 1890) appears to be an error, as the overwhelming majority of holoptychiid specimens from this deposit represent *Glyptolepis* (PEA, pers. obs). *Holoptychius* is known from both Euramerica and Gondwana, but tends to be much more common in Euramerica where it is often the most abundant osteichthyan in Late Devonian assemblages.

Palaeogeographic and stratigraphic implications

The fauna recorded from Valentia Slate Formation presents a biogeographic and stratigraphic puzzle that is rendered all the more important by the occurrence in

the same formation of some of the earliest known tetrapod trackways (Stössel, 1995; Stössel et al., 2016). The most common faunal component of the Valentia Slate Formation is the antiarch *Bothriolepis*, which represents the earliest record of this genus in Euramerica, though still older representatives are known from Gondwana and South China (Dupret et al., 2023). The record of *Holoptychius* is possibly the earliest in the world, and the lungfish and probable rhizodont both resemble Late Devonian taxa. Nevertheless, consistent mid-Givetian radiometric dates from the Enagh Tuff on Valentia Island (384.9 ± 0.7 Ma; Williams et al., 1997) and the Keel Tuff at St. Finan's Bay (385.0 ± 2.9 Ma; Williams et al., 2000) confirm a Middle Devonian age of the formation.

This directs attention to possible biogeographic explanations, where we can note that *Bothriolepis* and rhizodonts both have much longer histories in Gondwana than in Euramerica. The probable rhizodont coronoid specifically resembles that of *Gooloogongia* from the Famennian locality of Canowindra, New South Wales, Australia (Johanson & Ahlberg, 1998, 2001). As for the lungfish tooth plate, protruding teeth are found in the Euramerican *Andreyevichthys* from the Famennian of Russia, and in the Gondwanan "*Dipterus* sp." from the Famennian of Turkey. The Irish specimen appears to represent the earliest occurrence of this pattern in Euramerica.

Overall, we believe the unusual faunal composition of the Valentia Slate Formation is best explained by an early dispersal wave of some vertebrate groups from Gondwana to Euramerica. This would also be consistent with the location of the Munster Basin close to the south coast of Euramerica.

CONCLUSION

New remains of *Holoptychius* sp., Dipnoi and probably Rhizodontida have been discovered in the middle Givetian Valentia Slate Formation in south-western Ireland. *Holoptychius* and the rhizodont (if correctly identified) represent both the earliest examples of these taxa in Euramerica. *Bothriolepis*, the most abundant member of the Valentia Slate fauna, is also the earliest from Euramerica but is known from earlier deposits in Gondwana and South China (Dupret et al., 2023). The lungfish shows a derived tooth-plate morphology with procumbent teeth, otherwise only known from Late Devonian and later examples. The character of the assemblage sits somewhat uncomfortably with the mid-Givetian (approximately 385 My) isotopic age of the formation, but it may be explained as the result of a faunal dispersal from Gondwana into the southern coastlands of Euramerica.

Supplementary information. Supplementary material (CT-data, segmentation files, STLs, 3D pdfs) of this contribution is stored at the Swedish National Data Service (SND) (https://doi.org/10.57804/s0tg-cb09).

NHMUK PV P 59686_20220922.pdf: 3D-pdf of the specimen NHMUK PV P 59686 showing the Rhizodontida indet. fanged anterior coronoid and facial (or ethmoid) bone previously mistaken for an acanthodian spine, a Dipnoi indet. toothplate and two *Bothriolepis* plates. Scale cube is 1 cm^3.

Scale NMING:F35232.pdf: 3D pdf of an incomplete scale of *Holoptychius* sp. scale cube is 1 mm^3.

Author details. **Vincent Dupret**[1], **Hannah Byrne**[1], **Tom Challands**[2], **Øyvind Hammer**[3], **Kenneth Higgs**[4], **John Long**[5], **Grzegorz Niedźwiedzki**[1], **Martin Qvarnström**[1], **Iwan Stössel**[6] & **Per Erik Ahlberg**[1]. [1]Department of Organismal Biology, Uppsala University, Norbyvägen 18A, 752 36 Uppsala, Sweden; vincent.dupret@ebc.uu.se, Hannah.byrne@ebc.uu.se, grzegorz.niedzwiedzki@ebc.uu.se, martin.qvarnstom@ebc.uu.se, per.ahlberg@ebc.uu.se; [2]University of Edinburgh, School of Geosciences, Grant Institute of Earth Sciences, James Hutton Road, Edinburgh, EH9 3FE, UK; Tom.Challands@ed.ac.uk; [3]Natural History Museum, University of Oslo, P.O. Box 1172 Blindern, 0318 Oslo, Norway, oyvind.hammer@nhm.uio.no; [4]School of Biological, Earth and Environmental Sciences, University College Cork, Cork, T23 N73K, Ireland; K.Higgs@ucc.ie; [5]Flinders University, Biological Sciences (326), GPO Box 2100, Adelaide 5001, South Australia; john.long@flinders.edu.au; [6]ETH Zürich, Department of Earth Sciences, NO D 51.1, Sonneggstrasse 5, 8092 Zürich, Switzerland; istoessel@ethz.ch.

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