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1 **Fish and tetrapod communities across a marine to brackish salinity gradient in the**  
2 **Pennsylvanian (early Moscovian) Minto Formation of New Brunswick, Canada, and**  
3 **their palaeoecological and palaeogeographic implications**

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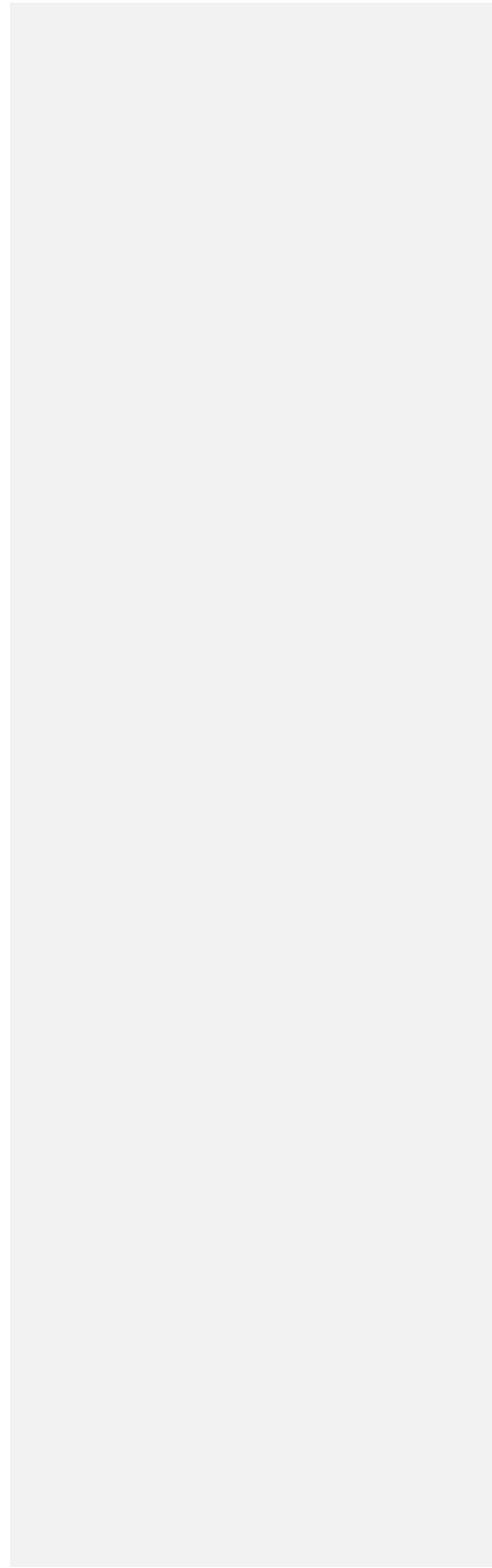
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27 **Abstract:** Fishes rapidly diversified into brackish coastal environments in Pennsylvanian  
28 times, and here we report new assemblages from New Brunswick, Canada, which shed light  
29 on this evolutionary event. Fish fossils from the early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

47

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

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53 INVASION of brackish coastal environments was a critical transitional phase in the  
54 Palaeozoic colonisation of continental freshwater ecospace (Buatois *et al.* 1998; Miller and  
55 Labandeira 2002; Park and Gierlowski-Kordesch 2007; Falcon-Lang *et al.* 2015a).  
56 Adaptation to lower and more variably saline (non-marine) water bodies may have  
57 commenced as early as the Ordovician (MacNaughton *et al.* 2002), with the abundance and  
58 complexity of brackish ecosystems steadily increasing through the Silurian–Carboniferous  
59 (Buatois *et al.* 2005). This pattern of colonisation closely parallels the Ordovician rise of  
60 hepatophytes, and the Silurian–Carboniferous diversification of tracheophytes (Gensel and  
61 Edwards 2001), implying the complex co-evolution of land plants, terrestrial-marine nutrient  
62 export patterns (Algeo and Scheckler 1998), and the carrying capacity of brackish (non-  
63 marine) coastal environments (Prescott *et al.* 2014).

64         Recent studies have identified a “mid-Carboniferous diversification event” when  
65 infiltration into brackish coastal settings appears to have sharply accelerated (Davies and  
66 Gibling 2013; Falcon-Lang *et al.* 2015a; Minter *et al.* 2016). This event commenced in the  
67 Serupukhovian and received its acme in the Bashkirian–Moscovian stages (Falcon-Lang *et al.*  
68 2015a). An intriguing characteristic of this episode was the apparent widespread adoption of  
69 a euryhaline habit amongst organisms as diverse as microconchids, ostracodes, xiphosurans  
70 and fish (Anderson and Shuster 2003; Carpenter *et al.* 2011; Bennett *et al.* 2012; Gierlowski-  
71 Kordesch and Cassle 2015). Euryhaline animals are relatively rare in modern ecosystems  
72 (Edwards and Marshall 2013; McCormick *et al.* 2013), and their dominance in Carboniferous  
73 times suggests marine communities converged on similar osmoregulatory strategies in order  
74 to utilise empty non-marine coastal ecospace for feeding and breeding (Williams *et al.* 2006;  
75 Carpenter *et al.* 2014), prior to the widespread colonisation of freshwater tracts further inland.

76         The mid-Carboniferous diversification event coincided with a sharp growth of  
77 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.* 2015b), 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

127 several million years of depositional hiatus (St Peter and Johnson 2009). In the course of this  
128 lengthy episode of landscape degradation, a NE-SW-trending valley system, c. 16 km wide,  
129 was cut into the basement, forming an erosional ‘container’ (depocentre) in which younger  
130 sediments of the Minto Formation accumulated (Hacquebard and Barss 1970).

131 This bedrock palaeovalley was bordered on either side by slates and lavas that formed  
132 subdued topographic highs with a palaeo-elevation of a few tens of metres above base level  
133 (Hacquebard and Barss 1970; Gray *et al.* 2012; Fig. 3A). Two lines of evidence suggest that  
134 the valley drained towards the southwest (Hacquebard and Barss 1970): (1) the thickness of  
135 the lower part of the formation, as measured from the basement contact to the base of the  
136 Minto Coal (a prominent chronostratigraphic marker bed) gradually increases from c. 15 m in  
137 northeast to > 90 m in the southwest (Fig. 3A), implying that the basin deepened towards the  
138 southwest, and sediment progressively onlapped towards the northeast; and (2) NE-SW-  
139 orientated ribbons of channelized sandstone, 1–1.5 km wide, in the ‘roof rock’ of the Minto  
140 Coal, fine towards the southwest (Fig. 3B) and suggest sediment transport in that direction.  
141 We note, however, that this inferred palaeoflow direction opposes regional patterns of  
142 sediment dispersal, which are directed towards the ENE (van der Poll 1973; Gibling *et al.*  
143 1992). This suggests that either drainage in the Minto Coalfield was strongly influenced by  
144 local bedrock topography, or that palaeoflow inferences based on grain size and isopachytes  
145 are incorrect. More reliable indicators of palaeoflow indicators, such as cross-bed arrays, have  
146 not been obtained to date.

147

#### 148 *Palaeoenvironments*

149 Despite its long history of geological study (Gesner 1841; Robb 1850; Bailey and Matthew  
150 1873), there have been no comprehensive studies of the sedimentary facies of the Minto  
151 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 2015a).

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,

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

253

#### 254 *Collection history*

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

261

#### 262 *Specimen preparation*

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

270

#### 271 *Specimen imaging*

272 Prepared specimens were photographed with a Nikon D700 digital SLR camera with a Nikon  
273 60 mm macro lens. Other specimens were photographed using a Panasonic Lumix DMC-ZS3  
274 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 PALAEOLOGY**

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, 1843a

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

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  $\geq 1$  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  $\leq 0.5$  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

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

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

339 Xenacanthiformes indet.

340 **Figure 9E**

341 *Material.* 32 specimens containing isolated teeth (NBMG 14966, 14985–14897, 14994,  
342 15835, 15837–15838, 15842, 15848, 16082, 16089, 18613, 19628–19846).

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

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

346 often have carinae on their lateral edges. Serration is absent in all specimens. A sub-circular  
347 coronal button is present in specimens with intact bases. In specimens not obscured by  
348 sediment there is no median foramen. A convex basal tubercle is present except where it has  
349 been broken off (Fig. 9E).

350 *Remarks.* The specimens are too fragmentary to identify beyond ordinal level. Some show  
351 individual features consistent with *Orthacanthus compressus*, such as the presence of carinae,  
352 but have not been included within *O. compressus* as these characteristics are shared by  
353 *Xenacanthus* (Johnson 1999).

354 Elasmobranchii indet.

355 Figure 9F, G

356 *Material.* 32 specimens containing 607 isolated scales (NBMG 19646–19677). Note that  
357 some of these specimens were obtained through the destructive dissolution of NBMG 14984,  
358 15834, and 15901, and then assigned new collection numbers.

359 *Diagnosis.* Scales with thin bases and cusps extending out from the free-face. Scales vary  
360 from polycuspid to fused cusps.

361 *Description.* Scales range from  $\leq 0.5$  mm to  $\leq 0.2$  mm in diameter and height (measured from  
362 the base outwards along the denticles). The base of the scales is thin and tends to be dotted  
363 with holes, which are likely to be a result of post-mortem degradation, as hole morphology is  
364 highly variable. Cusps range from polycuspid to fused cusps, which form a robust structure  
365 (Fig. 9F). The cusps of the polycuspid scales tend to have a degree of curvature, and all curve  
366 in the same direction.

367 *Remarks.* Elasmobranch scales from the Palaeozoic have been shown to have a high degree of  
368 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 Order *incertae sedis*

374 Family *incertae sedis*

375 Genus *AGELEODUS* Owen, 1867

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

377 *Ageleodus pectinatus* Agassiz, 1843a

378 **Figure 9H–J**

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 15175 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.*, 2000409 Genus *GYRACANTHIDES* Woodward, 1906410 *Type species.* *Gyracanthides murrayi* Woodward, 1906411 *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 42° between the IEB and the  
426 ornamented ridges and 25° 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

437 branch and converge in places and taper off both distally and proximally (Fig. 11D). There is  
438 a c. 20° angle between the striae and the IEB. The exertion area is covered by tubercles,  
439 which are arranged en échelon on the ornament ridges of NBMG 10739/1 and 4 (Fig. 11E),  
440 and as near straight ridges in NBMG 10739/2 and 5. The tubercles are elongated along the  
441 long axis and intersect as even chevrons along the leading edge (Fig. 11C, E). The length of  
442 the elongated tubercles varies from 400 to 910 µm between spine fragments. Any  
443 ornamentation originally present on the tubercles has been lost to abrasion. The angle  
444 between the ornament ridges and the IEB varies from c. 81° (Fig. 11B–C) in NBMG  
445 10739/1–2 to c. 52° in NBMG 10739/4 with the latter having more longitudinal elongate  
446 ridges to the long axis, suggesting that it is part of the distal end of a pelvic spine (Turner *et*  
447 *al.* 2005). Spines with varying levels of abrasion along their length may be indicative of wear  
448 during life (Turner *et al.* 2005); if abrasion was caused by post-mortem transportation, then a  
449 more even distribution of abrasion along the spine would be expected.

450 NBMG 10739/3–5, 7 and 10 are the only fragments complete enough for the cross-  
451 sectional shape to be determined; all are elliptical (Fig. 11F). Only a single ridge is visible on  
452 the trailing edge of NBMG 10739/3, as the surface is damaged where a second ridge would  
453 be expected in *Gyracanthides* (Turner *et al.* 2005). There is an infilled circular hollow in  
454 NBMG 10739/4 that narrows distally in proportion with the narrowing of the spine. This  
455 hollow represents the pulp cavity. All spine fragments are too small to show any distal  
456 curvature.

457 *Remarks.* Gyracanthid material from the Minto Formation has been previously reported as  
458 *Gyracanthus* cf. *G. duplicatus* (Gardiner 1966; Miller 1999), but since Dawson's  
459 *Gyracanthus duplicatus* is now known to be invalid (Carpenter *et al.* 2015), the Minto  
460 material merits re-classification. Specimens NBMG 15173 and NBMG 10739/1–11 have  
461 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, 1843b

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

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 (Faircler, 1966; Demson, 1979; Kennedy *et al.*, 2011), the only previously reported occurrence  
 494 of Acanthodidae is from the Tournaisian Horton Bluff Formation at Blue Beach, Nova Scotia  
 495 (Zidel, 1977; Minsky & Lucare, 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.

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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.*

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507

508 Class OSTEICHTHYES Huxley, 1880

509 Subclass SARCOPTERYGII Romer, 1955

510 Infraclass DIPNOMORPHA Ahlberg, 1991

511 Order DIPNOI Müller, 1845

512 Family *incertae sedis*513 Genus *CTENODUS* Agassiz, 1843a514 *Type species. Ctenodus cristatus* Agassiz, 1843a515 *Ctenodus interruptus* Barkas, 1869516 **Figure 12A–B**517 *Material.* Two specimens, each comprising an incomplete tooth plate (NBMG 10740, 15822).518 *Diagnosis.* Subtriangular tooth plate with ridges that are near-parallel to one another. The  
519 ridges are equipped with prominent, longitudinally compressed denticles with rounded apices.520 *Description.* NBMG 10740 is a broken fragment of a tooth plate. Only four near-parallel  
521 ridges are present (**Fig. 12A**) with lengths of 9 to 31 mm, but these measurements do not  
522 represent the original length of the ridges, as they are broken at both ends. There is a space of  
523 5 mm between ridges (measured from between the apices). Individual apex height reduces  
524 along each ridge from the centre out in both directions. Ridges are relatively straight. There is  
525 a prominent depression between two apices on one side of the specimen (**Fig. 12A**), seen in  
526 three of the ridges (not observable in the fourth ridge as this section of the ridge is not  
527 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 20° (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, 1881a 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, 1843b

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

673 *Megalichthys* sp.

674 **Figure 13**H–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 polyplacodont teeth, as  
725 present in *Megalichthys*, *Rhizodopsis*, *Rhizodus* and *Strepsodus* (Schultze 1970).  
726 Polyplacodont 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



728 cannot be determined and these teeth cannot be identified more precisely (Schultz 1970;  
 729 Vorobyeva 1977; Jeffery 2003). Therefore we identify these teeth as Tetrapodompha indet.

730

731 ~~Superclass~~-TETRAPODA ~~Ahlberg~~Goodrich, 1930~~91~~

732 **Figure 14–D**

733

734 *Material.* Fifteen specimens, including partial jaws (NBMG 15821, 15853, 15872, 20019,  
 735 20020, 20021), dermal cranial bones (NBMG 15785, 20028), vertebrae (NBMG 15783,  
 736 15784, 15870), ribs (NBMG 15782, 15914), possible limb bones (NBMG 15915), and scutes  
 737 (NBMG 15861).

738

739 *Description.* NBMG 15821 is a 14 mm long mandible, ~~14 mm long, and bears with~~ at least 17  
 740 elongate, straight, pointed (bullet-shaped) teeth that bear faint longitudinal striations confined  
 741 to the basal one-third of the visible portion of the crown (Fig. 14A). The jaw bone, although  
 742 somewhat damaged, appears to be narrow, barely as deep as the length of the tooth crowns,  
 743 and it bears a shallow, longitudinal sculpture of longitudinal ridges. NBMG xxxxx is a  
 744 vertebra comprising a disc-shaped ~~inter-~~inter- or pleurocentrum, ~~presumably bearing a striking~~  
 745 resemblance to anthracosaur inter-/pleurocentra of a temnospondyl, with nearly  
 746 equidimensional measurements in articular view (Fig. 14B), and anteroposteriorly short (Fig.  
 747 14C). ~~The articular faces are deeply amphicoelous, and there is central notochordal canal-a~~  
 748 central perforation from front to back. In lateral view (Fig. 14C), the portion of the lateral  
 749 surface comprised between the projecting, rolled edges around the articular faces ~~project, and~~  
 750 the intervening portion is depressed. The isolated osteoderm (Fig. 14D) is tiny, only 4 mm  
 751 across, with a thick keel extending from the centre of the scute to its edge, thus dividing the  
 752 scute 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 intercentrum is presumably of a  
 756 temnospondyl, reminiscent of those of embolomereous 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, colobodons and pycnodons (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

## BROMALITES

812

### Heteropolar microspiral coprolites

813

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 2012a). 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 xenacanthid 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.

847 *Description.* Light grey, calcareous coprolites, comprising a short cylindrical morphology  
848 with two rounded ends or an anterior taper resulting in a tear drop shape (Coprolite Types B1  
849 and B2 of Hunt and Lucas 2012a). Coprolites are 20 to 60 mm long and 6 to 20 mm diameter,  
850 and comprise a dense, solid posterior mass and a more diffuse anterior zone (Fig. 16D).

851 Invertebrate fragments, < 1 mm in granularity, are abundant, especially at the anterior end and  
852 include recognisable microconchids and bivalve fragments, possibly of *Naiadites* type (Fig.  
853 16C).

854 *Remarks.* The calcareous composition, and the presence of recognisable shelly fragments,  
855 indicates that the producer fed on invertebrates. The producer cannot be identified but the  
856 crushed shelly components suggest a duraphagous habit facilitated by grinding tooth plates,  
857 most consistent with the *Ctenodus* lungfish. The size of the coprolite suggests that the fish  
858 that produced it was relatively large.

859 *Subspherical coprolites*

860 *Figure 16F–G*

861 *Material.* One specimen (NBMG 19824).

862 *Diagnosis.* Short coprolite, approximately as wide as tall, rounded in all dimensions, showing  
863 a bilobed external appearance.

864 *Description.* The specimen is somewhat nondescript, and can simply be termed 'round', or as  
865 a subrounded small pellet (category C1), using the shape scheme of Hunt and Lucas (2012a,  
866 b). The coprolite is bilobed, with two equal-sized subspherical portions largely overlapping,  
867 and presumably reflecting the original structure. It measures 19 x 22 mm, and is, at most, 7  
868 mm thick. The thickness is probably reduced by compaction and by breakage; one side  
869 appears to be external, the other internal (Fig. 16F), showing numerous broken pieces of  
870 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 (*Gyracanthides*), 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



920 juvenile xenacanthid remains in heteropolar microspiral coprolites reported from the Minto  
921 Formation adds another dimension to our understanding of *Orthacanthus* behaviour. It  
922 suggests the genus was practising filial cannibalism of juvenile xenacanthids (as postulated at  
923 other sites; Hampe 1988; Soler-Gijon 1995; Heidke 1998; Johnson 1999; Beck *et al.* 2014),  
924 and may have been predated xenacanthid within protected nurseries developed within tidal  
925 estuaries (cf. Carpenter *et al.* 2014). The ecology of the other abundant shark, *Ageleodus*,  
926 remains completely unknown, and there is even uncertainty as to whether skeletal elements  
927 represent teeth or specialised brachial denticles (Lebedev 1996; Turner 2013). [The other](#)  
928 [common component \(20.5 %\) of the assemblage comprises diverse sarcopterygians](#)  
929 [\(rhizodontids, megalichthyids, rhizodopsids\)](#), which were, also, large predatory fish. The  
930 dominance of large predators (secondary and tertiary consumers) is inconsistent with a  
931 normal trophic pyramid. However, this inverted structure is commonly reported for  
932 Pennsylvanian assemblages (e.g., Carpenter *et al.* 2015), and may simply reflect a much  
933 lower preservation potential of, most soft-bodied, producers and primary consumers.

934 Within the fish assemblage, primary consumers are represented by [actinoptygians \(7.6](#)  
935 [%\) and acanthodians \(1.4 %\)](#), which likely fed on plankton, and the dipnoan, *Ctenodus*,  
936 whose crushing/grinding dentition suggests a duraphagous mode of life. Dipnoans were the  
937 most likely producer of the short ellipsoid coprolites that contain fragmentary invertebrate  
938 remains (microconchids, bivalves) and rare fish fragments. A *Ctenodus* tooth plate (NBMG  
939 10740) into which a tiny xenacanthid tooth is embedded, suggests that these lungfish may  
940 also have predated juvenile sharks.

941

#### 942 *Euryhaline tolerances*

943 The fish assemblage dates from the Bashkirian-Moscovian acme of a major diversification  
944 event within brackish/freshwater environments (Falcon-Lang *et al.* 2015a). 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.* 2015a; 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 ( $^{87}\text{Sr}/^{86}\text{Sr}$ ) 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. Chondrichthyans 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.* 2011). In  
 965 contrast, while also likely euryhaline, some acanthodians (*Gyracanthides*), 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

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

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

978

979 *Minto Acanthodids*

980 The Acanthodidae were a highly cosmopolitan mid to late Palaeozoic group, representatives  
 981 of which have been found on every continent except South America (Denison 1979; Long  
 982 1986; Burrow et al. 2008; Sallan et al. 2011); first appearing in the Middle Devonian, this  
 983 was the only acanthodiform family to persist into the Carboniferous and Permian (Beznosov  
 984 2009; Sallan et al. 2011). The best known acanthodidid genus, *Acanthodes*, was widely  
 985 distributed, occurring in Australia, South Africa, Europe, North America, Greenland, and  
 986 Siberia from the Middle Devonian to the late Permian (Denison 1979; Sallan et al. 2011).  
 987 However, the earliest known articulated specimens (*Acanthodes lopatini* Robson, 1889) are  
 988 from the Tournaisian of south-central Siberia (Beznosov 2009) and many earlier isolated  
 989 scales and ichthyoliths assigned to *Acanthodes* sp. are considered doubtful (Burrow et al.  
 990 2011).

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

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995 and Wilson 1996; Hanke 2008; Kennedy *et al.* 2012; Carpenter *et al.* 2014), and secondly  
996 because *Acanthodes* was distributed widely in North America (USA) and Europe (Germany,  
997 UK, Czech Republic) at this time (Demson 1978). Given *Acanthodes*' apparent ability, as a  
998 genus, to tolerate a wide range of salinity conditions, there was no obvious obstacle to prevent  
999 it from reaching Canada. The *Acanthodid* remains at Horton Bluff are tantalising, because if  
1000 they are in fact referable to *Acanthodes* this would indicate a substantial ghost lineage, and  
1001 suggest the lack of specimens from this interval is the result of collection failure or  
1002 taphonomic bias; it is to be hoped that further investigations at Blue Beach will provide  
1003 determinable material which will resolve this issue.

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#### 1004 *Evolutionary implications*

1005 The Maritimes Basin of Canada is a particularly informative area for studying the evolution  
1006 and ecology of fish populations during the mid-Carboniferous diversification into brackish  
1007 coastal waters. This depocentre is positioned near the continental interior of Pangaea (Falcon-  
1008 Lang *et al.* 2006) but was intermittently connected to marine water bodies in the course of  
1009 glacio-eustatic and tectonic fluctuations (Gibling *et al.* 2008). Fully marine incursions  
1010 occurred only during three brief intervals, during part of the Visean (Windsor Group), the  
1011 Bashkirian (Joggins and Tynemouth Creek formations; Grey *et al.* 2011; Falcon-Lang *et al.*  
1012 2015*b*) and early Moscovian stages (Minto Formation; this paper). However, brackish  
1013 incursions were far more common, spanning the entire Carboniferous interval (Archer *et al.*  
1014 1995; Tibert and Scott 1999; Falcon-Lang *et al.* 2006; McIlroy and Falcon-Lang 2006;  
1015 Gibling *et al.* 2008), and reflecting the periodic development of a brackish epicontinental sea,  
1016 in some ways, analogous to the present-day Baltic Sea (Calder 1998; Falcon-Lang 2005).

1017 These brackish-marine incursions contain rich but fragmentary fish faunas  
1018 (summarised in Fig. 17; see references in figure caption). A remarkable feature of these

1020 faunas in their conservative composition, with a consistent collection of taxa assembled by  
1021 Serpukhovian times (fauna of Pomquet Formation) and persisting for 20 million years, with  
1022 minimal variation, until late Moscovian times (fauna of Sydney Mines Formation).

1023

## 1024 CONCLUSIONS

- 1025 1. We describe a new fish fauna from the Carboniferous (Pennsylvanian; early  
1026 Moscovian) Minto Formation of New Brunswick, Canada
- 1027 2. The fauna includes chondrichthyans (xenacanthids, and the enigmatic *Ageleodus*),  
1028 acanthodians (gyracanthids and acanthodiforms), sarcopterygians (rhizodontids,  
1029 megalichthyids, rhizodopsids, and dipnoans), and actinopterygians.
- 1030 3. Facies analysis of taxa across a brackish-marine palaeosalinity gradient demonstrate  
1031 that almost all taxa were euryhaline, with chondrichthyans especially well equipped to  
1032 traverse into non-marine environments
- 1033 4. Documentation of widespread euryhalinity resolves a long-running debate about the  
1034 ecology of Carboniferous fishes, explaining how strontium isotope analyses of tooth  
1035 enamel indicate continental influence when other data point to marine dispersal.
- 1036 5. In the context of other rich Carboniferous fish faunas of the Maritimes Basin of  
1037 Atlantic Canada, fossils show the assembly of a conservative range of euryhaline taxa  
1038 over the 20 million year of the mid-Carboniferous diversification event into non-  
1039 marine settings.

1040

1041 **RANDY NOTES TO DEAL WITH LATER:** I assume that shark teeth may be better preserved  
1042 and easier to spot than bits and bobs of other fish – there may be a preservation bias that inflates  
1043 the numbers; Just to note then that Naiadites that is figured and any others are from Lithology 1 at  
1044 Coal Creek

1045  
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1058

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

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- 1584

1585 **FIGURE CAPTIONS**

1586

1587 **FIG. 1.** Location and geological context of the fossil sites. A, The Late Paleozoic Maritimes  
1588 Basin of Atlantic Canada, developed in the oblique convergence zone of Laurasia and  
1589 Gondwana (modified from Gibling *et al.* 2008). B, Geology of southern New Brunswick and  
1590 northwest Nova Scotia showing the fossil sites near Grand Lake, positioned on the stable  
1591 craton, adjacent to the active Moncton and Cumberland basins (modified from Falcon-Lang *et*  
1592 *al.* 2015a). C, Geology of the Pennsylvanian (early Moscovian) Minto Coalfield of New  
1593 Brunswick (after Hacquebard and Barss 1970; Ball *et al.* 1981; St Peter 2000) showing the  
1594 location of borehole DH62-1 illustrated in Fig. 4.

1595 **FIG. 2.** Geochronology and stratigraphic context of the fossil sites. A, The Pennsylvanian  
1596 Timescale (compiled from Peterson 2011; Waters and Condon 2012; Pointon *et al.* 2012;  
1597 Richards 2013). B., Stratigraphy of the Pennsylvanian (Bashkirian) Cumberland Group and  
1598 Pennsylvanian (Moscovian) Pictou Group of Atlantic Canada (modified from Gibling *et al.*  
1599 2008; Bashforth *et al.* 2014) showing the presence of Langsettian marine bands documented  
1600 in the Joggins (Grey *et al.* 2011) and Tynemouth Creek (Falcon-Lang *et al.* 2015b)  
1601 formations, and the new marine band (reported here) from the early to mid-Bolsovian part of  
1602 the Minto Formation.

1603 **FIG. 3.** Geology of the Pennsylvanian (early Bolsovian) Minto Coalfield (modified from  
1604 Hacquebard and Barss 1970). A, Isopachytes for (i) the Minto Coal and (ii) coal to basement,  
1605 the latter indicating onlap towards the northeast. B, Sandstone/mudstone ratio in the roof rock  
1606 of the Minto Coal showing NE-SW trending drainage channels that, locally, 'wash out' the  
1607 coal.

1608 **FIG. 4.** Sedimentary context of the fossil sites based on borehole core DH62-1. A, Graphic

1609 log of a short section of borehole DH62-1 (core boxes 44–52; depth 196–231 m) illustrating  
 1610 the three units of the Minto Formation (see text for explanation). The Minto Coal is removed  
 1611 from the core and limestone beds are believed to represent a roof facies as seen in the Joggins  
 1612 Formation (Davies and Gibling 2003). B, Erosive-based fluvial channel conglomerate facies  
 1613 in lower unit. C, Pin-stripe lamination in estuarine facies in middle unit. D, Red mudrock with  
 1614 carbonate glaeboles in upper unit. E, Close-up of paired mud-drapes in ripple cross-  
 1615 lamination in middle unit, a distinctive tidal indicator (cf. Naylor *et al.* 1998; Costain 2000).  
 1616 Scale bar is 30 mm (B–D), 4 mm (E).

1617 **FIG. 5.** Petrology of limestone Lithology 1 (shallow marine facies: A–G, NBMG 18779) and  
 1618 Lithology 2 (brackish embayment facies: H–I, NBMG 18611). A, Punctate brachiopods. B,  
 1619 fish skeletal fragments. C, Ostracodes. D, Punctate brachiopods and possible sponge spicules.  
 1620 E, Spirorbiform microconchids. F, Echinoderm spine mineralised with framboidal pyrite. G,  
 1621 putative foraminifera. H, Bivalves. I, Bivalves and phosphatic (francolite) nodule possibly of  
 1622 fish origin. Abbreviations: p.b., punctate brachiopods; f.s., fish skeletal fragments; o.v.,  
 1623 ostracode valves; s., sponge spicules; s.m., spirorbiform microconchids; e.s., echinoid spines;  
 1624 f.t., foraminifera test; f.p., framboidal pyrite; b.f., bivalve fragment. Scale bar is 1 mm (A–D,  
 1625 H–I), 0.5 mm (E–F), 0.25 mm (G).

1626 **FIG. 6.** Macroscopic invertebrates found in Lithology 2 (brackish embayment facies). A,  
 1627 Articulated *Naiadites* bivalves, NBMG 19967. B, Spirorbiform microconchid, NBMG 15841.  
 1628 C, Abundant spirorbiform microconchids, NBMG 15815. Abbreviations: s.m. spirorbiform  
 1629 microconchids. Scale bar is 5 mm (A), 1 mm (B), 1.5 mm (C).

1630 **FIG. 7.** Sedimentary and fossil characteristics of Lithology 3 (tidal estuary facies). A,  
 1631 Symmetrically-rippled siltstone to very fine-grained sandstone showing fish skeletal  
 1632 fragments concentrated within mud-rich ripple troughs. NBMG 15901 (specimen dissolved to

1633 extract fish fauna). B, Enlargement of area in (A) showing *Orthacanthus* tooth and macerated  
 1634 skeletal debris. Abbreviation: x.t., xenacanthid tooth. Scale bar as indicated (ruler divided into  
 1635 10 mm intervals) for A; 10 mm for B. .

1636 **FIG. 8.** Tip heaps adjacent to the former opencast mine at Iron Bound Cove (flooded area on  
 1637 the right; Latitude 46°08.67'N; Longitude 65°58.10'W), illustrating how material was  
 1638 collected by 'surface prospecting'.

1639 **FIG. 9.** Teeth of sharks from the Minto Formation (Pennsylvanian) of New Brunswick,  
 1640 Canada. A–D, Tricuspid tooth of *Orthacanthus compressus*, NBMG 19617, in aboral (A),  
 1641 oral (B), dorso-aboral (C), and ventro-oral (D) views. E, Tooth of Xenacanth indet., NBMG  
 1642 19629. F, Denticle of elasmobranch indet., NBMG 19667. G, Denticle of elasmobranch  
 1643 indet., NBMG 19647. H–J, Teeth of *Ageleodus pectinatus*: NBMG 19613 in aboral view (H),  
 1644 NBMG 19613 in oral view (I) and NBMG 15175 in aboral view (J). Abbreviations c.b:  
 1645 coronal button, n.f. nutrient foramen, m.f: median foramen. Scale bar is 2 mm (A–D), 1 mm  
 1646 (E), 0.25 mm (F–G), 0.5 mm (H–I), 2 mm (J).

1647 **FIG. 10.** Size ranges for shark teeth from the Minto Formation (Pennsylvanian), New  
 1648 Brunswick. A, Range of heights and frequencies for teeth of *Orthacanthus*. B, Cusp counts  
 1649 and frequencies for complete teeth of *Ageleodus*.

1650 **FIG. 11.** Spines of the Acanthodians from the Minto Formation (Pennsylvanian) of New  
 1651 Brunswick, Canada. A–F, *Gyracanthides* sp., G–H, *Acanthodes* sp. A–C, spines in lateral  
 1652 view: NBMG 15173 (A), NBMG 10739/1 (B), with indications of location of close-ups D  
 1653 and E, and NBMG 10739/2 (C). D, Striae on the insertion area and the angle between the  
 1654 striae and the exsertion area, NBMG 15173/1. E, Chevron pattern in ornament ridges on the  
 1655 leading edge, NBMG 15173/2. F, cross-section of a spine, NBMG 15173/4. G, spine in lateral  
 1656 view, NBMG 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, intercentrum 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 actinopterygian 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., actinopterygian 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.