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Spines of the stem chondrichthyan *Doliodus latispinosus* (Whiteaves) comb. nov. from the Lower Devonian of eastern Canada

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Abstract: The higher taxonomic affinities of fin spines from the Lower Devonian (Emsian) Atholville beds near Campbellton, New Brunswick, Canada, originally identified as *Ctenacanthus latispinosus*, have been uncertain since they were first described by Whiteaves in the late Nineteenth Century. Woodward subsequently referred the species to *Climatius*, because the isolated Canadian fin spines were similar to those preserved in articulated specimens of *Climatius reticulatus* from the Lower Old Red Sandstone (Lochkovian) of Scotland. Spines of the same form as the 'Atholville beds' specimens are also found in Emsian mudstones on the Gaspé Peninsula, Quebec. One of the fin spine forms appears identical to the pectoral fin spines on an articulated specimen from Atholville that has been assigned to the stem chondrichthyan *Doliodus problematicus*, a taxon erected for isolated diplodont teeth. By comparison with median and paired fin spine morphology on the climatiiform *Climatius reticulatus* from the Scottish Lower Old Red Sandstone and the spines preserved on the articulated *Doliodus*, isolated fin spines from Campbellton and several localities on the Gaspé Peninsula are now identified as belonging to *Doliodus latispinosus* comb. nov. The variety of spine morphotypes recognized – pectoral, prepelvic, prepectoral, and median – support a phylogenetic position within the "acanthodians" rather than "conventionally defined chondrichthyans".
Introduction

Fish-bearing beds of the Lower Devonian (Emsian) Campbellton Formation in New Brunswick, Canada, have been well known as a source of ostracoderms, arthrodires, acanthodians, and chondrichthyans (Whiteaves 1881; Woodward 1892a; Traquair 1893a) since the first fossils were discovered in 1881 by R.W. Ells (Ells 1883; Whiteaves 1889). The Campbellton Formation (Williams et al. 1985) is exposed along the banks of the Restigouche River–Chaleur Bay from Atholville, east toward Point La Nim, New Brunswick (Fig. 1).

R.W. Ells conducted geological surveys along the north shore of New Brunswick in 1879, 1880, and 1881. It was following the 1881 season that Ells first reported the discovery of fish fossils at Campbellton. The specimens came from argillaceous and brecciated limestones on the south bank of the Restigouche River about a half mile (0.8 km) above Campbellton (Fig. 1, locality 13). At the first opportunity, Ells contacted A.H. Foord, Assistant Palaeontologist to the Geological Survey of Canada, who was collecting at Scaumenac Bay across the river. Foord at once visited the Campbellton locality and devoted a week to the thorough examination of the fish-bearing beds (Whiteaves 1881). Foord's collection was examined by the Survey palaeontologist J.F. Whiteaves who identified the fish as *Coccosteus acadicus* (a placoderm), *Cephalaspis campbelltonensis* (an osteostracan agnathan), *Ctenacanthus latispinosus* (a chondrichthyan) and *Homacanthus* sp. (an acanthodian).

The discovery of Devonian fossils, especially fish, generated considerable interest for over a decade, perhaps in part due to the well known Upper Devonian (Frasnian) fossil locality a short distance across the estuary at Miguasha, Quebec. The British Museum (Natural History) (now the Natural History Museum of London) and the Royal Scottish Museum (now the National Museums of Scotland) were among the first foreign institutions to receive fossils from Campbellton. R.H. Traquair in Edinburgh and A.S. Woodward in London soon had specimens in hand and were able to
add to the earlier work of Whiteaves. Traquair and Woodward received specimens collected by Mr.
Jex, a supplier for the Weymouth fossil dealer R.F. Damon. Fossils were sent to England in 1888,
1891, and 1892. Based on these specimens, Traquair and Woodward published a series of papers
and reports from 1889 to 1900, often describing different specimens of each others’ species and
revising Whiteaves' work (Traquair 1890a–c, 1893a–c; Woodward 1889, 1891, 1892a, b, 1900).
The flurry of papers by three authors on the same fossils created some confusion, which still
persists.

North of Chaleur Bay, fossil fish faunas of similar age are found in the York River
Formation and the lower part of the Battery Point Formation on the Gaspé Peninsula, Quebec
(Burrow et al. 2008; Fig. 1). The farthest eastern sites include the Cap-aux-Os localities (Cap-aux-
Os Member, Battery Point Formation; Fig. 1, localities 7–11) including the Route 197 locality
(Desbiens 1994; Fig. 1, loc. 8) on the north side of Gaspé Bay, and the Anse-à-Brillant locality (Fig.
1, loc. 6) and other sites on the south side of Gaspé Bay (Pageau 1968, 1969a, b; Desbiens 1991;
Griffing et al. 2000), which are all in the upper part of the York River Formation. In central Gaspé,
rich fish bearing beds of the upper part of the York River Formation are found at several sites
including the Mont Lyall locality (Doyon et al. 1990, fig. 4; Desbiens 1991; Blieck et al. 2000, fig.
15; Fig. 1, loc. 2) and a locality southwest of Mont Tuzo (Burrow et al. 2008; Fig. 1, loc. 1).

The diverse fish fauna from east Gaspé includes osteostracans, placoderms, and acanthodians
(Pageau 1968, 1969a, 1969b; Blieck et al. 2000). The Gaspé assemblages of Emsian age have
affinities with those from the 'Atholville beds'. A preliminary list of the Mont Lyall vertebrate fauna
(Blieck et al. 2000, fig. 15) recorded taxa also found at the other Gaspé localities: the osteostracan
Yvonaspis sp.; the arthrodire placoderm Cartieraspis nigra, Phlyctaenius acadicus, and
Pageauaspis sp.; the acanthodian Climatius sp.; and the chondrichthyan Doliodus? sp. 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 revising *Gyracanthus incurvus*, assigning the species to a new genus *Ankylacanthus*. Some spines that Whiteaves (1889) described as *Homacanthus gracilis* were also assigned to *Ankylacanthus incurvus*.

A major development in the story of the 'spiny sharks' of these deposits came with the discovery of the first articulated specimen in the 'Atholville beds', assigned by Miller et al. (2003) to *Doliodus problematicus* Traquair, 1893. Although the fin spines on this specimen were not well exposed, it seemed likely that they could be of the *Climatius latispinosus* form. Recent 3D scanning work (Maisey et al. 2017) has confirmed this similarity.

Here we describe the new specimens of *Climatius latispinosus* from the Gaspé Peninsula as well as specimens from the 'Atholville beds', and based on the co-occurrence of *Doliodus problematicus* teeth and the *C. latispinosus* form of spines on the articulated fish from Atholville, we emend the name of the taxon.

**Geological and stratigraphic settings**

The Campbellton Formation unconformably overlies volcanics of the Lower Devonian Dalhousie Group. The unconformable upper contact with the overlying Carboniferous Bonaventure Formation (Williams et al. 1985) is beneath the Restigouche River (Dineley and Williams 1968).

Based on palynological data, the Campbellton Formation is dated as Emsian (Blieck et al. 2000). The miospore assemblage identified is the *Emphanisporites annulatus-Camarozonotriletes sextantii* Assemblage Zone (Richardson and McGregor 1986), which approximately corresponds to the *Polygnathus dehiscens* to *P. serotinus* Conodont zones of early Emsian to early late Emsian age.
(Blieck et al. 2000). Plant localities at the eastern exposures of the Formation (Kennedy et al. 2012a) contain spores from the *Grandispora* subzone of the *douglastownense–eurypterota* zone (Richardson and McGregor 1986), indicating a late Emsian to earliest Eifelian age (Wellman and Gensel 2004). By comparison the lowest fish-bearing ‘Atholville beds’ are in the older part of the Campbellton Formation within the early Emsian (Kennedy and Gibling 2011; Kennedy et al. 2012b). This would place the specimens between the Pragian-Emsian boundary at 407.6 ± 2.6 Ma (Cohen et al. 2016) and the terminal date for the Emsian at 393.2 ± 1.2 Ma (Cohen et al. 2016).

Some authors (e.g. Pageau 1968, 1969a, b) considered the Campbellton outcrops part of the Battery Point Formation found north of Chaleur Bay in Gaspé, Quebec.

The ‘Atholville beds’ (Dineley and Williams 1968) are exposed for over 2 km from Campbellton west of the New Brunswick-Quebec bridge to Atholville. They are composed of a steeply inclined basal coarse breccia overlain by a succession of interbedded sandstones and shales (Turner and Miller 2006). A total thickness of about 12 m is exposed (Miller 2007, fig. 2). The specimens collected in the 19th Century are from the lower breccia; further specimens, including the articulated *Doliodus*, have been recovered from calcareous shale or mudstone, argillaceous sediments, mostly exposed on the banks of the Restigouche River.

North of the river and bay, the Emsian-Eifelian Gaspé Sandstone Group is a major geological unit of the Gaspé Peninsula, cropping out from Gaspé in the east to the Matapedia Valley in the west, and more westward into the southern Rimouski area, at the frontier with the northernmost part of New Brunswick (Plusquellec et al. 2011, fig. 1). In Gaspé, the Group comprises in ascending stratigraphic sequence (Boucot et al. 1972), the deltaic York River Formation (Emsian), the estuarine-distal fluvial Battery Point Formation (Emsian-Eifelian), and the proximal fluvial Malbaie Formation (Eifelian). In the north-central part of the Gaspé Peninsula, the
Emsian York Lake Formation is overlain by the marine volcanic-influenced York River Formation (also Emsian) and the marine-continental Battery Point Formation (Emsian-Eifelian). In the Matapedia Valley and westward, the same units crop out, but clastic marine facies of the York River Formation persist into the lower Eifelian (Plusquellec et al. 2011, fig. 1B). Thus the marine-continental transition is diachronic, and the sediments record the progressive closure of the Gaspé Basin and the disappearance of the last residual sea ways of the Iapetus Ocean at the margin of Laurentia.

An historical overview of *Ctenacanthus latispinosus* Whiteaves, 1881

Whiteaves (1881) briefly described some of the isolated fin spines from the 'Atholville beds' as *Ctenacanthus latispinosus*, which he considered to be a chondrichthyan; spines that he assigned at that time to *Homacanthus* sp. undet., he subsequently assigned to *Homacanthus gracilis* N. Sp. (Whiteaves, 1889). However, *H. gracilis* (Eichwald, 1844) is an occupied name, being the type species of *Homacanthus*, with *H. arcuatus* Agassiz, 1845 its junior synonym. Burrow et al. (2016) have since synonymized *H. gracilis* with *Diplacanthus crassisimus* Duff, 1842, a species that is found in the Middle Devonian of Scotland, the Baltic countries, and Russia (Denison 1979, figs. 32I, J, 33F). Woodward (1889) assigned both *Ctenacanthus latispinosus* and Whiteaves’ *Homacanthus gracilis’* to the Acanthodii. Woodward (1889, p. 183) stated that the fossils were “misinterpreted and unrecognized” by Whiteaves, and could be compared with the spines of *Climatius* Agassiz, 1844, then known from both isolated spines and articulated fish from the Lower Old Red Sandstone (Lochkovian) of Turin Hill and elsewhere in the Midland Valley of Scotland (Egerton 1861; Powrie 1870). Woodward (1892a) subsequently provided a more formal, but no more detailed, description of *Climatius latispinosus*. Whiteaves’ *Homacanthus* was not included in his
synonymy. Although *Climatius latispinosus* was originally identified as the chondrichthyan
*Ctenacanthus* by Whiteaves (1881), it has since been considered a climatiid acanthodian (Denison 1979). Ultimately Whiteaves appeared to agree with Woodward’s interpretation. In 1907, Whiteaves again described the type *Ctenacanthus latispinosus* fin spines, this time as *Climatius? latispinosus*; in the same paper he listed the “*Homacanthus gracilis*” specimen only as a “Spine of (?) Acanthodian”. Confusion over the status of Whiteaves’ *Homacanthus* spines has only now been resolved. The type specimens from the 'Atholville beds' were originally catalogued as CMN 657 (Gardiner 1966). A hand-written note on their first catalogue card states that the number had already been used, so they would have to be re-numbered. The two specimens were apparently re-numbered as CMN 3245, and erroneously came to be listed as “part and counterpart” (an understandable assumption, given that they shared the same number). However, close examination by S. Cumbaa and M. Currie (pers. comm. 2007) shows that they are two separate specimens in different coloured matrix; both spines currently are assigned to *Ankylacanthus incurvus* (Traquair, 1890c) (see Burrow et al. 2008, fig. 2C, D; contra Denison 1979, p. 52, who stated the spines belong to *Climatius latispinosus*). The line-drawing in Whiteaves (1889, fig. 4) appears to be a rough composite of the two spines.

Traquair (1890a–c) added to the 'Atholville beds' fish assemblage by describing two new species, *Cephalaspis whiteavesi* (an osteostracan) and *Gyracanthus incurvus* (an acanthodian), and expanding descriptions of osteostracan *Cephalaspis campbelltonensis* and placoderm *Coccosteus acadicus*; he assigned the last to the genus *Phlyctaenius*. He also reiterated an earlier suggestion by Woodward (1889) that *Ctenacanthus latispinosus* and *Homacanthus* were not distinguishable from *Climatius*. Woodward (1892a) confirmed the identification of *Gyracanthus incurvus* based on four additional specimens acquired by the British Museum (Natural History). As noted earlier, this species is now assigned to *Ankylacanthus* (Burrow et al. 2008).
In his original description, Whiteaves (1881) had not compared the Campbellton fossils to *Ctenacanthus major*, Agassiz’s (1844) type for the genus, but rather to the Upper Silurian *Ctenacanthus ornatus* Agassiz, 1837. According to Maisey (1984, p. 10), the latter species is based on a climatiiform acanthodian spine referable to *Climatius*. Maisey (1981, 1982, 1984) discussed the problems that have arisen with *Ctenacanthus* since Agassiz established the genus in 1835 based on isolated spines from the Lower Carboniferous near Bristol, England. A number of specimens have been assigned to *Ctenacanthus* erroneously, in part, due to the flexible nature of the description of the genus which was amended numerous times following Agassiz’s original diagnosis. Over time *Ctenacanthus* became a ‘grab bag’ for fin spines; Maisey (1981) considered only eleven species to be correctly placed.

The fin spines of *Climatius latispinosus* are here considered highly likely to be attributable to the same taxon as the articulated specimen assigned by Miller et al. (2003; Fig. 2A) to *Doliodus problematicus* (Woodward, 1892a), a taxon originally erected for isolated diplodont teeth. Maisey et al. (2017; Fig. 2B) recently CT scanned the pectoral region of this articulated specimen, revealing hidden details of the number, distribution, and morphology of the fin spines, that permitted comparison with and identifications of some of the isolated spine forms.

**Materials and methods**

Campbellton specimens are reposited in many institutions, with most having been collected in the late 19th Century from mudstones towards the eastern end of the exposures. These mudstones are now only preserved as a thin veneer (Miller 2007). The structure of the spines collected in the 19th Century from these mudstones can be relatively well preserved. In 1971 one of us (JM), during his postgraduate work at the NHM, had thin sections made of one of the spines catalogued as NHMUK
PV P.6547. Spines collected from the 'Atholville Beds' in the 1800s are often compressed, whereas those collected from lithology similar to the Gaspé material are often uncrushed, but only preserved as molds or with friable bone. For the Gaspé material, specimens were collected from Mont Lyall in 2003 and from southwest of Mont Tuzo in 2002–2006. Most specimens were preserved only as impressions, 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 and Olympus SX40 dissecting microscope and DP12 imaging system. Thin sections were imaged using an Olympus BX50 transmission microscope and DP12 imaging system. Figures were compiled using Adobe Photoshop®.


**Systematic palaeontology**

Class Chondrichthyes

**REMARKS.** There is emerging consensus that all acanthodian fishes are stem chondrichthyans (Zhu et al. 2013; Long et al. 2015; Burrow et al. 2016), in much the same conceptual manner that
‘dinosaurs’ are nowadays considered stem birds. In most recently published phylogenetic analyses, *Doliodus* is nested within ‘conventionally defined chondrichthyans’ (Zhu et al. 2013), a character-based group defined by the presence of tessellated chondral mineralization. It is still unclear whether tessellated mineralization was actually present in *Doliodus*, although it shares numerous endoskeletal features with many other Palaeozoic shark-like fishes in its cranium, jaws, and pectoral region, as well as in its squamation and teeth (Miller et al. 2003, Turner and Miller 2008). However, *Doliodus* also possessed ‘acanthodian-like’ paired pectoral fin spines, prepectoral spines, and prepelvic spines (Maisey et al. 2017). Alternative phylogenetic positions for *Doliodus* are therefore possible, deeper within the chondrichthyan stem and below ‘conventionally defined chondrichthyans’.

Order, Family indet.

*Doliodus* Traquair, 1893

*Doliodus latispinosus* comb. nov. (Whiteaves, 1881)

Figs. 2–9

**REMARKS.** Structure of the spines, revealed by 3D scanning on the articulated specimen assigned by Miller et al. (2003) to *Doliodus problematicus* (Maisey et al. 2017), shows that the spines for which Whiteaves (1881) erected *Ctenacanthus latispinosus* should probably be assigned to the same species or at least to the same genus as the articulated specimen. *Ctenacanthus* spines differ in having a posterior face with a pronounced proximal median ridge and paired rows of posterior denticles (Maisey 1981), and *Climatius* spines differ in having only a thin inner layer and lacking posterior denticles (Burrow et al. 2013). Given that the isolated spines (1) do not conform to the
diagnosis for *Ctenacanthus* or *Climatius* and (2) have many features in common with those in the articulated *Doliodus* specimen, they are assigned to *Doliodus*. It is highly likely that the articulated specimen and the isolated spines are conspecific. Because Whiteaves erected the species name *latispinosus* in 1881, it has priority over *problematicus*, hence the spines are assigned to *Doliodus latispinosus* comb. nov.

SYNONYMS:

*Ctenacanthus latispinosus* Whiteaves, 1881, p. 99; Whiteaves 1883, p. 164; Whiteaves 1889, p. 95, pl. 10, fig. 3a, b

*Climatius latispinosus* (Whiteaves), Woodward 1889, p. 184; Traquair 1890a, p. 21; Woodward 1892a, p. 3; Gardiner 1966, p. 48; Pageau 1969a, p. 457, pl. 22, fig. 1–5, 10, pl. 24, fig. 1A, B; Denison 1979, p. 25

*Climatius? latispinosus* (Whiteaves): Whiteaves 1907, p. 257


“*Climatius*” *latispinosus*: Desbiens and Burrow 2004, p. 47; Burrow and Desbiens 2005, p. 27; Burrow et al. 2008, p. 906

*Doliodus problematicus*: Kennedy et al. 2012b, pl. 1j

cf. *Protodus jexi*: Kennedy et al. 2012b, pl. 1m
TYPE SPECIMENS: No holotype was formally designated. Fin spines collected by A.H. Foord in 1881 from the type locality include lectotype and paralectotypes: Lectotype: CMN 3242a (Figs. 3B, 4B; Whiteaves 1889, pl. 10.3; one of three syntype spines on CMN 3242 slab (Figs. 3A, 4A); label informally annotated by J. Zidek in 1977 to designate this spine as the holotype). Paralectotypes: CMN 3242b (Figs. 3C, 4C; Whiteaves 1889, pl. 10.3b), CMN 3242c (Figs. 3D; not previously figured), and CMN 12008 (Figs. 3E, F, 4D; Whiteaves 1889, pl. 10.3a).

TYPE LOCALITY AND HORIZON: Southern shore of Restigouche River section, c. 1 km west of Campbellton, New Brunswick, Canada; 'Atholville Beds' (Lower Devonian, ?lower Emsian), Campbellton Formation.

DISTRIBUTION: 'Atholville Beds'; Cap-aux-Os Member, Battery Point Formation, north side of Gaspé Bay; upper part of York River Formation, central Gaspé Peninsula, Québec, Canada.

median fin spine), NHM P.7081 (scales). Museum d’Histoire Naturelle de Miguasha: MHNM 02-10761.1, 2, 03-10001, 03-10003, 03-10010, 03-10011, 03-10012, 03-10013, 03-10021, 03-10023, 03-10026, 03-10027, 03-10039.2, 03-10078.1, 03-10080, 03-10097, 03-10099.1, 03-10099.2, 03-10122, 03-10138 (?prepelic spine surrounded by scales), 03-10146.1, 03-10148.1, 03-10150, 03-10153.1, 03-10213.2, 03-10215, 03-10216, 03-10217, 03-10219, 03-10220, 03-10240a, 03-10240b, 03-10310 from Mont Lyall locality; MHNM 03-10001, 03-120013 from southwest of Mont Tuzo; all preserved as impressions, some with fragmentary bone from which thin sections were ground. Redpath Museum: RM 14.104 (oblique section exposed), 1789 (slab with associated spines), 1825 (two spine specimens, labelled *Ctenacanthus latidentatus*; American Museum of Natural History: AMNH FF 7698 and 7699.

**DIAGNOSIS (SPINES):** All spines with longitudinal ridges ornamented with smooth or finely ribbed ‘bucket-in-bucket’ nodes; spines lack, or have a short, insertion base lacking ornament ridges; median fin spines straight with a single row of denticles along the distal third of the trailing edge; pectoral fin spines c. 50 mm long with a base one-third the length of the spine, insertion-exsertion boundary at c. 35° angle to leading edge, and a single row of small posterior denticles toward the tip; pelvic fin spines long-based triangular shape with a single row of hook-like denticles extending along the whole of the trailing edge; prepelvic spines inclined cone-shape with a wide open base and no posterior denticles; prepectoral and admedian? spines low, wide based, with ridges curving over towards the apex, and no posterior denticles.

**DESCRIPTION:** The articulated specimen of *Doliodus* (NBMG 10127, Fig. 2) shows few details of the fin spines on visual examination. A tomographic scan of the pectoral region in this specimen revealed two pairs of prepectoral spines, associated with the coracoid cartilages, anteromedial to the
pectoral fin spines (Maisey et al. 2017, figs. 2, 4, 5C, D, G–I, 6; Fig. 2B). The anterior pair are low with an oval base outline; the apex is towards the posterior, with noded straight ridges radiating to the perimeter of the base. The posterior pair have the same general shape, but are larger, with the base length almost half the length of the pectoral fin spine, and with longer ridges curving up to the apex. The pectoral fin spines (Maisey et al. 2017, figs. 2–4, 5A, B, E, F; Fig. 2) are 55 mm long with a slightly sigmoid trailing edge and almost straight leading edge, and are c. 8 mm maximum width; the insertion-exsertion boundary (IEB) is estimated to have been at a 35° angle to the leading edge. Unlike in many acanthodians, the spines did not project as far laterally as the fins themselves. The fin spines are twisted somewhat medially so that a diagonal transverse section is exposed distally on one of the slabs, showing a V-shaped cross section. Ridges are longitudinal, paralleling the trailing edge; a few places where impressions of ridge ornament are preserved show faintly ridged nodes. Small denticles are possibly preserved along the trailing edge of the left spine toward the distal tip. The specimen scans revealed two prepelvic spines with wide open bases and the base of a pelvic spine on the left side (Maisey et al. 2017, figs. 2, 6; Fig. 2). The base of a larger spine located in front of this series also was discovered in the scan (Maisey et al. 2017, fig. 2). In dorsal view, the external surface of this spine is exposed, whereas the internal surface of the prepelvic spines are exposed; the large spine was interpreted as a dorsal. Unfortunately it is not preserved well enough to resolve any notable features. Maisey et al. (2017, p. 10) also detected a fragmentary probable pelvic spine.

Whiteaves (1889, pl. 10.3, 3a) illustrated the type spines of *Doliodus latispinosus* comb. nov. with long ridges paralleling the leading edge, but re-examination of these specimens shows that the ridges are slightly oblique, converging on the leading edge, and more or less paralleling the trailing edge (Figs. 3, 4). Most isolated spines from the 'Atholville beds' (Fig. 3B) are elongate, straight or slightly curved, with a maximum length 90 mm, maximum width 20 mm for these
median (symmetrical) fin spines, and 10–20 longitudinal ridges; short ridges are intercalated between full-length ridges near the proximal end. The ridges are c. 2 mm wide and 2 mm apart near the proximal end, narrowing slightly towards the distal tip. Ornament on the ridges comprises short nodes c. 1 mm long, resembling flattened overlapping tubercles with fine ribbing toward the proximal ends of the spines (Fig. 5A, D, J, K), and longer smooth nodes c. 1.5 mm long toward the distal end of the spine. Ornament ridges often extend the whole length of the spines, although rare spines show a short differentiated insertion zone (Fig. 5A, D). A single row of thorn-like denticles runs along the distal third of the trailing edge of most of the spines. As these denticles are only on one side, impressions of the other side of a spine give no indication of the presence of a denticle row (Fig. 3E, F). Rare impressions of the trailing edge of spines (Fig. 5C) show evidence of the single denticle row and the relatively flat surface with striae between the two edges. The curved hooks have a base c. 0.4 mm long, are 1 mm apart, and recurve toward the proximal end of the spine (Figs. 3B, 6A, C–E). Slightly curved, laterally flattened, medium-length spines with c. 10 ridges per side, show the leading edge and IEB meeting at an angle c. 50° (Figs. 3E, F, 5I–K). CMN 12002 shows a spine with a patch of calcified (branchial?) cartilage and branchial denticles like those seen on the articulated Doliodus.

The main other general category of spine forms assigned to Doliodus latispinosus are the broad-based triangular spines, including the paralectotype spine CMN 3242b (Figs. 3C, 4C). Laterally flattened spines like the latter and NBMG 12072 (Fig. 5H), have a posterior denticle row that extends from the distal tip almost to the base of the spine. Some other triangular profiled spines have a base length equal to, or slightly greater than, the (inclined) height (i.e. length of trailing edge) with a wide open base (e.g. Fig. 5G: NBMG 11947, base length 30 mm, trailing edge length 25 mm; Fig. 6H). The 3D shape of this spine form is best illustrated by the Gaspé Peninsula specimens (see next paragraph). Rare spines including NHMUK PV P.6547(2) are short with a long base, with
ridges curving round to an apex above the presumed posterior end (Fig. 6G). By comparison with the structures revealed by the 3D scans of the articulated specimen, this spine is identified as an admedian. NBMG 12033 is the mold of a short low-angled spine (Fig. 5L), possibly a small prepectoral, and a patch of Doliodus type scales.

Most Doliodus latispinosus specimens from the Gaspé Peninsula are only spine fragments exposed in lateral view, but some are external impressions of whole elements. Nearly all of the different morphotypes are represented in the MHNM collection. Long relatively straight spines that projected at an angle of c. 50° to the body of the fish (e.g. Fig. 7B, D, E) and several imperfectly preserved, short relatively straight spines that projected at about 40° (Fig. 7C) to the body, have a broadly semicircular cross-sectional shape revealed in natural cross-section (Fig. 7F), indicating they are median fin spines. Other forms include the slightly recurved, laterally flattened, medium-length specimens (e.g. Fig. 7A), interpreted as pectoral spines, and asymmetrical inclined cone-like spines with long wide oval bases (Fig. 8A, E, J). Their broad shape is revealed in the molds of the uncompressed spines and on sawn sections of MHNM 03-100112 (Fig. 8B, C); these cone-shaped spines have much thinner walls than the median spines. Many have very well preserved ornament ridges, showing that the ribbed tubercular nodes sometimes extend along the whole length of the ridges (Fig. 8A, E, F, K); they lack posterior denticles. The proximal ends of the ridges are widely separated, with occasional short ridges intercalated between them. The long ridges coalesce in a random pattern along the ‘crest’ of the spine. Their shape compares closely to that of the posterior prepectoral spines on the articulated specimen, although the apex appears more pointed. With their wide open bases, they could possibly be large prepelvic spines. Other asymmetric paired fin spines have a triangular sagittal section, are laterally flattened and have a row of posterior denticles (Fig. 8G). By a process of elimination, these are interpreted as pelvic spines. One specimen MHNM 03-10138 shows a spine with an oval base and a low asymmetrical cone surrounded by typical
Doliodus scales (Fig. 8H), and is identified as a prepelvic rather than a prepectoral spine, because on
the latter the apex is strongly inclined.

Transverse thin sections of median fin spines (Fig. 9) show that, near the proximal end, vacuous
osteodentine fills most of the width of the walls, with an extremely narrow dense layer lining the
central cavity; thin trabeculae separate the osteodentinal spaces of the extensive middle layer,
grading into a denser osteo-mesodentine layer forming the ridges (Fig. 9A–D). The inner dense
layer increases in width distally; lamellae and possible bone cell lacunae and processes can be
distinguished close to the wellmarked boundary between the inner and middle layers (Fig. 9C).
Some of the interdenteonal lacunae-like structures (Fig. 9D) are possibly 'interglobular spaces',
rather than remnants of bone cells, as noted in spines of the acanthodian Machaeracanthus goujeti
Botella et al., 2012 and also in xenacanth sharks (e.g. Beck et al. 2016). The inner surface lining the
spine central cavity is very irregular toward the spine tip, as the cavity becomes centripetally infilled
by the dense lamellar inner tissue. Vascular canals between the trabeculae of the middle layer also
narrow toward the tip, as the osteodenteons in the older part of the spine are centrifugally infilled. In
the ornament ridges, the dentine tubules running into the vascular canals are orthodentine-like,
being fine calibre and straight, then branching and extending to the outer surface, without an
enameloid or tubule-free outer zone (Fig. 8E).

Two fin spines (Fig. 5D and E, F) show evidence of healed fractures, with the outer dentine
layer extending at least partially over the fracture. There is no evidence of resorption.

Discussion

Only the pectoral and small fragments of more posterior fin spines were exposed and identified by
Miller et al. (2003) on the partial articulated Doliodus specimen NBMG 10127 from Atholville,
New Brunswick. Both pectoral fin spines are partially eroded and/or buried in matrix and show limited detail. These pectoral spines are comparable in shape, having a relatively straight leading edge, a slightly sigmoidal trailing edge, and a similar orientation of ornament ridges, with one of the *Doliodus latispinosus* morphotypes known from isolated spines (Figs. 5E–F, 6B–C, 7A), leading us to interpret these also as pectoral fin spines. The articulated *Doliodus* specimen also has remnants of fin spines behind the branchial region, at least one of which has hook-like denticles. The 3D scan revealed that these include two prepelvic spines. These appear to have been very small on the articulated specimen; amongst the isolated material, specimen NBMG 12033 (Fig. 5L) could possibly be a prepelvic or prepectoral, although its apparently robust ridges could indicate this is not from *D. latispinosus*. The scan also revealed the base of a pelvic spine posterolateral to the prepelvic spines, but it is not preserved well enough to show details. Of the asymmetrical isolated spine forms, it seems likely that the triangular profile ones with posterior denticles must be pelvic spines (Figs. 3C, 5G, 6H, 7A), as we know of no instances where prepectoral or prepelvic series spines show such structures: the latter lack a posterior groove, having a circumferential insertion around the whole base. By comparison with similar elements in articulated specimens of Lower Old Red Sandstone climatiid acanthodians (e.g. Miles 1973) and the articulated *Doliodus*, small flattened cone-shaped spines (Fig. 8H) are interpreted as prepelvic spines. Larger low, open-based spines (Figs. 6G, 8A, E) are comparable with the posterior prepectoral spines revealed by scans of the articulated *Doliodus*.

Determining which median spine is which, however, is not necessarily helped by comparison with climatiid acanthodians, as the latter show great variation in relative lengths of median fin spines (e.g. Denison 1979, fig. 11). All of the complete isolated symmetrical spines (Figs. 3E, F, 5A, I–J, 6A, 7B) projected at an angle of c. 50° to the body. The only completely straight spine (Fig. 7B) has a markedly greater height to base length ratio (4.9:1) than the other spines, all of which are...
slightly convex along the leading edge. Given that the only median (dorsal) fin spine recognized so far on the articulated *Doliodus* appears fragmentary and only poorly preserved, we could only make an educated guess as to the original position of the isolated symmetrical spines.

Histological structure of *Doliodus latispinosus* median fin spines (Fig. 9) closely resembles that of *Parexus recurvus* spines (Burrow et al. 2013, fig. 7), with a wide osteodentinous middle layer. The main structural difference between spines of the two taxa is the type of dentine forming the outer zone of the ridges; *D. latispinosus* has branching orthodentine, whereas *Parexus recurvus* (Burrow et al. 2013) has a syncitial mesodentine sensu Valiukevičius and Burrow (2005). *Climatius reticulatus* Agassiz, 1844 spines also have a wide osteodentine layer, but the inner dense layer remains thin for the whole length of the spine (Burrow et al. 2015), unlike in *Parexus* and *Doliodus* where it increases in thickness towards the tip. The presumed prepelvic and prepectoral fin spines of *D. latispinosus* differ to its other spines in being very thin-walled, without a thick osteodentine layer, and only a thin inner layer. This structure resembles that in *Ankylacanthus incurvus* fin spines (Burrow et al. 2008, fig. 3F).

*Lupopsyrus pygmaeus* Bernacsek & Dineley, 1977 (see Hanke and Davis 2012), *Ankylacanthus incurvus*, and *Doliodus latispinosus*, though clearly distinguishable from each other based on fin spine ornament, show a unique combination of spine characters that are not found in other early gnathostomes with paired fin spines; specifically, they have a single row of posterior denticles and ‘protoctenacanth’ ornament on the ridges. *Lupopsyrus pygmaeus* only has denticles on the pectoral spines, not on the median or pelvic spines. Whereas no median, pelvic or prepelvic spines are known for *Ankylacanthus* (considered an early gyracanthid, see Burrow et al. 2008), the isolated spines of *D. latispinosus* include symmetrical forms that are clearly distinguishable as median spines. In *D. latispinosus*, all the median spine forms, as well as the pectoral and pelvic spines, have a single row of posterior denticles. *Doliodus* is the only taxon known to have this feature. In
Acanthodian taxa that have spines with posterior denticle rows, these denticles are on either a median spine (e.g. *Parexus recurvus* Agassiz, 1845: on the anterior dorsal) or the pectoral spines (e.g. *Ankylacanthus, Lupopsyrus, Vernicomacanthus, Gyracanthides*). Both *Doliodus* and *Ankylacanthus* appear to have had prepectoral and/or admedian spines.

With *Doliodus* and other early 'sharks' sinking deeper into the chondrichthyan stem (i.e. the acanthodian 'pool'), it is perhaps not surprising that many Devonian and Carboniferous (and other extinct and extant) sharks have fin spine morphologies that differ little within families, because most of these taxa probably evolved from a common ancestor within the climatiid grade of acanthodians.

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FIGURE CAPTIONS

**Fig. 1.** Locality map for eastern Canada showing occurrences of Lower Devonian (Emsian) vertebrate occurrences in central and eastern Gaspé (after Burrow et al. 2008, fig. 1).

**Fig. 2.** Articulated *Doliodus* specimen NBMG 10127 from the 'Atholville beds', New Brunswick. (A) Whole specimen, immersed in ethanol, dorsal view. (B) Reconstruction, ventral view, based on 3D scan images (see Maisey et al. 2017); prepectoral and dorsal spines buried in matrix and not visible on the exposed specimen. Scale bar = 10 cm. Abbreviations: dfs, dorsal fin spine; pectfs, pectoral fin spine; pps1, prepectoral spine 1; pps2, prepectoral spine 2 (or admedian spine); pelvfs, pelvic fin spine; prepelvs, prepelvic spines.

**Fig. 3.** *Doliodus latispinosus* (Whiteaves) comb. nov., CMN isolated fin spines from the 'Atholville beds', New Brunswick. (A) CMN 3242 slab with three spines, CMN 3242a–c; see outline drawing Figure 4A for identifications of the three individual spines. (B) Lectotype CMN 3242a. (C) Paralectotype CMN 3242b. (D) Paralectotype CMN 3242c. (E, F) CMN 12008, part and counterpart. (G) CMN 58593. (H) CMN 12002. Scale bars = 1 cm. Individual spine images all oriented with distal tip to top.

**Fig. 4.** *Doliodus latispinosus* (Whiteaves) comb. nov. isolated type fin spines from the 'Atholville beds', New Brunswick, outline drawings. (A) Block CMN 3242 with three spines; see photograph of slab in Figure 3A. (B) Lectotype CMN 3242a (Whiteaves 1889, pl. 10.3). (C) Paralectotype CMN 3242b (Whiteaves 1889, pl. 10.3b). (D) CMN 12008 (Whiteaves 1889, pl. 10.3a). Scale bar = 1 cm.
Fig. 5. *Doliodus latispinosus* (Whiteaves) comb. nov. isolated fin spines from the York River Formation, Quebec (A–D) and the 'Atholville beds', New Brunswick (E–L). (A) MHNM 03-10240a, cast of impression of non-denticulated side of whole spine. (B, C) MHNM 03-10240b, cast of lateral and trailing edge of distal tip and inner surface of one side of incomplete spine; bases of single denticle row visible near tip on the side of spine in the matrix, (B) lateral view; (C) posterolateral view of spine tip. (D) MHNM 03-10310, cast of fractured spine lacking distal end, showing regrowth over fracture; short base of insertion visible. (E, F) NBMG 9986a, b, two halves (part and counterpart) of spine with fractured, bent tip, also showing regrowth at fracture. (G) NBMG 11974, natural cast of inclined cone spine form, equalized in Photoshop to enhance contrast. (H) NBMG 12072, triangular spine with long posterior denticle row. (I, J) NBMG 12394a and b, two halves of one side of a medium sized spine (other side of spine still probably in matrix); (K) closeup of ornament tubercles/nodes in (J). (L) NBMG 12033, small low spine with patch of *Doliodus* type scales. Scale bars = 1 cm except in K = 1 mm.

Fig. 6. *Doliodus latispinosus* (Whiteaves) comb. nov. fin spines from the 'Atholville beds', New Brunswick. (A) NMS G.1897.51.62, median fin spine. (B) NMS G.1887.20.55, counterpart, ?pectoral fin spine. (C) NMS G.1887.20.55, part, ?pectoral fin spine. (D) NMS G.1897.51.63, ?median fin spine. (E) NMS G.1897.51.71, mid-section of median spine with well preserved posterior denticle row. (F) NMS G.1978.30.1, curved spine tip with well preserved denticles. (G) NHMUK PV P.6547(2), long-based low spine with apex overhanging posterior end. (H) NHMUK PV P.6547(3), long-based triangular spine with posterior denticle row. (I) RM 14.104, oblique natural section through median fin spine. Scale bars = 1 cm.
Fig. 7. *Doliodus latispinosus* (Whiteaves) comb. nov. isolated fin spines from the York River Formation, Gaspé Peninsula, Quebec. (A) MHNM 03-10219, partial impression of ?pectoral fin spine with well preserved posterior denticle row on distal half of spine. Scale bar = 1 cm. (B) MHNM 03-10010, cast of median fin spine. Scale bar = 1 cm. (C) MHNM 03-10003, cast of median fin spine missing tip. Scale bar = 1 cm. (D) MHNM 03-10215, impression of median fin spine. Scale bar = 1 cm. (E) MHNM 03-10021, cast of base of median fin spine. Scale bars = 1 cm. (F, G) MHNM 02-10761.1. (F) Cast of natural cross section of spine showing ribbed tubercles on longitudinal ridges. Scale bar = 1 mm. (G) Longitudinal section of tubercle on ridge showing vascular canals of osteodentine layer and ?syncitial mesodentine of outer layer of tubercle. Scale bar = 0.1 mm. (H) MHNM 03-10146.1, cast of fin spine. Scale bar = 1 mm. (I) MHNM 03-10001, cast of mid-spine fragment showing trailing edge with row of denticle bases on one side. Scale bar = 1 mm. Specimens A–H from Mont Lyall and specimen I from southwest of Mont Tuzo.

Abbreviations: d, denticle; ib, insertion base. Dotted white lines in A, H indicate presumed edge of spine.

Fig. 8. (A–K) *Doliodus latispinosus* (Whiteaves) comb. nov. isolated fin spines from the York River Formation, Gaspé Peninsula, Quebec. (A–D) MHNM 03-10012. (A) Cast of flattened cone-shaped spine, external view. Scale bar = 1 cm. (B, C) Cross sections of spines imbedded in the matrix. Scale bar = 1 mm. (D) Ground thin longitudinal section of spine ridge node/tubercle showing osteodentine extending full thickness of the spine ridge. Scale bar = 0.1 mm. (E, F) MHNM 03-10011 cast of flattened cone-shaped spine, external view. (E) Whole specimen. Scale bar = 1 cm. (F) Closeup showing ribbed overlapping tubercles/nodes on bifurcating ridges. Scale bar = 1 mm. (G) MHNM 03-10217, impression of ?pelvic fin spine, showing posterior denticles towards spine tip. Scale bar = 1 cm. (H) MHNM 03-10138, impression of ?prepelvic spine-platelet surrounded by
scales. Scale bar = 1 mm. (I) MHNM 03-10220, impression of spine showing proximal part of trailing edge that was probably covered with fin web. Scale bar = 1 cm. (J) MHNM 03-10099.1, impression of proximal half of flattened spine showing noded lateral and leading edge ridges. (K) MHNM 03-120013, cast of well-preserved paired (asymmetrical) spine tip with nodose ridges. Scale bar = 1 cm. Specimens A–J from Mont Lyall and specimen K from southwest of Mont Tuzo. Abbreviations: ost, osteodenteon; s, scale.

Fig. 9. Ground thin sections cut transversely through isolated spines of Doliodus latispinosus comb. nov. from the 'Atholville beds', New Brunswick. (A–D) Median spine NHMUK PV P.6547: (A, B) slide 71/8/36 mid-spine section, boxed area in A magnified and rotated 90° counterclockwise in B; (C, D) slide 19 section near tip, boxed area in C magnified in D. Scale bars = 1 mm. (E), closeup of tubercle vertical section in thin section NBMG 20973 showing dentine tubules extending from vascular canals. Scale bar = 0.1 mm. bcl, bone cell lacuna; dt, dentine tubules; idm, interdenteonal matrix; ?igsp, possible interglobular space; il, inner lamellar layer; ost, middle osteodentine layer; vc, vascular canal.