Fish and tetrapod communities across a marine to brackish salinity gradient in the

Pennsylvanian (early Moscovian) Minto Formation of New Brunswick, Canada, and

their palaeoecological and palaeogeographic implications

by AODHÁN Ó GOGÁIN[1], HOWARD J. FALCON-LANG[2], DAVID K. CARPENTER[3],

RANDALL F. MILLER[4], MICHAEL J. BENTON[1], PEIR K. PUFAHL[5], MARCELLO

RUTA[6], THOMAS DAVIES[1], STEVEN J. HINDS[7] *and* MATTHEW R. STIMSON[4, 7]

[1] School of Earth Sciences, University of Bristol, Bristol, BS8 1RJ, UK; e-mail:

ao14989.2014@my.bristol.ac.uk; mike.benton@bristol.ac.uk; thomas.davies@bristol.ac.uk

[2] Department of Earth Sciences, Royal Holloway, Egham, Surrey, TW20 0EX, UK; e-mail:

h.falcon-lang@es.rhul.ac.uk

[3] Ocean and Earth Science, National Oceanography Centre Southampton, University of

Southampton Waterfront Campus, European Way, Southampton, SO14 3ZH, UK; e-mail:

dkc1g12@soton.ac.uk

[4] Natural Science Department, New Brunswick Museum, 277 Douglas Avenue, Saint John,

New Brunswick, E2K 1E5, Canada; e-mail: Randall.Miller@nbm-mnb.ca,

mstimson29@gmail.com

[5] Department of Earth and Environmental Science, Acadia University, Wolfville, Nova

Scotia, B4P 2R6, Canada; e-mail: peir.pufahl@acadiau.ca

[6] ~~Department of Earth~~School of Life Sciences, University of Lincoln, ~~Riseholme Hall~~Green

Lane, ~~Riseholme Park,~~Lincoln

~~Lincolnshire,~~ LN6~~2~~ 7D2~~LG~~, UK; e-mail: mruta@lincoln.ac.uk

[7] New Brunswick Department of Energy and Mines, Geological Surveys Branch, Fredericton,

New Brunswick, E3B 5H1, Canada; e-mail: Steven.Hinds@gnb.ca

26

2
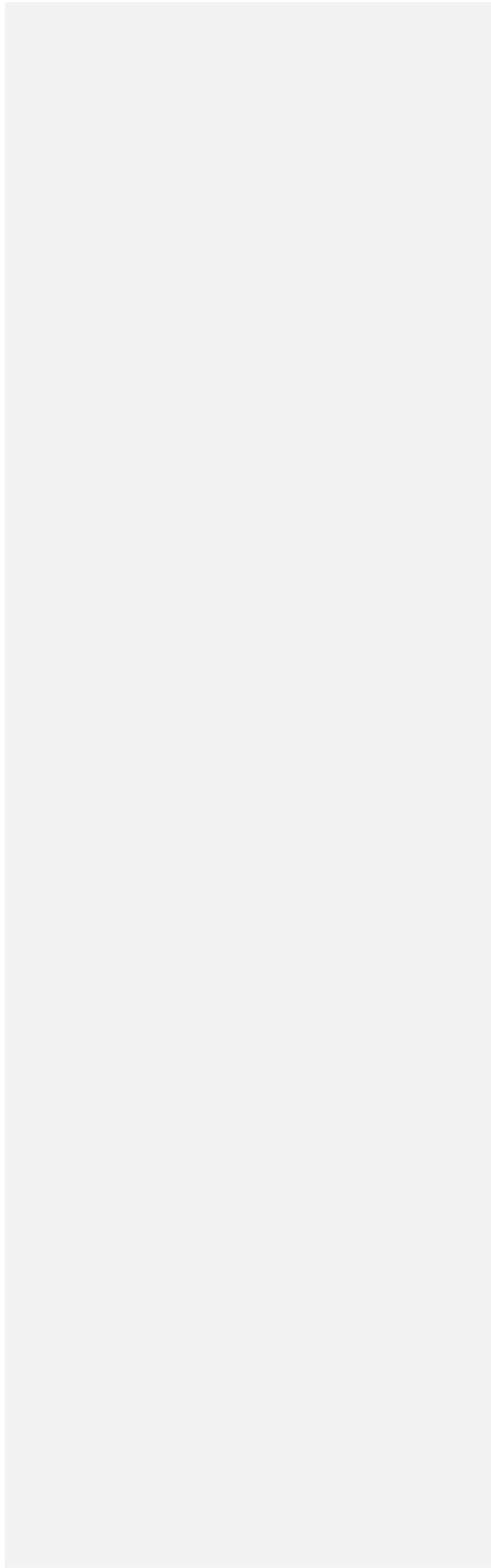
Abstract: Fishes rapidly diversified into brackish coastal environments in Pennsylvanian times, and here we report new assemblages from New Brunswick, Canada, which shed light on this evolutionary event. Fish fossils from the early Moscovian Minto Formation include chondrichthyans (xenacanthids, and the enigmatic *Ageleodus*), acanthodians (gyracanthids and acanthodiforms), sarcopterygians (rhizodontids, megalichthyids, rhizodopsids, and dipnoans), and actinopterygians. A key finding is that parautochthonous remains are preserved across a palaeosalinity gradient, with diversity (measured by the Simpson Index) declining from open marine environments, through brackish embayments, and reaching a nadir in tidal estuaries. Chondrichthyans were dominant across the entire palaeosalinity spectrum, comprising 70.5 % of fossils – a facies distribution that demonstrates a euryhaline mode of life. One large predatory chondrichthyan, *Orthacanthus*, appears to have practised filial cannibalism in coastal nurseries because its distinctive heteropolar coprolites are packed with juvenile xenacanthid teeth. In contrast, most other fishes are less common in coastal brackish waters. While still likely euryhaline, these organisms perhaps had less effective osmoregulation in brackish water, or were out-competed by chondrichthyans. The findings of this paper bring closure to a long-running debate about the ecology of Carboniferous fishes. The cosmopolitan biogeography of many fish genera strongly indicates marine-based dispersal, while strontium isotopic data suggest these same fish were exposed, at times, to continental water bodies. This apparent conflict is resolved by the demonstration of widespread euryhalinity. +TETRAPOD MATERIAL

Key words: Carboniferous, euryhaline, endemism, tidal, brackish, estuary

INVASION of brackish coastal environments was a critical transitional phase in the

Palaeozoic colonisation of continental freshwater ecospace (Buatois *et al.* 1998; Miller and

Labandeira 2002; Park and Gierlowski-Kordesch 2007; Falcon-Lang *et al.* 2015*a*).

Adaptation to lower and more variably saline (non-marine) water bodies may have

commenced as early as the Ordovician (MacNaughton *et al.* 2002), with the abundance and

complexity of brackish ecosystems steadily increasing through the Silurian–Carboniferous

(Buatois *et al.* 2005). This pattern of colonisation closely parallels the Ordovician rise of

hepatophytes, and the Silurian-Carboniferous diversification of tracheophytes (Gensel and

Edwards 2001), implying the complex co-evolution of land plants, terrestrial-marine nutrient

export patterns (Algeo and Scheckler 1998), and the carrying capacity of brackish (non-

marine) coastal environments (Prescott *et al.* 2014).

Recent studies have identified a "mid-Carboniferous diversification event" when

infiltration into brackish coastal settings appears to have sharply accelerated (Davies and

Gibling 2013; Falcon-Lang *et al.* 2015*a*; Minter *et al.* 2016). This event commenced in the

Serupukhovian and received its acme in the Bashkirian-Moscovian stages (Falcon-Lang *et al.*

2015*a*). An intriguing characteristic of this episode was the apparent widespread adoption of

a euryhaline habit amongst organisms as diverse as microconchids, ostracodes, xiphosurans

and fish (Anderson and Shuster 2003; Carpenter *et al.* 2011; Bennett *et al.* 2012; Gierlowski-

Kordesch and Cassle 2015). Euryhaline animals are relatively rare in modern ecosystems

(Edwards and Marshall 2013; McCormick *et al.* 2013), and their dominance in Carboniferous

times suggests marine communities converged on similar osmoregulatory strategies in order

to utilise empty non-marine coastal ecospace for feeding and breeding (Williams *et al.* 2006;

Carpenter *et al.* 2014), prior to the widespread colonisation of freshwater tracts further inland.

The mid-Carboniferous diversification event coincided with a sharp growth of

Gondwanan ice sheets and the onset of significant Milankovitch-driven glacio-eustatic

78   fluctuations (Fielding *et al.* 2008; Montañez and Poulsen 2013). These marine transgressions

79   with magnitudes of up to 120 m (Rygel *et al.* 2008) repeatedly flooded continental margins,

80   creating extensive epicontinental microtidal seaways (Wells *et al.* 2005), whose salinity

81   slowly decreased in a landward direction over many hundreds of kilometres (Falcon-Lang

82   2005; Falcon-Lang *et al.* 2015*b*), similar to the present-day Baltic Sea (Andersson *et al.* 1992,

83   1994). This palaeo-oceanographic context probably provided optimum conditions for

84   brackish colonisation, and Quaternary analogues have demonstrated that osmoregulatory

85   adaptation to such short-term brackish incursions is plausible over Milankovitch timescales of

86   as little as 10,000 years (Lee and Bell 1999).

87   Much recent attention has been given to the apparent dominance of a euryhaline mode

88   of life amongst mid-Carboniferous fish communities (Schultze 2009; Carpenter *et al.* 2011,

89   2014, 2015). However, consensus regarding ecology is currently lacking, with some

90   researchers arguing on palaeogeographic, sedimentological and geochemical grounds that fish

91   taxa, especially xenacanthid sharks (Masson and Rust 1984), may have been obligate

92   freshwater organisms (Štamberg and Zajíc 2008; Fischer *et al.* 2011, 2013; Montañez and

93   Cecil 2013). In this paper, we describe a new fish fauna from the Carboniferous

94   (Pennsylvanian) of New Brunswick, Canada (Fig. 1A), and demonstrate – based on

95   independent indicators of palaeo-salinity – that fish taxa existed across a brackish to marine

96   gradient, and that communities must therefore have been euryhaline. We discuss how these

97   new findings improve understanding of Carboniferous fish ecology and the mid-

98   Carboniferous diversification of non-marine ecosystems in particular.

99   +REVISE FOR TETRAPOD STORY

100

101   **GEOLOGICAL CONTEXT**

102 The fish fossils reported here were obtained from opencast mine sites (now reclaimed) within

103 the Minto Coalfield, Queens County, New Brunswick, Canada (Fig. 1A–C). The rocks of the

104 Minto Coalfield are of considerable historical interest, having been the first place in North

105 America where coal was mined, beginning in 1639, and they are even mentioned in a 1667

106 entry of Samuel Pepys' famous diary (Smith 1989; Falcon-Lang 2009; Quann *et al.* 2010).

107

108 *Stratigraphy, age and basin analysis*

109 Rocks of the Minto Coalfield belong to the Pennsylvanian Minto Formation (*sensu* St Peter

110 and Johnson 2009), the lowest unit of the Pictou Group. They were deposited on the New

111 Brunswick Platform (Fig. 1B-C), a stable cratonic region that lay to the north of the oblique

112 collisional zone between Laurasia and Gondwana (Gibling *et al.* 2008). Based on combined

113 megafloral and palynofloral biostratigraphy, the Minto Formation is thought to be latest

114 Duckmantian to Bolsovian in age (Hacquebard and Barss 1970; St Peter 1997, 2000), with

115 the economically important Minto Coal specifically dated as early Bolsovian (Kalkreuth *et al.*

116 2000). Radiometric ages recently obtained from immediately below and above the Aegiranum

117 Marine Band, which marks the Duckmantian–Bolsovian [boundary?] in western Europe

118 (Pointon *et al.* 2012; Waters and Condon 2012), suggest an age of c. 314 Ma for this

119 boundary. The Minto Formation therefore correlates with the early part of the Moscovian

120 global stage (Peterson 2011; Richards 2013; Fig. 2A).

121   Within the Minto Coalfield, sediments of the Minto Formation were deposited

122 unconformably over the top of basement rocks of Mississippian age and older, as the cratonic

123 New Brunswick Platform underwent thermal subsidence (Gibling *et al.* 2008; Fig. 2B).

124 Extensive borehole arrays indicate that this basal unconformity is marked by a major silcrete

125 paleosol, up to 9 m thick in places (Sullivan 1981; St Peter 2000), which mantles the

126 basement complex and indicates seasonally-dry climate weathering over the preceding

several million years of depositional hiatus (St Peter and Johnson 2009). In the course of this

lengthy episode of landscape degradation, a NE-SW-trending valley system, c. 16 km wide,

was cut into the basement, forming an erosional 'container' (depocentre) in which younger

sediments of the Minto Formation accumulated (Hacquebard and Barss 1970).

This bedrock palaeovalley was bordered on either side by slates and lavas that formed

subdued topographic highs with a palaeo-elevation of a few tens of metres above base level

(Hacquebard and Barss 1970; Gray *et al.* 2012; Fig. 3A). Two lines of evidence suggest that

the valley drained towards the southwest (Hacquebard and Barss 1970): (1) the thickness of

the lower part of the formation, as measured from the basement contact to the base of the

Minto Coal (a prominent chronostratigraphic marker bed) gradually increases from c. 15 m in

northeast to > 90 m in the southwest (Fig. 3A), implying that the basin deepened towards the

southwest, and sediment progressively onlapped towards the northeast; and (2) NE-SW-

orientated ribbons of channelized sandstone, 1–1.5 km wide, in the 'roof rock' of the Minto

Coal, fine towards the southwest (Fig. 3B) and suggest sediment transport in that direction.

We note, however, that this inferred palaeoflow direction opposes regional patterns of

sediment dispersal, which are directed towards the ENE (van der Poll 1973; Gibling *et al.*

1992). This suggests that either drainage in the Minto Coalfield was strongly influenced by

local bedrock topography, or that palaeoflow inferences based on grain size and isopachytes

are incorrect. More reliable indicators of palaeoflow indicators, such as cross-bed arrays, have

not been obtained to date.

Palaeoenvironments

Despite its long history of geological study (Gesner 1841; Robb 1850; Bailey and Matthew

1873), there have been no comprehensive studies of the sedimentary facies of the Minto

Formation (St Peter 2000; Clark 2004; St Peter and Johnson 2009). Three units are generally

152 recognised, and their lithologies are described below, based on our studies of borehole cores

153 (DH62-1 to 3) accessioned at the New Brunswick Department of Energy and Mines,

154 Geological Surveys Branch, Fredericton (Fig. 4A).

155   The lowermost unit, up to 60 m thick (uppermost part only is shown in Fig. 4A),

156 comprises quartz pebble and intraclast conglomerate, fine- to very coarse-grained trough

157 cross-bedded sandstone, and grey siltstone arranged in fining-upward successions. These beds

158 resemble the broadly coeval South Bar Formation of Nova Scotia, which formed under

159 braided fluvial conditions (Rust and Gibling 1990), and the Waddens Cove Formation of

160 Nova Scotia, which show similar silicrete paleosols (Gibling and Rust 1992). The beds are

161 interpreted as the fluvial channel deposits of a poorly drained coastal plain.

162   The middle unit, up to 15 m thick (Fig. 4A), comprises grey laminated shale with

163 distinctive 'pin strip' laminations of very fine-grained to fine-grained sandstone. Sedimentary

164 structures include ripple cross-lamination showing mud drape pairs, flaser bedding, and

165 symmetrical ripples (Fig. 4B, C). At one level is developed the < 0.8 m thick Minto Coal,

166 underlain by a seat earth, 1 m thick (rooted bleached palaeosol). These beds resemble those of

167 the broadly coeval Malagash Formation of Nova Scotia, interpreted as tidal deposits (Naylor

168 *et al.* 1998; Costain 2000), with the coal being formed in a calamite-dominated coastal peat

169 mire (Kalkreuth *et al.* 2000). Proximity of the peat mire to an open brackish-marine

170 embayment is supported by the relatively high (5–9%) sulphur content of the Minto Coal,

171 which increases towards the southwest and the basin centre (Fig. 3A; Hacquebard and Barss

172 1970). Sandstone ribbons, up to 1.5 km wide, that have been mapped in the succession

173 overlying the Minto Coal, and locally 'wash out' the coal (Fig. 3B) may represent incised

174 valleys, flooded to form tidal estuaries; however, this interpretation cannot be confirmed

175 because the boreholes do not intersect this facies.

176　　　　The uppermost unit, c. 100 m thick (lowermost part only shown in Fig. 4A),

177　comprises units of pebbly sandstone, thin sandstone sheets, and relatively thick intervals of

178　massive, red mudrock, locally showing slickensides and small, scattered carbonate nodules.

179　These beds were formerly assigned to the Hurley Creek Formation, but were amalgamated

180　into the Minto Formation by St Peter (2000), based on regional mapping. The succession

181　probably represents the deposits of a relatively well-drained alluvial plain (cf. Davies and

182　Gibling 2003), but borehole characteristics are insufficient for detailed analysis.

183

184　*Fish- and tetrapod-bearing lithologies*

185　Fish and tetrapod assemblages reported here were not collected *in situ* within a logged

186　succession, but obtained from the tip heap piles of opencast mines exploiting the Minto Coal

187　at relatively shallow depth, and must have come from the overburden. A careful review of all

188　fossiliferous specimens shows that the fossils occur in four different lithologies, and can be

189　related to the logged section, with varying degrees of confidence. All fossils are inferred to

190　have come from the middle unit (tidal/estuarine facies), as shown on Fig. 4A.

191　　　　Lithology 1 comprises a medium grey limestone bed, up to 24 mm thick, which shows

192　abundant fish skeletal fragments throughout. Although no macroscopic fossils are visible in

193　hand specimen, except spirorbiform microconchids, in petrographic thin section, the rock

194　comprises a wackestone containing scattered bioclasts of punctate brachiopods (Fig. 5A, D),

195　fish bones (Fig. 5B), ostracodes (Fig. 5C), putative sponge spicules (Fig. 5D), spirorbiform

196　microconchids (Fig. 5E), echinoid spines (Fig. 5F), and putative forams (Fig. 5G). An early

197　diagenetic phase of framboidal pyrite (Fig. 5F) commonly infills voids, followed by a later

198　phase of sparry calcite (Fig. 5C, E, G). The invertebrate assemblage, together with the

199　presence of framboidal pyrite, indicates deposition under stenohaline marine conditions

200　(Maliva 1989; Tucker and Wright 1990; Schieber 2002). The high micrite content indicates

201 rather quiet bottom waters, and the absence of siliciclastic grains suggests that the marine

202 embayment was relatively extensive (Gibling and Kalreuth 1991). Similar marine limestones

203 have been documented elsewhere in the Maritimes Basin, in the Pennsylvanian (Langsettian)

204 Joggins Formation (Grey *et al.* 2011) and Tynemouth Creek Formation (Falcon-Lang *et al.*

205 2015*a*).

206   Lithology 2 comprises dark grey, bituminous limestone, up to 28 mm thick, showing

207 abundant bivalve fragments, spirorbiform microconchids, and a large quantity of comminuted

208 fossil plant debris. In petrographic thin section, these lithologies comprise bivalve-dominated

209 packstone with minimal micrite matrix (Fig. 5H, I), and rare fish fragments (Fig. 5I). The

210 only recognisable invertebrates are the bivalve *Naiadites*, which may be locally preserved

211 intact and articulated (Fig. 6A), but more commonly is highly fragmented, and spirorbiform

212 microconchids. Three subtypes are recognised: Lithology 2a lacking microconchids,

213 Lithology 2b with abundant microconchids (Fig. 6B), and Lithology 2c with few

214 microconchids but prominent fish fragments in winnowed lenses. Calver (1968) interpreted

215 *Naiadites* as a brackish bivalve, and it is known also from identical lithologies in the

216 Pennsylvanian Joggins, Port Hood, Parrsboro, and Sydney Mines formations of nearby Nova

217 Scotia, where they have been interpreted as the deposits of extensive brackish embayments

218 (Gibling and Kalkreuth 1991; Calder 1998). The environment was probably shallow and

219 wave-agitated given that micrite matrix has largely been winnowed away and bivalves are

220 commonly fragmented (Davies and Gibling 2003; Falcon-Lang 2005; Carpenter *et al.* 2015).

221   Neither limestone lithology was observed in the logged boreholes. However, in the

222 Joggins Formation of Nova Scotia, such thin limestone beds form the roof of coal seams

223 (Davies and Gibling 2003; Falcon-Lang 2005), and represent brackish-marine flooding

224 surfaces, possibly triggered by glacio-eustatic or tectonic factors (Falcon-Lang *et al.* 2006). In

225 all the boreholes that we studied, the interval containing the Minto Coal had been removed

226   for coal petrographic analysis, and possibly with it, evidence for the stratigraphic position of

227   overlying limestone beds. Clearly, the two limestone lithologies represent open water facies,

228   and the presence of comminuted plant debris in Lithology 2 suggests proximity to coastal

229   vegetation. Based on fossil content and lithology, we infer that Lithology 1 was formed in the

230   deepest part of the marine embayment and Lithology 2 represents the shallow coastal

231   embayed zone where fluvial discharge led to lower and most variable salinities.

232   Lithology 3 comprises thinly bedded, pale grey siltstone to very fine-grained

233   sandstone showing symmetrical ripple marks with mud drapes (Fig. 7A). In thin section, it

234   shows a poorly developed micritic matrix. Fish skeletal fragments are particularly

235   concentrated within the mud-rich ripple troughs (Fig. 7B). Lithology 4 comprises a medium-

236   to dark-grey, laminated mudstone, with thin partings of very fine-grained sandstone, and

237   isolated fish fragments. These latter two lithologies are identical to those found in the

238   tidal/estuarine facies reported from the borehole core overlying the Minto Coal, and therefore

239   can be directly related to the logged succession with a high degree of confidence. These

240   clastic beds probably represent the most proximal of the fossiliferous lithologies, probably

241   deposited within a tidal estuary developed on the coast of the brackish-marine epicontinental

242   sea represented by the limestone beds.

243

244   **MATERIAL AND METHODS**

245   All fossil material reported here was obtained by 'surface prospecting' on weathered tip heaps

246   adjacent to back-filled opencast coal mines within the Minto Coalfield (Fig. 8), and no

247   material was directly obtained in a sedimentary context. Almost all specimens were collected

248   from either Iron Bound Cove (Latitude 46°08.67'N; Longitude 65°58.10'W) (404 specimens)

249   or Coal Creek (Latitude 46°06.09'N; Longitude 65°53.39'W) (60 specimens + 230 more with

250   indet.) on the Northeast Arm of Grand Lake, c. 10 km NE of Minto, Queens County (Fig. 1B,

C). A small collection (28 specimens) was also obtained from unrecorded locations in the Minto Coalfield.

Collection history

The fossil material reported here was collected in four phases. Prior to 1988, William H. Forbes obtained a few specimens without detailed locality data (Miller and Forbes 2001). A much larger collection was obtained by Michael Lee between c. 1991 and 2000 at Iron Bound Cove and Coal Creek. Further collections were made at the Iron Bound Cove site by Michael Lee in collaboration with one of us (RFM) in 2002, and a final phase of collecting was undertaken by three of us (AÓG, RFM, MRS) from the same locality in 2015.

Specimen preparation

Fossils visible on bedding surfaces were prepared through a combination of mechanical and chemical removal of surrounding matrix. Mechanical preparation was by means of a pin-vice, assorted fine-tipped brushes, and tweezers. Where the matrix was too hard for this to work, specimens were immersed in a 5% acetic acid solution, buffered with calcium acetate, following the approach of Jeppsson *et al.* (1985). To reduce the risk of fracture and to provide a barrier against acid attack, fossil material was lightly coated with a weak, ethanol-based contact adhesive ('Mowital') before acid digestion.

Specimen imaging

Prepared specimens were photographed with a Nikon D700 digital SLR camera with a Nikon 60 mm macro lens. Other specimens were photographed using a Panasonic Lumix DMC-ZS3 digital camera or a Canon Eos 40D digital camera using a Canon Ultrasonic 100mm macro

275 lens or mounted on a Leica MS5 microscope. Figures were prepared with Adobe Photoshop

276 Illustrator in Creative Suite 5.

277

278 *Specimens and museum repository*

279 Fossil specimens are accessioned as follows: NBMG, New Brunswick Museum (Geology),

280 Saint John, New Brunswick, Canada.

281

282 **SYSTEMATIC PALAEONTOLOGY**

283 A comprehensive review of 492 rock specimens containing c. 2462 individual fish skeletal

284 fragments in the NBMG collections from the Minto Formation is given in the supplementary

285 material (see Appendix S1). Miller (1999) published a preliminary list of taxa known up to

286 that date, but no detailed study of the material has been undertaken hitherto. We present the

287 materials in the sequence Chondrichthyes, Sarcopterygii, Actinopterygii (Table 1).

288

289   Class CHONDRICHTHYES Huxley, 1880

290   Subclass ELASMOBRANCHII Bonaparte, 1838

291   Superorder XENACANTHIMORPHA Nelson, 1976

292   Order XENACANTHIFORMES Berg, 1937

293   Family DIPLODOSELACHIDAE Dick, 1981

294   Genus *ORTHACANTHUS* Agassiz, 1843*a*

295 *Type species. Orthacanthus cylindricus* Agassiz, 1843*a*

296   *Orthacanthus compressus* Newberry, 1856

297   Figure 9A–D

298 *Material.* 71 specimens bearing isolated teeth (NBMG 9948, 10740 (juvenile specimen

299 attached to *Ctenodus* tooth plate), 10746–10748, 10757, 14953–14965, 14967–14968,

300 14983–14984, 14991–14993, 14996, 15823, 15825, 15832–15834, 15836, 15838, 15841,

301 15843, 15846–15847, 15849, 15902–15903, 15905–15910, 15916, 16088, 16090, 16093,

302 16095, 19614–19626, 19850, 19852–19854, 19856).

303 *Diagnosis.* Teeth bi- or tricuspid, with two lateral cusps flanking a median cusp in tricuspid

304 teeth. Where present, the median cusp is smaller than the lateral cusps. Carinae may be

305 present on the edges of the lateral cusps. Tooth base is thin with a round to oval shape. A

306 coronal button is present which does not contact any cusps. A median foramen is present on

307 the labial side of the coronal button. A basal tubercle may be present, which extends in a

308 labial direction and has an oval shape.

309 *Description.* Teeth range in height, as measured from the basal surface to the apex of the

310 largest cusp, from 0.5 to 11.0 mm (Fig. 10A). In larger teeth (> 1 mm) one lateral cusp is

311 typically larger than the other with both showing a degree of lateral divergence; the 'major

312 cusp' tends to diverge more than the 'minor cusps' (Fig. 9A–C), with some 'minor cusps'

313 having near vertical orientations. Lateral cusps have a lanceolate cross section. Carinae are

314 present on lateral cusps ≥ 1 mm. Serration is absent from all specimens. Median cusps,

315 although present in the majority of specimens, are absent in several teeth. The median cusps

316 of teeth > 0.5 mm high are on average less than 1/3 the height of associated lateral cusps,

317 whereas the median cusps of teeth ≤ 0.5 mm high are roughly the same height as the lateral

318 cusps. A median foramen is present in all specimens. The shape of the coronal button is

319 variable, and may be rounded, oval or heart-shaped (Fig. 9D), and oval coronal buttons are

320 elongated along the labial-lingual axis. Lingual to the coronal button are 1–4 nutritive

321 foramina except in one specimen where the button is absent; the precise placement of the

322 nutritive foramina also varies between teeth. The bases of the teeth vary in shape from

circular to oval and have a 'scarred' appearance. Oval bases may be either elongated along
the labial-lingual axis or along the lateral axis. Base thickness shows a positive linear
correlation with base length and tooth height ($R^2 = 0.8132$, 0.816 respectively). A convex
basal tubercle is present in some specimens and forms a bulbous shape, which protrudes
beyond the labial margin of the base.

Remarks. Tooth size is unimodal (Fig. 10A), suggesting we have a single population and a
single species. Assigning small teeth and teeth which lack serration to the genus
Orthacanthus has been argued against by Hampe (1988). Johnson (1999), on the other hand,
shows that *Orthacanthus* teeth can lack serration and have small sizes. It is difficult to
distinguish *Orthacanthus compressus* from *Orthacanthus texensis*; *O. texensis* has been ruled
out as a possible identity here, as teeth of this species typically have thicker bases, whereas *O.*
compressus teeth are characterised by having thin bases, although this is not always the case
(Johnson 1999). Also our specimens lack serration, whereas serration has been recorded in
thin-based teeth of *O. texensis* (Johnson 1999). Based on the placement of teeth within the
jaw for *O. texensis* (Johnson 1999), it is reasonable to assume a posterior curvature of the
'major cusp' in the teeth of *O. compressus.*

<div align="center">Xenacanthiformes indet.</div>

<div align="center">Figure 9E</div>

Material. 32 specimens containing isolated teeth (NBMG 14966, 14985–14897, 14994,
15835, 15837–15838, 15842, 15848, 16082, 16089, 18613, 19628–19846).

Diagnosis. Bicuspid or tricuspid teeth with a base that extends lingually.

Description. Bi- or tricuspid teeth with a base that extends in a lingual to anterio-lingual
direction. Cusps are lanceolate to oval in cross section and lateral cusps larger than 1 mm

often have carinae on their lateral edges. Serration is absent in all specimens. A sub-circular

coronal button is present in specimens with intact bases. In specimens not obscured by

sediment there is no median foramen. A convex basal tubercle is present except where it has

been broken off (Fig. 9E).

Remarks. The specimens are too fragmentary to identify beyond ordinal level. Some show

individual features consistent with *Orthacanthus compressus*, such as the presence of carinae,

but have not been included within *O. compressus* as these characteristics are shared by

Xenacanthus (Johnson 1999).

Elasmobranchii indet.

Figure 9F, G

Material. 32 specimens containing 607 isolated scales (NBMG 19646–19677). Note that

some of these specimens were obtained through the destructive dissolution of NBMG 14984,

15834, and 15901, and then assigned new collection numbers.

Diagnosis. Scales with thin bases and cusps extending out from the free-face. Scales vary

from polycuspid to fused cusps.

Description. Scales range from ≤ 0.5 mm to ≤ 0.2 mm in diameter and height (measured from

the base outwards along the denticles). The base of the scales is thin and tends to be dotted

with holes, which are likely to be a result of post-mortem degradation, as hole morphology is

highly variable. Cusps range from polycuspid to fused cusps, which form a robust structure

(Fig. 9F). The cusps of the polycuspid scales tend to have a degree of curvature, and all curve

in the same direction.

Remarks. Elasmobranch scales from the Palaeozoic have been shown to have a high degree of

morphological variability, depending on which part of the body they are from (Dick 1981).

369 This variability can be more pronounced than that seen between species, making the

370 assignment of scales a difficult task. The Minto specimens show similarities to denticles

371 depicted by Lebedev (1996, fig 6d–f), characterised there as "*Ctenacanthus*" type denticles

372 (Karatajute-Talimaa 1992; Lebedev 1996).

373 <div align="center">Order *incertae sedis*</div>

374 <div align="center">Family *incertae sedis*</div>

375 <div align="center">Genus *AGELEODUS* Owen, 1867</div>

376 *Type species. Ageleodus pectinatus* Agassiz, 1843*a*

377 <div align="center">*Ageleodus pectinatus* Agassiz, 1843*a*</div>

378 <div align="center">Figure 9H–J</div>

379 *Material.* 67 specimens containing isolated teeth (NBMG 9973b, 10800, 12067, 14965,

380 14969–14982, 14995, 14997–15004, 15175, 15806, 15838, 15858–15861, 15863, 15868,

381 15890–15893, 15895, 15897–15900, 16070–16072, 16095, 19600–19613, 19717, 19851).

382 *Diagnosis.* Mesio-distally elongated teeth with multiple sharp-conical cusps arranged in a row

383 along the crown. The base is long, narrow and deep, and lacks imbrications.

384 *Description.* The teeth are mesio-distally elongated, giving an impression of anterior-

385 posterior compression: the crown is bulbous on one side and flattened on the opposite side

386 (Fig. 9H–J). The number of cusps on the crown varies from 9–18 (Fig. 10B) in complete

387 specimens, with the exception of NBMG 15715, which has 35 (Fig. 9J). The cusps are sharp-

388 conical, except where rounded by abrasion, and are situated along the crown, with 1-2

389 marginal cusps in a slightly ventral position at each edge. The root of the tooth is compressed

390 and is punctuated by nutritive channels.

391 *Remarks.* As *A. pectinatus* is known only from disarticulated teeth, the arrangement of teeth

392 within the jaws is unknown; we follow the terminology established by Downs and Daeschler

393 (2001). Cusp count appears to be continuous and unimodal within the sample, with a mean of

394 14, and all specimens lie within the first standard deviation except for NBMG 15175 (Fig.

395 10B). This is similar to the variation in other samples (e.g. Downs and Daeschler 2001, fig.

396 3); in that example, the majority of specimens had 3 to 16 cusps, though rare teeth with as

397 many as 33 cusps were found. Given the much smaller sample size here, the fact that

398 specimens from Minto show less variation than those from Red Hill is not surprising;

399 nonetheless, all specimens except NBMG 15715 fall within the range of variation established

400 by Downs and Daeschler (2001) for *A. pectinatus*. Controversy continues to surround the

401 interpretation and affinity of *Ageleodus* (Turner 2013). Here we have followed the

402 conservative view that these features represent the teeth of a basal elasmobranch of uncertain

403 placement; however, we note that Lebedev (1996) proposed a rather different hypothesis, i.e.,

404 that they are not teeth at all, but rather specialised brachial denticles.

405

406 Class ACANTHODII Owen, 1846

407 Order *incertae sedis*

408 Family GYRACANTHIDAE Woodward, 1906 emend. Warren *et al.,* 2000

409 Genus *GYRACANTHIDES* Woodward, 1906

410 *Type species. Gyracanthides murrayi* Woodward, 1906

411 *Gyracanthides* sp.

412 Figure 11A–F

413 *Material.* One specimen containing 11 individual spine fragments (NBMG 10739/1–11) and

414 two further specimens containing single spines (NBMG 15173, 15826).

415 *Diagnosis.* Laterally compressed spines with a V-shaped to U-shaped cross section. Striated

416 insertion area with an exsertion area covered by tubercles that form ornament ridges.

417 Ornament ridges intersect in a chevron arrangement along the leading edge. Ridges are

418 oblique to the long axis near the insertion area, but become parallel to the long axis towards

419 the distal end in pectoral spines. This is not seen in dorsal and pelvic spines, where tubercle

420 ridges are consistently oblique towards the distal end.

421 *Description.* NBMG 151173 is a partially exposed spine 84 mm long. The long axis shows a

422 very small degree of curvature (Fig. 11A). The cross section of the spine does not show

423 curvature, but this may be a result of the sediment obscuring parts of the spine. The

424 insertion/exsertion boundary (IEB); Fig. 11A) is hard to distinguish due to the high degree of

425 abrasion on the ornament ridges. There is an angle of 42º between the IEB and the

426 ornamented ridges and 25º between the IEB and the striae. Ornament ridges more distal to the

427 IEB show less abrasion, allowing individual ridges to be traced, but the damage is still

428 sufficient that individual tubercles on the ridges are heavily worn and difficult to discern.

429 Seven ridges cross a line drawn perpendicular to the leading edge at the posterior limit of the

430 insertion area (Fig. 14A, cf. Turner *et al.* 2005, fig. 2a).

431   NBMG 10739 is composed of 11 fragments from several different spines. In NBMG

432 10739/1–2 the ornament ridges of the exsertion area are pinched out by the insertion area

433 along the leading line (Fig 11B–C). Specimens NBMG 10739/1–2 measure 46 mm and 44

434 mm along their long axes respectively, with broken surfaces on the distal and proximal ends.

435 The cross-sectional shape of NBMG 10739/1–2 is difficult to determine because it is

436 fragmentary. The insertion area is covered by parallel to sub-parallel incomplete striae that

branch and converge in places and taper off both distally and proximally (Fig. 11D). There is

a c. 20º angle between the striae and the IEB. The exsertion area is covered by tubercles,

which are arranged en échelon on the ornament ridges of NBMG 10739/1 and 4 (Fig. 11E),

and as near straight ridges in NBMG 10739/2 and 5. The tubercles are elongated along the

long axis and intersect as even chevrons along the leading edge (Fig. 11C, E). The length of

the elongated tubercles varies from 400 to 910 µm between spine fragments. Any

ornamentation originally present on the tubercles has been lost to abrasion. The angle

between the ornament ridges and the IEB varies from c. 81º (Fig. 11B–C) in NBMG

10739/1–2 to c. 52º in NBMG 10739/4 with the latter having more longitudinal elongate

ridges to the long axis, suggesting that it is part of the distal end of a pelvic spine (Turner *et*

al. 2005). Spines with varying levels of abrasion along their length may be indicative of wear

during life (Turner *et al.* 2005); if abrasion was caused by post-mortem transportation, then a

more even distribution of abrasion along the spine would be expected.

NBMG 10739/3–5, 7 and 10 are the only fragments complete enough for the cross-

sectional shape to be determined; all are elliptical (Fig. 11F). Only a single ridge is visible on

the trailing edge of NBMG 10739/3, as the surface is damaged where a second ridge would

be expected in *Gyracanthides* (Turner *et al.* 2005). There is an infilled circular hollow in

NBMG 10739/4 that narrows distally in proportion with the narrowing of the spine. This

hollow represents the pulp cavity. All spine fragments are too small to show any distal

curvature.

Remarks. Gyracanthid material from the Minto Formation has been previously reported as

Gyracanthus cf. *G. duplicatus* (Gardiner 1966; Miller 1999), but since Dawson's

Gyracanthus duplicatus is now known to be invalid (Carpenter *et al.* 2015), the Minto

material merits re-classification. Specimens NBMG 15173 and NBMG 10739/1–11 have

been removed from the genus *Gyracanthus* based on having spines with ellipsoid cross

462 sections, open grooved hollows and ornament ridges showing a change in angle from oblique

463 to parallel along the long axis of the pectoral spines. These features are not characteristic of

464 *Gyracanthus*, the spines of which have circular cross sections and ornament ridges that are

465 consistently oblique, but are characteristic of the genus *Gyracanthides* (Turner *et al.* 2005;

466 Snyder 2011). Therefore we have assigned our specimens to the genus *Gyracanthides*.

467 Species-level classification of *Gyracanthides* is based on tubercle orientation, ornamentation

468 and arrangement along the ornament ridges (Warren *et al.* 2000; Turner *et al.* 2005). As

469 NBMG 15173 is highly abraded, this specimen cannot be assigned to a species. NBMG

470 10739/1 and NBMG 10739/2 (Fig. 11B–C) show a much lesser degree of abrasion, yet no

471 striae on the tubercles can be seen, as in *Gyracanthides murrayi* (Warren *et al.* 2000, fig. 8e–

472 f), indicating that these spines still underwent a small degree of abrasion. The en échelon

473 packaging of tubercles on the ornament ridges better fits *Gyracanthides hawkinsi* than the

474 straight ornament ridges of *G. murrayi*, but ornamented ridges in *G. hawkinsi* meet along the

475 leading edge in uneven chevrons, which is not seen in specimen NBMG 10739/1–11, and

476 tubercles have three projections which converge towards the apex, again not seen in this

477 specimen. Therefore we assign both specimens to *Gyracanthides* sp.

478   Order ACANTHODIDA Berg, 1940

479   Family ACANTHODIDAE Huxley, 1861

480   Genus *ACANTHODES* Agassiz, 1843*b*

481 *Type species. Acanthodes bronni* Agassiz, 1843*b*

482   *Acanthodes* sp.

483   Figure 11G–H

484 *Material.* Four isolated spines (NBMG 15174 15852, 15869, 15913).

485 *Diagnosis.* Slender, gently curving spines with a rounded anterior rib; lateral surfaces smooth

486 except for a single longitudinal groove on each side.

487 *Description.* Isolated, incomplete spines 10 to 32.5 mm in length and 0.5 to 2.5 mm wide,

488 exposed in lateral view. A rounded rib runs along the anterior surface, and is flanked on each

489 side by a prominent longitudinal groove; this is visible as an external mould in the matrix

490 where parts of the spine have been lost, confirming its presence on both sides. The spines are

491 otherwise smooth.

492 *Remarks.* Though other acanthodiforms were common in eastern Canada during the Devonian

493 (Gardiner 1966; Denison 1979; Kennedy *et al*. 2012), the only previously reported occurrence

494 of Acanthodidae is from the Tournaisian Horton Bluff Formation at Blue Beach, Nova Scotia

495 (Zidek 1977; Mansky & Lucas 2013, fig. 13A), identified as Acanthodidae indet. Thus, this is

496 the first Canadian example of *Acanthodes* and extends the known range of the Acanthodidae

497 in Canada by some 35 million years.

498 Acanthodidae indet.

499 *Material*. Ten specimens containing multiple isolated spines (NBMG 15822, 15835, 15838,

500 15844, 15873, 16082, 16094, 16095, 20013, 20016).

501 *Diagnosis*. Slender, gently curving spines, unornamented except for a single prominent

502 longitudinal groove.

503 *Description*. Isolated, incomplete spines 5 to 25 mm long and 0.5 to 1.75 mm wide, exposed

504 in various aspects. Several have been crushed and badly damaged, such that no further

505 diagnostic features can be discerned.

506 *Remarks.*

507

Class OSTEICHTHYES Huxley, 1880

Subclass SARCOPTERYGII Romer, 1955

Infraclass DIPNOMORPHA Ahlberg, 1991

Order DIPNOI Müller, 1845

Family *incertae sedis*

Genus *CTENODUS* Agassiz, 1843*a*

Type species. Ctenodus cristatus Agassiz, 1843*a*

Ctenodus interruptus Barkas, 1869

Figure 12A–B

Material. Two specimens, each comprising an incomplete tooth plate (NBMG 10740, 15822).

Diagnosis. Subtriangular tooth plate with ridges that are near-parallel to one another. The ridges are equipped with prominent, longitudinally compressed denticles with rounded apices.

Description. NBMG 10740 is a broken fragment of a tooth plate. Only four near-parallel ridges are present (Fig. 12A) with lengths of 9 to 31 mm, but these measurements do not represent the original length of the ridges, as they are broken at both ends. There is a space of 5 mm between ridges (measured from between the apices). Individual apex height reduces along each ridge from the centre out in both directions. Ridges are relatively straight. There is a prominent depression between two apices on one side of the specimen (Fig. 12A), seen in three of the ridges (not observable in the fourth ridge as this section of the ridge is not preserved). Apices vary randomly along the ridge between conical and rounded (Fig. 12A);

528   rounded apices are likely a result of abrasion. All apices are laterally compressed towards the

529   apex. The basal surface is encased in sediment.

530   *Remarks.* Only two species of *Ctenodus* have been reported from the North American

531   continent: *C. cristatus* and *C. interruptus*, with *C. murchisoni* from Nova Scotia being

532   assigned to *Conchodus plicatus* (Baird 1978). NBMG 10740 shows more prominent

533   separated apices than *C. cristatus* (Sharp and Clack 2013, fig. 2) and *C. murchisoni*

534   (Sternberg 1941, fig. 1–3). These prominent apices are similar to *C. interruptus* (see Sharp

535   and Clack 2013, fig. 5, 14). Therefore NBMG 10740 has been assigned to *C. interruptus*. The

536   dental plate bears some small xenacanth teeth on the occlusal surfaces (Fig. 12B).

537   Dipnoi indet.

538   Figure 12C, D

539   *Material*. Six specimens, each comprising isolated tooth-plate fragments (NBMG 18609,

540   19698–19701, 19833).

541   *Diagnosis.* Triangular tooth-plates equipped with ridges of denticles.

542   *Description.* Fragmentary tooth-plates, each bearing two ridges, converging at an angle of c.

543   20º (Fig. 12C). There is no evidence that any other ridges were originally present. Denticles

544   are laterally compressed, and this is consistently more pronounced in one ridge than the other

545   (Fig. 12D). Tooth-plates show broken surfaces near the edges.

546   *Remarks*. Dipnoan tooth-plates show substantial variation attributed to tooth wear (Schultze

547   and Chorn 1997) and to developmental anomalies (Kemp 1996, 2003), making the

548   identification of isolated specimens difficult. Most diagnostic characters are associated with

549   cranial bones rather than tooth-plates (Sharp and Clack 2013), although isolated tooth-plates

550 can often be identified to species level when complete (Sharp and Clack 2013). Due to the

551 fragmentary nature of the specimens they have been assigned to Dipnoi indet.

552

553 Infraclass TETRAPODOMORPHA Ahlberg, 1991

554 Order RHIZODONTIDA Andrews and Westoll, 1970 emend. Johanson and Ahlberg, 2001

555 Family RHIZODONTIDAE Traquair, 1881*a* emend. Andrews and Westoll, 1970

556 NBMG 20014, 20015 need to be assigned to taxa (currently given as Rhizodontidae)

557 Genus *STREPSODUS* Huxley, *in* Huxley and Etheridge, 1865

558 *Type species. Strepsodus sauroides* Binney, 1841

559 *Strepsodus sauroides* Binney, 1841

560 Figure 13A

561 *Material.* Nine specimens containing isolated teeth (NBMG 9969, 15005, 15007, 15788,

562 15815, 15820, 15829–15830, 19688).

563 *Diagnosis.* Tall, slender teeth that are recurved lingually. Teeth are oval in cross section.

564 Reversed curvature is present towards the apex of the crown. Raised parallel striae are present

565 on the lingual side and on the lingual portions of the distal and mesial sides of the teeth. Striae

566 are longitudinal and show minor to no degree of curvature.

567 *Description*. Incomplete teeth varying in length from 7 mm in NBMG 9969 to 17 mm in

568 NBMG 15820. Teeth have an oval cross section. Teeth are recurved and show reverse-

569 curvature near the apex (Fig. 13A), giving them a sigmoidal shape. Raised striae are

570 longitudinal and some show minor curvature, particularly towards the apex, causing

571 individual striae to cross from the lingual surface to the mesial/distal sides. Striae subside

572 near the apex and are absent on the apex itself. Striae may appear to converge apically as a

573 result of recurvature, yet they never come into direct contact. Instead a stria caught between

574 two converging striae will taper out. Striae show a maximum spacing of 0.1 mm prior to

575 convergence. This distance is consistent irrespective of tooth size; larger teeth simply bear

576 more striae. The base of the crown is absent in all specimens.

577 *Remarks*. Reverse curvature seen in NBMG 9969 and possibly present in NBMG 15820

578 suggests that these may be symphyseal tusks, but the small size of NBMG 9969 and the lack

579 of well-preserved *Strepsodus* mandibles makes this uncertain (Jeffery 2003, 2006).

580 Genus *ARCHICHTHYS* Hancock and Atthey, 1870

581 *Type species. Archichthys portlocki* Portlock, 1843 ex Agassiz MS

582 *Archichthys portlocki* Portlock, 1843 ex Agassiz MS

583 Figure 13B–C

584 *Material.* Three specimens, each containing an isolated tooth (NBMG 15799, 15818, 19972).

585 *Diagnosis.* Robust, gently curved tooth with 11 plications around the base. A 'woven' pattern

586 of striation is present above the plications.

587 *Description.* NBMG 19972 is a robust tooth 14 mm long. The tooth shows gentle lingual

588 curvature (Fig. 13B) with an oval cross section, and is equipped with 11 basal plications (Fig.

589 13C). Striations on the exposed parts of the tooth surface form a "woven" texture; these are

590 most pronounced at the base of the tooth, and become fainter apically, disappearing

591 completely at the apex. Although the labial surface is partially covered in sediment, an

592 exposed part lacks striations.

593 *Remarks.* The 11 plications reported from NBMG 19972 are less than the 16 to 18 recorded

594 by Jeffery (2006). This does not rule NBMG 19972 out of being assigned to *Archichthys*

595 *portlocki* as the plication count did not form part of the diagnostic section in Jeffery (2006). A

596 plication count of 11 agrees with the estimated 10 to 12 for *A. portlocki* in Carpenter *et al.*

597 (2015). Although the striations in NBMG 19972 are similar to those of *Letognathus* (Brazeau

598 2005), this assignment has been ruled out as striations are present on the labial surface of

599 *Letognathus*, whereas striations in NBMG 19972 are absent from the labial surface, which is

600 seen in the teeth of *A. portlocki* (Jeffery 2006). The teeth of *Letognathus* are long and slender

601 (Brazeau 2005), unlike the robust tooth of NBMG 19972, again supporting our identification.

602 cf. *Archichthys portlocki* Portlock, 1843 ex Agassiz MS

603 Figure 13D–E

604 *Material.* Two isolated scales (NBMG 15831, 19689).

605 *Diagnosis.* Sub-hexagonal scales with more prominent concentric growth lines on the outer

606 than the inner surface. Median boss in the inner centre.

607 *Description.* Two incomplete sub-hexagonal scales with the inner surface exposed. NBMG

608 19689 has a diameter of 25 mm (Fig. 13D) and NBMG 15831 has a length of 16 mm and a

609 width of 24 mm (Fig. 13E). Concentric growth rings are most prominent at the periphery of

610 the scale and diminish towards the centre. NBMG 19689 has an elongated median boss 4 mm

611 long and 2 mm wide. NBMG 15831 has a pentagon-shaped median boss 1 mm across.

612 *Remarks* NBMG 15831 and NBMG 19689 resemble scales, which formed part of the type

613 series for *Archichthys portlocki* (Portlock 1843, reproduced in Jeffery 2006, fig. 1). Surface

614 detail is partially obscured by a light coating of very fine sediment. Attempts were made to

615 remove the sediment cover, but this resulted in damage to the scale and so was abandoned.

616   Genus *RHIZODUS* Owen, 1840

617   *Type species. Rhizodus hibberti* Owen, 1840

618   Rhizodontidae cf. *Rhizodus hibberti* Owen, 1840

619   Figure 13F

620   *Material.* 16 specimens comprising isolated symphyseal tusks (NBMG 15787, 15789-15791,

621   15795, 15798, 15809-15810, 15812-15813, 15816-15817, 15862, 15862, 15866, 16074).

622   *Diagnosis.* Large tusk with lenticulate cross-section. There are approximately 24 plications

623   around the base of the tusk.

624   *Description.* NBMG 15809 is a single robust tusk partially covered in matrix. The exposed

625   portion is 29 mm long. The apex of the crown is either covered in matrix or absent. The

626   exposed surface of the base of the crown is equipped with 12 plications. Recurvature, if any,

627   cannot be observed due to matrix cover. The tusk is slightly compressed which has resulted in

628   longitudinal fractures.

629   *Remarks.* Based on the number of plications (n = 12) visible on the exposed portion of

630   NBMG 15809, it is likely that the tooth bears 22 to 26 in total. Similar tusk morphotypes

631   from different genera of rhizodont are differentiated based on the number of plications

632   (Jeffery 2003). This tusk cannot be *Archichthys portlocki* or *Letognathus hardingi* because

633   they bear 16 to 18 and around 14 plications, respectively (Brazeau 2005; Jeffery 2006).

634   *Strepsodus sauroides* is also excluded because it lacks striations. An estimated plication count

635   of 22 to 26 is consistent with *Rhizodus hibberti* (20 to 22) and *Barameda decipiens* (20 to 26)

636   (Jeffery 2003; Holland *et al.* 2007). As *B. decipiens* is known mostly from Australia, whilst

637   *R. hibberti* is found in North American and European localities, this is more likely *R. hibberti*.

638   Isolated tusks of *R. hibberti* and *Screbinodus ornatus* are only distinguishable based on size

639 (Jeffery 2003); with a minimum crown height of 26 mm, we assign NBMG 15809 to

640 Rhizodontidae cf. *Rhizodus hibberti*.

641 Order *incertae sedis*

642 Family RHIZODOPSIDAE Berg, 1940

643 Genus *RHIZODOPSIS* Young, 1866 ex Huxley MS emend. Traquair, 1881*b*

644 *Type species. Rhizodopsis sauroides* Williamson, 1849

645 cf. *Rhizodopsis sauroides* Williamson, 1849

646 Figure 13G

647 *Material*. One specimen comprising a single isolated scale (NBMG 15901).

648 *Diagnosis.* Ovoid scale, divided into four quadrants. Concentric growth lines present in all

649 quadrants. Radial striae present in only the posterior and anterior quadrants. A median boss

650 and concentric growth lines are present on the inner surface.

651 *Description.* Elongated ovoid scale with a length of 26.5 mm and a maximum width of 14

652 mm. The scale is imbedded in the matrix with the inner surface exposed. The scale is

653 fractured, but almost complete with only a small section of the outer edge broken off (Fig.

654 13G). Quadrants can be identified but with great difficulty and concentric growth lines can

655 only be seen along the very edges. Radial striae can only be seen in parts along the outer

656 edge. There is a median boss on the inner surface, elongated along the long axis. The median

657 boss is 4 mm long and 1 mm thick. The scale is marked by punctae, 400 µm in diameter.

658 *Remarks*. Detail on the surface of NBMG 15901 has been lost, seen in the lack of concentric

659 growth lines towards the centre of the scale, making identification uncertain. Overall scale

660 morphology looks similar to that illustrated by Williamson (1837, fig. 1, 4), with NMBG

661 15901 being slightly more ovoid. This less rhombic morphology is seen in other *Rhizodopsis*

662 *sauroides* scales (e.g. Holland *et al*. 2010, fig 6f reproduced from Woodward 1891). The

663 median boss of NBMG 15901 matches the median boss illustrated by Williamson (1837, fig.

664 1, 4). *Megalichthys* scales with the cosmine removed have been misidentified as the scales of

665 *Rhizodopsis* (Holland *et al*. 2010), but as the scales of *Megalichthys* lack a median boss

666 (Andrew and Westoll 1970) it is certain that NBMG 15901 does not belong to *Megalichthys*.

667 For the present, NBMG 15901 is placed in Tetrapodomorpha indet. cf. *Rhizodopsis*

668 *sauroides*.

669 Order Sarcopterygii *incertae sedis*

670 Family MEGALICHTHYIDAE Hay, 1902

671 Genus *MEGALICHTHYS* Agassiz, 1843*b*

672 *Type species. Megalichthys hibberti* Agassiz, 1843*b*

673 *Megalichthys* sp.

674 Figure 13H–J

675 *Material.* Four specimens (NBMG 10741 in two parts, 15794, 19974). One of these blocks

676 contains up to eleven identifiable fragmented scales (NBMG 10741/1) and seven complete

677 scales in the other part (NBMG 10741/2–7).

678 *Diagnosis*. Sub-rhombic scales with a cosmine-covered outer surface.

679 *Description.* Fractured rhombic scales c. 25 mm in length where complete (Fig. 13H).

680 Cosmine-covered outer surface with very low relief ripple-like ornamentation (Fig. 13I).

681 There is a cosmine-free ridge at the margin of the cosmine-covered outer surface, which

682 gradually thins towards the outer edge of the scale. Where the cosmine covering has been

683 worn away from the scales, the surface is covered by closely spaced punctae. On the inner

684 surface is a prominent ridge, which follows the line of contact between the cosmine-covered

685 portion and the ridge on the free field. The ridge on the inner surface does not extend to the

686 margins and tapers off sharply in a stepwise fashion (Fig. 13J). This gives the ridge an

687 elongated rectangular shape.

688 *Remarks*. Genus- and species-level identification of megalichthyids is based on cranial

689 characters (Thompson 1964; Andrews 1985, Fox *et al*. 1995), but as *Megalichthys* is common

690 throughout the Carboniferous Maritime Basin it is reasonable to associate these rhombic

691 scales with the genus (e.g., Carpenter *et al.* 2015).

692 cf. *Megalichthys* sp.

693 Figure 13K–L

694 *Material.* One specimen, a single isolated centrum (NBMG 19958).

695 *Diagnosis.* Annular centrum with a relatively large notochordal canal.

696 *Description.* NBMG 19958 is a single annular centrum with an outer diameter of 27 mm (Fig.

697 13K) and a thickness of 5.5 mm (Fig. 13L). The inner surface tapers to form a ridge-like

698 structure, and a relatively large notochordal canal (diameter 16 mm) is inferred. Therefore the

699 inner/outer diameter ratio is 1.69. The inner and outer surface is rough and has a worn

700 appearance. There is no evidence of a neural arch or spine.

701 *Remarks.* The worn texture of the centrum suggests that smooth or wrinkled periosteal bone is

702 absent, which may be the reason why triangular areas over the posteroventral regions are

703 absent (see Andrews and Westoll 1970, fig. 7d). The inner/outer diameter ratio of NBMG

704 19958 is slightly larger than the typical ratio seen in *Megalichthys hibberti*, but ratios in

705 excess of 1.6 have been noted (Andrews and Westoll 1970). Based on its size, this centrum

706   would have been from the trunk of the fish. Neural arches are present in some, but not all,

707   megalichthyid trunk vertebrae, meaning that the lack of a neural arch does not exclude this

708   specimen from the trunk (Andrews and Westoll 1970). The higher outer/inner diameter ratio

709   of specimen NBMG 19958 compared to *Megalichthys hibberti*, along with the difficulty of

710   assigning a single isolated worn centrum to a species, means we assign it to cf. *Megalichthys*

711   sp.

712   Tetrapodomorpha indet.

713   Figure 13M–N

714   *Material.* Twelve specimens, comprising incomplete, isolated teeth (NBMG 9968, 10776,

715   10777, 10783, 10785, 19691-19697).

716   *Diagnosis.* Recurved conical teeth with a smooth surface, lacking cutting edges.

717   *Description.* Conical teeth that are recurved (Fig. 13M), except for NBMG 10785, which has

718   been flattened to such a degree that it is impossible to tell if the tooth was ever recurved.

719   NBMG 19696 has a circular cross section exposing a pulp cavity that has been infilled with

720   sediment. NBMG 10777 (Fig. 13N) has a broken face exposing part of the pulp cavity that

721   has likewise been infilled with sediment. The base is absent in all specimens.

722   *Remarks*. Apical caps lacking acrodin exclude these teeth from Actinopterygii, so have been

723   placed within the sarcopterygians. Sediment-filled pulp cavities suggest that NBMG 19696

724   and NBMG 10777 had hollow pulp cavities, which are indicative of polyplocodont teeth, as

725   present in *Megalichthys*, *Rhizodopsis*, *Rhizodus* and *Strepsodus* (Schultze 1970).

726   Polyplocodont teeth are also present in crown tetrapods, so a tetrapod affinity cannot be ruled

727   out. Without further histological investigation and as all teeth lack a base, plication folding

cannot be determined and these teeth cannot be identified more precisely (Schultz 1970;

Vorobyeva 1977; Jeffery 2003). Therefore we identify these teeth as Tetrapodomopha indet.

Superclass TETRAPODA ~~Ahlberg~~Goodrich, 19~~30~~09~~1~~

Figure 14 D

Material. Fifteen specimens, including partial jaws (NBMG 15821, 15853, 15872, 20019,

20020, 20021), dermal cranial bones (NBMG 15785, 20028), vertebrae (NBMG 15783,

15784, 15870), ribs (NBMG 15782, 15914), possible limb bones (NBMG 15915), and scutes

(NBMG 15861).

Description. NBMG 15821 is a 14 mm long mandible, ~~14 mm long, and bears~~with at least 17

elongate, straight, pointed (bullet-shaped) teeth that bear faint longitudinal striations confined

to the basal one-third of the visible portion of the crown (Fig. 14A). The jaw bone, although

somewhat damaged, appears to be narrow, barely as deep as the length of the tooth crowns,

and it bears a shallow~~, longitudinal~~ sculpture of longitudinal ridges. NMBG xxxxx is a

vertebra comprising a disc-shaped ~~inter~~inter- or pleurocentrum, ~~presumably~~bearing a striking

resemblance to anthracosaur inter-/pleurocentra~~of a temnospondyl~~, with nearly

equidimensional measurements in articular view (Fig. 14B), and anteroposteriorly short (Fig.

14C). ~~The articular faces are deeply amphicoelous, and there is~~central notochordal canal~~a~~

~~central perforation from front to back~~. In lateral view (Fig. 14C), the portion of the lateral

surface comprised between the projecting, rolled edges around the articular faces ~~project, and~~

~~the intervening portion~~ is depressed. The isolated osteoderm (Fig. 14D) is tiny, only 4 mm

across, with a thick keel extending from the centre of the scute to its edge, thus dividing the

scurte into two approximately symmetrical halves.~~.~~

753 *Remarks.* There are several small jaw bones that do not appear to correspond to any of the

754 fishes just described, and some at least show superficial resemblance to ~~temnospondyls such~~

755 ~~as~~those of colosteids ~~,~~ and embolomeres. The vertebral ~~inter~~centrum is ~~presumably of a~~

756 ~~temnospondyl~~reminiscent of those of embolomerous anthracosaurs. The isolated osteoderm is

757 problematic, as no osteoderms of comparable shape are known from early tetrapods that we

758 know of.~~resembles those of temnospondyls such as Eryops (Pawley and Warren, 2006).~~

759

760

761 Subclass ACTINOPTERYGII Cope, 1887

762 Actinopterygii indet.

763 Figure 15A–D

764 *Material.* Seven specimens containing 24 isolated scales (NBMG 18608, 19678–19683), ten

765 specimens containing 172 cranial bone fragments (NBMG 19799–19808), one isolated tooth

766 (NBMG 19684), and four isolated centra (NBMG 19834, 19685–19687).

767 *Diagnosis.* Rhombic scales with a covering of ganoine, peg-and-socket articulation and

768 asymmetrical serrations. Disc shaped scutes with elongated ridges on the outer surface.

769 Conical teeth with a distinct apical cap. Hour-glass shaped centra with concave depressions.

770 *Description. Scales:* Rhombic scales 0.5 to 1 mm in size. Four scales have asymmetrical

771 serrations on the posterior margin (Fig. 15A–B). Dorsal and ventral margins are straight with

772 slight curvature near the anterior and posterior margins. The anterior margins are slightly

773 curved along their entire extent. Peg-and-socket articulation is present in seven of the scales

774 (Fig. 15B). *Cranial Bone Fragments:* Elongated sub-rectangular shaped bone plates with a

775 maximum long axis of 2.5 mm. NBMG 19804 has closely packed, branching ridges present

776 on the outer surface (Fig. 15C), which vary along the surface from longitudinal to curved.

777 The inner surface is smooth lacking a peg-and-socket articulation. *Tooth:* NBMG 19684 is a

778 slender, recurved conical tooth with translucent apical cap (Fig. 15D). *Centra:* NBMG 19686

779 measures 1.22 mm from anterior to posterior margin and 0.5 mm in maximum height, giving

780 a height:length ratio of 2.44. The centrum becomes constricted towards the centre (Fig. 15E)

781 producing an 'hour glass-shape' (Schultz and Chorn 1986). Concave posterior and anterior

782 margins form 'cup' shapes on either end that are infilled with sediment. On the dorsal surface

783 there are two sockets elongated along the long axis and separated by a trough. These sockets

784 would have housed the neural arches. A rounded attachment site is present only on one of the

785 lateral sides, which extends laterally (Fig. 15E). On the other lateral side it is likely that an

786 attachment site was present, but has been broken off. A thin ridge runs along the long axis of

787 the ventral surface.

788 *Remarks*. The interrelationships of basal Actinopterygii are poorly understood (Patterson

789 1982; Gardiner 1984; Gardiner and Schaeffer 1989; Sallan 2014), and certain groups, such as

790 the Palaeonisciformes, are likely paraphyletic (Janvier 1996), making the placement of

791 ichthyoliths in mid-level taxonomic groups problematic. Peg-and-socket articulation in

792 NBMG 19679/1 is similar to that depicted by Schultze (1966, fig. 1a–b) and was previously

793 thought characteristic of ganoid fishes, but the discovery of cladistian scales with peg-and-

794 socket articulation suggests that it is plesiomorphic within the Actinopterygii (Schultze 1977;

795 Patterson 1982). The ridge patterns on the cranial bone fragments, from the Minto specimen,

796 resemble to a limited degree the pattern of ridges seen in the rostral and premaxilla of

797 *Gogosardia coatesi* illustrated in Choo *et al*. (2009, fig. 8a-b) suggesting they are of

798 palaeoniscoid-type. Due to the variation seen in the ridges of cranial bones (Choo *et al.* 2009;

799 Choo 2011, 2015) identification of fragmented cranial bones is problematic. The high

800 variability of scale morphologies in early Actinopterygii means that it is difficult to say

801 whether scales and cranial bone fragments from the Minto specimen represent one or more

802 species (Choo 2011). The apical cap of NBMG 19684 is composed of modified dentine called

803 acrodin (Ørvig 1978), a characteristic found only in the teeth of Actinopterygii, including

804 cladistians, some palaeonisciformes, colobodonts and pycnodonts (Ørvig 1978; Patterson

805 1982), though it is absent in pachycormids, *Cheirolepis* and *Severnichthys* (Patterson 1982;

806 Carpenter *et al*. 2014). The centra resemble those of palaeoniscoids illustrated by Schultz and

807 Chorn (1986, fig 3.1–2). The presence of lateral attachment sites, which would have served as

808 attachment points for the ribs, and a height:length ratio of 1:2.44 suggests that these centra

809 formed part of the abdominal region (Schultz and Chorn 1986), although this is higher than a

810 ratio of 1:1.5 recorded by Schultz and Chorn (1986).

811

812   BROMALITES

813   Heteropolar microspiral coprolites

814   Figure 16A–B, E

815 *Material.* Thirty-three specimens (NBMG 18789, 19975–11998, 20004–20011).

816 *Diagnosis.* Spiral coprolites, with coils concentrated at the posterior end, covering < 50% of

817 the total length, and striae parallel to the long-axis at the anterior end.

818 *Description*. Spiral coprolites, dark grey to brown in colour, 12 to 37 mm long and 5 to 14

819 mm diameter (Fig. 16A). Coprolites characterised by 6 to 12 coils, typically 1 to 2.5 mm

820 wide, concentrated at the posterior end, and comprising up to 50 % of the total length

821 (Coprolite Type F3 of Hunt and Lucas 2012*a*). The anterior end is characterised by prominent

822 striae, parallel to the long axis, but twisted into a corkscrew. In thin section, posterior coils

823 are recognisable (Fig. 16B), and the bulk of the coprolites comprise amorphous to pelleted

824 phosphatic grains. Abundant fish skeletal material is also present including recognisable

825 bicupsid xenacantid teeth, although their very small size, suggests an origin in a juvenile

826 shark (Fig. 16E).

827 *Remarks.* Heteropolar spiral coprolites were produced by fishes with valvular intestines

828 (McAllister 1987), and represent fully evacuated coprolites rather than enterolites preserved

829 *in situ* (Hunt *et al.* 2012; Hunt and Lucas 2012*ab*). The phylogenetic distribution of this

830 intestinal structure is not well understood, but it is generally considered to be a primitive

831 feature, most characteristic of elasmobranchs; it is absent in more derived fishes such as

832 actinopterygians and teleosts (Hunt and Lucas 2012*a*). Various authors have argued that

833 xenacanthiform sharks were the most likely producer of spiral coprolites in the

834 Pennsylvanian-Permian of U.S.A. (Williams 1972; McAllister 1985; Hampe 1988), and

835 Johnson (1999) and Hunt *et al.* (2012) described similar coprolites to those reported here

836 from the Pennsylvanian-Permian of U.S.A. and related them to *Orthacanthus* sharks, in

837 particular, based on quantitative co-occurrence data. Given the large size of our coprolites and

838 the abundance of *Orthacanthus* teeth in the Coal Creek assemblages where the heteropolar

839 coprolites co-occur, a biological association is considered very likely. Based on the

840 occurrence of small xenacanthid teeth within the coprolite, *Orthacanthus* may have fed on

841 juvenile sharks amongst other prey.

842   Short cylindrical coprolites

843   Figure 16C–D

844 *Material.* Four specimens (NBMG 19999–12002).

845 *Diagnosis.* Short cylindrical coprolites with the posterior end, rounded, and the anterior end,

846 slightly to strongly tapered.

Description. Light grey, calcareous coprolites, comprising a short cylindrical morphology

with two rounded ends or an anterior taper resulting in a tear drop shape (Coprolite Types B1

and B2 of Hunt and Lucas 2012*a*). Coprolites are 20 to 60 mm long and 6 to 20 mm diameter,

and comprise a dense, solid posterior mass and a more diffuse anterior zone (Fig. 16D).

Invertebrate fragments, < 1 mm in granularity, are abundant, especially at the anterior end and

include recognisable microconchids and bivalve fragments, possibly of *Naiadites* type (Fig.

16C).

Remarks. The calcareous composition, and the presence of recognisable shelly fragments,

indicates that the producer fed on invertebrates. The producer cannot be identified but the

crushed shelly components suggest a duraphagous habit facilitated by grinding tooth plates,

most consistent with the *Ctenodus* lungfish. The size of the coprolite suggests that the fish

that produced it was relatively large.

<div align="center">Subspherical coprolites</div>

<div align="center">Figure 16F–G</div>

Material. One specimen (NBMG 19824).

Diagnosis. Short coprolite, approximately as wide as tall, rounded in all dimensions, showing

a bilobed external appearance.

Description. The specimen is somewhat nondescript, and can simply be termed 'round', or as

a subrounded small pellet (category C1), using the shape scheme of Hunt and Lucas (2012*a*,

b). The coprolite is bilobed, with two equal-sized subspherical portions largely overlapping,

and presumably reflecting the original structure. It measures 19 x 22 mm, and is, at most, 7

mm thick. The thickness is probably reduced by compaction and by breakage; one side

appears to be external, the other internal (Fig. 16F), showing numerous broken pieces of

bone, scales, and teeth preserved. These fish skeletal fragments (Fig. 16G) include a portion

871 of a ridged tooth, preserved shiny and black, possibly from a rhizodont, as well as

872 unidentifiable portions of scales and bones.

873 *Remarks*. The coprolite is not especially distinctive; however, based on its size and its

874 contents, it is assignable to a relatively large predatory fish, perhaps a xenacanth shark or

875 rhizodont.

876

877 **DOMINANCE-DIVERSITY ANALYSIS**

878 The taxonomic make-up of a total of 483 hand specimens, each containing at least one

879 fish fragment, was analysed, quantitatively, at order/class and generic level, with

880 indeterminate material discarded (Table 2). At order/class level, the assemblage (n = 288

881 identifiable hand specimens) is dominated by chondrichthyans (70.5 %), with common

882 sarcopterygians (20.5 %) and rare actinopterygians (7.6 %) and acanthodians (1.4 %). At

883 generic level (n = 182 identifiable hand specimens), chondrichthyans are even more dominant

884 with *Ageleodus* (37.0 %) and *Orthacanthus* (39.2 %) comprising nearly four fifths of the

885 assemblage, while four sarcopterygians, *Rhizodus* (8.8 %), *Strepsodus* (5.0 %), *Megalichthys*

886 (2.8 %), and *Archichthys* (2.8 %) make up most of the rest of the total.

887 In order to examine palaeoecological patterns, specimens were assigned to one of the

888 four sedimentary facies (Supplementary Dataset 1) and analysed in a palaeoenvironmental

889 context: shallow marine (Lithology 1), brackish embayment facies (Lithology 2), or brackish

890 tidal estuary (Lithology 3 and 4). We note that analysis of the facies distribution of fishes

891 across this offshore to onshore salinity gradient is hampered by the fact that three-quarters of

892 determinate specimens derive from the brackish embayment facies (Lithology 2) whereas

893 fossils in the offshore shallow marine facies (Lithology 1) and onshore tidal estuary facies

894 (Lithology 3 and 4) are relatively rare. Acknowledging this limitation, genus-level data was

895 analysed using the inverse of the Simpson Index given by the equation:

896
$$D = 1 - \left(\sum \frac{n(n-1)}{N(N-1)} \right)$$

897 where n is the total number of specimens of a particular genus and N is the total number of

898 specimens of all genera. This analysis shows that diversity is highest in the shallow marine

899 environment (D = 0.805) and progressively declines in the brackish embayment (D = 0.641)

900 and tidal estuary (D = 0.428). Examining these data qualitatively also reveals patterns. It is

901 noteworthy that both shark genera, *Ageleodus* and *Orthacanthus*, are distributed across the

902 salinity gradient (Lithology 1 – 4) in relatively high proportions. In contrast, some

903 acanthodians (*Gyrancanthides*), dipnoans (*Ctenodus*), rhizodonts (*Archichthys*, *Strepsodus*)

904 and *Megalichthys* occur in higher proportions in the marine facies (Lithology 1) while some

905 other rhizodonts (*Rhizodus*, *Rhizodopsis*) are more common in brackish tidal estuaries.

906

907 **DISCUSSION**

908 In this paper, we document a new diverse assemblage of fish in its facies context in the

909 Pennsylvanian (early Moscovian) Minto Formation of New Brunswick, Canada. Findings

910 improve knowledge of the biodiversity, food webs, and ecology of fish communities during a

911 critical evolutionary phase.

912

913 *Biodiversity and food webs*

914 Based on specimen counts, the dominant fish were chondrichthyans, comprising 70.5 % of

915 the assemblage based on class-level counts. Two genera are co-dominant. Most common

916 (39.2 %) is *Orthacanthus*, a large predatory shark that reached its acme in Pennsylvanian

917 times. The diet of *Orthacanthus* was diverse including actinopterygians, acanthodians,

918 dipnoans, xenacanthids, and tetrapods, based on analysis of coprolites (Williams 1972;

919 Hampe 1988; Johnson 1999) and gut contents (Kriwet *et al.* 2008). The presence of suspected

juvenile xenacanthid remains in heteropolar microspiral coprolites reported from the Minto

Formation adds another dimension to our understanding of *Orthacanthus* behaviour. It

suggests the genus was practising filial cannibalism of juvenile xenacanthids (as postulated at

other sites; Hampe 1988; Soler-Gijon 1995; Heidke 1998; Johnson 1999; Beck *et al.* 2014),

and may have been predating xenacanthid within protected nurseries developed within tidal

estuaries (cf. Carpenter *et al.* 2014). The ecology of the other abundant shark, *Ageleodus*,

remains completely unknown, and there is even uncertainty as to whether skeletal elements

represent teeth or specialised brachial denticles (Lebedev 1996; Turner 2013). The other

common component (20.5 %) of the assemblage comprises diverse sarcopterygians

(rhizodontids, megalichthyids, rhizodopsids), which were, also, large predatory fish. The

dominance of large predators (secondary and tertiary consumers) is inconsistent with a

normal trophic pyramid. However, this inverted structure is commonly reported for

Pennsylvanian assemblages (e.g., Carpenter *et al.* 2015), and may simply reflect a much

lower preservation potential of, most soft-bodied, producers and primary consumers.

Within the fish assemblage, primary consumers are represented by actinoptygians (7.6

%) and acanthodians (1.4 %), which likely fed on plankton, and the dipnoan, *Ctenodus*,

whose crushing/grinding dentition suggests a duraphagous mode of life. Dipnoans were the

most likely producer of the short ellipsoid coprolites that contain fragmentary invertebrate

remains (microconchids, bivalves) and rare fish fragments. A *Ctenodus* tooth plate (NBMG

10740) into which a tiny xenacanthid tooth is embedded, suggests that these lungfish may

also have predated juvenile sharks.

Euryhaline tolerances

The fish assemblage dates from the Bashkirian-Moscovian acme of a major diversification

event within brackish/freshwater environments (Falcon-Lang *et al.* 2015*a*). A key feature of

945   this phase of coastal invasion was the apparent widespread adoption of a euryhaline habit

946   with diverse marine-based organisms exploring lower salinity waters along coasts and

947   estuaries (Bennett *et al.* 2012; Davies and Gibling 2013; Falcon-Lang *et al.* 2015*a*; Minter *et*

948   *al.* 2016; Gierlowski-Kordesch *et al.* 2016). However, there is considerable disagreement as

949   to whether Carboniferous fish communities documented from continental facies were part of

950   this euryhaline invasion. Some authors agree that fish communities were, indeed, temporary

951   visitors from adjacent marine environments because their cosmopolitan distribution implies

952   dispersal via marine seaways (Schultze 2009; Carpenter *et al.* 2011, 2014, 2015). In contrast,

953   others have maintained that they comprised elements of an endemic freshwater ecosystem

954   because the strontium isotope ratio ($^{87}Sr/^{86}Sr$) of apatite tooth enamel (0.70824 to 0.71216)

955   suggests substantial contact with continental-influenced water bodies (Masson and Rust 1984;

956   Štamberg and Zajíc 2008; Fischer *et al.* 2011, 2013; Montañez and Cecil 2013).

957   Quantitative analysis of fish remains in a detailed facies context, reported here,

958   provides unequivocal demonstration that, at least, some fish taxa were euryhaline, but also

959   reveals previously unsuspected ecological heterogeneity. Chondrichthyians appear to have

960   been particularly successful in colonising the full salinity gradient, and both *Orthacanthus*

961   and *Ageleodus* have been found in apparently freshwater fluviolacustrine facies upstream of

962   the marine coast at other sites (Carpenter *et al.* 2014; ref). This is also the case for

963   *Acanthodes*, which been reported from a variety of lacustrine, fluvial, estuarine/deltaic, and

964   fully marine settings (Zidek 1976; Beznosov 2009; Burrow *et al.* 2010; Sallan *et al.* 2010). In

965   contrast, while also likely euryhaline, some acanthodians (*Gyrancanthides*), dipnoans

966   (*Ctenodus*), rhizodonts (*Archichthys*, *Strepsodus*) and *Megalichthys* appear to have been

967   better adapted to marine environments, while some other rhizodonts (*Rhizodus*, *Rhizodopsis*)

968   appear to be better suited to life in brackish tidal estuaries based on facies distribution data

969   (Table 1). This heterogeneity is reflected by the Simpson Index, which shows that fish

Formatted: Font: Italic

Formatted: Highlight

diversity declines from open marine environments towards more variably saline estuaries, suggesting that not all taxa were equally successful at infiltrating brackish water coastal tracts.

The inferred widespread euryhalinity of Carboniferous fish in the Minto Formation helps resolve the long-running debate regarding ecology. If the taxa were freely migrating beneath marine and freshwater settings, or even occupying brackish coastal settings, it is possible for them to both have a marine-based dispersal pattern but also show strontium isotope values (Schmitz et al. 1991) indicative of continental/freshwater influences.

Minto Acanthodidids

The Acanthodidae were a highly cosmopolitan mid to late Palaeozoic group, representatives of which have been found on every continent except South America (Denison 1979; Long 1986; Burrow *et al.* 2008; Sallan *et al.* 2010); first appearing in the Middle Devonian, this was the only acanthodiform family to persist into the Carboniferous and Permian (Beznosov 2009; Sallan *et al.* 2010). The best known acanthodidid genus, *Acanthodes,* was widely distributed, occurring in Australia, South Africa, Europe, North America, Greenland, and Siberia from the Middle Devonian to the late Permian (Denison 1979; Sallan *et al.* 2010). However, the earliest known articulated specimens (*Acanthodes lopatini* Rohon, 1889) are from the Tournaisian of south-central Siberia (Beznosov 2009) and many earlier isolated scales and ichthyoliths assigned to *Acanthodes* sp. are considered doubtful (Burrow *et al.* 2010).

Acanthodes has not hitherto been reported from Canada, and the family Acanthodidae is known only from a single Tournaisian locality at Blue Beach, Nova Scotia (Zidek 1977; Mansky and Lucas 2013). This is surprising, firstly because other acanthodian groups are well represented through the Devonian and Carboniferous (Gardiner 1966; Denison 1979; Gagnier

and Wilson 1996; Hanke 2008; Kennedy *et al.* 2012; Carpenter *et al.* 2015), and secondly because *Acanthodes* was distributed widely in North America (USA) and Europe (Germany, UK, Czech Republic) at this time (Denison 1979). Given *Acanthodes'* apparent ability, as a genus, to tolerate a wide range of salinity conditions, there was no obvious obstacle to prevent it from reaching Canada. The Acanthodid remains at Horton Bluff are tantalising, because if they are in fact referable to *Acanthodes* this would indicate a substantial ghost lineage, and suggest the lack of specimens from this interval is the result of collection failure or taphonomic bias; it is to be hoped that further investigations at Blue Beach will provide determinable material which will resolve this issue.

Evolutionary implications

The Maritimes Basin of Canada is a particularly informative area for studying the evolution and ecology of fish populations during the mid-Carboniferous diversification into brackish coastal waters. This depocentre is positioned near the continental interior of Pangaea (Falcon-Lang *et al.* 2006) but was intermittently connected to marine water bodies in the course of glacio-eustatic and tectonic fluctuations (Gibing *et al.* 2008). Fully marine incursions occurred only during three brief intervals, during part of the Visean (Windsor Group), the Bashkirian (Joggins and Tynemouth Creek formations; Grey *et al.* 2011; Falcon-Lang et al. 2015*b*) and early Moscovian stages (Minto Formation; this paper). However, brackish incursions were far more common, spanning the entire Carboniferous interval (Archer *et al.* 1995; Tibert and Scott 1999; Falcon-Lang *et al.* 2006; McIlroy and Falcon-Lang 2006; Gibling *et al.* 2008), and reflecting the periodic development of a brackish epicontinental sea, in some ways, analogous to the present-day Baltic Sea (Calder 1998; Falcon-Lang 2005).

These brackish-marine incursions contain rich but fragmentary fish faunas (summarised in Fig. 17; see references in figure caption). A remarkable feature of these

faunas in their conservative composition, with a consistent collection of taxa assembled by

Serpukhovian times (fauna of Pomquet Formation) and persisting for 20 millon years, with

minimal variation, until late Moscovian times (fauna of Sydney Mines Formation).

CONCLUSIONS

1. We describe a new fish fauna from the Carboniferous (Pennsylvanian; early
   Moscovian) Minto Formation of New Brunswick, Canada

2. The fauna includes chondrichthyans (xenacanthids, and the enigmatic *Ageleodus*),
   acanthodians (gyracanthids and acanthodiforms), sarcopterygians (rhizodontids,
   megalichthyids, rhizodopsids, and dipnoans), and actinopterygians.

3. Facies analysis of taxa across a brackish-marine palaeosalinity gradient demonstrate
   that almost all taxa were euryhaline, with chondrichthyans especially well equipped to
   traverse into non-marine environments

4. Documentation of widespread euryhalinity resolves a long-running debate about the
   ecology of Carboniferous fishes, explaining how strontium isotope analyses of tooth
   enamel indicate continental influence when other data point to marine dispersal.

5. In the context of other rich Carboniferous fish faunas of the Maritimes Basin of
   Atlantic Canada, fossils show the assembly of a conservative range of euryhaline taxa
   over the 20 million year of the mid-Carboniferous diversification event into non-
   marine settings.

RANDY NOTES TO DEAL WITH LATER: I assume that shark teeth may be better preserved
and easier to spot than bits and bobs of other fish – there may be a preservation bias that inflates
the numbers; Just to note then that Naiadites that is figured and any others are from Lithology 1 at
Coal Creek

1045

1058

1059 **DATA ARCHIVING STATEMENT**

1060 Data for this study are available in the Dryad Digital Repository: http://dx.doi.org/xxxx

1061

1062 **REFERENCES**

1063 AGASSIZ, L. J. R. 1843*a* (1837–1843). *Recherches sur les poissons fossiles*, **3**. Petitpierre,

1064 Neuchâtel et Soleure, viii + 390 + 32 pp.

1065 — 1843*b* (1837–1843). *Recherches sur les poissons fossiles*, **2**. Petitpierre, Neuchâtel et

1066 Soleure, xii + 310 + 336 pp.

1067 AHLBERG, P. E. 1991. A re-examination of sarcopterygian interrelationships, with special

1068 reference to the Porolepiformes. *Zoological Journal of the Linnean Society*, **103**, 241–

1069 287.

1070 ALGEO, T. J. and SCHECKLER, S. E. 1998. Terrestrial-marine telecommunications in the

1071 Devonian: Links between the evolution of land plants, weathering processes, and marine

1072 anoxic events. *Philosophical Transactions of the Royal Society, London, Series B*,

1073 **353**, 113–130.

1074 ANDERSON, L. I. and SHUSTER, C. N. 2003. Throughout geological time: where have they

1075 lived. *In* SHUSTER, C. N., BARLOW, R. B., and BROCKMANN, H. J. (eds.), *The*

1076 *American Horseshoe Crab.* Harvard University Press, Cambridge, Massachusetts, 189–

1077 223.

1078 ANDERSSON, P. S., WASSERBURG, G. J. and INGRI, J. 1992. The sources and transport

1079 of Sr and Nd isotopes in the Baltic Sea. *Earth and Planetary Science Letters*, **113**, 459–

1080 472.

1081 — , — and STORDAL, M. C. 1994. Strontium, dissolved and particulate loads in fresh and

1082 brackish waters: the Baltic Sea and Mississippi Delta. *Earth and Planetary Science*

1083 *Letters*, **124**, 195–210.

1084 ANDREWS, S. M. 1985. Rhizodont crossopterygian fish from the Dinantian of Foulden,

1085 Berwickshire, Scotland, with a re-evaluation of this group. *Transactions of the Royal*

1086 *Society of Edinburgh, Earth Sciences*, **76**, 67–95.

1087 — and WESTOLL, T. S. 1970. The postcranial skeleton of rhipidistian fishes excluding

1088 *Eusthenopteron*. *Transactions of the Royal Society of Edinburgh*, **68**, 391–489.

1089 ARCHER, A. W., CALDER, J. H., GIBLING, M. R., NAYLOR, R. D., REID, D. R. and

1090 WIGHTMAN, W. G. 1995. Invertebrate trace fossils and agglutinated foraminifera as

indicators of marine influences within the classic Carboniferous section at Joggins, Nova Scotia, Canada. *Canadian Journal of Earth Sciences*, **32**, 2027–2039.

BAILEY, L.W. and MATTHEW, G. F. 1873. Report of observations on the Carboniferous system of New Brunswick in the counties of Queens, Sunbury and a portion of York. *Geological Survey of Canada, Report of Progress for 1872–1873*, Part 8, 180–230.

BAIRD, D. 1962. A haplolepid fish fauna in the Early Pennsylvanian of Nova Scotia. *Palaeontology*, **5**, 22–29.

— 1978. Studies on Carboniferous freshwater fishes. *American Museum Novitates*, **1641**, 1–22.

BALL, F. D., SULLIVAN, R. M. and PEACH, A. R. 1981. Carboniferous Drilling Project. Report Investigation 18. New Brunswick Department of Natural Resources, 109 pp.

BARKAS, T. P. 1869. *Ctenodus interruptus. Scientific Opinion*, **2**, 113–114.

BASHFORTH, A. R., CLEAL, C. J., GIBLING, M. R., FALCON-LANG, H. J., MILLER, R. F., 2014. Early Pennsylvanian plant communities on a seasonal tropical fluvial landscape (Tynemouth Creek Formation, New Brunswick, Canada). *Review of Palaeobotany and Palynology,* **200**, 229–263.

BECK, K. G., SOLER-GIJÓN, R., CARLUCCI, J. R. and WILLIS, R. E. 2014. Morphology and histology of dorsal spines of the xenacanthid shark *Orthacanthus platypternus* from the Lower Permian of Texas, USA: palaeobiological and palaeoenvironmental implications. *Acta Palaeontologica Polonica*, **61**, 97–117.

BENNETT, C. E., SIVETER, D.J., DAVIES, S. J., WILLIAMS, M., WILKINSON, I. P., BROWNE, M. and MILLER, C. G. 2012. Ostracods from freshwater and brackish environments of the Carboniferous of the Midland Valley of Scotland: the early colonization of terrestrial water bodies. *Geological Magazine*, **149**, 366–396.

1115 BERG, L. S. 1937. A classification of fish-like vertebrates. *Bulletin de l'Académie des*

1116 *Sciences de l'URSS*, **20**, 1277–1280.

1117 — 1940. Classification of fishes, both living and fossil. *Trudy Zoologischeskovo Instituta*, **5**,

1118 85–517.

1119 BEZNOSOV, P. 2009. A redescription of the Early Carboniferous acanthodian *Acanthodes*

1120 *lopatini* Rohon, 1889. *Acta Zoologica*, **90**, 183–193.

1121 BINNEY, E. W. 1841. On the fossil fishes of the Pendleton coal field. *Transactions of the*

1122 *Manchester Geological Society*, **1**, 153–178.

1123 BONAPARTE, C. L. 1838. *Iconografia della fauna Italiana per le quattro classi degli*

1124 *Animali Vertebrati, 3*. Salviucci, Rome, 266 pp.

1125 BRAZEAU, M. D. 2005. A new genus of rhizodontid (Sarcopterygii, Tetrapodomorpha) from

1126 the Lower Carboniferous Horton Bluff Formation of Nova Scotia, and the evolution of

1127 the lower jaws in this group. *Canadian Journal of Earth Sciences*, **42**, 1481–1499.

1128 BUATOIS, L. A., MÁNGANO, M. G., GENISE, J. F. and TAYLOR, T. N. 1998. The

1129 ichnological record of the continental invertebrate invasion: evolutionary trends,

1130 environmental expansion, ecospace utilization, and behavioral complexity. *Palaios*, **13**,

1131 217–240.

1132 —, GINGRAS, M. K., MACEACHERN, J., MÁNGANO, M. G., ZOONEVELD, J. P.,

1133 PEMBERTON, S. G., NETTO, R. G., MARTIN, A., 2005. Colonization of brackish-

1134 water systems through time: evidence from the trace-fossil record. *Palaios*, **20**, 321–347.

1135 BURROW, C. J., LONG, J. L. AND TRINAJSTIC, K. 2008. Disarticulated acanthodian and

1136 chondrichthyan remains from the upper Middle Devonian Aztec Siltstone, Southern

1137 Victoria Land, Antarctica. *Antarctic Science*, **21**, 71–88.

1138 —, TURNER, S. and YOUNG, G. C. 2010. Middle Palaeozoic microvertebrate assemblages

1139 and biogeography of East Gondwana (Australasia, Antarctica). *Palaeoworld*, **19**, 37–54.

CALDER, J. H. 1998. The Carboniferous evolution of Nova Scotia. 261–302. *In*
BLUNDELL, D. J. and SCOTT, A. C. (eds.). *Lyell: the past is the key to the present.*
Geological Society of London, Special Publication, **143**, 376 pp.

CALVER, M. A. 1968. Invertebrate faunas. 147–177. *In* MURCHISON, D. and WESTOLL,
T. S. (eds.) *Coal and coal-bearing strata*. Oliver and Boyd, Edinburgh, 418 pp.

CARPENTER, D. K., FALCON-LANG, H. J., BENTON, M. J. and NELSON, W. J. 2011.
Fishes and tetrapods from the Pennsylvanian (Kasimovian) Cohn Coal Member of the
Mattoon Formation, Illinois, USA: systematics, palaeoecology and palaeoenvironments.
Palaios, **26**, 639–658.

—, —, —, and HENDERSON, E. 2014. Carboniferous (late Tournaisian) fish assemblages
from the Isle of Bute, Scotland: systematics and palaeoecology. *Palaeontology*, **57**,
1215–1240.

—, —, —, and GREY, M. 2015. Early Pennsylvanian (Langsettian) fish assemblages from
the Joggins Formation, Canada, and their implications for palaeoecology and
palaeogeography. *Palaeontology*, **58**, 661–690.

CARROLL, R. L., BELT, E. S., DINELEY, D. L., BAIRD, D. and MCGREGOR, D. C.
1972. *Field excursion A59, vertebrate paleontology of Eastern Canada*, *guidebook*. 24th
International Geological Congress, Montreal, 113 pp.

CHOO. B. 2011. Revision of the actinopterygian genus *Mimipiscis* (=*Mimia*) from the Upper
Devonian Gog formation of Western Australia and the interrelationships of the early
Actinopterygii. *Earth and Environmental Science Transactions of the Royal Society of
Edinburgh*, **102**, 77–104.

— 2015. A new species of the Devonian actinopterygian *Moythomasia* from Bergisch
Gladbach, Germany, and fresh observations on *M. durgaringa* from the Gogo Formation

of Western Australia. *Journal of Vertebrate Paleontology*, **35**, e952817 (doi: 10.
1080/02724634.2015.952817).

—, LONG, J.A. and TRINAJSTIC, K. 2009. A new genus and species of basal
actinopterygian fish from the Upper Devonian Gogo Formation of Western Australia.
Acta Zoologica, **90** (Suppl 1), 194–210.

CLARK, P. 2004. *The Sedimentology of Minto Salmon Harbour Mine site and its high sulfur coals*. Unpublished Honours thesis, University of New Brunswick, Fredericton, New Brunswick, 74 pp.

COPE, E. D. 1887. Geology and palaeontology. *American Naturalist*, **1887**, 1014–1019.

COSTAIN, T. 2000. *Stratigraphic analysis and possible tidal influences in the Thorburn Member and Coal Brook Member, Stellarton Formation, Nova Scotia.* Unpublished BSc thesis, Dalhousie University, 77 pp.

DAVIES, N. S. and GIBLING, M. R. 2013. The sedimentary record of Carboniferous rivers: continuing influence of land plant evolution on alluvial processes and Palaeozoic ecosystems. *Earth Science Reviews*, **120**, 40–79

DAVIES, S. J. and GIBLING, M. R. 2003. Architecture of coastal and alluvial deposits in an extensional basin: the Carboniferous Joggins Formation of eastern Canada. *Sedimentology*, 50, 415–439.

DAWSON, J. W. 1868. *Acadian Geology* or *The Geology of Nova Scotia, New Brunswick and Prince Edward Island*, 2nd Edition. Oliver and Boyd, Edinburgh, 694 p.

DENISON, R. 1979. Acanthodii. 1–62. *In* SCHULTZE, H-P. (ed.). *Handbook of Paleoichthyology Volume 5*. Gustav Fischer Verlag, Stuttgart and New York, 62 pp.

DICK, J. R. F. 1981. *Diplodoselache woodi* gen. et sp. nov., an early Carboniferous shark from the Midland Valley of Scotland. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **72**, 99–113.

1189 DOWNS, J. P. and DAESCHLER, E. B. 2001. Variation within a large sample of *Ageleodus*

1190   *pectinatus* teeth (Chondrichthyes) from the late Devonian of Pennsylvania, USA. *Journal*

1191   *of Vertebrate Paleontology*, **21**, 811–814.

1192 EDWARDS, S. L. and MARSHALL, W. S. 2013. Principles and patterns of osmoregulation

1193   and euryhalinity in fishes. 1–44. *In* McCORMICK, S. D., FARRELL, A.P., and

1194   BRAUNER, C.J. (eds.), *Fish Physiology, Vol. 32, Euryhaline Fishes*, Elsevier, New

1195   York.

1196 FALCON-LANG, H. J. 2005. Small cordaitalean trees in a marine-influenced coastal habitat

1197   in the Pennsylvanian Joggins Formation, Nova Scotia, Canada. *Journal of the Geological*

1198   *Society, London*, **162**, 485–500.

1199 — 2009. The earliest history of coal mining and grindstone quarrying at Joggins, Nova Scotia

1200   and its implications for the meaning of the place-name "Joggins". *Atlantic Geology*, **45**,

1201   1–21.

1202 — BENTON, M. J., BRADDY, S. J. and DAVIES, S. J. 2006. The Pennsylvanian tropical

1203   biome reconstructed from the Joggins Formation of Canada. *Journal of the Geological*

1204   *Society, London*, **163**, 561–576.

1205 — MINTER, N. J., BASHFORTH, A. R., GIBLING, M. R., MILLER, R. F. 2015*a*. Mid-

1206   Carboniferous diversification of continental ecosystems inferred from trace fossil suites

1207   in the Tynemouth Creek Formation of New Brunswick, Canada. *Palaeogeography,*

1208   *Palaeoclimatology, Palaeoecology*, **440**, 142–160.

1209 — , PUFAHL, P. K., BASHFORTH, A. R., GIBLING, M. R., MILLER, R. F. and MINTER,

1210   N.J. 2015*b*. A marine incursion in the Lower Pennsylvanian Tynemouth Creek

1211   Formation, Canada: implications for paleogeography, stratigraphy and paleoecology.

1212   *Palaios*, **30**, 779–791.

1213 FIELDING, C.R., FRANK, T.D., BIRGENHEIER, L.P., RYGEL, M.C., JONES, A.T. and

1214   ROBERTS, J. 2008. Stratigraphic imprint of the Late Palaeozoic Ice Age in eastern

1215   Australia: a record of alternating glacial and nonglacial climate regime. *Journal of the*

1216   *Geological Society*, **165**, 129–140.

1217   FISCHER, J., VOIGT, S., SCHNEIDER, J.W., BUCHWITZ, M. and VOIGT, S. 2011. A

1218   selachian freshwater fauna from the Triassic of Kyrgyzstan and its implication for

1219   Mesozoic shark nurseries. *Journal of Vertebrate Paleontology*, **31**, 937-953.

1220   —, SCHNEIDER, J. W., VOIGT. S., JOACHIMSKI, M. M., TICHOMIROWA, M.,

1221   TUTKEN, T., GOTZE, J. and BERNER, U. 2013. Oxygen and strontium isotopes from

1222   fossil shark teeth: Environmental and ecological implications for Late Palaeozoic

1223   European basins. *Chemical Geology*, **342**, 44–62.

1224   FOX, R. C., CAMPBELL, K. S. W., BARWICK, R. E. and LONG, J. A. 1995. A new

1225   osteolepiform fish from the Lower Carboniferous Raymond Formation, Drummond

1226   Basin, Queensland. *Memoirs of the Queensland Museum*, **38**, 99–221.

1227   GAGNIER, P-Y. and WILSON, M. V. H. 1996. Early Devonian acanthodians from northern

1228   Canada. *Palaeontology*, **39**, 241–258.

1229   GARDINER, B. G. 1966. *Catalogue of Canadian fossil fishes.* Contribution No. 68, Life

1230   Sciences. Royal Ontario Museum, University of Toronto, 154 pp.

1231   — 1984. The relationship of the palaeoniscid fishes, a review based on new specimens of

1232   *Mimia* and *Moythomasia* from the Upper Devonian of western Australia. *Bulletin of the*

1233   *British Museum, Natural History (Geology)*, **37**, 173–428

1234   — and SCHAEFFER, B. 1989. Interrelationships of lower actinopterygian fishes. *Zoological*

1235   *Journal of the Linnean Society*, **97**, 135–187.

1236   GENSEL, P. G. and EDWARDS, D. 2001. *Plants invade the land*. Columbia University

1237   Press, New York, 304 pp.

1238   GESNER, A. 1841. *Third report on the Geological Survey of the Province of New Brunswick.*

1239   Henry Chubb, Saint John, New Brunswick, 88 pp.

1240   GIBLING, M. R. and KALKREUTH, W .D. 1991. Petrology of selected carbonaceous

1241   limestones and shales in Late Carboniferous coal basins of Atlantic Canada.

1242   *International Journal of Coal Geology*, **17**, 239–271.

1243   — and RUST, B. R. 1992. Silica-cemented palaeosols (ganisters) in the Pennsylvanian

1244   Waddens Cove Formation, Nova Scotia, Canada. *In* WOLF, K. H. and

1245   CHILINGARIAN, G. V. (eds), *Diagenesis III: Developments in Sedimentology 47*,

1246   Amsterdam, Elsevier, p. 621–655.

1247   — CALDER, J. H., RYAN, R., VAN DER POLL, H. W. and YEO, G. M. 1992. Late

1248   Carboniferous and Early Permian drainage patterns in Atlantic Canada. *Canadian*

1249   *Journal of Earth Sciences*, **29**, 338–352.

1250   — CULSHAW, N., RYGEL, M. C. and PASCUCCI, V. 2008. The Maritimes Basin of

1251   Atlantic Canada: basin creation and destruction in the collisional zone of Pangea. 211–

1252   244. *In* MIALL, A. D. (ed.). *The sedimentary basins of the United States and Canada*.

1253   Elsevier, Oxford, 624 pp.

1254   GIERLOWSKI-KORDESCH, E. H. and CASSLE, C. F. 2015. The "*Spirorbis*" problem

1255   revisited: sedimentology and biology of microconchids in marine-nonmarine transitions.

1256   *Earth-Science Reviews*, **148**, 209–227.

1257   — FALCON-LANG, H. J. and CASSLE, C. F. 2016. Reply to comment on the paper of

1258   Gierlowski and Cassle, The "*Spirorbis*" problem revisited [Earth-Science Reviews, 148,

1259   209–227]. *Earth-Science Reviews*, **152**, 201–204]

1260   GRAY, T. R., DOSTAL, J., McLEOD, M., KEPPIE, D. and ZHANG, Y. 2012.

1261   Geochemistry of Carboniferous peralkaline felsic volcanic rocks, central New

1262   Brunswick, Canada: examination of uranium potential. *Atlantic Geology*, **46**, 173–184.

1263 GREINER, H. 1977. Crossopterygian fauna from the Albert Formation, New Brunswick,

1264 Canada, and its stratigraphic-paleoecologic significance. *Journal of Paleontology*, **51**,

1265 44–56.

1266 GREY, M., PUFAHL, P. K. and AZIZ, A. A. 2011. Using multiple environmental proxies to

1267 determine degree of marine influence and paleogeographical position of the Joggins

1268 Fossil Cliffs UNESCO World Heritage Site. *Palaios*, **26**, 256–263.

1269 HACQUEBARD, P. A. and BARSS, M. S. 1970. Paleogeography and facies aspects of the

1270 Minto Coal seam, New Brunswick, Canada, C.R. *Sixth International Congress of*

1271 *Carboniferous Stratigraphy and Geology*, **3**, 861–872.

1272 HAMPE, O. 1988. Über die Bezahnung des *Orthacanthus* (Chondrichthyes: Xenacanthida;

1273 Oberkarbon-Unterperm). *Paläontologische Zeitschrift*, **62**, 285–296.

1274 HANCOCK, A. and ATTHEY, T. 1870. Note on an undescribed fossil fish from the

1275 Newsham coal-shale near Newcastle-upon-Tyne. *Annals and Magazine of Natural*

1276 *History Series 4*, **5**, 266–268.

1277 HANKE, G. F. 2008. *Promesacanthus eppleri* n. gen., n. sp., a mesacanthid (Acanthodii,

1278 Acanthodiformes) from the Lower Devonian of northern Canada. *Geodiversitas*, **30**,

1279 287–302.

1280 HAY, O. P. 1902. Bibliography and catalogue of the fossil Vertebrata of North America.

1281 *Bulletin of the United States Geological Survey*, **179**, 1–868.

1282 HEIDKE, U. H. J. 1998. Revision of the genus *Orthacanthus* Agassiz 1843 (Chondrichthyes:

1283 Xenacanthida). *Paläontologische Zeitschrift*, **72**, 135–147.

1284 HOLLAND, T., WARREN, A., JOHANSON, Z., LONG, J., PARKER, K. and GARVEY, J.

1285 2007. A new species of *Barameda* (Rhizodontida) and heterochrony in the rhizodontid

1286 pectoral fin. *Journal of Vertebrate Paleontology*, **27**, 295–315.

— LONG, J. and SNITTING, D. 2010. New information on the enigmatic tetrapodomorph fish *Marsdenichthys longioccipitus* (Long 1985). *Journal of Vertebrate Paleontology*, **30**, 68–77.

HUNT, A. P. and LUCAS, S. G. 2012*a*. Descriptive terminology of coprolites and Recent feces. *New Mexico Museum of Natural History and Science, Bulletin*, **57**, 153–160.

— and — 2012*b*. Classification of vertebrate coprolites and related trace fossils. *New Mexico Museum of Natural History and Science, Bulletin*, **57**, 137–146.

—, —, SPIELMANN, J. A., CANTRELL, A., SUAZO, T. and LERNER, A. J. 2012. Bromalites from the Tinajas Lagerstätte (Late Pennsylvanian: Late Missourian), central New Mexico, USA. *New Mexico Museum of Natural History and Science, Bulletin*, **57**, 175–183.

HUXLEY, T. H. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata, and more particularly of the Mammalia. *Proceedings of the Zoological Society of London*, **1880**, 649–662.

— and ETHERIDGE, R. 1865. *A catalogue of the collection of fossils in the Museum of Practical Geology, with an explanatory introduction*. G. E. Eyre and W. Spottiswoode, London, 381 pp.

JANVIER, P. 1996. *Early vertebrates*. Oxford Monographs on Geology and Geophysics, **33**, 393 pp.

JEFFERY, J. E. 2003. Mandibles of rhizodontids: anatomy, function, and evolution within the tetrapod stem-group. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **93**, 255–276.

— 2006. The Carboniferous fish genera *Strepsodus* and *Archichthys* (Sarcopterygii: Rhizodontida): clarifying 150 years of confusion. *Palaeontology*, **49**, 113–132.

1311 JEPPSSON, L., FREDHOLM, D. and MATTIASSON, B. 1985. Acetic acid and phosphatic

1312   fossils – a warning. *Journal of Paleontology*, **59**, 952–956.

1313 JOHANSON, Z. and AHLBERG, P. E. 2001. Devonian rhizodontids and tristichopterids

1314   (Sarcopterygii; Tetrapodomorpha) from East Gondwana. *Transactions of the Royal*

1315   *Society of Edinburgh, Earth Sciences*, **92**, 43–74.

1316 JOHNSON, G. D. 1979. *Early Permian vertebrates from Texas: Actinopterygii*

1317   *(Schaefferichthys), Chondrichthyes (including North American Pennsylvanian and*

1318   *Triassic Xenacanthodii, and Acanthodii).* Unpublished Ph.D. thesis, Southern Methodist

1319   University, Dallas, Texas, 653 pp.

1320 —— 1999. Dentitions of Late Palaeozoic *Orthacanthus* species and new species of

1321   ?*Xenacanthus* (Chondrichthyes: Xenacanthiformes) from North America. *Acta*

1322   *Geologica Polonica*, **49**, 215–266

1323 KALKREUTH, W. MARCHIONI, D. and UTTING, J. 2000. Petrology, palynology, coal

1324   facies, and depositional environments of an Upper Carboniferous coal seam, Minto

1325   Coalfield, New Brunswick, Canada. *Canadian Journal of Earth Sciences*, **37**, 1209–

1326   1228.

1327 KARATAJUTE-TALIMAA, V. N. 1992. The early stages of the dermal skeleton formation

1328   in chondrichthyans. *In* MARK-KURIK, E. (ed.) *Fossil Fishes as Living Animals.*

1329   Proceedings of the II International Colloquium on the study of Palaeozoic fishes, Tallinn,

1330   1898. *Academia*, **1**, 223–231.

1331 KEMP, A. 1996. *Sagenodus* (*Proceratodus*) *carlinvillensis* (Romer and Smith 1934),

1332   (Osteichthyes: Dipnoi), short ridge anomaly and classification of dipnoans. *Journal of*

1333   *Vertebrate Paleontology*, **16**, 16–19.

1334 —— 2003. Development anomalies in the tooth plates and jaw bones of lungfish. *Journal of*

1335   *Vertebrate Paleontology*, **23**, 517–531.

KENNEDY, K. L., MILLER, R. F. and GIBLING, M. R. 2012. Palaeoenvironments of Early Devonian fish and other aquatic fauna of the Campbellton Formation, New Brunswick, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 361–362, 61–72.

KRIWET, J., WITZMANN, F., KLUG, S. and HEIDTKE, U. H. J. 2008. First direct evidence of a vertebrate three-level trophic chain in the fossil record. *Proceedings of the Royal Society B*, **275**, 181–186.

LAMBE, L. M. 1910. Palaeoniscid fishes from the Albert Shales of New Brunswick. *Geological Survery of Canada, Contributions to Canadian Paleontology, Memoir*, **3**, 1–69.

LEBEDEV, O. A. 1996. Fish assemblages in the Tournaisian – Viséan environments of the East European Platform. 387–415. *In* STROGEN, P., SOMERVILLE, I. D. and JONES, G. Ll. (eds.). *Recent advances in Lower Carboniferous geology*. Geological Society Special Publication **107**, The Geological Society Publishing House, Bath, 464 pp.

LEE, C. E. and BELL, M. A. 1999. Causes and consequences of recent freshwater invasions by saltwater animals. *Trends in Ecology and Evolution*, **14**, 284-288.

LONG, J. A. 1986. A new Late Devonian acanthodian fish from Mt. Howitt, Victoria, Australia, with remarks on acanthodian biogeography. *Proceedings of the Royal Society of Victoria*, **98**, 1–17.

MacNAUGHTON, R. B., COLE, J. M., DALRYMPLE, R. W., BRADDY, S. J., BRIGGS, D. E. G., and LUKIE, T. D. 2002. First steps on land: arthropod trackways in Cambrian-Ordovician eolian sandstone, southeastern Ontario, Canada. *Geology*, **30**, 391–394.

MALIVA, R. G. 1989. Displacive calcite syntaxial overgrowths in open marine limestones. *Journal of Sedimentary Research*, **59**, 397–403.

MANSKY, C. F. and LUCAS, S. G. 2013. Romer's Gap revisited: continental assemblages and ichno-assemblages from the basal Carboniferous of Blue Beach, Nova Scotia,

Canada. *In* LUCAS, S. G., DiMICHELE, W. A., BARRICK, J. E., SCHNEIDER, J. W. and SPEILMAN, J. A. (eds.) *The Carboniferous–Permian Transition.* New Mexico Museum of Natural History and Science, **60**, 244–273.

MASSON, A. G. and RUST, B. R. 1984. Freshwater shark teeth as environmental indicators in the Upper Pennsylvanian coal-bearing succession near Sydney, Nova Scotia. *Canadian Journal of Earth Sciences*, **21**, 1151–1155.

McALLISTER, J. A. 1985. Reevaluation of the formation of spiral coprolites. *The University of Kansas Paleontological Contributions*, *Paper,* **114**, 1–12.

— 1987. Phylogenetic distribution and morphological reassessment (SIC) of the intestines of fossil and modern fishes. *Zoologische Jahrbücher. Abteilung für Anatomie und Ontogenie der Tiere*, **115**, 281–294.

McCORMICK, S. D., FARRELL, A. P. and BRAUNER, C. J. (eds) 2013. *Euryhaline fishes*. *Fish Physiology*, **32**, Elsevier, London, 594 pp.

McILROY, D. and FALCON-LANG, H. J. 2006. Discovery and paleoenvironmental implications of a *Zoophycos*-group trace fossil (? *Echinospira*) from the Middle Pennsylvanian Sydney Mines Formation of Nova Scotia. *Atlantic Canada*, **42**, 31–35.

MILLER, R. F. 1999. Report of *Gyracanthus* (Chordata: Acanthodii) and other Upper Carboniferous fish from the Minto Formation, New Brunswick (NTS 21 1/4). 37–43. *In* CARROLL, B. M. W. (ed.). *Current Research 1998*. New Brunswick Department of Natural Resources and Energy, Minerals and Energy Division, Mineral Resource Report **99-4**, New Brunswick Department of Natural Resources and Energy, Fredericton, 163 pp.

— and FORBES, W. H. 2001. An Upper Carboniferous trigonotarbid, *Aphantomartus pustulatus* (Scudder 1884) from the Maritimes Basin (Euramerican Coal Province), New Brunswick, Canada. *Atlantic Geology*, **37**, 191–196.

— and McGOVERN, J. H. 1997. Preliminary report of fossil fish (Actinopterygii:
Palaeonisciformes) from the Lower Carboniferous Albert Formation at Norton, New
Brunswick (NTS 21 H/12). *In* CARROLL. B. M. W. (ed.) *Current Research 1996*. New
Brunswick Department of Natural Resources, Resource Report, **97**, 191–200.

MILLER, M. F. and LABANDEIRA, C. C. 2002. Slow crawl across the salinity divide:
delayed colonization of freshwater ecosystems by invertebrates. *GSA Today*, **12**, 4–10.

MINTER, N. J., BUATOIS, L. A., MÁNGANO, M. G., DAVIES, N. S., GIBLING, M. R.
and LABANDEIRA, C. C. 2016. The establishment of terrestrial ecosystems. In:
MÁNGANO, M.G. and BUATOIS, L.A. (eds.), The trace-fossil record of major
evolutionary events. Topics in Geobiology 39, xxx–xxx. Springer.

MONTAÑEZ, I. P. and CECIL, C. B. 2013. Paleoenvironmental clues archived in non-
marine Pennsylvanian-lower Permian limestones of the Central Appalachian Basin, USA.
International Journal of Coal Geology, **119**, 41–55.

— and POULSEN, C.J. 2013. The Late Paleozoic Ice Age: an evolving paradigm. *Annual
Review of Earth and Planetary Sciences*, **41**, 629–656.

MÜLLER, J. 1845. Über den Bau und die Grenzen der Ganoiden, und über das natürliche
System der Fische. *Archiv für Naturgeschichte*, **1845**, 91–142.

NAYLOR, R. D., ARCHER, A. W., CHANDLER, F. W. and FRALICK, P. W. 1998.
Fluvioestuarine sedimentation in the Late Carboniferous Malagash Formation of Nova
Scotia, Canada. *Nova Scotia Department of Natural Resources, Report of Activities 1998*,
Report ME 1999-1, p. 71–89.

NELSON, J. S. 1976. *Fishes of the world.* Wiley & Sons, New York, 416 pp.

NEWBERRY, J. S. 1856. Description of several new genera and species of fossil fishes, from
the Carboniferous strata of Ohio. *Proceedings of the Academy of Natural Sciences of
Philadelphia*, **8**, 96–100.

ØRVIG, T. 1978. Microstructure and growth of the dermal skeleton in fossil actinopterygian
fishes: *Nephrotus* and *Colobodus*, with remarks on the dentition in other forms.
Zoologica Scripta, **7**, 297–326.

OWEN, R. 1840. *Odontography; or, a treatise on the comparative anatomy of the teeth; their physiological relations, mode of development, and microscopic structure in the vertebrate animals. Volume 1, text*. Hippolyte Baillière, London, 655 pp.

— 1846. *Lectures on the comparative anatomy and physiology of the vertebrate animals delivered at the Royal College of Surgeons, England in 1844 and 1846*. Part 1, fishes. Longman, Brown, Green and Longmans, London, 304 pp.

— 1867. On the dental characters of genera and species, chiefly of fishes, from the Low Main Seam and shales of coal, Northumberland. *Transactions of the Odontological Society of Great Britain*, **1**, 323–391.

PAGEAU, Y. 1969. Nouvelle faune ichthyologique du Dévonien moyen dans les Grès de Gaspé (Québec). II. Morphologie et systématique. Première section: A. Euryptérides, B. Ostracodermes, C. Acanthodiens et Sélaciens. *Naturaliste Canadien*, **96**, 399–478.

PARK, L. E. and GIERLOWSKI-KORDESCH, E. H. 2007. Paleozoic lake faunas: establishing aquatic life on land. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **249**, 160–179.

PATTERSON, C. 1982. Morphology and interrelationship of primitive actinopterygian fishes. *American Zoologist*, **22**, 241–259.

PAWLEY, K. and WARREN, A. A. 2006. The appendicular skeleton of Eryops megacephalus Cope, 1877 (Temnospondyli: Eryopoidea) from the Lower Permian of North America. *Journal of Paleontology*, **80**, 561–580.

PETERSON, J. A. 2011. Better mathematical constraints on ages of Carboniferous stage boundaries using radiometric tuff dates and cyclostratigraphy. *Geochemistry, Geophysics, Geosystems*, **12**, Q0AA15, doi: 10.1029/2010GC003467.

POINTON, M. A., CHEW, D. M., OVTCHAROVA, M., SEVASTOPULO, G. D. and CROWLEY, Q. G. 2012. New high-precision U-Pb dates from western European Carboniferous tuffs; implications for time scale calibration, the periodicity of late Carboniferous cycles and stratigraphical correlation. *Journal of the Geological Society*, **169**, 713–721.

PORTLOCK, J. E. 1843. *Report on the geology of the County of Londonderry, and of parts of Tyrone and Fermanagh*. A. Milliken, Dublin, 784 pp.

PRESCOTT, Z., STIMSON, M. R., DEFOE, L. T., GIBLING, M. R., MACRAE, R. A., CALDER, J. H. and HEBERT, B. 2014. Microbial mats and ichnofauna of a fluvial-tidal channel in the Lower Pennsylvanian Joggins Formation, Canada. *Palaios*, **29**, 624–645.

QUANN, S., YOUNG, A., LAROQUE, C., FALCON-LANG, H. J. and GIBLING, M. R. 2010. Dendrochronologic dating of coal mine workings at the famous Joggins Fossil Cliffs of Nova Scotia, Canada. *Atlantic Geology*, **46**, 185–194.

RICHARDS, B. C. 2013. Current status of the international Carboniferous time scale. *New Mexico Museum of Natural History and Science, Bulletin*, **60**, 348–353.

ROBB, J. 1850. Report of coal in New Brunswick. 38–47. *In* JOHNSTON, J.F.W. (ed) *Report of the Agricultural Capabilities of the Province of New Brunswick.* Queen's Printer, Fredericton, New Brunswick.

ROHON, J. V. 1889. Über fossile Fische vom oberen Jenissei. *Memoires de L'Académie Impériale des Sciences de St-Pétersbourg, VII Séri*, **36**, 1–17.

ROMER, R. S. 1955. *Herpetichthys*, Amphiboidei, Choanichthyes or Sarcopterygii? *Nature*, **176**, 126–127.

1458 RUST, B. R. and GIBLING, M. R. 1990. Braidplain evolution in the Pennsylvanian South

1459 Bar Formation, Sydney Basin, Nova Scotia, Canada. *Journal of Sedimentary Research*, **1**,

1460 59–72.

1461 RYGEL, M.C., FIELDING, C.R., FRANK, T.D. and BIRGENHEIER, L.P. 2008. The

1462 magnitude of Late Paleozoic glacioeustatic fluctuations: a synthesis. *Journal of*

1463 *Sedimentary Research*, **78**, 500–511.

1464

1465 SALLAN, L. C., COATES, M. I. and CLACK, J. 2010. End-Devonian extinction and a

1466 bottleneck in the early evolution of modern jawed vertebrates. *Proceedings of the*

1467 *National Academy of Sciences*, **107**, 10131–10135.

1468 SALLAN, L. C. ── 2014. Major issues in the origin of ray-finned fish (Actinopterygii)

1469 biodiversity. *Biological Reviews*, **89**, 950–971.

1470 SCHIEBER, J. 2002, Sedimentary pyrite: a window into the microbial past. *Geology*, **30**,

1471 531–534.

1472 SCHMITZ, B., ABERG, G., WERDLIN, L., FOREY, P. and BENDIX-ALMGREEN, S. E.

1473 1991. $^{87}Sr/^{86}Sr$, Na, F, Sr, and La in skeletal fish debris as a measure of the paleosalinity

1474 of fossil–fish habitats. *Geological Society of America Bulletin*, **103,** 786–794.

1475 SCHULTZE, H.–P. 1966. Morphologische und histologische Untersuchungen an Schuppen

1476 mesozoischer Actinopterygier (Ubergang von Ganoid- zu Rund-Schuppen). *Neues*

1477 *Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **126**, 232–314.

1478 ── 1970. Folded teeth and the monophyletic origin of tetrapods. *American Museum*

1479 *Novitates*, **2408**, 1–10

1480 ── 1977. Ausgangsform und Entwicklung der rhombischen Schuppen der Osteichthyes

1481 (Pisces). *Paläontologische Zeitschrift*, **51**, 152–168.

— 2009. Interpretation of marine and freshwater paleoenvironments in Permo-Carboniferous deposits. Palaeogeography, Palaeoclimatology, Palaeoecology 281, 126–136.

— and CHORN, J. 1986. Palaeoniscoid (Actinopterygii, Pisces) vertebrae from the Late Paleozoic of central North America. *Journal of Paleontology*, **60**, 744–757.

— and — 1997. The Permo-Carboniferous genus *Sagenodus* and the beginning of modern lungfish. *Contributions to Zoology*, **67**, 9–70.

SHARP, E. L. and CLACK, J. A. 2013. A review of the Carboniferous lungfish *Ctenodus* Agassiz, 1838 from the United Kingdom, with new data from an articulated specimen of *Ctenodus interruptus* Barkas, 1869. *Transactions of the Royal Society of Edinburgh: Earth and Environmental Sciences*, **104**, 169–204.

SMITH, G. 1989. Coal in Canada. *Geological Survey of Canada, Paper* 89-4.

SNYDER, D. 2011. Gyracanthid gnathostome remains from the Carboniferous of Illinois. *Journal of Vertebrate Paleontology*, **31**, 902–906.

SOLER-GIJÓN, R. 1995. Evidence of predator–prey relationship in xenacanth sharks of the Upper Carboniferous (Stephanian C) from Puertollano, Spain. *Geobios*, **19**, 151–156.

ST. PETER, C. 1997. Bedrock geology of the Chipman/Canaan River map area (NTS 21 I/04 and part of 21 H/13), Sunbury, Queens and Kings counties, New Brunswick. *New Brunswick Department of Natural Resources and Energy, Minerals and Energy Division*, Plate 97-34.

— 2000. Carboniferous geology of the southwestern New Brunswick platform (Maugerville Subbasin). *New Brunswick Department of Natural Resources and Energy, Mineral Resources*, Plate 2000-16.

—, and JOHNSON, S.C. 2009. Stratigraphy and structural history of the late Paleozoic Maritimes Basin in southeastern New Brunswick, Canada. New Brunswick. *Department of Natural Resources; Minerals, Policy and Planning Division, Memoir*, **3**, 348 p.

ŚTAMBERG, S. and ZAJÍC, J. 2008. *Carboniferous and Permian faunas and their occurrence in the limnic basins of the Czech Republic*. Museum of Eastern Bohemia. 224 pp.

STERNBERG, R. M. 1941. Carboniferous dipnoans from Nova Scotia. *American Journal of Science*, **239**, 836–838.

SUES, H.-D., HOOK, R. W. and OLSEN, P. E. 2013. Donald Baird and his discoveries of Carboniferous and early Mesozoic vertebrates in Nova Scotia. *Atlantic Geology*, **49**, 90–103.

SULLIVAN, R.M. 1981. *A brief petrographic study of the rock stratigraphic unit Mississippian-Pennsylvanian felsic volcanics (MPfv) near Stanley, New Brunswick.* Supplementary Report No. 4 of the Carboniferous Drilling Project, New Brunswick Department of Natural Resources, Mineral Development Branch, Open File Report 81 3, 20 pp.

THOMPSON, K. S. 1964. Revised generic diagnoses of the fossil fishes *Megalichthys* and *Ectosteorhachis* (family Osteolepidae). *Bulletin of the Museum of Comparative Zoology*, **131**, 283–311.

TIBERT, N. E. and SCOTT, D. B. 1999. Ostracodes and agglutinated foraminifera as indicators of paleoenvironmental change in an Early Carboniferous brackish bay, Atlantic Canada. *Palaios*, **14**, 246–260.

TRAQUAIR, R. H. 1881*a*. Report on the fossil fishes collected by the Geological Survey of Scotland in Eskdale and Liddlesdale, part 1, Ganoidei. *Edinburgh Philosophical Transactions*, **30**, 15–71.

1530 — 1881*b*. On the cranial osteology of *Rhizodopsis*. *Transactions of the Royal Society of*
1531   *Edinburgh*, **30**, 167–179.

1532 TUCKER, M.E. and WRIGHT, V.P. 1990. *Carbonate Sedimentology*. Blackwell Scientific
1533   Publications, London, 482 pp.

1534 TURNER, S. 2013. *Ageleodus*: widespread mid-Palaeozoic sharks known only from teeth.
1535   61st Symposium on Vertebrate Palaeontology and Comparative Anatomy, Abstracts with
1536   Programme, Edinburgh, p. 43.

1537 — , BURROW, C. and WARREN, A. 2005. *Gyracanthides hawkinsi* sp. nov. (Acanthodii,
1538   Gyracanthidae) from the Lower Carboniferous of Queensland, Australia, with a review of
1539   gyracanthid taxa. *Palaeontology*, **48**, 963–1006.

1540 VAN DER POLL, H. W. 1973. Stratigraphy, sediment dispersal and facies analysis of the
1541   Pennsylvanian Pictou Group in New Brunswick. *Maritime Sediments*, **9**, 72–77.

1542 VOROBYEVA, E. I. 1977. Evolutionary modifications of the teeth structure in the
1543   Palaeozoic Crossopterygii. *Journal of the Palaeontological Society of India*, **20**, 16-20

1544 WARREN, A., CURRIE, B. P., BURROW, C. and TURNER, S. 2000. A redescription and
1545   reinterpretation of *Gyracanthides murrayi* Woodward 1906 (Acanthodii, Gyracanthidae)
1546   from the Lower Carboniferous of the Mansfield Basin, Victoria, Australia. *Journal of*
1547   *Vertebrate Paleontology*, **20**, 225–242.

1548 WATERS, C. N. and CONDON, D. J. 2012. Nature and timing of Late Mississippian to Mid-
1549   Pennsylvanian glacio-eustatic sea-level changes of the Pennine Basin, UK. *Journal of the*
1550   *Geological Society of London*, **169**, 37–51.

1551 WELLS, M. R., ALLISON, P. A., PIGGOTT, M. D., PAIN, C. C., HAMPSON, G. J. and DE
1552   OLIVIERA, C. R. E. 2005. Large sea, small tides: the Late Carboniferous seaway of NW
1553   Europe. *Journal of the Geological Society of London*, **162**, 417–420.

1554 WILLIAMS, M., LENG, M. J., STEPHENSON, M. H., ANDREWS, J. E., WILKINSON, I.

1555 P., SIVETER, D. J., HORNE, D. J. and VANNIER, J. M. C. 2006. Evidence that Early

1556 Carboniferous ostracods colonised coastal flood plain brackish water environments.

1557 *Palaeogeography, Palaeoclimatology, Palaeoecology*, **230**, 299–318.

1558 WILLIAMS, M. E. 1972. The origin of "spiral coprolites." *The University of Kansas*

1559 *Paleontological Contributions*, **59**, 1–19.

1560 WILLIAMS, S. C. and LUCAS, S. L. 2013. Taphonomy and paleoecology of Pennsylvanian

1561 fishes from Kinney Brick Quarry, New Mexico, USA. *In* LUCAS, S. G., NELSON, W. J.

1562 , DiMICHELE, W. A., SPEILMAN, J. A., KRAINER, K., BARRICK, J. E., ELRICK,

1563 S., VOIGT, S. (eds.) *The Carboniferous–Permian Transition in Central New Mexico.*

1564 New Mexico Museum of Natural History and Science, **59**, 371–398.

1565 WILLIAMSON, W. C. 1837. On the affinity of some fossil scales of fish from the Lancashire

1566 Coal Measures with those of the recent Salmonidæ. *Philosophical Magazine Series 3*, **11**,

1567 300–301.

1568 — 1849. On the microscopic structure of the scales and dermal teeth of some ganoid and

1569 placoid Fish. *Philosophical Transactions of the Royal Society of London*, **139**, 435–475.

1570 WOODWARD, A. S. 1891. *Catalogue of the fossil fishes in the British Museum (Natural*

1571 *History). Part II. Containing the Elasmobranchii (Acanthodii), Holocephali,*

1572 *Ichthodorulites, Ostracodermi, Dipnoi and Teleostomi*. British Museum of Natural

1573 History, London, 553 pp.

1574 — 1906. On a Carboniferous fish fauna from the Mansfield District, Victoria. *Memoirs of the*

1575 *National Museum of Victoria*, **1**, 1–32.

1576 YOUNG, J. 1866. On the affinities of *Chondrosteus*, Ag. *Quarterly Journal of the Geological*

1577 *Society*, **22**, 569.

1578   ZIDEK, J. 1976. Kansas Hamilton Quarry (Upper Pennsylvanian) *Acanthodes*, with remarks

1579   on the previously reported occurrences of the genus. *University of Kansas*

1580   *Paleontological Contributions*, **83**, 1–41.

1581   — 1977. An Acanthodid shoulder girdle from Lower Mississippian of Nova Scotia. *Journal*

1582   *of Paleontology*, **51**, 199–200.

1583

1584

FIGURE CAPTIONS

FIG. 1. Location and geological context of the fossil sites. A, The Late Paleozoic Maritimes Basin of Atlantic Canada, developed in the oblique convergence zone of Laurasia and Gondwana (modified from Gibling *et al.* 2008). B, Geology of southern New Brunswick and northwest Nova Scotia showing the fossil sites near Grand Lake, positioned on the stable craton, adjacent to the active Moncton and Cumberland basins (modified from Falcon-Lang *et al.* 2015*a*). C, Geology of the Pennsylvanian (early Moscovian) Minto Coalfield of New Brunswick (after Hacquebard and Barss 1970; Ball *et al.* 1981; St Peter 2000) showing the location of borehole DH62-1 illustrated in Fig. 4.

FIG. 2. Geochronology and stratigraphic context of the fossil sites. A, The Pennsylvanian Timescale (compiled from Peterson 2011; Waters and Condon 2012; Pointon *et al.* 2012; Richards 2013). B., Stratigraphy of the Pennsylvanian (Bashkirian) Cumberland Group and Pennsylvanian (Moscovian) Pictou Group of Atlantic Canada (modified from Gibling *et al.* 2008; Bashforth *et al.* 2014) showing the presence of Langsettian marine bands documented in the Joggins (Grey *et al.* 2011) and Tynemouth Creek (Falcon-Lang *et al.* 2015*b*) formations, and the new marine band (reported here) from the early to mid-Bolsovian part of the Minto Formation.

FIG. 3. Geology of the Pennsylvanian (early Bolsovian) Minto Coalfield (modified from Hacquebard and Barss 1970). A, Isopachytes for (i) the Minto Coal and (ii) coal to basement, the latter indicating onlap towards the northeast. B, Sandstone/mudstone ratio in the roof rock of the Minto Coal showing NE-SW trending drainage channels that, locally, 'wash out' the coal.

FIG. 4. Sedimentary context of the fossil sites based on borehole core DH62-1. A, Graphic

log of a short section of borehole DH62-1 (core boxes 44–52; depth 196–231 m) illustrating

the three units of the Minto Formation (see text for explanation). The Minto Coal is removed

from the core and limestone beds are believed to represent a roof facies as seen in the Joggins

Formation (Davies and Gibling 2003). B, Erosive-based fluvial channel conglomerate facies

in lower unit. C, Pin-stripe lamination in estuarine facies in middle unit. D, Red mudrock with

carbonate glaebules in upper unit. E, Close-up of paired mud-drapes in ripple cross-

lamination in middle unit, a distinctive tidal indicator (cf. Naylor *et al.* 1998; Costain 2000).

Scale bar is 30 mm (B–D), 4 mm (F).

FIG. 5. Petrology of limestone Lithology 1 (shallow marine facies: A–G, NBMG 18779) and

Lithology 2 (brackish embayment facies: H–I, NBMG 18611). A, Punctate brachiopods. B,

fish skeletal fragments. C, Ostracodes. D, Punctate brachiopods and possible sponge spicules.

E, Spirorbiform microconchids. F, Echinoderm spine mineralised with framboidal pyrite. G,

putative foraminifera. H, Bivalves. I. Bivalves and phosphatic (francolite) nodule possibly of

fish origin. Abbreviations: p.b., punctate brachiopods; f.s., fish skeletal fragments; o.v.,

ostracode valves; s., sponge spicules; s.m., spirorbiform microconchids; e.s., echinoid spines;

f.t., foraminifera test; f.p., framboidal pyrite; b.f., bivalve fragment. Scale bar is 1 mm (A–D,

H–I), 0.5 mm (E–F), 0.25 mm (G).

FIG. 6. Macroscopic invertebrates found in Lithology 2 (brackish embayment facies). A,

Articulated *Naiadites* bivalves, NBMG 19967. B, Spirorbiform microconchid, NBMG 15841.

C, Abundant spirorbiform microconchids, NBMG 15815. Abbreviations: s.m. spirorbiform

microconchids. Scale bar is 5 mm (A), 1 mm (B), 1.5 mm (C).

FIG. 7. Sedimentary and fossil characteristics of Lithology 3 (tidal estuary facies). A,

Symmetrically-rippled siltstone to very fine-grained sandstone showing fish skeletal

fragments concentrated within mud-rich ripple troughs. NBMG 15901 (specimen dissolved to

extract fish fauna). B, Enlargement of area in (A) showing *Orthacanthus* tooth and macerated

skeletal debris. Abbreviation: x.t., xenacanthid tooth. Scale bar as indicated (ruler divided into

10 mm intervals) for A; 10 mm for B. .

FIG. 8. Tip heaps adjacent to the former opencast mine at Iron Bound Cove (flooded area on

the right; Latitude 46°08.67'N; Longitude 65°58.10'W), illustrating how material was

collected by 'surface prospecting'.

FIG. 9. Teeth of sharks from the Minto Formation (Pennsylvanian) of New Brunswick,

Canada. A–D, Tricuspid tooth of *Orthacanthus compressus*, NBMG 19617, in aboral (A),

oral (B), dorso-aboral (C), and ventro-oral (D) views. E, Tooth of Xenacanth indet., NBMG

19629. F, Denticle of elasmobranch indet., NBMG 19667. G, Denticle of elasmobranch

indet., NBMG 19647. H–J, Teeth of *Ageleodus pectinatus*: NBMG 19613 in aboral view (H),

NBMG 19613 in oral view (I) and NBMG 15175 in aboral view (J). Abbreviations c.b:

coronal button, n.f. nutrient foramen, m.f: median foramen. Scale bar is 2 mm (A–D), 1 mm

(E), 0.25 mm (F–G), 0.5 mm (H–I), 2 mm (J).

FIG. 10. Size ranges for shark teeth from the Minto Formation (Pennsylvanian), New

Brunswick. A, Range of heights and frequencies for teeth of *Orthacanthus*. B, Cusp counts

and frequencies for complete teeth of *Ageleodus*.

FIG. 11. Spines of the Acanthodians from the Minto Formation (Pennsylvanian) of New

Brunswick, Canada. A–F, *Gyracanthides* sp., G–H, *Acanthodes* sp. A–C, spines in lateral

view: NBMG 15173 (A), NBMG 10739/1 (B), with indications of location of close-ups D

and E, and NBMG 10739/2 (C). D, Striae on the insertion area and the angle between the

striae and the exsertion area, NBMG 15173/1. E, Chevron pattern in ornament ridges on the

leading edge, NBMG 15173/2. F, cross-section of a spine, NBMG 15173/4. G, spine in lateral

view, NMBG 15174. H, spine in lateral view, NBMG 15852. Line at r-s represents the

1657 insertion/exsertion boundary (IEB). Line at x-y represents a line perpendicular to the leading

1658 edge. Scale bar is 20 mm (B, C), 10 mm (A, G, and H), 2 mm (F), 1 mm (D and E).

1659 **FIG. 12.** Feeding plates of dipnoans from the Minto Formation (Pennsylvanian) of New

1660 Brunswick, Canada. A–B, Feeding plate of *Ctenodus interruptus*, NBMG 10740 (A), with

1661 close-ups of isolated xenacanth teeth sitting on the surface (B). C–D, Fragments of the

1662 feeding plates of Dipnoi indet., NBMG 18609 showing convergent ridges (C), and NBMG

1663 19699, showing differential apical elongations (D). Scale bar is 4 mm (A), 1 mm (B–D).

1664 **FIG. 13.** Teeth and scales of rhizodonts and tetrapodomorphs from the Minto Formation

1665 (Pennsylvanian) of New Brunswick, Canada. A, Tooth of *Strepsodus sauroides*: NBMG

1666 15820 in lateral view. B, C, Tooth of *Archichthys portlocki*, NBMG 19972, showing

1667 striations, in lateral view (B), and plication count on the base (C). D–E, Scales of cf.

1668 *Archichthys portlocki*, NBMG 19689 (D), NBMG 15831 (E). F, Tooth of cf. *Rhizodus*

1669 *hibberti* NBMG 15809. G, Scale of cf. *Rhizodopsis sauroides* NBMG 15901 showing the

1670 attachment side. H–J, Scales of *Megalichthys* indet.: NBMG 10741/1, showing the free field

1671 (H), and close-up image of the cosmine cover of the free field (I), and NBMG 19974a,

1672 showing the attached surface (J). K–L, Centrum of *Megalichthys* sp., in articular (K) and

1673 lateral (L) views. M–N, Teeth of Tetrapodomorpha indet., NBMG 10776 (M), and NBMG

1674 10777 (N). Scale bar is 2 mm (A–C, M, and N); 20 mm (F), 10 mm (D, E, G, K, L), 20 mm

1675 (H, J), separate 2 mm scale bar (I).

1676 **FIG. 14.** Tetrapod remains, with provisional identifications. A, Small dentary of a possible

1677 ?colosteid ~~temnospondyl~~ bearing teeth, NMBG 15821. B, C, intecentrum of a ~~temnospondyl~~

1678 possible embolomerous anthracosaur vertebra, in ~~particular~~ ?anterior (B) and lateral (C)

1679 views, NMBG xxxxx. D, ~~Temnospondyl~~ osteoderm,~~,~~ NMBG xxxxx. Scale bar is 80 mm (A),

1680 10 mm (B and C), 50 mm (D).

1681 **FIG. 15.** Remains of indeterminate actinopterygians from the Minto Formation

1682 (Pennsylvanian) of New Brunswick, Canada. A–B, Scale, NBMG 19679/1 showing the free

1683 field (A), and the attached surface (B). C, Sculptured scale or dermal skull bone, NBMG

1684 19048a. D, Tooth, NBMG 19684. E, Vertebra, NBMG 19686. Abbreviations: l.a.s, lateral

1685 attachment site; v.r., ventral ridge. Scale bar is 0.5 mm (A, B, and E), 0.4 mm (D).

1686 **FIG. 16.** Fish coprolites (bromalites). A., Heteropolar microspiral coprolite, NBMG 19979.

1687 showing coils and posterior spire. B, Thin section of heteropolar microspiral coprolite

1688 containing fish skeletal fragments including probable juvenile xenacanthid tooth (box: F),

1689 NBMG 18789. C., Large, short cylindrical coprolite composed of calcareous material (box:

1690 E), NBMG 20000. D., Rounded, bilobed coprolite (box: G), NBMG 19824. E., Expanded

1691 view of spirorbiform microconchids and bivalve fragments in coprolite shown (C), NBMG

1692 20000. F., Expanded view of xenacanthid tooth in coprolite (B), NBMG 18789. G., Expanded

1693 view of rhizodont tooth and actinoptergian scale (D), NBMG 18789. Abbreviations: p.s.,

1694 posterior spiral; x.t., xenacanthid tooth; s.m., spirorbiform microconchids; b.f., bivalve

1695 fragments; r.t., rhizodont tooth; a.s., actinoptergian scale. Scale bars are 4 mm (A–B, D), 6

1696 mm (C), 1.5 mm (E), 1 mm (F, G).

1697 **FIG. 17.** Summary of 10 fish faunas from brackish-marine facies in the Carboniferous

1698 Maritimes Basin of Atlantic Canada. Carboniferous timescale based on critical synthesis of

1699 recent papers (Peterson 2011; Waters and Condon 2012; Pointon *et al.* 2012; Richards 2013)

1700 and age of key formations in the Maritimes Basin based on various sources (see Gibling *et al.*

1701 2008 for discussion). Faunas based on illustrations in published records, revised in light of

1702 modern nomenclature. Principal sources for the compilation (Dawson 1868; Gardiner 1966;

1703 Carroll *et al.* 1972; Calder 1998) were supplemented by the following additional sources

1704 (Lambe 1910; Baird 1962, 1978; Greiner 1977; Johnson 1979, 1999; Miller and McGovern

1705 1997; Turner *et al.* 2005; Brazeau 2005; Jeffrey 2006; Sues *et al.* 2013; Mansky and Lucas

1706   2013; Carpenter *et al.* 2015; this paper; Yale Peabody Museum collections database:

1707   http://collections.peabody.yale.edu/search/)

1708

1709 **TABLE CAPTIONS**

1710 **Table 1.** Summary of fish taxa from the Pennsylvanian (early Moscovian; early Bolsolvian)

1711 Minto Formation of New Brunswick, Canada (cf. Bashkirian fish fauna in Joggins Formation;

1712 Carpenter *et al.* 2015, fig. 5).

1713 **Table 2.** Quantitative data for the facies distribution of fish specimen ranked at class/order

1714 and generic level. Note that the number of specimens at class/order level (n = 288) is higher

1715 than at generic level (n = 181) because some specimens can be assigned to class/order but not

1716 to genus. Percentage values at class/order and genus level differ because of they are based on

1717 these different datasets. The inverse of the Simpson Index (1 – H) is calculated for generic

1718 level data only.