Spanish Journal of Palaeontology 38 (1), 15–22, 2023
https://doi.org/10.7203/sjp.26372
Sociedad Española de Paleontología ISSN 2255-0550 / eISSN 2660-9568

OPEN ACCESS RESEARCH PAPER

Teeth and tooth whorls of the stem chondrichthyan *Doliodus* from the Early Devonian of the Gaspé Sandstone Group, Gaspé Peninsula, Quebec, Canada

Dientes y diente en espiral del condrictio troncal *Doliodus* del Devónico Inferior del Grupo Areniscas de Gaspé, Península de Gaspé, Quebec, Canadá

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Abstract: The Early Devonian (Emsian) vertebrate fauna of the Gaspé Peninsula, Quebec (Canada) shows close affinity with the Emsian fauna from the Atholville beds, New Brunswick (Canada). Specimens collected in the early 2000s from several localities in central Gaspé include molds of tooth whorls and isolated teeth that we assign to the stem chondrichthyan *Doliodus*. Isolated teeth of this taxon were first described from the Atholville beds in the late 1800s by Arthur Smith Woodward, who erected a new species *Diplodus problematicus*. Whereas the Atholville beds teeth are usually preserved individually or in tooth families, and as hard tissue, the Gaspé teeth are mostly preserved as molds of tooth whorls, with individual teeth sharing a thin bone base. Thin sections of *Doliodus* teeth from the Atholville beds show parallel close-set vascular canals extending above the base plate and through tooth bases, with teeth formed of osteodentine and orthodentine. We consider that all the known dental elements assigned to *Doliodus* are conspecific with the articulated *Doliodus* specimen from the Atholville beds and thus all are assigned to the same species *D. latispinosus*. The teeth are compared with the diplodont teeth of other stem chondrichthyan taxa, in particular the Omalodontiformes.

Resumen: La fauna de vertebrados del Devónico Inferior (Emsiense) de la Península de Gaspé, Quebec (Canadá) muestra una estrecha afinidad con la fauna del Emsiense de las capas de Atholville, New Brunswick (Canadá). Los especímenes recogidos a principios de la década de los 2000 en varias localidades del centro de Gaspé incluyen moldes de dientes en espiral y dientes aislados que son asignados al condrictio basal *Doliodus*. Los dientes aislados de este taxón fueron descritos por primera vez en los yacimientos de Atholville a finales del siglo XIX por Arthur Smith Woodward, quien erigió una nueva especie *Diplodus problematicus*. Mientras que los dientes de estos últimos suelen conservarse individualmente o en familias de dientes, y como restos directos (tejidos duros), los de Gaspé se conservan sobre todo como moldes de dientes en espirales, donde los dientes individuales comparten una fina base de hueso. Las láminas delgadas de los dientes de *Doliodus* de los yacimientos de Atholville muestran canales vasculares paralelos y cerrados que se extienden por encima de la placa basal y a través de las bases de los dientes, con dientes formados de osteodentina y ortodentina. Consideramos que todos los elementos dentales conocidos asignados a *Doliodus* son conespecíficos con el espécimen articulado de *Doliodus* de las capas de Atholville y, por lo tanto, todos se asignan a la misma especie *D. latispinosus*. Los dientes se comparan con los dientes diplodontos de otros taxones de condrictios troncales, en particular los Omalodontiformes.

Received: 29 November 2022
Accepted: 28 March 2023
Published: 5 April 2023

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Keywords:
Emsian
Gaspé Sandstone Group
Teeth
York River Formation

Palabras-clave:
Emsiense
Grupo Areniscas de Gaspé
Dientes
Formación York River

INTRODUCTION

Vertebrate assemblages of Emsian age are long-known from the Atholville beds at Campbellton, New Brunswick in eastern Canada, being first described in the late 1800s (*e.g.*, Whiteaves, 1881; Woodward, 1892; Traquair, 1893). Assemblages (possibly of a similar age, or slightly younger) from the lower Battery Point Formation in eastern Gaspé Peninsula, Quebec were described in detail much later by Pageau (1968, 1969a, 1969b, 1982, 2021), and a preliminary list of a vertebrate fauna from the upper York River Formation at Mt Lyall in central Gaspé was published by Blieck *et al*. (2000, fig. 15). The taxa found at the latter locality were assigned by those authors to the osteostracan *Yvonaspis* sp., the arthrodire placoderms *Cartieraspis nigra*, *Phlyctaenius acadicus* and *Pageauaspis* sp., the acanthodian *Climatius* sp., and

the chondrichthyan *Doliodus*? sp. Subsequently, Burrow and Desbiens (2005) listed the Emsian York River Formation acanthodian and chondrichthyan fauna as comprising *Cheiracanthus costellatus*, *Climatius latispinosus*, *Gyracanthus incurvus*, *Doliodus problematicus*, and an ischnacanthiform acanthodian, but noted that the taxonomy of all species needed revision. Burrow *et al*. (2008) commenced this process by assigning the spine-based taxon *Gyracanthus incurvus* to a new genus, *Ankylacanthus*, and Burrow *et al*. (2017) assigned the spine-based taxon *Climatius latispinosus* and tooth-based taxon *Doliodus problematicus* to *Doliodus latispinosus* nov. comb., based on identification of spines and teeth considered identical to these on an articulated fish from the Atholville beds that was originally assigned by Miller *et al*. (2003) to *Doliodus problematicus*. Here we describe the dental elements from the York River Formation and compare them with the isolated teeth of *Doliodus*, including the type specimen (Fig. 1), and the teeth on the articulated fish from the Atholville beds of New Brunswick.

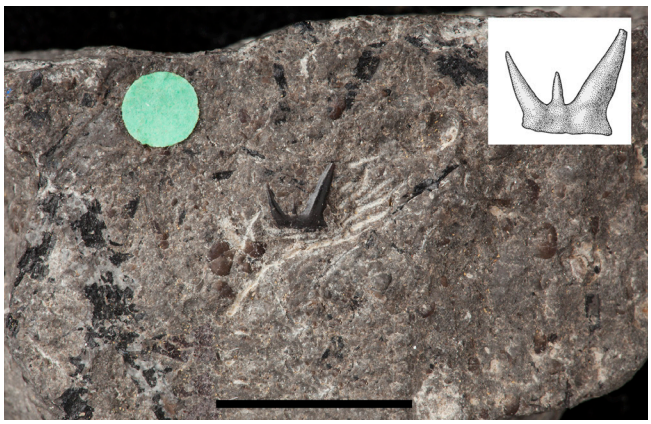

Figure 1. *Diplodus problematicus* Woodward holotype tooth NHMUK PVP.6540: main image CC0-1.0 Licence, retrieved: 21 Mar 2023 12:02:35 (UTC) https://data.nhm.ac.uk/object/55926f0f-e3a9-4272-a841-fa98639b7e04/1678924800000, inset drawing from Denison (1979, fig. 27D); scale bar = 20 mm.

GEOLOGICAL SETTING

The Emsian–Eifelian Gaspé Sandstone Group is a major geological unit of the Gaspé Peninsula, outcropping from Gaspé in the east to the southern Rimouski area in the west near the northernmost border of New Brunswick (Plusquellec *et al*., 2011). In Gaspé, fossil fish faunas are found in the Group in the deltaic York River Formation (Emsian) and the lowermost part of the estuarine-distal fluvial Battery Point Formation (Emsian–Eifelian) (see Burrow *et al*., 2008, 2017 for more detailed descriptions of the geology and depositional history of the Group). Sites in Gaspé where *Doliodus* teeth have been collected are in volcanites of the upper York River Formation, central Gaspé – at the Mont Lyall locality (Blieck *et al*., 2000, fig. 15) where siltstones are sandwiched between basalt flows, and a locality southwest of Mont Tuzo, where fish remains occur at many levels in tuffs and tuffaceous sediments underlying a thick basaltic sequence of the Tuzo-Lyall volcanic member (Burrow *et al*., 2017, fig. 1). The Mt Lyall siltstone commonly contains a linguloid species, and the Mt Tuzo fish beds are closely associated with *in situ* plant beds (SD, pers. observ.). These littoral and shallow water lithofacies overly marine sandstones and shales containing a shelly fauna of the Appalachian *Etymothyris* brachiopod range Zone (lower Emsian, Boucot & Johnson, 1967).

MATERIALS AND METHODS

Specimens were collected from Mont Lyall in 2003 and from southwest of Mont Tuzo in 2002–2006. Most specimens were preserved only as impressions or molds, although a few had fragmentary hard tissues left *in situ*. In the latter case, fragments were removed for thin sectioning, with the rest of the bone cleared with 10% HCl and by manual cleaning with fine needles. Casts were made with latex or Exaflex®, a hydrophilic vinyl polysiloxane, whitened with ammonium chloride or magnesium oxide, and images taken with a Fuji S1 Pro camera, or Olympus SX40 dissecting microscope and DP12 imaging system. Small isolated teeth were picked from acetic acid residues of a sample collected at Atholville in 2004, platinum-coated and imaged in a JEOL JSM-6300F scanning electron microscope (**SEM**). Thin sections were imaged using an Olympus BX50 transmission microscope and DP12 imaging system. Figures were compiled using Adobe Photoshop®.

Institutional abbreviations. MHNM, Museum of Natural History, Miguasha; **NHMUK PVP,** palaeontology collection of the Natural History Museum, London; **NMS,** National Museums of Scotland, Edinburgh.

SYSTEMATIC PALAEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Order, Family indet.
Genus *Doliodus* Traquair, 1893

Type-species. *Doliodus latispinosus* (Whiteaves, 1881). Early Devonian, Emsian, Canada.

Doliodus latispinosus

Figure 2

2000 *Doliodus*? sp.; Blieck *et al*., fig. 15.
2016 *Doliodus problematicus*; Burrow *et al*., p. 1249.

Material. Tooth whorls and teeth: MHNM 02-10135.1, 02-10170.1, 02-10762.1, 03-10014.1, 03-10148, 03-10160, 03-10212.1 (part and counterpart) from Mont Lyall locality; MHNM 02-10000.1, 02-10087.1, 03-10224.1, from locality southwest of Mont Tuzo; all preserved as impressions, sometimes with fractured remnants of hard tissues.

Description. MHNM 03-10212.1, part and counterpart (Fig. 2A, 2B), is a small diplodont tooth, *ca.* 2.5 mm high, comparable in shape to NHMUK PVP.6540 (a single tricuspid tooth lacking a base, the holotype designated for *Diplodus problematicus* Woodward, 1892; Fig. 1), but with only the base of a central cusp preserved. A weakly developed carina extends apically from the base adjacent to the median cusp on each main cusp (Fig. 2A). Although not described by Woodward (1892), the holotype tooth also has similar carinae visible on the exposed surface of the main cusps (Fig. 1). The base of tooth MHNM 03-10212.1 shows an incomplete surface at the level of the parallel canals that form the network extending through the bases of the teeth in each tooth family. MHNM 03-10212.2 (Fig. 2C–2F), from the same slab, is a tooth whorl 8.5 mm long between anterior and posterior tooth tips, with a base length of 5 mm. The arched base bears five teeth, which appear to have a maximum of three cusps each. The largest tooth cusp is 2.5 mm high and has a mostly smooth surface with a carina running from its junction with the medial cusp to its tip. Vascular canal foramina form a row where the tooth base merges with the bone base plate. The inner surface of the plate is relatively smooth and continuous, with fine parallel ridges running antero-posteriorly. The base of the most posterior tooth shows a fracture surface where the tooth has separated from the base plate at the level of the main vascular canal network. MHNM 03-10224.1 (Fig. 2G–2J) is part and counterpart of a complete tooth whorl with an arched-concave base plate, 13 mm long and 10 mm wide, bearing five teeth. Before casting of the part, the infilling of the parallel vascular canals running longitudinally through the tooth bases was visible (Fig. 2J). The teeth each bear seven cusps, comprising two large lateral cusps which are 3 mm high, a 2 mm high median cusp, and two smaller cusps between the median cusp and each of the lateral cusps. Based on the evidence of tooth whorls MHNM 03-10212.2 and 03-10224.1, the longitudinal canals appear to have run on top of the base between the teeth (Fig. 2F, 2I–2J). MHNM 02-10762.1 (Fig. 2K, 2L) is the impression of the inner surface of a tooth whorl base with most of one tooth visible. The base is 5 mm long with maximum width 4 mm, and is scored by thin sub-parallel striations and ridges running antero-posteriorly. The tooth had five conical cusps comprising two large lateral cusps 2.5 mm high and 1.0 mm basal diameter, a medial cusp 2.5 mm high, and two small cusps 0.7 mm high between the medial and each of the lateral cusps. Part and counterpart of MHNM 02-10170.1 (Fig. 2M, 2N) were preserved, showing the impressions of the occlusal and basal surfaces of a tooth whorl 4 mm long with a maximum width 4 mm. The base outline is sub-circular, with the basal surface being concavely bowl-shaped and bearing fine longitudinal striations and ridges. The occlusal surface shows four teeth, with the smallest having two divergent lateral cusps and a smaller cusp between them. Other teeth have four cusps, with the two lateral cusps largest, and one medium and one small cusp between them (interpreted from the relative diameters of the cusp bases). The upper surface of the base (Fig. 2N) shows eight or nine parallel canals running between the teeth. Specimen MHNM 02-10135.1 (Fig. 2O) shows the remnants of a whorl 7 mm long, comprising at least three teeth, exposed in occluso-lateral view. The specimen differs from the other whorls described in that the most completely preserved tooth cusp, interpreted as the lateral cusp of the largest tooth, has a sigmoidal shape and is almost 3 mm high. The cusps have a circular cross-section, without any visible cristae or carinae; however, no medial surfaces of cusps are preserved. Part of the vascular network in the base of the middle tooth is exposed; this tooth had two lateral cusps with a smaller central cusp. A fracture runs through the base of the tooth, at the level where the vascular canals are densest.

Other tooth whorls not figured include MHNM 02-10000.1, MHNM 03-10148 and 03-10160, which are all similar to each other, with three tricuspid teeth. No division is visible between the teeth; the upper surface of the base between each tooth is scored by about ten close-set parallel longitudinal grooves. MHNM 02-10087.1 shows an oblique view of the inner basal surface of a tooth whorl, and the base of just one tooth cusp.

Only rare specimens had some of the hard tissue preserved. These show that the tooth and base plate tissue is continuous, but fine histological structure is not discernible.

The CT scans of NBMG 10127 1a in Maisey *et al*. (2014, figs. 3–5) show its dentition exhibits both monognathic and dignathic heterodonty. By comparison of the isolated Gaspé tooth whorls with that dentition, specimens which appear to have a base that is much longer than wide, with relatively symmetrical cusps (*e.g.*, Fig. 2C–2E, 2F, 2K–2L) would have been positioned towards the front of the jaw, and those which are of a similar length and width with relatively low cusp apices (*e.g.*, Fig. 2M–2N, ?2I–2J) were towards the back of the jaw. None of the Gaspé specimens show the more asymmetrical main cusps that characterise the mid-jaw teeth in NBMG 10127, but the whole range of possible forms could hardly be expected with such a small sample size and imperfect preservation.

Comparison. In publications prepared before the description by Miller *et al*. (2003) of the articulated *Doliodus* specimen from the Atholville beds, several authors (Ginter, 2004; Hampe *et al*., 2004; Turner, 2004) addressed the question of the relationship of *Doliodus problematicus* (Woodward) with younger chondrichthyans, and with *Leonodus carlsi* Mader, 1986 from the Lochkovian of Spain (the oldest taxon based on undeniably chondrichthyan teeth), purely based on the isolated teeth and tooth families/whorls from the Atholville beds. Ginter *et al*. (2010) subsequently assigned *Doliodus* to the Order Omalodontiformes, a group characterized by

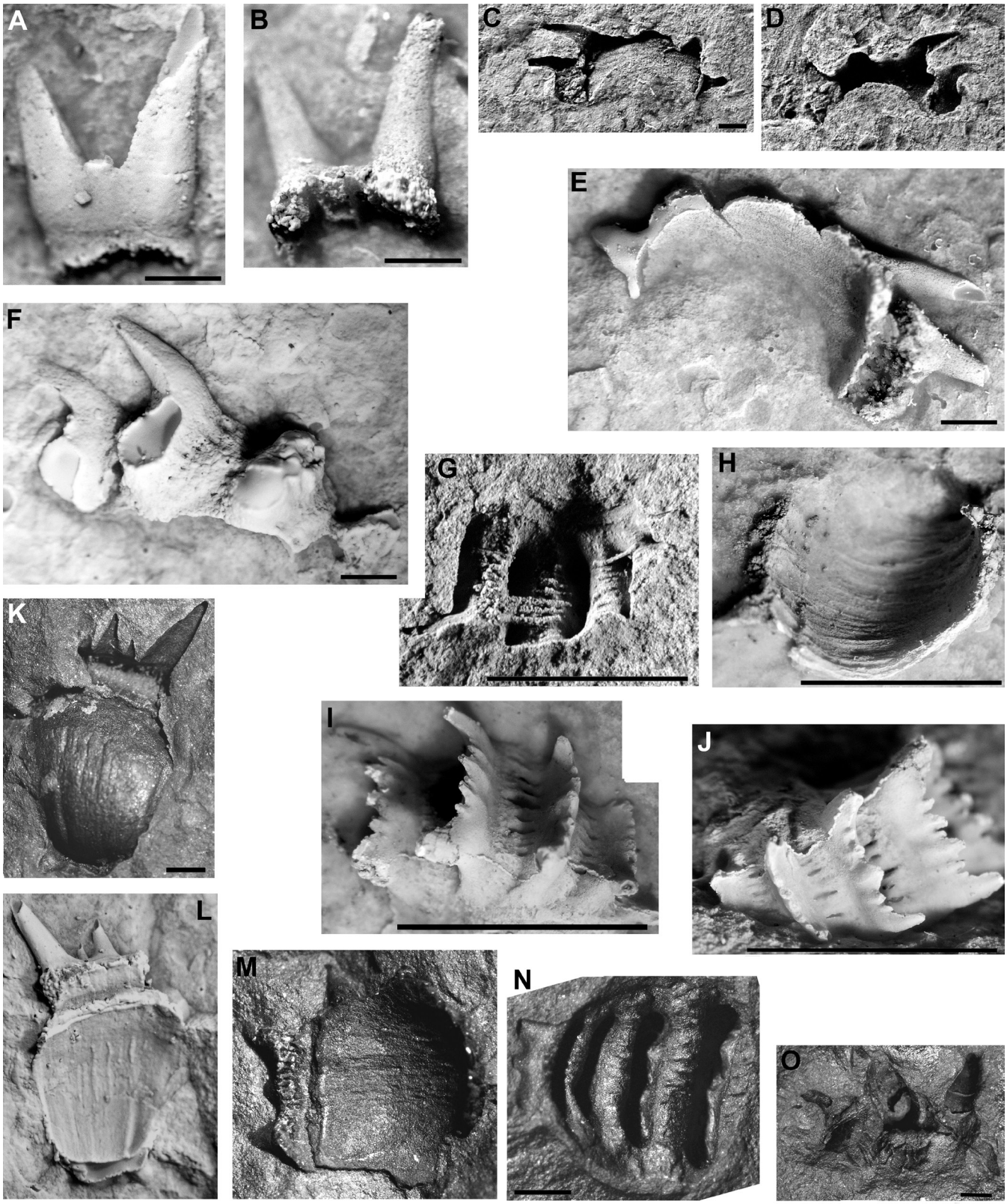

Figure 2. *Doliodus latispinosus* teeth from the York River Formation, Gaspé Peninsula. **A**–**B,** MHNM 03-10212.2, casts of isolated diplodont tooth crowns; **C**–**F,** tooth whorl MHNM 03-10212.1; **C**–**D,** molds of tooth whorl on part and counterpart; **E**–**F,** casts of tooth whorl on part and counterpart (two cusps not cast); **G**–**J,** small tooth whorl MHNM 03-10224; **G**–**H,** molds on part and counterpart, with remnants of vascular canal infillings on part; **I**–**J,** casts of tooth whorl on part and counterpart; **K**–**L,** MHNM 02-10762.1, mold and cast of tooth whorl base with one tooth, lateral cusp missing; **M**–**N,** tooth whorl MHNM 03-10170.1, mold of tooth whorl base on part and occlusal surface on counterpart; **O,** larger tooth whorl MHNM 02-10135, mold of large tooth whorl with a sigmoidal cusp on fractured? base. G–J is from southwest of Mont Tuzo, and all other specimens are from Mont Lyall; scale bars = 10 mm in G–J, 1.0 mm in A–F, K–N, 0.1 mm in O.

having tooth bases lacking a lingual extension. Maisey *et al*. (2019) classified the genus as Chondrichthyes *incertae sedis* because most of the teeth on the articulated specimen form continuous whorls with a common base plate (Maisey *et al*., 2014), thus differing from the separate teeth of omalodontiforms, and because tooth overlap was interpreted as the opposite of that inferred for omalodontiforms. That is, overlap in *Doliodus* was considered to be the 'normal' cladodont shark teeth arrangement where the replacement tooth sits on top of the preceding tooth's labial projection (J. Maisey, pers. comm., 2023), whereas omalodontiform teeth are considered to have labial extensions (Ginter *et al*., 2010). However, our investigations indicate that there is no tooth base overlap in *Doliodus* as the teeth lack basal extensions and are separated by the thin basal plate.

The 19 isolated specimens in the NMS collection that were examined by Traquair (1893) in erecting the genus *Doliodus* are mostly tooth whorls (Turner, 2004, figs. 4B–4I, 5, 6, 7A–7D), some of which preserve part of the arched basal bone plate between the teeth (Turner, 2004, fig. 6A, 6H). On one specimen (Turner, 2004, fig. 6K) the lingual surface of the basal bone plate is exposed, and another specimen (Turner, 2004, fig. 7C) is exposed in lateral view showing the thin continuous basal plate under and between the teeth. Previously, this bony basal plate has been interpreted as a calcified dental membrane (Ginter *et al*., 2010), but thin sections show that it is bone, and presumably the basement membrane (a connective tissue 'conveyor belt' which underlay this bony basal plate as the tooth whorl grew) produced the parallel longitudinal ridging preserved on its lingual surface (*e.g*., Fig. 2E, 2H). The thinness of the inter-tooth base plate, combined with the close-set canals running through the base of the teeth onto the surface of the interconnecting base, presumably created a zone of weakness resulting in isolated teeth such as the holotype of *D. problematicus* lacking complete bases. Alternatively, some of the isolated teeth with an incomplete base could be developing teeth from the lingual end of the tooth family which had not yet fused to the whorl, as seen in CT scans of the articulated *Doliodus* specimen NBMG 10127 (Maisey *et al*., 2014, fig. 7). It seems clear that both the isolated dental elements and the articulated fish from the Atholville beds assigned to *Doliodus* uniquely share the character of teeth forming a whorl on a thin basal bone plate. There is no evidence from the articulated fish or isolated dental elements to indicate that individual teeth or tooth whorls were shed, and it is most likely that the isolated elements represent disarticulated remains.

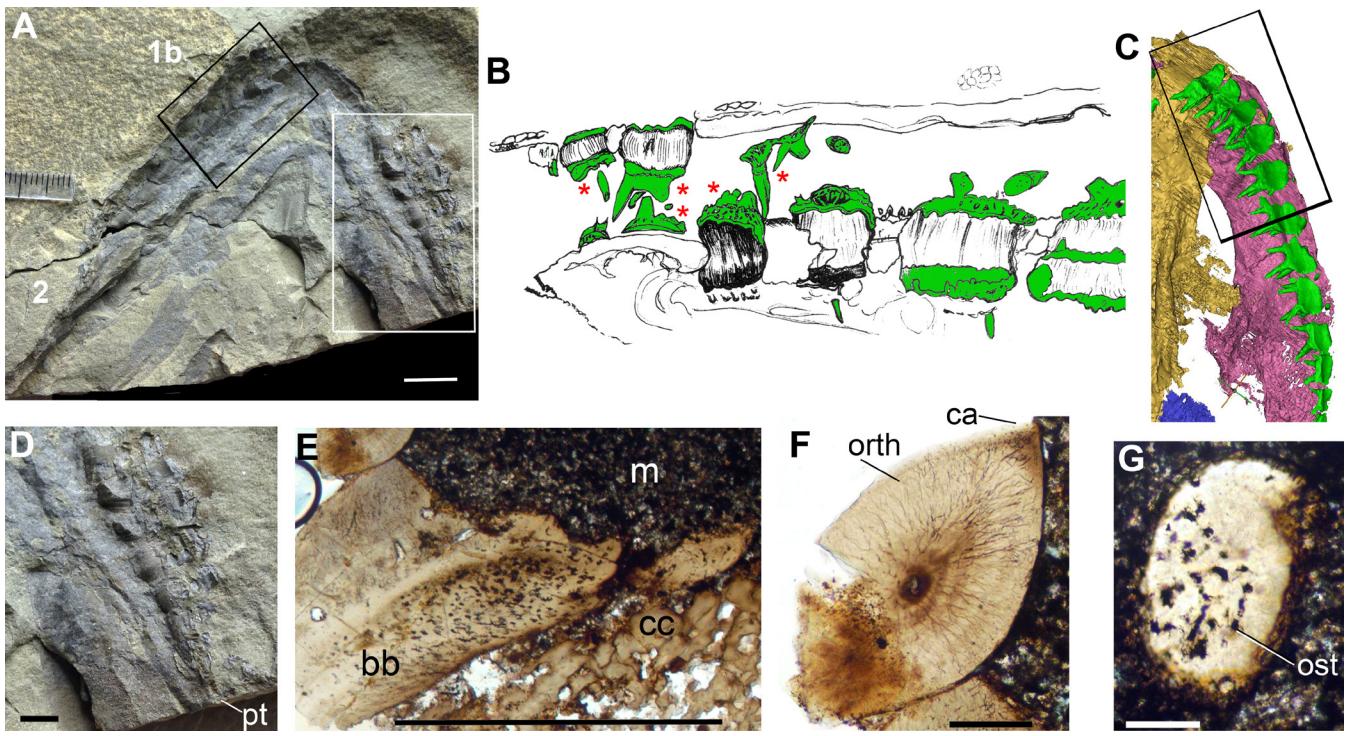

Figure 3. *Doliodus latispinosus* articulated specimen NBMG 10127, dentition. **A,** NBMG 10127 1b+2, showing the counterpart of the area sketched in **B** (image courtesy of Randall Miller); **B,** teeth (in green) of the left lower (and upper) jaws exposed on the surface of NBMG 10127 1a (area indicated by the black box in **A**; sketch by Susan Turner), showing teeth (red asterisks) with main and intermediate cusps; **C,** CT scan reconstitution of the left palatoquadrate (pink) and lower jaw teeth (green) of NBMG 10127 1a, in ventral view (image courtesy of John Maisey); **D,** closeup of NBMG 10127 1b (white box in **A**) showing fractured teeth and impression of four-cusped posterior tooth; **E–G,** thin section 10127-06 from NBMG 10127 2 (labelled as 2 in **A**); **E,** section through a tooth, tooth cusp, and jaw calcified cartilage; **F,** closeup of transverse section through tooth cusp; **G,** transverse section through base osteodentine of small (?intermediate) tooth cusp. **bb,** basal bone; **ca,** carina; **cc,** calcified cartilage; **m,** matrix; **orth,** orthodentine; **ost,** osteodentine; **pt,** posterior tooth; scale bars = 10 mm in A, B, 1.0 mm in D, E, 0.1 mm in F, G.

One possible difference between the isolated teeth and those on the articulated fish NBMG 10127 is the distribution of intermediate cusps between the two main lateral cusps. Teeth are preserved on three of the pieces of the specimen, designated 1a, 1b, and 2 (Fig. 3A–3D). The 3D scan reconstitutions by Maisey *et al*. (2014) of NBMG 10127 1a show only rare evidence for intermediate cusps, although the resolution is relatively poor, especially for the small posterior teeth, and digital smoothing occurred during processing of the scan data. An impression of one small posterior tooth exposed on the articulated specimen appears to show four small cusps (Fig. 3D). Given that nearly all isolated *Doliodus* teeth have between one and three intermediate cusps (Turner, 2004, tab. 2), the possibility that there are two different species should be considered. Higher resolution scans of the teeth on the articulated fish could help resolve this issue, but visual examina-

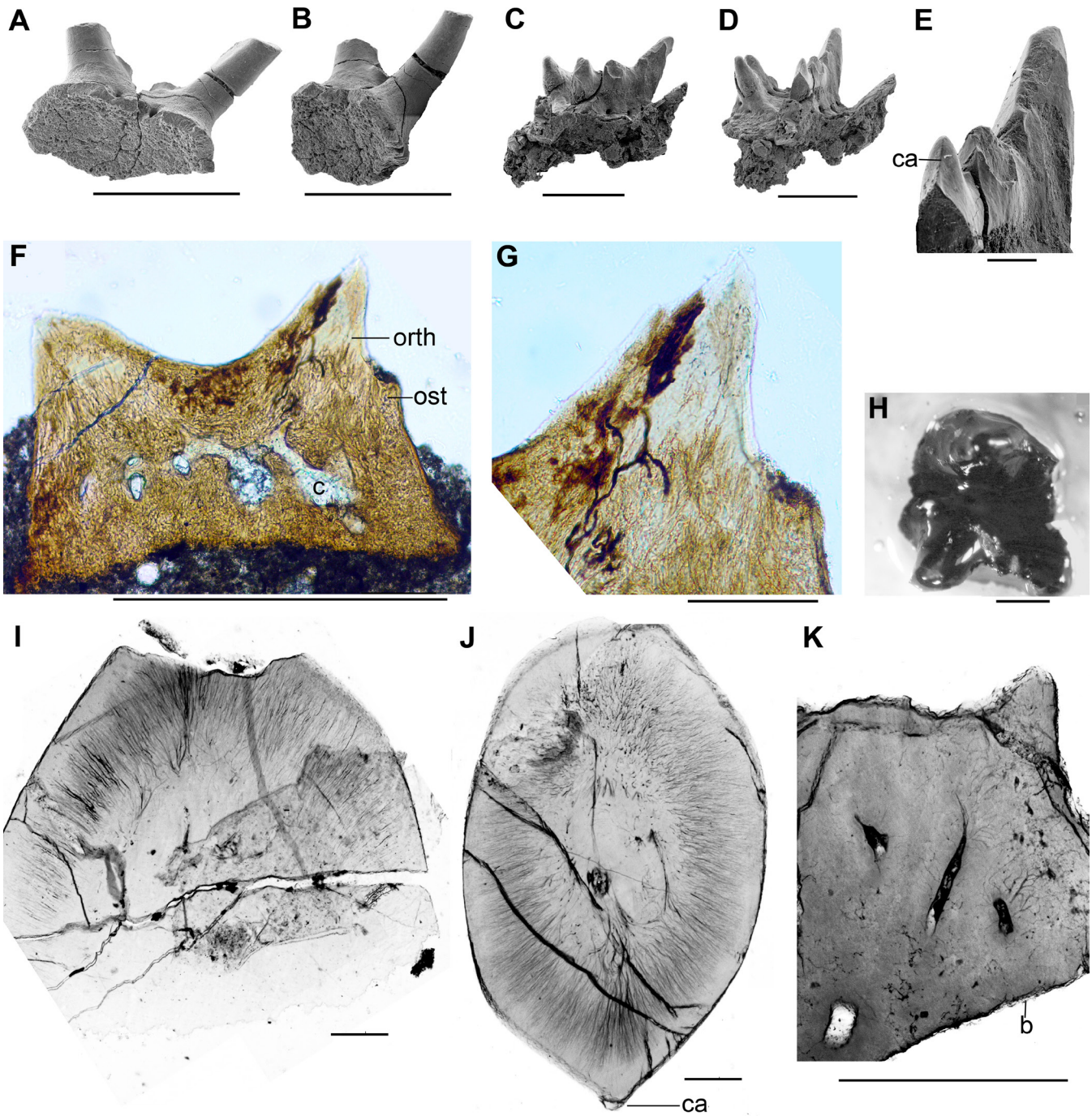

Figure 4. *Doliodus latispinosus* isolated dental elements from the Atholville beds. **A**–**E,** SEM images of small teeth from acetic acid-etched sample; **A**–**B,** NBMG 22420, detached tooth in **A**, anterobasal view and **B**, laterobasal view; **C**–**E,** NBMG 22430, tooth whorl with three teeth in **C**, anterior?, **D**, lateral, and **E**, closeup lateral view of middle tooth; **F**–**G,** uncatalogued detached tooth, vertical section; **H**–**K,** NBMG 22440, detached tooth; **H,** tooth embedded in resin before sectioning; **I,** oblique section through cusp; **J,** transverse section through other cusp; **K,** vertical section through tooth base and base of cusp; **c,** canal; **ca,** carina; **orth,** orthodentine; **ost,** osteodentine; scale bars = 1.0 mm in H, K, 0.5 mm in A-D, F, 0.1 mm in E, G, I, J.

tion of the specimen indicates that most teeth do have intermediate cusps (Fig. 3B), and there is no good reason to suppose that the isolated dental elements and the articulated fish are from different species.

Isolated *Doliodus* teeth from the Atholville Beds (Fig. 4A–4K) provide evidence that parallel close-set vascular canals ran through the base of teeth and above the base plate. Thin sections (Fig. 4F, 4G, 4I–4K) show that these canals extended into the osteodentine of the tooth bases to form a network with several branches running up into the tooth cusps. Fine, branching orthodentine tubules radiate out from the canals. The thin outermost zone of the cusps is tubule-free, but not clearly separated from the dentinous tissue. Thin sections of teeth on the articulated specimen NBMG 10127 (Fig. 3E–3G) show a similar structure, except that these teeth are attached to the basal bone plate (Fig. 3E).

Histologically, the tissues forming *Doliodus* teeth are barely distinguishable from those on ischnacanthiform acanthodian tooth whorls, which have a thin outer layer lacking dentine tubules, branching syncitial mesodentine or orthodentine forming the teeth, osteodentine and/or vascular bone forming the base, and vascular canal foramina at the tooth base/basal bone junction (Gross, 1957; Burrow, 1995, figs. 4B, 4C, 6C). The ischnacanthiform tooth whorls differ from those of *Doliodus* in having the largest (or only) cusp of each tooth centrally, a thicker, more robust base without longitudinal ridges and striations on the inner surface, the vascular canal network deep in the base of the whorl, and a spiralling base. Indeed, *Doliodus* teeth appear to be intermediate between acanthodian tooth whorls and diplodont chondrichthyan tooth families. Perhaps surprisingly, considering the climatiid-like distribution of spines on the articulated *Doliodus* (Maisey *et al*., 2017), the tooth whorl histology is more similar to that of ischnacanthiforms than *Climatius reticulatus*, which has mesodentine rather than orthodentine forming the cusps (Burrow *et al*., 2015, fig. 3K).

DISCUSSION

Whorls with 'diplodont' teeth are known (if rarely) from Silurian microvertebrate assemblages. For example, Vergoossen (1999, fig. 29, 'Acanthodii') figured one from the Psammosteus Limestones (Lochkovian) of the Welsh Borderlands. Similar elements are also found in microvertebrate assemblages from the early Emsian Jawf Formation in Saudi Arabia (Burrow *et al*., 2006, fig. 9.6–9.9, 9.12, 9.13). *Leonodus carlsi* from the Lochkovian of Spain is based on diplodont teeth, but these differ from those of *Doliodus* (and the last two examples) in being separate teeth with a lingual shelf and boss, and a basolabial projection (Ginter *et al*., 2010). The monocuspid teeth of *Protodus jexi* Woodward, 1892 which co-occur with *Doliodus* teeth in the Atholville beds are much larger than those of *Doliodus*; Woodward assigned the genus to a new family Protodontidae but its relationship to other chondrichthyans is not known (Turner & Miller, 2008). Certainly, there is no evidence for *Protodus* being closely related to *Doliodus* or the Omalodontiformes. Given the similarity between the tooth crown morphology and tooth base and crown histology of the omalodontiforms to *Doliodus*, it seems possible that they could have derived from a *Doliodus*-like ancestor. However, the distinguishing feature of omalodontiform teeth–a labial basal extension–is not developed in *Doliodus*.

Supplementary information. This article has no additional data.

Author contributions. CB and SD conceived the study, analysed the data, and wrote the manuscript;

Competing Interest. We declare no competing interests

Funding. We received no funding for this study.

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Acknowledgments. Our thanks go to Sue Turner (Geosciences, Queensland Museum) and Michal Ginter (University of Warsaw) for discussions about *Doliodus* teeth, Johanne Kerr, Jason A. Willett and Norman Parent (MHNM) for participation in the diggings at the Mont Lyall and Mont Tuzo localities, Randy Miller (NBMG) for images and access to the NBMG collection, Sue Turner for providing her sketch, and John Maisey (American Museum of Natural History) for CT scan reconstitution images. Reviewers John Maisey and Michal Ginter are thanked for their helpful and stimulating comments, and the Valencia meeting committee for their wonderful organisation. This work is a contribution to the Special Volume dedicated to Dr Philippe Janvier and Dr Tiiu Märss.

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