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# *Protodus jexi* Woodward, 1892 (Chondrichthyes), from the Lower Devonian Campbellton Formation, New Brunswick, Canada

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ABSTRACT:

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*Protodus jexi* from the early Emsian 'Atholville beds', Campbellton Formation between Atholville and Campbellton, northern New Brunswick, Canada, is redescribed from material studied by R. H. Traquair and new specimens. *Protodus* is a valid monotypic genus with rows of shark-like serrated teeth. The taxon is based solely on teeth, some of which are associated. The teeth have monocuspid crowns with a thin enameloid layer and distinctive labial depressions or grooves, and large subrectangular to D-shaped cladodont-like bases some laterally and downwards extended. Crown histology is orthodentine merging down into the osteodentine of the base. A possible relationship with cladodont-bearing sharks is mooted and *Protodus* and other putative late Silurian to early Devonian chondrichthyan teeth are referred to a redefined family Protodontidae WOODWARD.

**Key words:** Early gnathostomes, Early chondrichthyans, *Protodus*, Teeth, Early Devonian, Canada, Taxonomy, Morphology.

## INTRODUCTION

In 1892 WOODWARD described two "chondrichthyans", *Diplodus problematicus* and *Protodus jexi,* based on teeth from the Lower Devonian Campbellton Formation, New Brunswick, Canada (TURNER & MILLER 2005a). TRAQUAIR (1893) renamed *Doliodus problematicus*, which he reaffirmed was chondrichthyan (MILLER & *al.* 2003; TURNER 2004) and noted (p. 145) that the many specimens of *Protodus jexi* described (but not illustrated) were collected subsequent to Woodward's description. He thought that the selachian nature (of the tooth) was "proved beyond doubt, not merely by its shape, but by its occasionally occurring in transverse bands, three or four being in apposition in a row back to front".

New material of *Protodus jexi* from the 'Atholville beds', Campbellton Formation, and examination of the type and Traquair's specimens provide a reassessment of the taxon. Despite Woodward and Traquair's chondrichthyan claims, from the mid-20th century *Protodus jexi* was placed into Acanthodii (e.g., DENISON 1979) until the senior author began a review of Campbellton material following a visit to Museum of Comparative Zoology of the Harvard University, Cambridge, USA in 1983. However, we must not forget that when first described chondrichthyans per se and acanthodians ('spiny sharks') were united. The

transference to acanthodians probably occurred and persisted because of a perceived similarity of *Doliodus problematicus* and *Protodus jexi* teeth to those of so-called "*Protodus*" *scoticus* from the Lower Old Red Sandstone of Scotland, with tooth files, whorls, and scales, which TRAQUAIR (1898) reassigned to *Protodus*, and then which were referred to ischnacanthiform acanthodians (WOODWARD 1917; not 1915, see DENISON 1979, fig. 27E caption). This position for the Campbellton taxa was most probably accepted based on the type illustrations of thin, concave bases and similarities to ischnacanthiform toothlets (see e.g., GARDINER 1966; DENISON 1979, p. 39). The Scottish specimen is now known to be the head of a *Nostolepis* (BURROW & TURNER in press).

*Protodus jexi*, as far as we can ascertain, has not been re-examined since TRAQUAIR's (1893, 1898) studies and here we illustrate the NMS specimens for the first time with detailed descriptions provided as Appendix 1.

**Institutional Abbreviations**: Carnegie Museum, Pittsburgh, USA – CM; Museum of Comparative Zoology, University of Harvard, Cambridge, USA – MCZ; Natural History Museum, London, UK, Fossil Fish collection – NHM P; National Museum of Scotland, Edinburgh, Scotland, UK (formerly Royal Scottish Museum, RSM) – NMS; New Brunswick Museum, Saint John, Canada – NBMG.

## GEOLOGICAL SETTING

*Protodus jexi* teeth have only been found in the basal vertebrate-bearing Atholville beds (TURNER & MILLER 2005a). These deposits represent the basal Campbellton Formation and outcrop from Atholville to Campbellton along the banks of the Restigouche River (Bay of Chaleur); MILLER (2007 and figs therein) recently reviewed the location, fossil assemblage and stratigraphy. The beds comprise a steeply inclined basal coarse mudstone breccia overlain by a succession of interbedded sandstones and mudstones that unconformably overlie rhyolite of the Lower Devonian Val d'Amour Formation dated at 407.4 ± 0.8 Ma (WILSON & *al.* 2004). Miospores indicated an early Emsian age (see BLIECK & CLOUTIER 2000, MILLER 2007 for earlier references) for part of the formation, although WILSON & *al.* (2004) proposed an Emsian/Eifelian age based on an angular unconformity separating the Val d'Amour and Campbellton formations. However, in terms of the international timescale (GRADSTEIN & *al.* 2004), the basal Atholville beds could be as old as late Pragian.

The Atholville beds are well known as a source of cephalaspid ostracoderms, arthrodires, acanthodians and again for chondrichthyans since the first fossils were discovered in 1881 whereas the palaeoenvironment has been uncertain (e.g., DINELEY & WILLIAMS 1968). The dark grey fossiliferous mudstone-breccia containing rhyolite fragments and blocks of sandstone or finer mudstone rich in ostracodes and gastropods, with eurypterids and plants are mainly unbedded. The chaotic mess of remains, fragments and enclosed jumbled beds of rock in mud suggest that all was deposited in a single event; we have suggested that the geographically-limited basal beds might represent a fossilized mudflow or lahar (TURNER & MILLER 2003).

*Protodus jex*i has not been found in the top Lagerstätte mudstone at Atholville, which yielded well-preserved *Doliodus problematicus* (MILLER & *al.* 2003), cephalaspids, placoderms and the eurypterid *Pterygotus anglicus* (MILLER 2007).

## SYSTEMATIC PALAEONTOLOGY

### Class Chondrichthyes HUXLEY, 1880
### Order Incertae sedis

REMARKS: Unlike *Doliodus* and other early Devonian taxa such as *Omalodus, Protodus* does not possess a thin labially-directed base and so cannot be placed in the Omalodontiformes TURNER, 1997. A new order Protodontiformes might be warranted when more is known of the earliest toothed sharks.

### Family Protodontidae WOODWARD, 1932

REVISED DIAGNOSIS: Cartilaginous fish bearing a dentition of separate primarily monocuspid teeth; cusp formed of distal orthodentine with an enameloid surface; a large solid subrectangular to D-shaped base formed of osteodentine; arranged in short tooth files (at least four in series); teeth apposite without interlocking devices; not ankylosed to cartilaginous jawbones.

REFERRED AND PROBABLE INCLUDED GENERA: *Protodus*, *Stigmodus* (which might be synonymous with *Protodus*), *Celtiberina*, *Dendrodus*.

REMARKS: WOODWARD's original (1932) definition of "Teeth cuspidate, in transverse series curving around the cartilage of the jaw, those of each series fused together by their expanded bases" was in part in-

fluenced by TRAQUAIR's (1898) uniting of "*Protodus*" *scoticus* with *P. jexi*. WOODWARD (1917) thought that more primitive elasmobranch teeth possessed a horizontally expanded base (or root), while antero-poste-

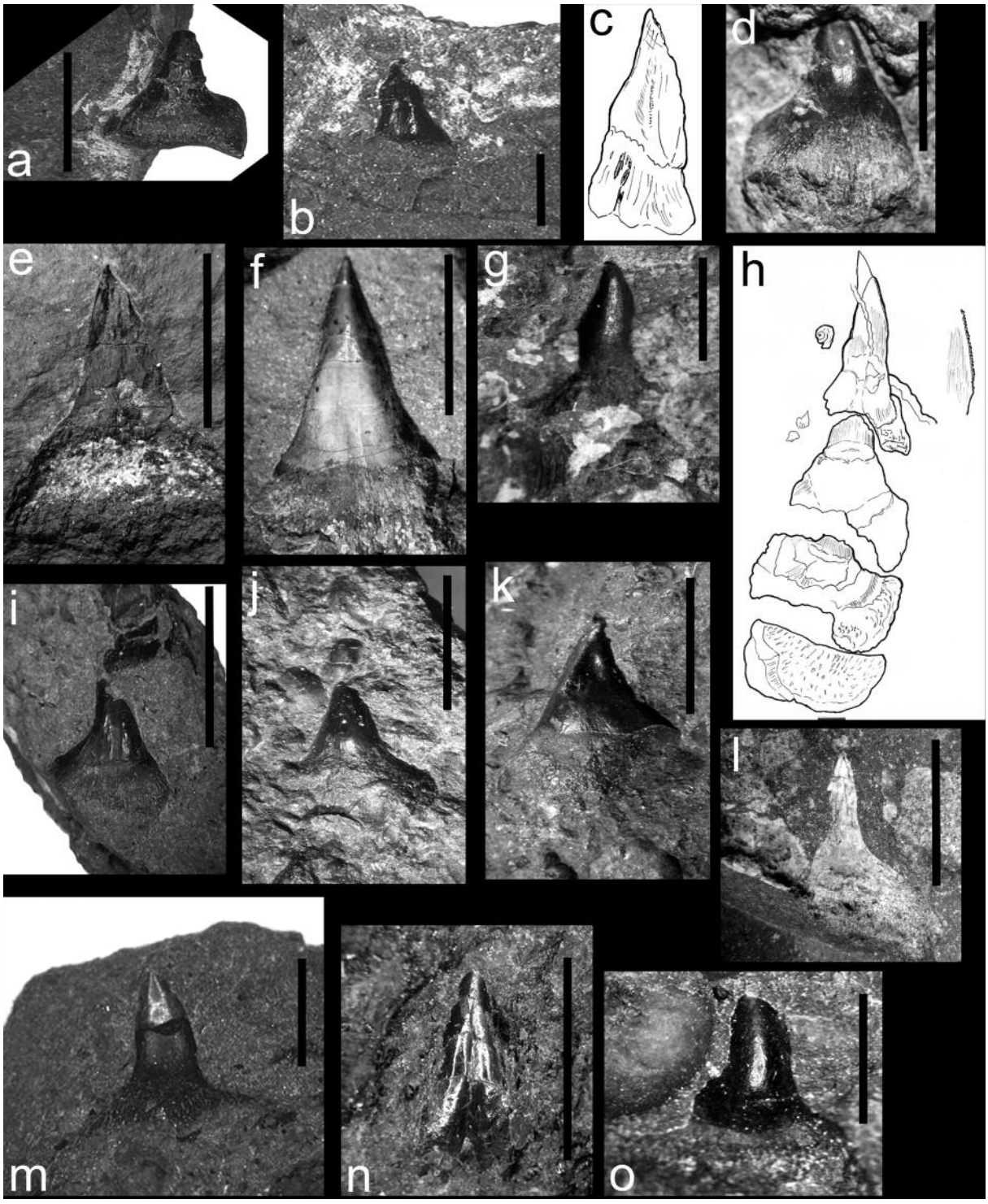


Fig. 1. *Protodus jexi* WOODWARD, 1892, a – NHM P6538, Holotype; b – NHM P6539c, scale = 2mm; c – NMS 1897.51.30; d – NBMG 3083; e – NBMG 13927; f – NBMG 11983; g) NBMG 13929, scale = 2mm; h – NMS 1897.51.39, tooth file of four conjoined teeth, first described but never figured by Traquair (1893), anterior to bottom?; scale = approx. 1cm; detail of serrated edge not to scale; i – NHM P7077; j) CM 5141(1); k – CM 5141(2); l – NBMG 12402; m – NHM P6568, scale = 2mm; n – NHM P60654; o – NHM In 59054 scale = 2mm. Scale = 5mm except where indicated

rior compression was the result of specialization. He also considered that *Protodus jexi* was a specialized form of a 'simple type' of tooth. His assessment later led him to create the family based on this tooth form, and in that we consider he was justified (see also TURNER & *al.* 2004).

A patch of partially articulated complex dermal denticles with one associated fin spine has been recovered in a horizon that has yielded several *P. jexi* teeth but we cannot confidently attribute these specimens to the taxon; they might belong to *D. problematicus*, which has 'ctenacanth' or *Antarctilamna* type scales, or might be plesiomorphic in these early spined sharks. Large disarticulated fin spines have been identified at Campbellton and at least one spine type identified as *Climatius latispinosus* is attributable to *D. problematicus*. Whether protodontids had fin spines will not be resolved unless an articulated *P. jexi* is found.

Genus *Protodus* WOODWARD, 1892

REVISED DIAGNOSIS: Noticeable heterodonty and asymmetry of small to medium sized teeth (<~12 mm) in tooth files of at least four teeth. Base large, undivided, laterally expanded, sometimes bilobed, and anteroposteriorly compressed. No discernible basal button.

TYPE AND POSSIBLY ONLY SPECIES: *Protodus jexi* WOODWARD, 1892

*Protodus jexi* WOODWARD, 1892
(Text-figs 1-3)

SYNTYPES: NHM P6538 (Fig. 1a, holotype), P6539a-c (Text-figs 1b, 2c, 3d thin section): similar teeth collected by Mr Jex, c. 1891.

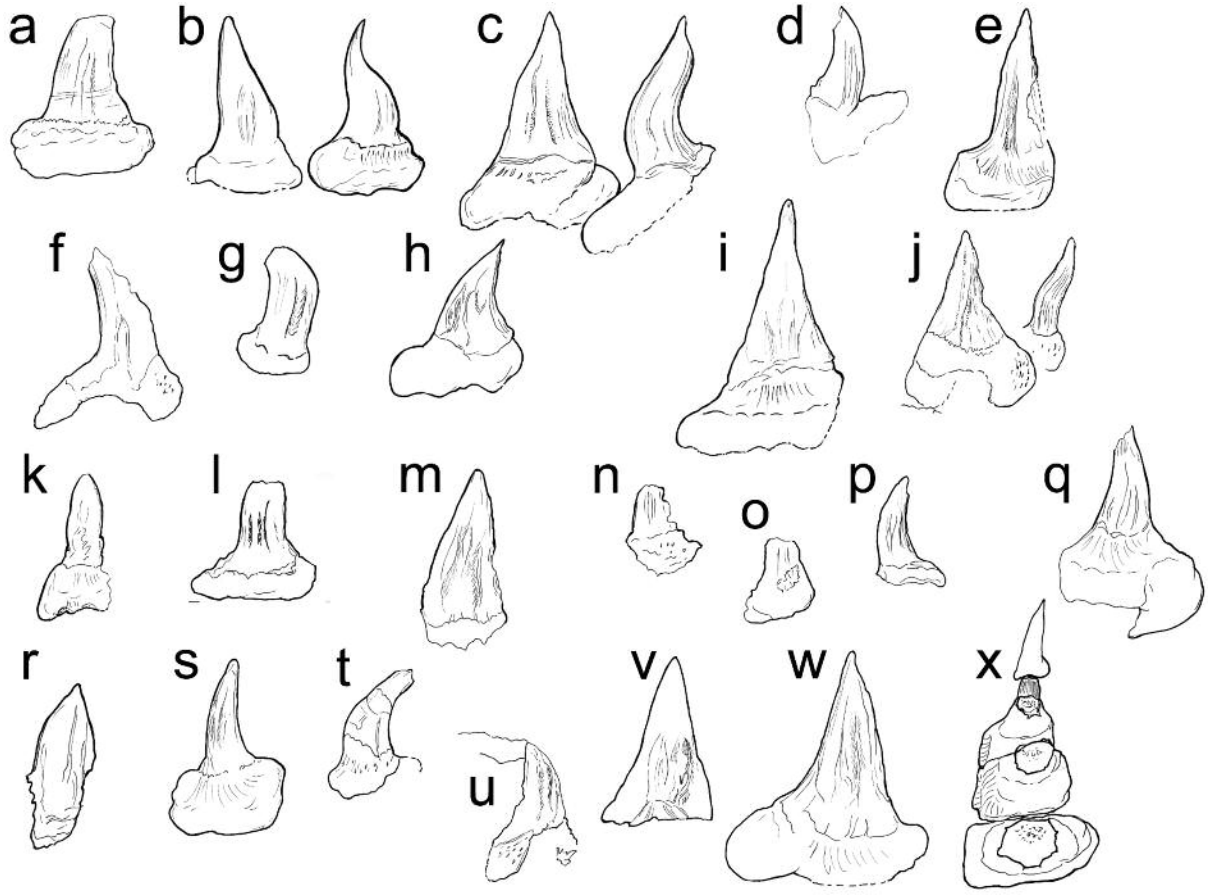


Fig. 2. *Protodus jexi* WOODWARD, 1892, interpretive drawings of TRAQUAIR's specimens, a) NMS 1897.51.14; b) NMS 1897.51.15; c) NMS 1897.51.16; d) NMS 1897.51.17; e) NMS 1897.51.18; f) NMS 1897.51.19; g) NMS 1897.51.20; h) NMS 1897.51.21; i) NMS 1897.51.22; j) NMS 1897.51.23; k) NMS 1897.51.24; l) NMS 1897.51.25; m) NMS 1897.51.26; n) NMS 1897.51.27; o) NMS 1897.51.28; p) NMS 1897.51.29; q) NMS 1897.51.30a; r) NMS 1897.51.31; s) NMS 1897.51.32; t) NMS 1897.51.33.1; u) NMS 1897.51.35 v) NMS 1897.51.36; w) NMS 1897.51.37; x) NMS 1897.51.38

PARATYPES: NMS 1897.51.14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37.1,2, 38a-c/39a-d: the important latter associated teeth were among those found by Mr Jex, R.F. Damon's collector (CLEEVELY 1983), and purchased from Damon by Traquair, as were the holotype/syntypes (see Text-figs 1c-h, 2a-x).

OTHER TOPOTYPE MATERIAL includes: CM5141 (1-2); NBMG 3083, 11983, 12402, 13918, 13919, 13920, 13922, 13923, 13924, 13927, 13928, 13929, 13930, 13933, 14506, 14507; NHM P6568; NHM P 7077; NHM P7081; NHM P59030; NHM P59043; NHM P59054; NHM P60645; MCZ 548, MCZ 8505 isolated teeth (see selected examples Text-figs 1d-g, i-o).

PLACE AND RANGE: Atholville beds, shoreline approximately 1.3 km W of the interprovincial bridge crossing the Restigouche River, near Campbellton, northern New Brunswick, Canada (palaeogeographically eastern Euramerica); most specimens from near 48°00.13'N; 66°41.68'W. Lower Devonian, late Pragian/early Emsian.

EXTENDED DIAGNOSIS: Dental crown (between 2-12 mm high) consisting of a single, robust, solid, conical sometimes nearly triangular cusp with biconvex cross-section, with a rounded point distally and lateral crista that can be finely serrated; generally five-sided cross section at cusp base and ellipsoid at distal point; labial surface with a single or double central depression and groove/s in proximal part; cusp formed of orthodentine mainly invested with finely-striated enameloid on surface down to interface with the cusp-base interface; sigmoidal in lateral view, sometimes topping a short splayed concave labial zone that grades into a large labially-rounded and downturned but lingually short horizontal base varying from undivided laterally expanded, D-shaped and anteroposteriorly compressed, to bulbous and bilobed, formed of osteodentine.

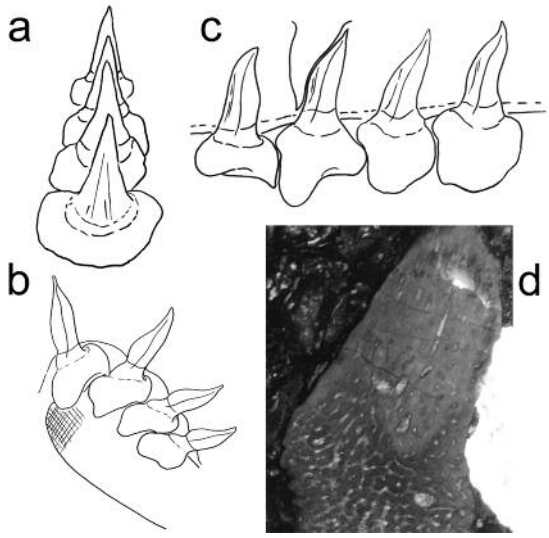


Fig. 3. *Protodus jexi*, a – restoration of tooth file based on NMS1897.51.38 and 39; b and c – possible tooth row reconstructions shown diagrammatically in lateral view, with upper cusp contact shown in (c), position 2; d – histological structure from vertical transverse section of syntype NHM P6539a, part of the cusp plus part of the base, measuring approximately 5.25 mm in height

REMARKS: The diagnoses of genus and species are basically the same but we leave the genus more open to encompass possible synonyms such as *Stigmodus*. The original (WOODWARD 1892, p. 1) stated that there was a "dental crown consisting of a single, robust, solid, conical cusp", which in essence is the case, "invested with gano-dentine", which we now interpret as thin enameloid. He went on: "root large, undivided, laterally expanded, and anteroposteriorly compressed", which was true of the holotype tooth as far as he could judge from its position in the matrix (see appendix for descriptions). He concluded that *Protodus jexi* was "the earliest tooth referable to the Elasmobranchii hitherto determined, and is especially remarkable on account of the form of the root". TRAQUAIR (1893) supported WOODWARD's view based on the new material from Campbellton including for him an indisputable elasmobranch-like tooth row (here figured as Text-fig. 1h).

DESCRIPTION: There are around 65 teeth now referable to this species and two (Text-figs 1l, 2u) sit on possible jaw cartilage (see appendix for descriptions). All teeth are robust and relatively small to medium-sized, the largest being estimated as 12 mm high by 10 mm across the base. In the holotype (NHM P6538, Text-fig. 1a), shown by WOODWARD (1892, figs 1, 1a) in lateral and labial view, the crown is about 5 mm high with basal width of about 3 mm. The apical half of the crown is sharply bent linguad, the lateral margins are keeled, the labial face more convex, and with median longitudinal pair of ridges and intermediate groove. In general these grooves and ridges can be asymmetrically placed, imparting to some teeth a twisted appearance. The coronal face is smooth or very delicately striated. The labial zone below the shiny enameloid of the cusp has a pock-marked appearance with small foramina. The base below is rectangular to deeply rounded and often extends laterally

beyond the interface with the crown. The base is often embedded in the matrix but basal shape can be seen in some (e.g. Text-figs 1a, c, e, h, l). Putative pectoral spines and scales will be described elsewhere.

HISTOLOGY: WOODWARD (1892) made but did not figure thin sections (NHM P6539a, Text-fig. 3c), proving to himself that the tooth was not a crossopterygian laniary. His sections show coarser osteodentine in the base becoming more regular in the labial zone to lower cusp with only a few wider vessels and no clearly larger foramina. A section through the cusp of one of the paratypes (NMS 1897.51.21) showed orthodentine with a thin clear outer layer, interpreted here as enameloid. Further study using CT or synchrotron technology is planned.

GROSS (e.g. 1957) studied "*Protodus*" but now it is clear that all his material was from acanthodians, cf. *Nostolepis scotica* (BURROW & TURNER in press).

Broken or worn specimens of *P. jexi* allow some observations. The cusp orthodentine is seen clearly when the tip is broken. The thin enameloid layer invests most of the cusp and seems thicker on the labial surface (and more obvious in some specimens, see Text-fig. 1). Fine horizontal striae or distinct lines can sometimes be seen towards the cusp-base interface (e.g. Text-fig. 1f, o), which might reflect incremental growth or growth spurts/damage; one tooth cusp (Text-fig. 2o) has a percussion hole.

The internal structure of the base is a cancellous osteodentine with generally smaller foramina in a narrow labial zone just below the proximal cusp interface. Larger elongate foramina can be seen on the base (Text-figs 1c, 2b, c) and in NMS 1897.51.30 there is an embayment housing a foramen and two above it to the left side and a large foramen to the left of that. NBMG 3083 (Text-fig. 1c) shows the upper parts of some elongate foramina in the upper basal surface. Histological structure is seen in NMS specimens (Text-figs 1h, 2f, j, n, u, x).

DENTITION: Two main size classes of teeth have been found, those approximately 2.5-4 mm long and those 7-10+ mm long; one, NBMG 13926, might be that of a juvenile. Some cusps are high and relatively straight (Text-fig. 1, 2e, s, x) whereas others are broadly triangular and quite sigmoidal in lateral view (e.g. Text-fig. 2c); one or two are rather hook-like (Text-fig. 2g, t), the larger broken cusps being as high as 12 mm or more. The two NMS counterpart sets of four associated teeth show a presumed tooth row or Zähnreihe (Text-figs 1h, 2x) and one or two other specimens show two or three associated teeth (e.g. Text-fig. 1i, l).

Several *Protodus jexi* teeth exhibit a well-developed labial zone on the area below the cusp where there is no shiny external layer (e.g. Text-figs 1f, k, m; 21, q); this area would not have been exposed in life. Mature teeth exhibit a wide triangular cusp (e.g. Text-fig. 2c, v) and there is some variation suggesting heterodonty. Deep expanding even swollen bilobed bases occur in some (Text-fig. 2c, j, w) and the lingual view is seen in NHM P7081, similar to those of the tooth row (Text-fig. 1h).

Possible reconstruction of tooth file and dentition based especially on NMS 1897.51.38 and 39 is shown diagrammatically in Text-fig. 3a-c. In general the single cusps are sigmoidal with a shiny enameloid surface, and usually a prominent anteriomedial labial groove. The labial cusp is angular in cross section, wide, high and pointed, with a fine microornament extends short striae, not ankylosed to presumed cartilaginous jawbones. The crown invariably has a single, large wide central triangular or conical cusp, which is generally robust with no sign of lateral cusplets; it is sigmoidal in lateral view, labial surface with a central depression or groove in proximal part, pointed distally, lateral crista can be finely serrated, osteodentine in base, cusp has five-sided cross section at the base and ellipsoid at point, orthodentine in cusps, finely striated enameloid on surface of cusp extends down to interface with the base. A splayed concave area at the base of the cusp grades into the base. The crown sits on a rounded to D-shaped base, which is wider than the crown, undivided, laterally expanded, and anteroposteriorly compressed; it can be bulbous and ventrally extended sometimes giving a bilobed appearance.

We are not sure if the small and large teeth were associated in the same dentition or represent age classes. There are clear signs of moderate asymmetry to guide in building a right and left dentition. However, the heterodont variation is slight and teeth embedded in matrix so not all is clear. Possible wear patterns are seen on a few teeth (e.g. Text-fig. 2 g, j, and see below). Interestingly, unlike *Leonodus* there is no sign of a dorso-basal button or articulating device with the next tooth or any specialized extended labial or lingual structures. The bases seem to have sat side by side, in the manner which WOODWARD (1917) saw as typical of hybodonts and modern elasmobranchs. In this they are comparable also with shark embryonic teeth (e.g. SHIMADA 2002, fig. 6C), which are small, blunt and peg-like and almost acrodont in their simple position and attachment to the jaw with a symphysial tooth in the upper jaws. Others (quoted in SHIMADA 2002) have noted that early stage adult teeth in lam-

niforms have bluntly pointed crowns without distinct cutting edges, serration and/or lateral cusplets, a pattern seen in the Protodontidae. SHIMADA (2002, p. 316) explained these adaptations as guards against wounding the mother's uterus or other internal organs. The special feature of *Protodus jexi* is the apposition of the distal cusp of the alternating upper tooth against the front of the following lower fitting into the labial grooves.

FUNCTIONAL MORPHOLOGY: The cusps of *Protodus jexi* teeth are high and sharp (Text-figs 1e, f), but not extremely so as in modern stabbing shark teeth. The distal point is rounded with sharp lateral cristae. In some specimens a fine serrated edge is seen near the distal tip of the crista (Text-fig. 1h). *P. jexi* probably had a clutching-penetrating or puncturing dentition. Considering the associated teeth and the interaction structures seen on the cusps, it would seem that upper and lower dentition did come into contact, with the upper teeth fitting against the deep grooves and creating the observed wear patterns (e.g. Text-fig. 3c).

Most distinct in *P. jexi* is the presence of the prominent anteriomedial labial groove or embayment that might have functioned as the 'blood draining' groove (as in samurai swords or Bowie-type knives), seen nicely in NBMG 11983 and NHM P60645 (Text-figs 1f, n). This style of tooth supports the interpretation of the species as a predator, or alternatively an opportunistic scavenger. The robust nature of the sharp, serrate cusps also bolsters this interpretation. *Protodus jexi* would presumably have been able to attack (or scavenge on) and penetrate the armour of contemporary cephalaspids and placoderms and even *Doliodus*, other various scaled fish such as acanthodians, perhaps even young pterygotid eurypterids.

## RELATIONSHIPS

What were the earliest chondrichthyan teeth like? We now have various 'sharks' in the Silurian based on scales but no certain teeth until end Pridoli (e.g., TURNER & MILLER 2005b), a 40-Ma gap between putative scales and teeth. By earliest Devonian there are three distinct tooth patterns: the xenacanth-like *Leonodus*; then the Campbellton sharks, omalodontiform-like *Doliodus*, the latter two multicuspid; and monocuspid *Protodus*. MADER'S (1986) tentative cladogram for such early teeth placed the xenacanth-like *Leonodus* at the base, probably because it was the oldest tooth then known.

TRAQUAIR (1893) reaffirmed the chondrichthyan nature of *Protodus jexi* based on the teeth in transverse bands; in fact only one specimen seen (Text-fig. 1h, 2x) exhibits the toothrow. Spiral whorls and unsocketed Dornzähne, typical acanthodian spiny teeth, are not seen in *Protodus* as far as we can determine, although *Doliodus* does possess anterior tooth sets like tooth whorls.

*Protodus jexi* teeth with the large central cusp and laterally expanded D-shaped basal root, seem to fit the general 'cladodont' type of tooth. As noted by TURNER & *al.* (2004), it is most similar to contemporary *Celtiberina maderi* WANG, 1993 (cf. his pl. 4, figs 1a, 2a). WANG (1993, p. 95) referred *Celtiberina* to the Hybodontoidea ZANGERL, 1981 but described a large-cusped "elasmobranch" tooth, with occasional small lateral cusplets, and a thick, long, and 'kraftig' base. The cusp is massive, 'stark' linguad, and ribbed with no sharp lateral cristae seen but his specimens are somewhat worn. In his pl. 4, fig. 2, two teeth are seen joined in a row "Verband". These teeth like those of *P. jexi* might seem to be good candidates for a basal or 'stem' cladodont. However, unlike most cladodont teeth, the *P. jexi* tooth form is uniformly monocuspid, with no special labial or lingual protrusion, or any boss on the base providing an interlocking adaptation. Some other mid-Devonian taxa illustrated by DE POMEROY (1996, fig. 4 K-J) show such simplicity of monocuspid crown and a deep rounded or laterally extended base with no projections and these might also belong to the protodontidid clade.

Nor is the *Protodus jexi* tooth as splayed out labially as *Doliodus* (TURNER 2004) and other Omalodontiformes. Instead, *Protodus jexi* has a concave upper labial zone penetrated by a series of small foramina, comparable with a similar area in some cladodont teeth, and a rather bulbous lingual protrusion. IVANOV & RODINA (2004) threw doubt on the monophyletic status of omalodonts and preferred to consider a labial extension as a functional strategy in early shark teeth, and this is quite feasible. However, in *Protodus* there seems to be a unique structure with the cusp of the following tooth fitting into the embayment of the base of the one in front.

There are other possible shark candidates, however, based on older teeth. WHITEAVES (1897) described *Dendrodus arisaigensis* from the Upper Silurian (Pridoli) Knoydart or Stonehouse Formation of McDonald Brook, near Arisaig, Nova Scotia; the specimen cannot been located. GARDINER (1966) dismissed it as sarcopterygian. It might be ischnacanthiform but shows similarities in its robust triangulariform cusp and base to *Protodus*, as noted by DENISON

(1979, p. 56). Equally interesting as a candidate is the robust tooth called *Stigmodus gracilis* by BROTZEN (1934), and possibly also *Plectrodus hamatus* BROTZEN, 1934, which like *Protodus* also have a high isosceles-triangular monocusp and apparently a rectangular base although they are not well enough illustrated to be sure; DENISON (1979, fig. 35) placed these in his 'unknowns'. We tentatively refer these to the Protodontidae.

## CONCLUSIONS

*Protodus jexi* is known from one locality on the Campbellton shoreline of northern New Brunswick and represents the first chondrichthyan with predator style teeth. Given the nature of shark dentitions, the known 60 or so teeth might belong to one dentition. The paratypes and probably the syntypes include a tooth file of four associated dagger-like teeth with serrated cristae. The large subrectangular to D-shaped *Protodus* toothbase is similar and might be phylogenetically related to the cladodont type. Contemporaries *Celtiberina* and *Stigmodus* might be closely related or the similar tooth features might reflect functionality, with large laterally extended bases providing such 'protodontidid' teeth with a 'solid' root resisting movement and assisting an efficient predatory bite.

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# APPENDIX – *Protodus jexi* WOODWARD, 1892, full descriptions and measurements of teeth.

Institutional Abbreviations: Carnegie Museum, Pittsburgh, USA – CM; Geologisk Museum, Copenhagen, Denmark – GMV; Museum of Comparative Zoology, University of Harvard, Cambridge, USA – MCZ; Natural History Museum, London, UK, Fossil Fish collection – NHM P; National Museum of Scotland, Edinburgh, Scotland, UK (formerly Royal Scottish Museum, RSM) – NMS; New Brunswick Museum, Saint John, Canada – NBMG.

**NHM COLLECTION (data from 10 specimens)**

HOLOTYPE/ SYNTYPE: NHM P6538 (Text-fig. 1a), a medium-sized tooth in the round, showing lateral crista but worn; labial median groove; cusp-base interface with a distinct embayment at the base of the lingual side of the crown; basal surface is concave, ? basal foramen; by exchange, R. Damon, Nov. 1891. NB. photo PF C is actually 6538.

SYNTYPES: NHM P6539a-c: three similar teeth from Damon, Nov. 1891. Thin section (Text-fig. 3d) is c. On the slide it says that it is a 'vertical trans. sect. of the base of the tooth'. The part of the tooth shown in the thin section, which comprises part of the of the cusp plus part of the base, measures approximately 5.25 mm in height.

NHM P 6567 shadowy grey shapes to the left of the *Doliodus* toothwhorl might be *Protodus* teeth. Purchased Damon 1893.

NHM P 6568; sharp pointed shiny cusp broken in half; labial view; base in matrix. There might be a second tooth to the right. Purchased Damon 1893.

NHM P 7077; a large tooth, about 7 mm high but the distal part of the cusp appears to be embedded in the matrix, with a wide and deep labial base but flaring out to extend the base laterally; two other possible teeth bases to its upper right; this specimen needs preparation as it might be a tooth row. Purchased Damon 1893.

NHM P7081-3; this poorly preserved specimen (ht?) shows a rounded (worn?) cusp on a deep lobed base possibly bilobed apparently in lingual view.

NHM P7085; doubtfully - may all be *Doliodus*, also smaller in size?

NHM P59030; medium-sized tooth in labial view with sharp but worn cusp and a distinct embayment at the cusp-labial skirt interface; massive laterally expanded D-shaped base.

NHM P59043; Not seen.

NHM P59054; small-sized tooth in labial view with very shiny cusp with one distinct line near the lower edge of the enameloid (possible incremental or slowing of growth line or trauma); labial skirt and top of expanding base, especially to left, preserved showing osteodentine.

NHM P60645; small short very shiny cusp with blunt rounded tip on less distinct rounded base; associated with spines.

**NMS PARATYPES**

NMS 1897.51.14: large tooth, cusp nearly 10 mm high with broken tip so over 10 mm high preserved in labial view with the cusp broken off about midway. The median labial depression is shallow. There are horizontal striae on the labial surface. The surface of the cusp is severely marked with what appear to be serrated cuts. The large laterally expanded base needs preparing.

NMS 1897.51.15: large tooth, about 7 mm total height, slightly asymmetric with a good sigmoidal curve seen in lateral view.

NMS 1897.51.16: large tooth with an 8 mm high cusp as seen in labial view, wide at the base and complete cusp triangular, with deep grooves to either side of a central part (Text-fig. 3f). There is a labial concavity (skirt). As seen from this tooth, the extension of the base is labiad at the base of the cusp in the enameloid. There are growth lines and swells to either side. In lateral view (or second tooth) the sigmoidal nature of the cusp can be seen with the base extending some mm at an angle of 45 degrees. There is a sharp lateral crista and some undulations on the labial cusp surface, whereas the lingual surface is smoother and with fine striae.

NMS 1897.51.17: small tooth about 3-4 mm high, preserved in labio-lateral view (or else slightly asymmetrical curving to the left). Labial ridges and a

slight concavity are seen. The distal cusp tip is broken. The base is not fully exposed but a wide right extension is apparent.

NMS 1897.51.18: high tooth with large high-angled sharp cusp about 7-8 mm on a wide apparently D-shaped base, although the lateral extensions are not exposed.

NMS 1897.51.19: large tooth probably over 10 mm and possibly 12 high as the tip is broken. The labial view exhibits a wide triangular depression and steep side. The enameloid surface is irregular at the cusp-base interface. The base is wide about 8 mm across, and splayed bilobed with the right side lobe broken so that the internal structure of the osteodentine can be seen.

NMS 1897.51.20: small tooth about 3 mm high preserved in labial view. The cusp is assymmetrical appearing to curve to the left, with the tip broken off. The labial surface is well grooved with a deep rounded central, almost U-shaped, groove. The base is hardly exposed in the sediment.

NMS 1897.51.21 used for histological section.

NMS 1897.51.22: large triangular high tooth about 7 – 8 mm total height with a well preserved tip showing a labial angled surface. A wide concave labial proximal embayment flanked by striae and ridges. There is a well pronounced labial skirt with the lateral extensions of the base not well exposed.

NMS 1897.51.23: large triangular tooth 8 mm total height, 4 mm across lateral width, well preserved with a deep narrow labial groove and further striae. The cusp is high angled but slightly sigmoidal in lateral view with a distinct labial bulge mid-way up the crown. The lateral crista is pronounced on the right and many lingual striae can be seen. The enameloid edge is crenulated at the base of the cusp. The labial skirt is pronounced and the base is wide and bilobed, the left side not fully exposed and the internal osteodentine exhibited on the right.

NMS 1897.51.24: small 'battered' looking tooth (or perhaps head or other denticle) only about 2.5 mm high preserved in labial view, distal tip broken. The cusp is more blade-like than the others although it still possesses a median labial depression. The base is deep but not so wide. Two large concavities (vascular or pulp openings) can be seen on the basal rim.

NMS 1897.51.25: small tooth preserved in labial view with the cusp broken off about half way. It is well grooved on the labial surface with a series of ridges beside the central depression. The base is expanded laterally but not fully exposed.

NMS 1897.51.26: is a medium-sized tooth about 3-4 mm high preserved in labial view showing mainly a high triangular cusp and almost no base, only the upper part of the basal skirt. The labial surface has a very wide median depression flanked by ridges and striae.

NMS 1897.51.27: small tooth about 2.5 mm high preserved in labial view but not well preserved; it looks very worn. The bottom part of the cusp only is seen with several striae. The labial skirt exhibits a few small foramina but the base is not well exposed.

NMS 1897.51.28: small badly preserved tooth (or perhaps head or other denticle) 2-3 mm high, preserved in labial view, with only the basal half of the cusp in view, tip broken, and a small segment of labial skirt on the left. There is a depression in the middle of the cusp just right of the median labial groove with a jagged edge, which might be a depressed puncture mark.

NMS 1897.51.29: small tooth about 3 mm high by 1.5 mm across preserved base, in lateral view (or is it asymmetrical). The cusp is broken at the tip and has a strong lateral crista on the right side and fine lingual striae apparent. The right lateral expansion or lingula base is exposed.

NMS 1897.51.30a: two medium-sized teeth, wider and shorter than most about 6-7 mm high and preserved (b) in lateral view, with cusps slightly curved. Specimen is slightly asymmetrical in the cusp with the tip broken off; it has a wide labial skirt and a deep base with the right lobed extension exposed. Specimen b has sharp cristae placed well linguad but the flatter lingual surface is striated, the labial surface has depressions and ridges. The bulbous base is extended forward labiad.

NMS 1897.51.31: tooth about 3-4 mm high, cusp only preserved in labial view, but with only the cusp exposed. The base is covered with sediment on the sides.

NMS 1897.51.32: is a large tooth about 7-8 mm high and 4-5 mm across, in labio-lateral view to the right

with a curved cusp and a well developed median depression with two grooves. The labial skirt is clear and the base laterally expanded and rounded.

NMS 1897.51. 33. 1, 2: exhibits two teeth, one larger than the other, which is quite small, both curved. 33.1 is abt 4 mm high but has a broken tip; 33.2 about 3-4 mm high but with broken tip.

NMS 1897.51.34: small badly preserved tooth preserved in labial or lingual view, with only the basal half of the cusp in view (cusp broken off halfway) and the upper segment of the laterally expanded labial base. The cusp shows three clear striae (may be lingual).

NMS 1897.51.35: small tooth with a robust wide triangular cusp about 3 mm high by 3 mm across preserved base. The median depression is wide and concave with prominent lateral ridges. The base appears to be bilobed and the internal structure can be seen on the broken surface of the left lobe of the base; the right side is not well exposed. Just to the left of the distal tip of the tooth is a band of black material that might be cartilage or plant.

NMS 1897.51.36: large mature tooth preserved only as a wide triangular cusp about 8-9 mm high seen in labial view. The median depression is wide, double and concave with prominent ridges.

NMS 1897.51.37: a) large mature tooth with a wide triangular cusp preserved in labial view. The median depression is wide and concave with prominent ridges. A deep expanding base is not fully exposed but is lobed to the left; b-c); two more teeth were found on the obverse.

NMS 1897.51.38a-c, d?: shows four teeth, long and curved (Text-fig. 3b). The paratype counterpart 1897.51.38 + 39 (described below) is an associated dentition, a tooth row or Zahnreihe of four teeth. NMS 1897.51.38 shows three teeth with the fourth to anterior (labiad) in natural mold, about a 1 cm span?, cusp of second broken above base. Seen cross-section in 3; the outline of the base is rectangular and the cusp is seen at the basal cross section, 4 likewise. The basal widths increase linguad in the tooth row so that base four is almost twice the width of one and even 2.

NMS 1897.51.39a-d: counterpart of NMS 1897.51.38. There are four teeth en echelon, large pyramidal to rectangular bases, touching each other (Text-fig. 3c, d). The tooth cusp is large and single, with fine lateral crista with very fine serrations. Cusp 1-3 in mould only, but basal part of cusp with enameloid is present in 1-2. Basal bony tissue seen well in 4 as the base is broken across the middle. Basal extensions are seen to the right hand side. A possible reconstruction of the tooth file is illustrated in lateral view (Text-fig. 3e ).

**NEW MATERIAL (NBMG) COLLECTED BY RM SINCE 2001** (except NBMG 3083) (16 specimens)

NBMG 3083: large tooth 9+ mm high and 9+ mm across wide triangular base exhibiting fine microornament striations (Text-fig. 1d).

NBMG 11983: large tooth with a 10+ mm high and 9 mm across wide triangular base exhibiting fine microornament striations (Text-fig. 1f).

NBMG 12402: shows what appears to be two teeth en echelon possibly sitting on a narrow cartilaginous jawbone cartilage, and associated with multi-hooked spine (which might also be that of *Doliodus*). Tooth 7 mm high and 6 mm across wide triangular base, cusp constricted near base.

NBMG 13918: small tooth with curved cusp, 7 mm high and about 5 mm wide across base.

NBMG 13919: poorly preserved curved tooth more than 7 mm high, cusp broken cusp and base buried.

NBMG 13920: triangular tooth, partly buried, 7+ mm high and 5+ mm wide across base.

NBMG 13922: triangular tooth, partly buried, 8+ mm high and 3+ mm wide across base.

NBMG 13923: tooth 6+ mm high and 4+ mm across wide triangular base, cusp constricted at base.

NBMG 13924: tooth 5 mm high and 3+ mm across wide triangular base, cusp constricted near base.

NBMG 13927: is a large tooth with a triangular cusp 9 mm high and 8 mm across a wide triangular base.

NBMG 13928: two teeth on slab, one tooth with a triangular cusp 6 mm high and 5 mm across the base, and one tooth 5+ mm high and 5 mm across wide triangular base, cusp constricted at base.

NBMG 13929: two teeth on slab, one tooth with a curved cusp 9 mm high and 5 mm across the base, and one partly buried tooth with 5+ mm high and 2+ mm wide.

NBMG 13930: one partly buried tooth with 3+ mm high and 5 mm wide.

NBMG 13933: small fragment of cusp, not measured

NBMG 14506: small tooth with curved cusp, 5 mm high and about 3 mm wide across base.

NBMG 14507: tooth 7 mm high and 5+ mm across wide triangular base, cusp constricted near base.

**OTHER MUSEUM COLLECTIONS** (7-9 specimens)

CM 5141 (1-2): two specimens (Text-fig. 1j, k) (probably acquired from Damon), triangular cusp, one about 7 mm high and 5+ mm wide across the base, the other 5 mm high and 5 mm across the base.

MCZ 548 ex-Damon;

MCZ 8505 isolated tooth.

NB 22-11-07, medium sized tooth with cusp about 3.5 cm and total height about 6.5; lateral crista clear but not sharp; poorly preserved base showing osteodentine and expanding laterally and linguad.

GMV2007-16, two or three possible teeth (C. Burrow, pers. comm.).

NB. This appendix will be updated when possible. Please inform the authors of any more specimens in collections worldwide.