

FISH AND TETRAPOD COMMUNITIES ACROSS A MARINE TO BRACKISH SALINITY GRADIENT IN THE PENNSYLVANIAN (EARLY MOSCOVIAN) MINTO FORMATION OF NEW BRUNSWICK, CANADA, AND THEIR PALAEOECOLOGICAL AND PALAEOGEOGRAPHICAL IMPLICATIONS

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Abstract: Euryhaline adaptations in Pennsylvanian vertebrates allowed them to inhabit the marine to freshwater spectrum. This is illustrated by new assemblages of fish and tetrapods from the early Moscovian Minto Formation of New Brunswick, Canada. Fish include chondrichthyans (xenacanthids and the enigmatic *Ageleodus*), acanthodians (gyracanthids and acanthodiforms), sarcopterygians (rhizodontids, megalichthyids and dipnoans), and actinopterygians (eurynotiforms). Tetrapods include small- to medium-sized, and largely aquatic, stem tetrapods (colosteids) and anthracosaurs (embolomeres). A key finding is that the parautochthonous fossil assemblages are preserved across a salinity gradient, with diversity (measured by the Simpson Index) declining from open marine environments, through brackish embayments, and reaching a nadir in tidal estuaries. Chondrichthyans dominate the entire salinity spectrum (65% of fossils), a distribution that demonstrates a euryhaline mode of life, and one large predatory chondrichthyan, *Orthacanthus*, may have

practised filial cannibalism in coastal nurseries because its heteropolar coprolites contain juvenile xenacanthid teeth. In contrast, other fish communities were more common in open marine settings while tetrapods were more common in coastal brackish waters. While all these faunas were also likely to have been euryhaline, their osmoregulation was, perhaps, less versatile. The demonstration of widespread euryhalinity among fish and aquatic tetrapods explains why Pennsylvanian faunas generally show a cosmopolitan biogeography because taxa were able to disperse via seaways. It also resolves the paradox of enriched strontium isotopic signatures observed in these faunas because organisms would have been, at times, exposed to continental water bodies as well. Therefore, our new findings contribute to the long-running debate about the ecology of Pennsylvanian fishes and tetrapods.

Key words: Pennsylvanian, fish communities, salinity gradient, euryhaline, cosmopolitan, New Brunswick.

EURYHALINE animals are relatively rare in modern ecosystems (Edwards & Marshall 2013; McCormick *et al.* 2013), with less than 10% of organisms adopting this

osmoregulatory strategy (Schultz & McCormick 2013). In contrast, euryhaline adaptations appear to have been much more widespread at certain times in the geological

past (Minter *et al.* in press) and, in fact, may have played a critical transitional role in the Palaeozoic colonization of continental freshwater ecospace (Buatois *et al.* 1998; Miller & Labandeira 2002; Park & Gierlowski-Kordesch 2007; Falcon-Lang *et al.* 2015a). Adaptation to lower and more variably saline (brackish to fresh) water bodies commenced as early as the Ordovician (MacNaughton *et al.* 2002; Davies & Sansom 2009; Sansom *et al.* 2009) and the abundance and complexity of these ecosystems steadily increased through the Silurian–Carboniferous (Jones & Dixon 1977; Buatois *et al.* 2005; Kennedy *et al.* 2012). Colonization patterns closely parallel the Ordovician rise of hepatophytes and the Silurian–Carboniferous diversification of tracheophytes (Gensel & Edwards 2001), indicating co-evolutionary teleconnections between land plants, terrestrial–marine nutrient export patterns (Algeo & Scheckler 1998), and the carrying capacity of ‘non-marine’ coastal environments (Prescott *et al.* 2014).

Adoption of euryhalinity appears to have peaked during a ‘mid-Carboniferous diversification’ when this mode of life, temporarily, became dominant (Davies & Gibling 2013; Falcon-Lang *et al.* 2015a) among organisms as diverse as microconchids, ostracodes, xiphosurans and fish (Anderson & Shuster 2003; Carpenter *et al.* 2011; Bennett *et al.* 2012; Gierlowski-Kordesch & Cassle 2015; Gierlowski-Kordesch *et al.* 2016) in order, perhaps, to utilize depauperate non-marine coastal ecospace for feeding and breeding (Williams *et al.* 2006; Carpenter *et al.* 2014). Rapid diversification coincided with the sharp growth of Gondwanan ice sheets and the onset of significant Milankovitch-driven glacio-eustatic fluctuations (Fielding *et al.* 2008; Montañez & Poulsen 2013). These marine transgressions, with magnitudes of up to 120 m (Rygel *et al.* 2008), repeatedly flooded continental margins, creating extensive epicontinental microtidal seaways (Wells *et al.* 2005), whose salinity slowly decreased in a landward direction over many hundreds of kilometres (Falcon-Lang 2005; Falcon-Lang *et al.* 2015b), similar to the present-day Baltic Sea (Andersson *et al.* 1992, 1994). This palaeoceanographic context probably provided optimum conditions for euryhaline organisms to exploit brackish environments.

In this paper, we describe euryhalinity in Late Palaeozoic vertebrate communities. Facies analysis suggests that a wide range of fish, including gyraacanthids, elasmobranchs, dipnoans, rhizodonts and megalichthyids, as well as tetrapods, existed in freshwater to brackish environments in Devonian–Carboniferous times (Friedman & Sallan 2012), and much recent attention has been given to the apparent dominance of a euryhaline mode of life among mid-Carboniferous vertebrate communities (Schultze 2009; Carpenter *et al.* 2011, 2014, 2015). However, consensus regarding ecology is currently lacking, with some researchers arguing on palaeogeographical, sedimentological and geochemical grounds that fish taxa,

especially xenacanthid sharks (Masson & Rust 1984) and tetrapods, may have been obligate freshwater organisms (Johnson 1979, 1999; Stamberger & Zajíc 2008; Fischer *et al.* 2011, 2013; Montañez & Cecil 2013). In this paper, we describe a new fauna of fish and tetrapods from the Carboniferous (Pennsylvanian; early Moscovian) of New Brunswick, Canada (Fig. 1A), and demonstrate (based on independent indicators of palaeosalinity) that certain fish and tetrapod taxa existed across a brackish to marine gradient, and that communities must therefore have been euryhaline. We discuss how these new findings improve our understanding of Carboniferous fish and tetrapod ecology.

GEOLOGICAL CONTEXT

The fish and tetrapod fossils reported here were obtained from opencast mine sites (now reclaimed) within the Minto Coalfield, Queens County, New Brunswick, Canada (Fig. 1). The rocks of the Minto Coalfield are of historical interest, having been the first place in North America where coal was mined, beginning in 1639, and they are mentioned in a 1667 entry of Samuel Pepys’ famous diary (Smith 1989; Falcon-Lang 2009; Quann *et al.* 2010).

Stratigraphy, age and basin analysis

Rocks of the Minto Coalfield belong to the Pennsylvanian Minto Formation (*sensu* St Peter & Johnson 2009), the lowest unit of the Pictou Group. They were deposited on the New Brunswick Platform (Fig. 1B–C), a stable cratonic region that lay to the north of the oblique collisional zone between Laurasia and Gondwana (Gibling *et al.* 2008). Based on combined megafloral and palynofloral biostratigraphy, the Minto Formation is thought to be latest Duckmantian to Bolsovian in age (Hacquetard & Bars 1970; St Peter 1997, 2000), with the economically important Minto Coal specifically dated as early Bolsovian (Kalkreuth *et al.* 2000). Radiometric ages recently obtained from immediately below and above the Aegiranum Marine Band, which marks the Duckmantian–Bolsovian in western Europe (Pointon *et al.* 2012; Waters & Condon 2012), suggest an age of *c.* 314 Ma for this boundary. The Minto Formation therefore correlates with the early part of the Moscovian Stage (Peterson 2011; Richards 2013; Fig. 2A).

Within the Minto Coalfield, sediments of the Minto Formation were deposited unconformably over the top of basement rocks of Mississippian age and older, as the cratonic New Brunswick Platform underwent thermal subsidence (Gibling *et al.* 2008; Fig. 2B). Extensive borehole arrays indicate that this basal unconformity is marked by

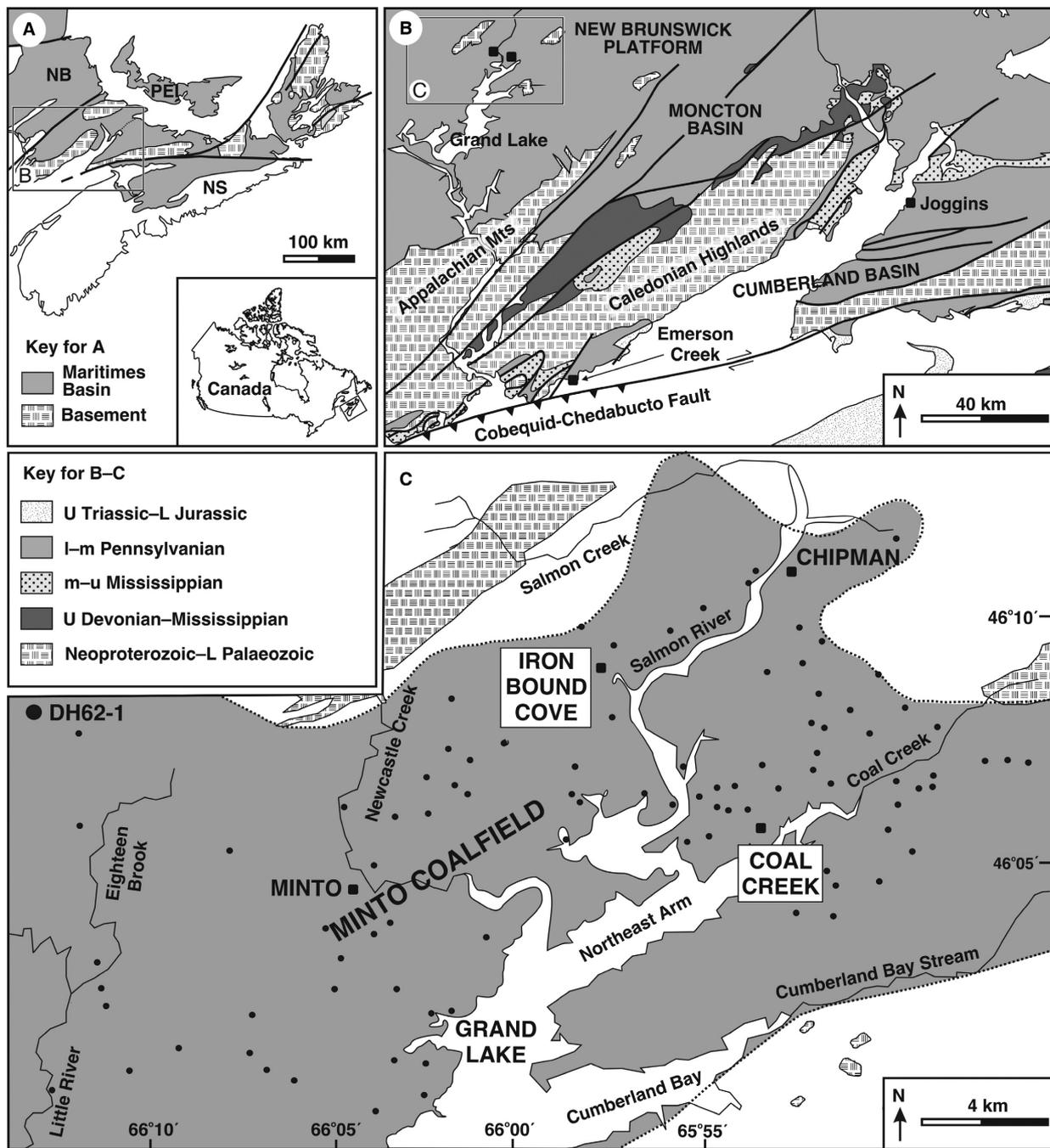


FIG. 1. Location and geological context of the fossil sites. A, the Late Palaeozoic Maritimes Basin of Atlantic Canada, developed in the oblique convergence zone of Laurasia and Gondwana (modified from Gibling *et al.* 2008); inset map gives location within Canada. B, geology of southern New Brunswick and north-west Nova Scotia showing the fossil sites near Grand Lake, positioned on the stable craton, adjacent to the active Moncton and Cumberland basins (modified from Falcon-Lang *et al.* 2015a); other Pennsylvanian sites with marine beds (Joggins, Emerson Creek) are also shown. C, geology of the Pennsylvanian (early Moscovian) Minto Coalfield of New Brunswick (after Hacquebard & Barss 1970; Ball *et al.* 1981; St Peter 2000) showing the location of the two fossil sites, borehole DH62-1 illustrated in Figure 4, and other boreholes (closed circles). *Abbreviations:* NB, New Brunswick; NS, Nova Scotia; PEI, Prince Edward Island.

a major silcrete palaeosol, up to 9 m thick in places (Sullivan 1981; St Peter 2000), which mantles the basement complex and indicates seasonally dry-climate weathering

over the preceding several million years of depositional hiatus (St Peter & Johnson 2009). In the course of this lengthy episode of landscape degradation, a NE-SW-

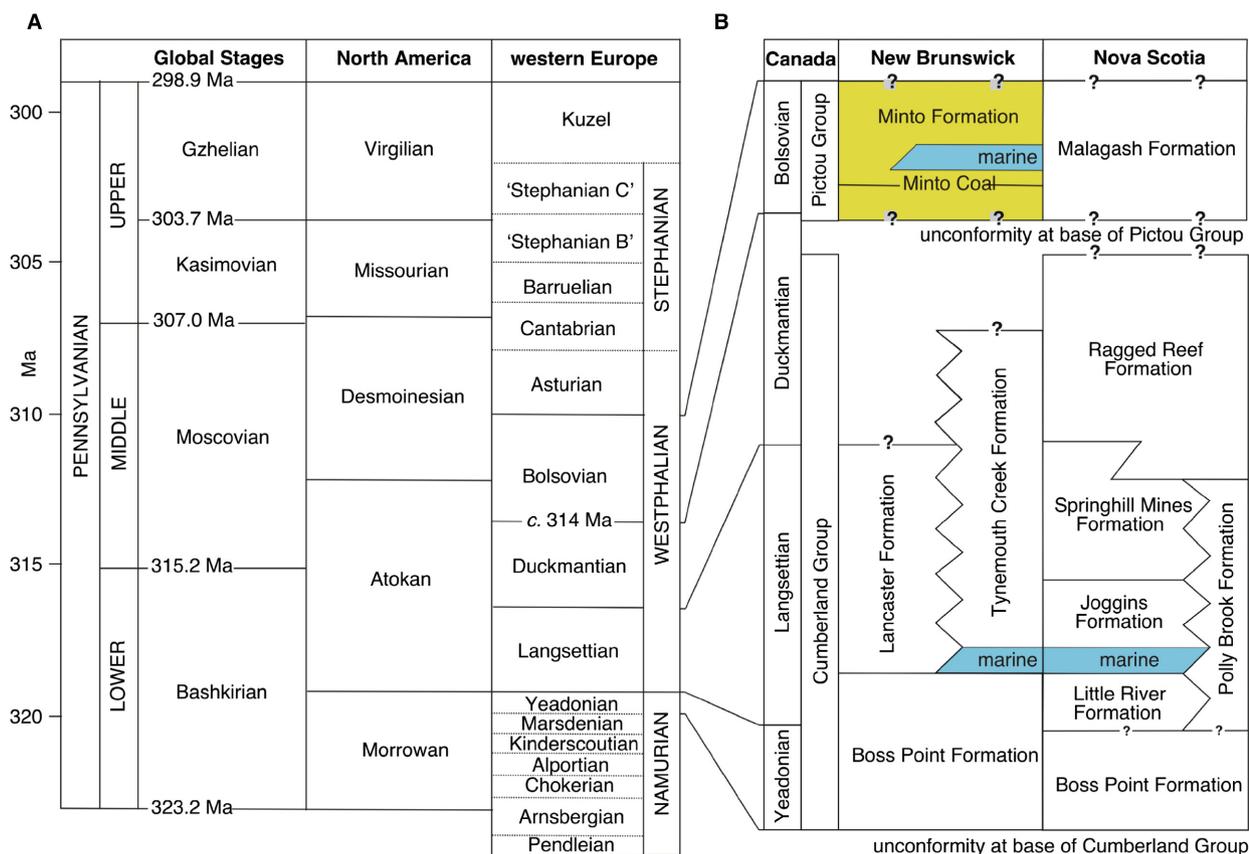


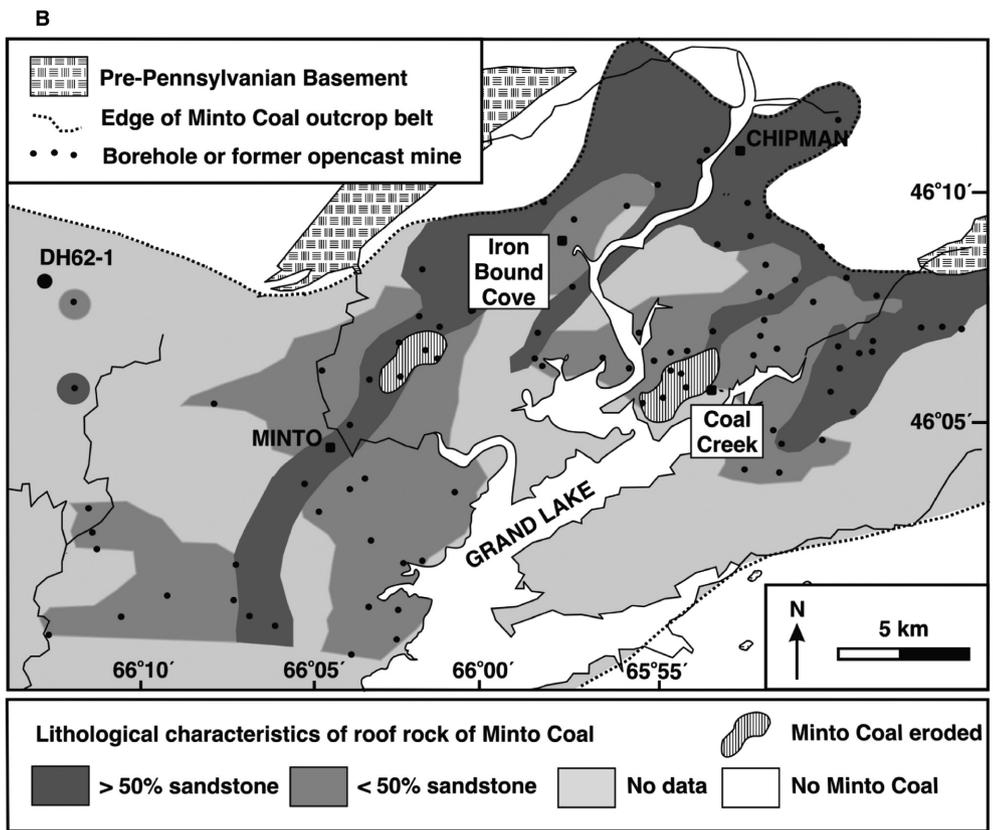
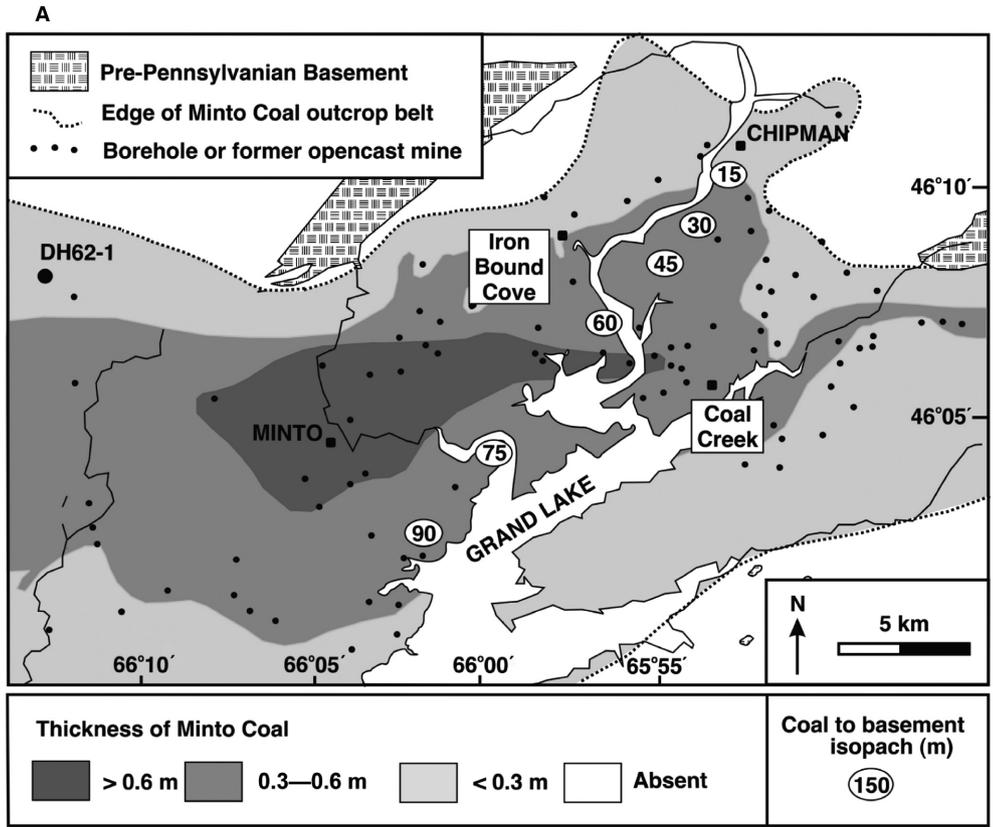
FIG. 2. Geochronology and stratigraphical context of the fossil sites. A, the Pennsylvanian timescale (compiled from Peterson 2011; Waters & Condon 2012; Pointon *et al.* 2012; Richards 2013). B, stratigraphy of the Pennsylvanian (Bashkirian) Cumberland Group and Pennsylvanian (Moscovian) Pictou Group of Atlantic Canada (modified from Gibling *et al.* 2008; Bashforth *et al.* 2014) showing the presence of Langsetian marine bands documented in the Joggins (Grey *et al.* 2011) and Tynemouth Creek (Falcon-Lang *et al.* 2015b) formations, and the new marine band (reported here) from the early to mid-Bolsovian part of the Minto Formation. Colour online.

trending valley system, *c.* 16 km wide, was cut into the basement, forming an erosional 'container' (degradational depocentre) in which younger sediments of the Minto Formation accumulated (Hacquebard & Barss 1970).

This bedrock palaeovalley was bordered on either side by slates and lavas that formed subdued topographical highs with a palaeoelevation of a few tens of metres above base level (Hacquebard & Barss 1970; Gray *et al.* 2012; Fig. 3A). Two lines of evidence suggest that the valley drained towards the southwest (Hacquebard & Barss 1970): (1) the thickness of the lower part of the formation, as measured from the basement contact to the base of the Minto Coal (a prominent chronostratigraphic marker bed) gradually increases from *c.* 15 m in the north-east to >90 m in the south-west (Fig. 3A), implying that

the basin deepened towards the south-west, and sediment progressively overlapped towards the north-east; and (2) NE-SW-orientated ribbons of channelized sandstone, 1–1.5 km wide, in the 'roof rock' of the Minto Coal, fine towards the south-west (Fig. 3B) and suggest sediment transport in that direction. We note, however, that this inferred palaeoflow direction opposes regional patterns of sediment dispersal, which are directed towards the ENE (van de Poll 1973; Gibling *et al.* 1992). This suggests that either drainage in the Minto Coalfield was strongly influenced by local bedrock topography, or that palaeoflow inferences based on grain size and isopachytes are incorrect. More reliable palaeoflow indicators, such as cross-bed arrays, have not been obtained to date due to poor surface exposure.

FIG. 3. Geology of the Pennsylvanian (early Bolsovian) Minto Coalfield (modified from Hacquebard & Barss 1970). A, isopachytes for the Minto Coal and coal to basement, the latter indicating onlap towards the north-east. B, sandstone/mudstone ratio in the roof rock of the Minto Coal showing NE-SW trending drainage channels that, locally, 'wash out' the coal (i.e. areas where Minto Coal is eroded).



Palaeoenvironments

Despite its long history of geological study (Gesner 1841; Robb 1850; Bailey & Matthew 1873), there have been no comprehensive studies of the sedimentary facies of the Minto Formation (St Peter 2000; Clark 2004; St Peter & Johnson 2009). Three units are generally recognized, and their lithologies are described below, based on our own studies of borehole cores (DH62-1 to 3) accessioned at the New Brunswick Department of Energy and Mines, Geological Surveys Branch, Fredericton (Fig. 4A).

The lowest unit, up to 60 m thick (uppermost part only is shown in Fig. 4A), comprises quartz pebble and intraclast conglomerate, fine- to very coarse-grained trough cross-bedded sandstone, and grey siltstone arranged in fining-upward successions, with intermittent silcrete palaeosols. These beds resemble the broadly coeval (early Moscovian) South Bar Formation of Nova Scotia, which formed under braided fluvial conditions (Rust & Gibling 1990), and the early Moscovian Waddens Cove Formation of Nova Scotia, which shows similar silcrete palaeosols (Gibling & Rust 1992). The beds are interpreted as the fluvial channel deposits of a poorly- to well-drained coastal plain.

The middle unit, up to 15 m thick (Fig. 4A), comprises grey laminated shale with distinctive 'pinstripe' laminations of very fine-grained to fine-grained sandstone. Sedimentary structures include ripple cross-lamination showing mud drape pairs, flaser bedding, and symmetrical ripples (Fig. 4B–C). At one level the <0.8 m thick Minto Coal is developed, underlain by a seat earth, 1 m thick (rooted, bleached palaeosol). These beds resemble those of the broadly coeval (early Moscovian) Malagash Formation of Nova Scotia, interpreted as tidal deposits (Naylor *et al.* 1998; Costain 2000), with the coal being formed in a calamite-dominated coastal peat mire (Kalkreuth *et al.* 2000). Proximity of the peat mire to an open brackish-marine embayment is supported by the relatively high (5–9%) sulphur content of the Minto Coal, which increases towards the south-west and the basin centre (Fig. 3A; Hacquebard & Barss 1970). Sandstone ribbons, up to 1.5 km wide, that have been mapped in the succession overlying the Minto Coal, and locally 'wash out' the coal (Fig. 3B) may represent incised valleys, flooded to form tidal estuaries; however, this interpretation cannot be confirmed because the boreholes do not intersect this facies.

The uppermost unit, *c.* 100 m thick (lowermost part only shown in Fig. 4A), comprises units of pebbly sandstone, thin sandstone sheets, and relatively thick intervals of massive, red mudrock, locally showing slickensides and small, scattered carbonate nodules. These beds were formerly assigned to the Hurley Creek Formation, but were amalgamated into the Minto Formation by St Peter

(2000), based on regional mapping. The succession probably represents the deposits of a relatively well-drained alluvial plain (cf. Davies & Gibling 2003), but borehole characteristics are insufficient for detailed analysis.

Fish- and tetrapod-bearing lithologies

Fish and tetrapod assemblages reported here were not collected *in situ* within a logged succession, but obtained from the tip heap piles of opencast mines exploiting the Minto Coal at relatively shallow depth, and must have come from the overburden of the coal. A careful review of all fossiliferous specimens shows that the fossils occur in four different lithologies, and can be related to the logged section, with varying degrees of confidence. All fossils are inferred to have come from the middle unit (tidal/estuarine facies), as shown on Fig. 4A.

Lithology 1 comprises a medium grey limestone bed, up to 24 mm thick, which shows abundant fish skeletal fragments throughout. In petrographic thin section, the lithology comprises a wackestone containing scattered bioclasts of punctate brachiopods (Fig. 5A, D), fish bones (Fig. 5B), ostracodes (Fig. 5C), putative sponge spicules (Fig. 5D), spirorbiform microconchids (Fig. 5E), echinoid spines (Fig. 5F), and putative forams (Fig. 5G). An early diagenetic phase of framboidal pyrite (Fig. 5F) commonly infills voids, followed by a later phase of sparry calcite (Fig. 5C, E, G). The only macroscopic invertebrate fossils that are visible in hand specimen are rare spirorbiform microconchids (Fig. 6A–B). The invertebrate assemblage, together with the presence of framboidal pyrite, indicates deposition under fully marine conditions (Maliva 1989; Tucker & Wright 1990; Schieber 2002). The high micrite content indicates quiet bottom waters, and the absence of siliciclastic grains suggests that the marine embayment was relatively extensive (Gibling & Kalkreuth 1991). Similar marine limestone beds have been documented elsewhere in the Maritimes Basin, in the Pennsylvanian (Langsettian) Joggins Formation (Grey *et al.* 2011) and Tynemouth Creek Formation (Falcon-Lang *et al.* 2015a).

Lithology 2 comprises dark grey, bituminous limestone, up to 28 mm thick, showing abundant fragments and rare articulated examples of the bivalve *Naiadites* (Fig. 6C), spirorbiform microconchids and a large quantity of comminuted fossil plant debris. In petrographic thin section, these lithologies comprise bivalve-dominated packstone with minimal micrite matrix (Fig. 5H–I), rare fish fragments (Fig. 5I) and spirorbiform microconchids. Calver (1968) interpreted *Naiadites* as a mostly brackish bivalve, and it is known also from identical lithologies in the Pennsylvanian Joggins, Port Hood, Parrsboro and Sydney Mines Formations of nearby Nova Scotia, where they have been interpreted as the deposits of extensive

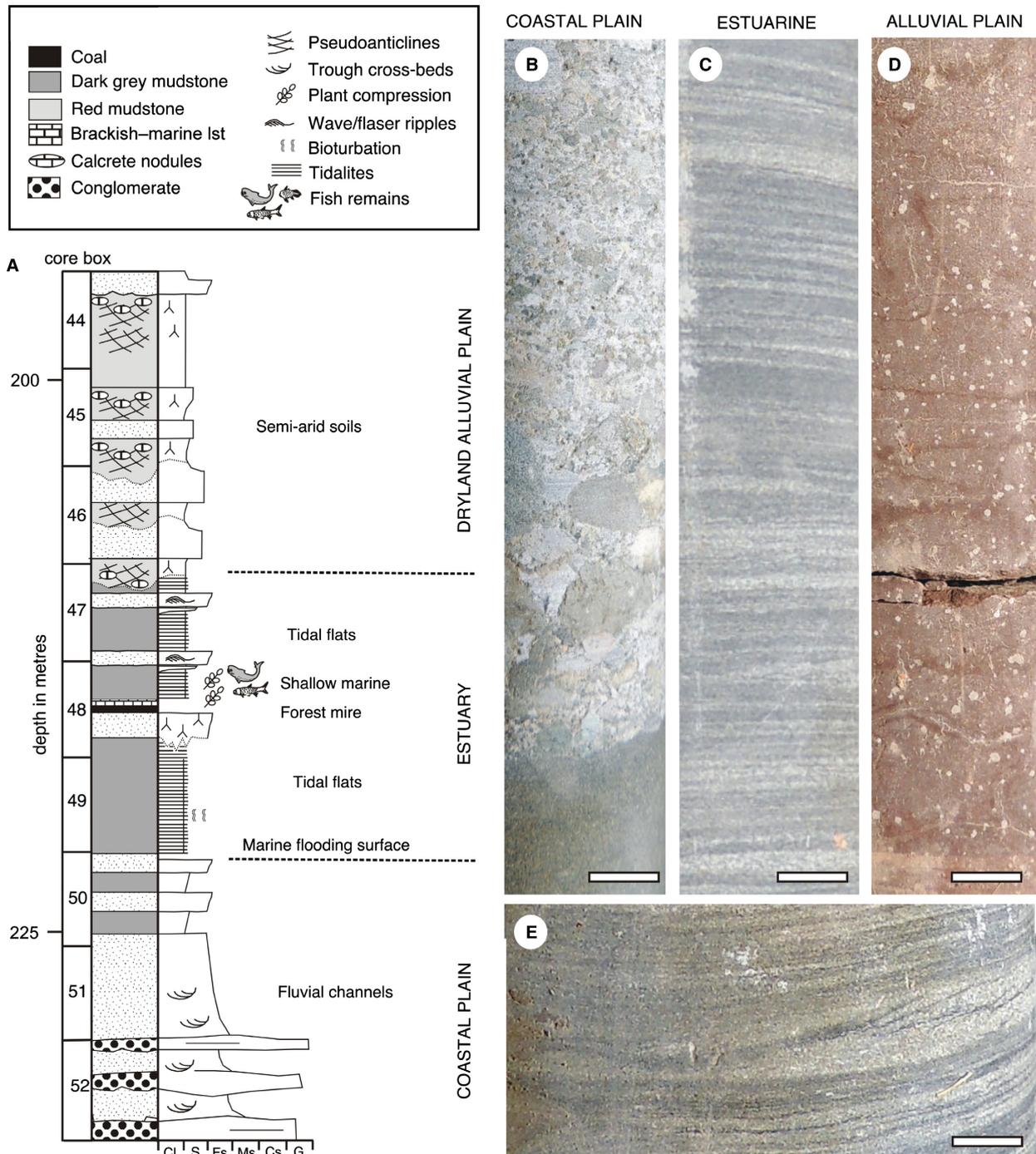


FIG. 4. Sedimentary context of the fossil sites based on borehole core DH62-1. A, graphic log of a short section of borehole DH62-1 (core boxes 44–52; depth 196–231 m) illustrating the three units of the Minto Formation (see text for explanation). The Minto Coal is removed from the core and limestone beds are believed to represent a roof facies as seen in the Joggins Formation (Davies & Gibling 2003). B, erosive-based fluvial channel conglomerate facies in lower unit. C, pin-stripe lamination in estuarine facies in middle unit. D, red mudrock with carbonate glaebules in upper unit. E, Close-up of paired mud-drapes in ripple cross-lamination in middle unit, a distinctive tidal indicator (cf. Naylor *et al.* 1998; Costain 2000). Scale bars represent 30 mm (B–D); 4 mm (E). Colour online.

brackish embayments (Gibling & Kalkreuth 1991; Calder 1998; Falcon-Lang *et al.* 2006). The environment was probably shallow and wave-agitated given that the micrite

matrix has largely been winnowed away and bivalves are commonly fragmented (Davies & Gibling 2003; Falcon-Lang 2005; Carpenter *et al.* 2015).

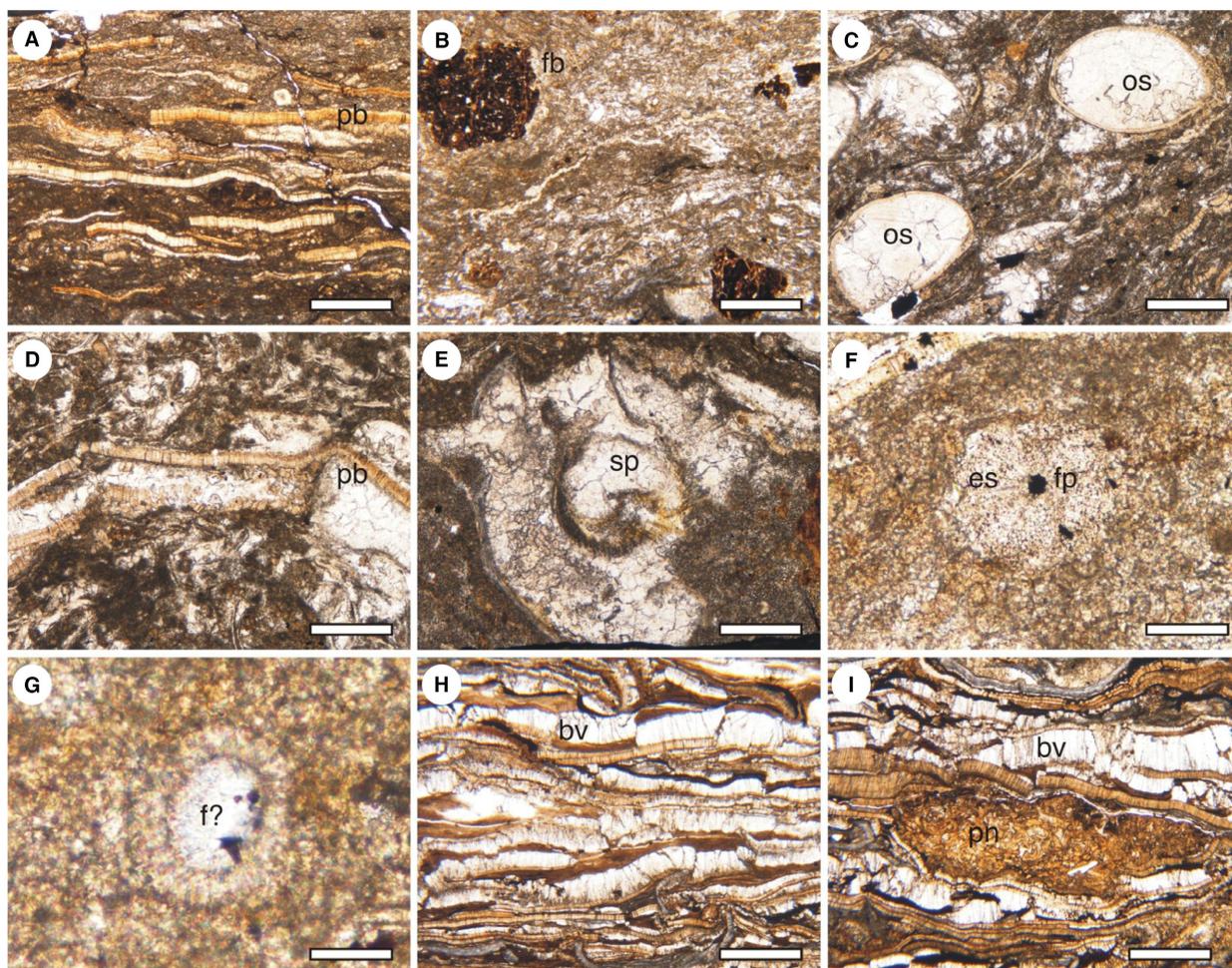


FIG. 5. Petrology of limestone Lithology 1 (shallow marine facies at Iron Bound Cove: A–G, NBMG 18789) and Lithology 2 (brackish embayment facies at Coal Creek: H–I, NBMG 18611). A, punctate brachiopods. B, fish skeletal fragments. C, ostracodes. D, punctate brachiopods and possible sponge spicules. E, spirorbiform microconchids. F, echinoderm spine mineralized with framboidal pyrite. G, putative foraminifera. H, bivalves. I, bivalves and phosphatic (francolite) nodule possibly of fish origin. *Abbreviations:* bv, bivalve fragment; es, echinoid spines; f, foraminifera test; fb, fish skeletal fragments; fp, framboidal pyrite; os, ostracode carapace; pb, punctate brachiopods; pn, phosphatic nodule, sp, spirorbiform microconchids; Scale bars represent 1 mm (A–D, H–I); 0.5 mm (E–F); 0.25 mm (G). Colour online.

Neither limestone lithology was observed in the logged boreholes. However, in the Joggins Formation of Nova Scotia, such thin limestone beds form the roof of coal seams (Davies & Gibling 2003; Falcon-Lang 2005), and represent brackish-marine flooding surfaces, possibly triggered by glacio-eustatic or tectonic factors (Falcon-Lang *et al.* 2006). In all the boreholes that we studied, the interval containing the Minto Coal has been removed for coal petrographic analysis, and possibly with it, evidence for the stratigraphical position of overlying limestone beds. Clearly, the two limestone lithologies represent open-water facies, and the presence of comminuted plant debris in Lithology 2 suggests proximity to coastal vegetation. Based on fossil content and lithology, we infer that Lithology 1 was formed in the offshore marine part of

the embayment and Lithology 2 represents the coastal embayed zone where fluvial discharge led to lower and most variable salinities.

Lithology 3 comprises thinly bedded, pale grey siltstone to very fine-grained sandstone showing symmetrical ripple marks with mud drapes (Fig. 7A). In thin section, it shows a poorly developed micritic matrix. Fish skeletal fragments, included xenacanthid teeth, are particularly concentrated within the mud-rich ripple troughs (Fig. 7B). Lithology 4 comprises a medium- to dark-grey, laminated mudstone, with thin partings of very fine-grained sandstone, and isolated fish fragments. These latter two lithologies are identical to those found in the tidal/estuarine facies reported from the borehole core overlying the Minto Coal, and therefore can be directly

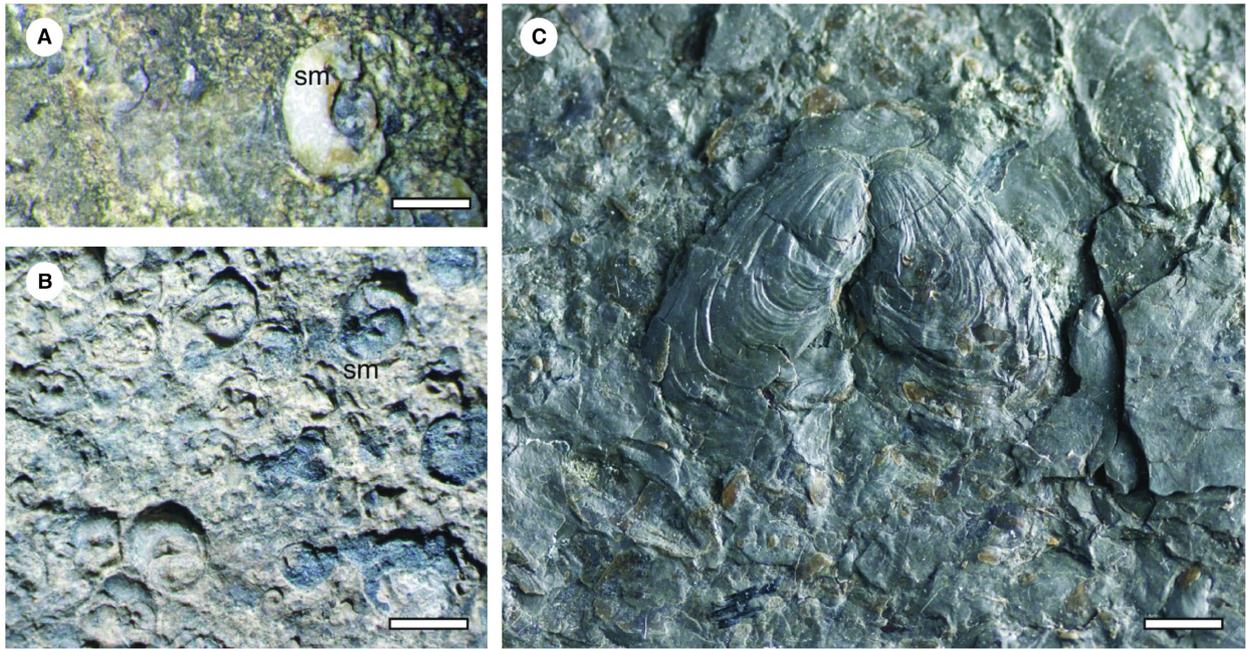


FIG. 6. A–B, macroscopic invertebrates found in Lithology 1 (shallow marine facies at Iron bound Cove); A, spirorbiform microconchid, NBMG 15841; B, abundant spirorbiform microconchids, NBMG 15815. C, articulated *Naiadites* bivalves, NBMG 19967; found in Lithology 2 (brackish embayment facies at Coal Creek). *Abbreviation:* sm, spirorbiform microconchids. Scale bars represent 1 mm (A); 1.5 mm (B); 5 mm (C). Colour online.

related to the logged succession with a high degree of confidence. These clastic beds probably represent the most proximal of the fossiliferous lithologies, probably deposited within a tidal estuary developed on the coast of the brackish-marine epicontinental sea represented by the limestone beds.

MATERIAL AND METHOD

All fossil material reported here was obtained by surface prospecting on weathered tip heaps adjacent to back-filled opencast coal mines within the Minto Coalfield (Fig. 8), and no material was directly obtained in a sedimentary context.

Localities, collections and collections history

Fossil material was collected in four phases. Prior to 1988, William H. Forbes obtained 28 specimens from various sites in the Minto Coalfield, but without detailed locality data (Miller & Forbes 2001). Between c. 1991 and 2000, amateur palaeontologist Michael Lee obtained a much larger collection at Iron Bound Cove (46°08.67'N; 65°58.10'W) and Coal Creek (46°06.09'N; 65°53.39'W) on the Northeast Arm of Grand Lake, c. 10 km NE of Minto, Queens County (Fig. 1B–C). Those collections

were augmented by one of us (RFM) in collaboration with Michael Lee, at Iron Bound Cove in 2002, and by three of us (AÓG, RFM, MRS) at Iron Bound Cove in 2015. There are 404 catalogued hand specimens from Iron Bound Cove and 60 catalogued hand specimens from Coal Creek, together with a further 230 specimens from Coal Creek that are currently uncatalogued but show indeterminate fish skeletal material only.

Specimen preparation and imaging

Fossils visible on bedding surfaces were prepared using a combination of mechanical and chemical removal of surrounding matrix. Mechanical preparation was by means of a pin-vice, assorted fine-tipped brushes, and tweezers. Where the matrix was too hard for this to work, specimens were immersed in a 5% acetic acid solution, buffered with calcium acetate, following the approach of Jeppsson *et al.* (1985). To minimize risk of fracture and to provide a barrier against acid attack, fossils were coated with a weak, ethanol-based contact adhesive ('Mowital') before acid digestion. Specimens prepared in this way were photographed with a Nikon D700 digital SLR camera with a Nikon 60 mm macro lens. Other specimens were photographed using a Panasonic Lumix DMC-ZS3 digital camera or a Canon Eos 40D digital camera using a Canon Ultrasonic 100 mm



FIG. 7. Sedimentary and fossil characteristics of Lithology 3 (tidal estuary facies). A, symmetrically-rippled siltstone to very fine-grained sandstone showing fish skeletal fragments concentrated within mud-rich ripple troughs. NBMG 15901 (specimen dissolved to extract fish fauna). B, enlargement of boxed area in A showing *Orthacanthus* tooth and macerated skeletal debris. Abbreviation: xt, xenacanthid tooth. Scale bar divided into 10 mm intervals (A); 5 mm (B). Colour online.

macro lens or mounted on a Leica MS5 microscope. Figures were prepared with Adobe Photoshop Illustrator in Creative Suite 5.

Institutional abbreviation. NBMG, New Brunswick Museum (Geology), Saint John, New Brunswick, Canada.

SYSTEMATIC PALAEOLOGY

A comprehensive review of 722 hand specimens containing >2692 individual fish skeletal fragments in the NBMG collections from the Minto Formation is given in Ó Gogáin *et al.* (2016, S1). Miller (1999) published a preliminary list of taxa known up to that date, but

no detailed study of the material has been undertaken hitherto. We present the materials in the sequence Chondrichthyes, Acanthodii, Sarcopterygii, Actinopterygii (Table 1).

Class CHONDRICHTHYES Huxley, 1880
 Subclass ELASMOBRANCHII Bonaparte, 1838
 Superorder XENACANTHIMORPHA Nelson, 1976
 Order XENACANTHIFORMES Berg, 1937
 Family DIPLODOSELACHIDAE Dick, 1981

Genus ORTHACANTHUS Agassiz, 1843a

Type species. *Orthacanthus cylindricus* Agassiz, 1843a



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

Orthacanthus compressus Newberry, 1856
Figure 9A–D

Material. 70 specimens bearing isolated teeth (NBMG 9948, 10740 (juvenile specimen attached to *Ctenodus* tooth plate), 10746–10748, 10757, 14953–14965, 14967–14968, 14983–14984, 14991–14993, 14996, 15823, 15825, 15832–15834, 15836, 15838, 15841, 15843, 15846–15847, 15849, 15902–15903, 15905–15910, 15916, 16088, 16090, 16093, 16095, 19614–19626, 19850, 19852–19854, 19856).

Diagnosis. Teeth bi- or tricuspid, with two lateral cusps flanking a median cusp in tricuspid teeth. Where present, the median cusp is smaller than the lateral cusps. Carinae may be present on the edges of the lateral cusps. Tooth base is thin with a round to oval shape. A coronal button is present which does not contact any cusps. A median foramen is present on the labial side of the coronal button. A basal tubercle may be present, which extends in a labial direction and has a bulbous shape.

Description. Teeth range in height, as measured from the basal surface to the apex of the largest cusp, from 0.5 to 11.0 mm (Fig. 10A). In larger teeth (>1 mm) one lateral cusp is typically larger than the other with both showing a degree of lateral divergence; the 'major cusp' tends to diverge more than the 'minor cusps' (Fig. 9A–D), with some 'minor cusps' having near vertical orientations. Lateral cusps have a lanceolate cross-section. Carinae are present on lateral cusps ≥ 1 mm. Serration is absent from all specimens. Median cusps, although present in the majority of specimens, are absent in several teeth. The median cusps of teeth >0.5 mm high are on average less than one-third the height of associated lateral cusps, whereas the median cusps of teeth ≤ 0.5 mm high are roughly the same height as the lateral cusps. A median foramen is present in all specimens. The

TABLE 1. Summary of fish taxa from the Pennsylvanian (early Moscovian; early Bolsolvian) Minto Formation of New Brunswick, Canada (cf. Bashkirian fish fauna in Joggins Formation; Carpenter *et al.* 2015, fig. 5).

Class CHONDRICHTHYES
Subclass ELASMOBRANCHII
Superorder XENACANTHIMORPHA
Order XENACANTHIFORMES
Family DIPLODOSELACHIDAE
Genus <i>ORTHACANTHUS</i>
<i>Orthacanthus compressus</i>
Order <i>incertae sedis</i>
Family <i>incertae sedis</i>
Genus <i>AGELEODUS</i>
<i>Ageleodus pectinatus</i>
Class ACANTHODII Owen, 1846
Order <i>incertae sedis</i>
Family GYRACANTHIDAE
Genus <i>GYRACANTHIDES</i>
<i>Gyracanthides</i> sp.
Order ACANTHODIDA
Family ACANTHODIDAE
Genus <i>ACANTHODES</i>
<i>Acanthodes</i> sp.
Class OSTEICHTHYES
Subclass SARCOPTERYGII
Infraclass DIPNOMORPHA
Order DIPNOI
Family <i>incertae sedis</i>
Genus <i>CTENODUS</i>
<i>Ctenodus interruptus</i>
Infraclass TETRAPODOMORPHA
Order RHIZODONTIDA
Family RHIZODONTIDAE
Genus <i>STREPSODUS</i>
<i>Strepsodus sauroides</i>
Genus <i>ARCHICHTHYS</i>
<i>Archichthys portlocki</i>
Genus <i>RHIZODUS</i>
cf. <i>Rhizodus hibberti</i>
Order <i>incertae sedis</i>
Family RHIZODOPSIDAE
Genus <i>RHIZODOPSIS</i>
cf. <i>Rhizodopsis sauroides</i>
Order Sarcopterygii <i>incertae sedis</i>
Family MEGALICHTHYIDAE
Genus <i>MEGALICHTHYS</i>
<i>Megalichthys</i> sp.
Subclass ACTINOPTERYGII Cope, 1887
Order EURYNOTIFORMES
<i>Actinopterygii indet.</i>

shape of the coronal button is variable, and may be rounded, oval or heart-shaped (Fig. 9D), and oval coronal buttons are elongated along the labial-lingual axis. Lingual to the coronal button are 1–4 nutritive foramina except in one specimen where the button is absent; the precise placement of the nutritive

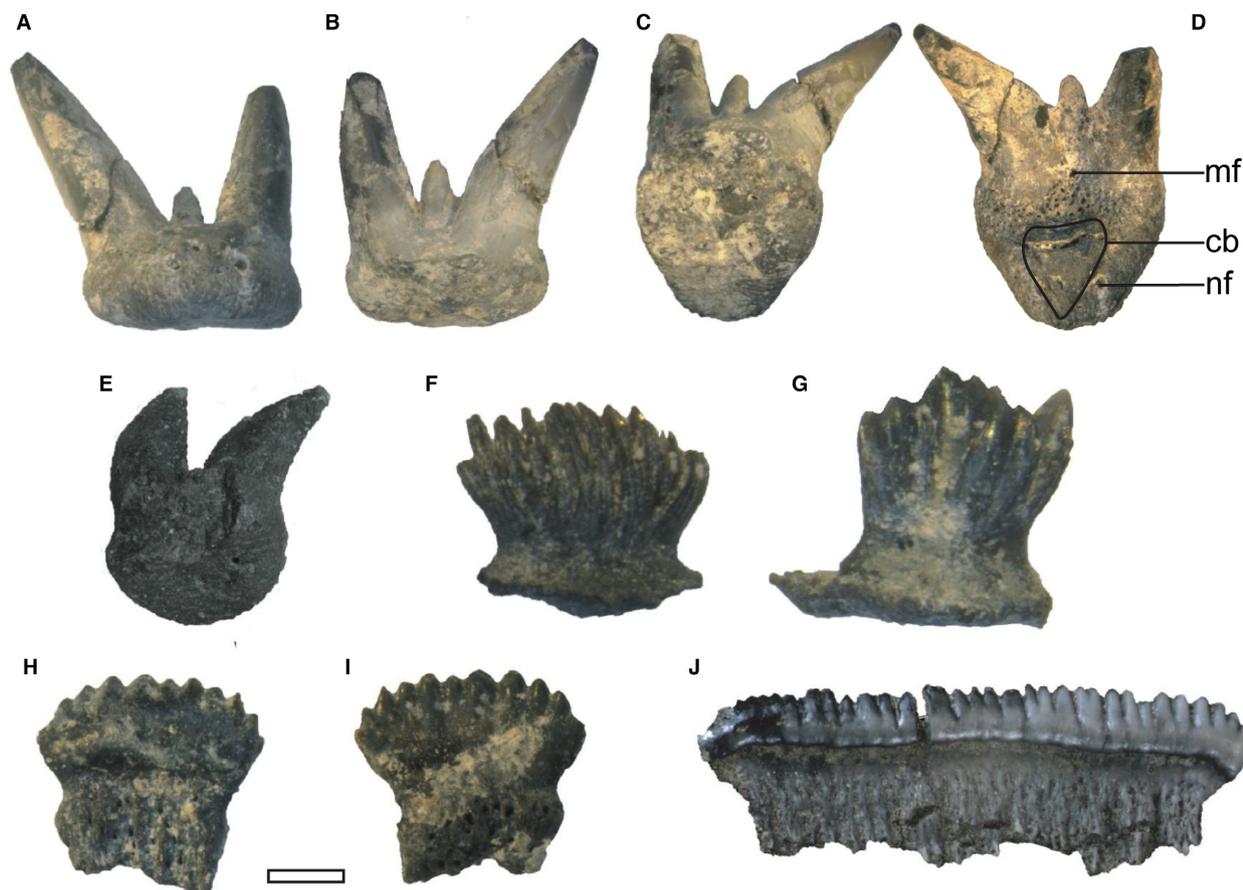


FIG. 9. Teeth of chondrichthyans from the Minto Formation (Pennsylvanian) of New Brunswick, Canada. A–D, tricuspid tooth of *Orthacanthus compressus*, NBMG 19617, in: A, oral; B, aboral; C, ventro-aboral; D, dorso-oral views. E, tooth of xenacanth indet., NBMG 19629. F, denticle of elasmobranch indet., NBMG 19667. G, denticle of elasmobranch indet., NBMG 19647. H–J, teeth of *Ageleodus pectinatus*: H, NBMG 19613 in aboral view; I, NBMG 19613 in oral view; J, NBMG 15175 in aboral view. *Abbreviations:* cb, coronal button; nf, nutrient foramen; mf, median foramen. Scale bar represents 2 mm (A–D); 1 mm (E); 0.25 mm (F–G); 0.5 mm (H–I); 2 mm (J). Colour online.

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

Remarks. Tooth size is unimodal (Fig. 10A), suggesting that we have a single population and a single species. Assigning small teeth and teeth which lack serration to the genus *Orthacanthus* has been argued against by Hampe (1988). Johnson (1999), on the other hand, showed that *Orthacanthus* teeth can lack serration and have small sizes. It is difficult to distinguish *Orthacanthus compressus* from *Orthacanthus texensis*; *O. texensis* has been ruled out as a possible identity here, as teeth of this species typically have thicker bases, whereas *O. compressus* teeth are

characterized by having thin bases, although this is not always the case (Johnson 1999). Also our specimens lack serration, whereas serration has been recorded in thin-based teeth of *O. texensis* (Johnson 1999). Based on the placement of teeth within the jaw for *O. texensis* (Johnson 1999), it is reasonable to assume a posterior curvature of the ‘major cusp’ in the teeth of *O. compressus*.

Xenacanthiformes indet.

Figure 9E

Material. 33 specimens containing isolated teeth (NBMG 14966, 14985–14987, 14994, 15835, 15837–15838, 15842, 15848, 16082, 16089, 18613, 19628–19645, 19846, 20003).

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

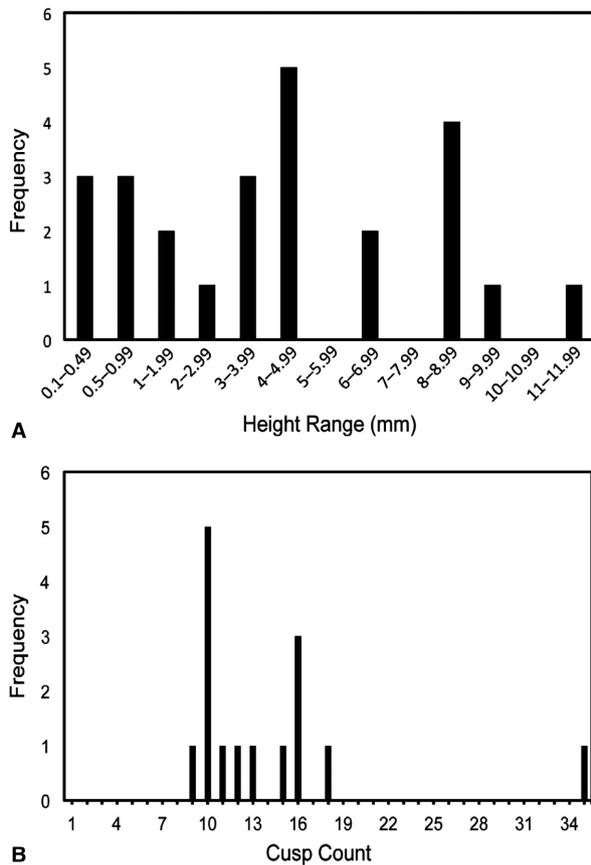


FIG. 10. Size ranges for Chondrichthyan teeth from the Minto Formation (Pennsylvanian), New Brunswick. A, range of heights and frequencies for teeth of *Orthacanthus*. B, cusp counts and frequencies for complete teeth of *Ageleodus*.

Description. Bi- or tricuspid teeth with a base that extends in a lingual to antero-lingual direction. Cusps are lanceolate to oval in cross-section and lateral cusps larger than 1 mm often have carinae on their lateral edges. Serration is absent in all specimens. A sub-circular coronal button is present in specimens with intact bases. In specimens not obscured by sediment there is no median foramen. A convex basal tubercle is present except where it has been broken off (Fig. 9E).

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

Elasmobranchii indet.
Figure 9F–G

Material. 32 specimens containing 607 isolated scales (NBMG 19646–19677). Note that some of these specimens were obtained

through the destructive dissolution of NBMG 14984, 15834, and 15901, and then assigned new collection numbers.

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

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

Remarks. Elasmobranch scales from the Palaeozoic have been shown to have a high degree of morphological variability, depending on which part of the body they are from (Dick 1981). This variability can be more pronounced than that seen between species, making the assignment of scales a difficult task. The Minto specimens show similarities to denticles depicted by Lebedev (1996, fig 6d–f), characterized there as ‘*Ctenacanthus*’ type denticles (Karatajute-Talimaa 1992; Lebedev 1996).

Order INCERTAE SEDIS
Family INCERTAE SEDIS

Genus AGELEODUS Owen, 1867

Type species. *Ageleodus pectinatus* Agassiz, 1843a

Ageleodus pectinatus Agassiz, 1843a
Figure 9H–J

Material. 67 specimens containing isolated teeth (NBMG 9973b, 10800, 12067, 14965, 14969–14982, 14995, 14997–15004, 15175, 15806, 15838, 15858–15861, 15863, 15868, 15890–15893, 15895, 15897–15900, 16070–16072, 16095, 19600–19613, 19717, 19851).

Diagnosis. Mesio-distally elongated teeth with multiple sharp-conical cusps arranged in a row along the crown. The base is long, narrow and deep, and lacks imbrications.

Description. The teeth are mesio-distally elongated, giving an impression of anterior–posterior compression: the crown is bulbous on one side and flattened on the opposite side (Fig. 9H–J). The number of cusps on the crown varies from 9 to 18 (Fig. 10B) in complete specimens, with the exception of NBMG 15175, which has 35 (Fig. 9J). The cusps are sharp-conical, except where rounded by abrasion, and are situated along the crown, with 1–2 marginal cusps in a slightly ventral position at

each edge. The root of the tooth is compressed and is punctuated by nutritive channels.

Remarks. As *A. pectinatus* is known only from disarticulated teeth, the arrangement of dentition within the jaws is unknown; we follow the terminology established by Downs & Daeschler (2001). Cusp count appears to be continuous and unimodal within the sample, with a mean of 14, and all specimens lie within the first standard deviation except for NBMG 15175 (Fig. 10B). This is similar to the variation in other samples (e.g. Downs & Daeschler 2001, fig. 3); in that example, the majority of specimens had 3–16 cusps, though rare teeth with as many as 33 cusps were found. Given the much smaller sample size here, the fact that specimens from Minto show less variation than those from Red Hill is not surprising; nonetheless, all specimens except NBMG 15175 fall within the range of variation established by Downs & Daeschler (2001) for *A. pectinatus*. Controversy continues to surround the interpretation and affinity of *Ageleodus* (Turner 2013). Here we have followed the conservative view that these features represent the teeth of a basal elasmobranch of uncertain placement; however, we note that Lebedev (1996) proposed a rather different hypothesis: that they are not teeth at all, but rather specialized branchial denticles.

Class ACANTHODII Owen, 1846

Order INCERTAE SEDIS

Family GYRACANTHIDAE Woodward, 1906 emend.

Warren *et al.*, 2000

Genus GYRACANTHIDES Woodward, 1906

Type species. *Gyracanthides murrayi* Woodward, 1906.

Gyracanthides sp.

Figure 11A–F

Material. One specimen containing 11 individual spine fragments (NBMG 10739/1–11) and two further specimens containing single spines (NBMG 10736, 15173, 15826, 19969, 19970).

Diagnosis. Laterally compressed spines with a V- to U-shaped cross-section. Striated insertion area with an exertion area covered by tubercles that form ornament ridges. Ornament ridges intersect in a chevron arrangement along the leading edge. Ridges are oblique to the long axis near the insertion area, but become parallel to the long axis towards the distal end in pectoral spines. This is not seen in dorsal and pelvic spines,

where tubercle ridges are consistently oblique towards the distal end.

Description. NBMG 15173 is a partially exposed spine 84 mm long. The long axis shows a very small degree of curvature (Fig. 11A). The cross-section of the spine does not show curvature, but this may be a result of the sediment obscuring parts of the spine. The insertion/exsertion boundary (IEB; Fig. 11A) is hard to distinguish due to the high degree of abrasion on the ornament ridges. There is an angle of 42° between the IEB and the ornamented ridges and 25° between the IEB and the striae. Ornament ridges more distal to the IEB show less abrasion, allowing individual ridges to be traced, but the damage is still sufficient that individual tubercles on the ridges are heavily worn and difficult to discern. Seven ridges cross a line drawn perpendicular to the leading edge at the posterior limit of the insertion area (Fig. 11A, cf. Turner *et al.* 2005, fig. 2a).

NBMG 10739 is composed of 11 fragments from several different spines. In NBMG 10739/1–2 the ornament ridges of the exertion area are pinched out by the insertion area along the leading line (Fig. 11B–C). Specimens NBMG 10739/1–2 measure 46 mm and 44 mm along their long axes respectively, with broken surfaces on the distal and proximal ends. The cross-sectional shape of NBMG 10739/1–2 is difficult to determine because it is fragmentary. The insertion area is covered by parallel to sub-parallel incomplete striae that branch and converge in places and taper off both distally and proximally (Fig. 11D). There is a c. 20° angle between the striae and the IEB. The exertion area is covered by tubercles, which are arranged en échelon on the ornament ridges of NBMG 10739/1 and 4 (Fig. 11E), and as near-straight ridges in NBMG 10739/2 and 5. The tubercles are elongated along the long axis and intersect as even chevrons along the leading edge (Fig. 11C, E). The lengths of the elongated tubercles vary from 400 to 910 µm in different spine fragments. Any ornamentation originally present on the tubercles has been lost to abrasion. The angle between the ornament ridges and the IEB varies from c. 81° (Fig. 11B–C) in NBMG 10739/1–2 to c. 52° in NBMG 10739/4 with the latter having more longitudinal elongate ridges to the long axis, suggesting that it is part of the distal end of a pelvic spine (Turner *et al.* 2005). Spines with varying levels of abrasion along their length may be indicative of wear during life (Turner *et al.* 2005); if abrasion was caused by post-mortem transportation, then a more even distribution of abrasion along the spine would be expected.

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

Remarks. Gyracanthid material from the Minto Formation has been reported previously as *Gyracanthus* cf. *G. duplicatus* (Gardiner 1966; Miller 1999), but since Dawson's *Gyracanthus duplicatus* is now known to be

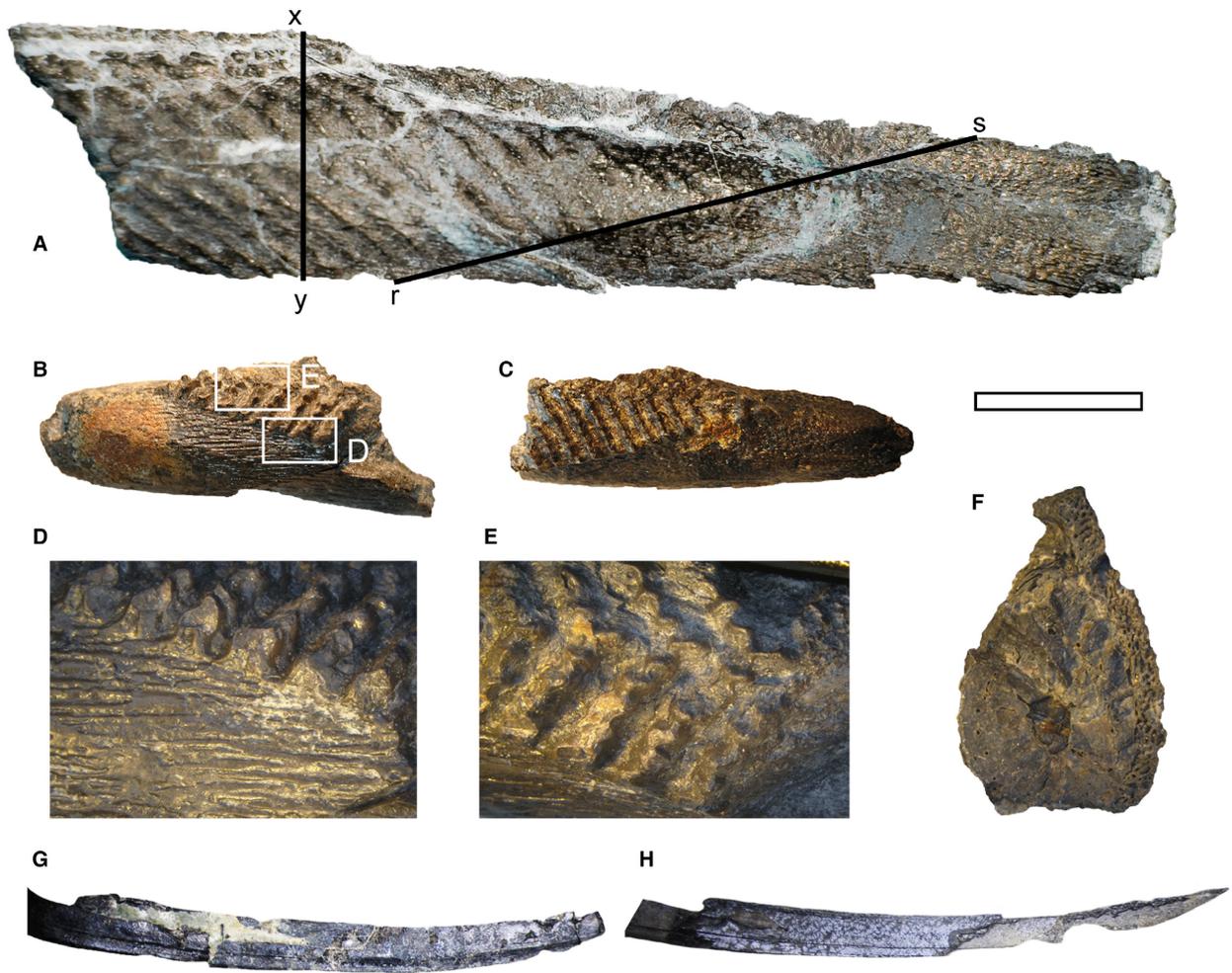


FIG. 11. Spines of the acanthodians from the Minto Formation (Pennsylvanian) of New Brunswick, Canada. A–F, *Gyracanthides* sp.; A–C, spines in lateral view: A, NBMG 15173; B, NBMG 10739/1, boxes indicate locations of D and E; C, NBMG 10739/2; D, striae on the insertion area and the angle between the striae and the exsertion area, NBMG 10739/1; E, chevron pattern in ornament ridges on the leading edge, NBMG 10739/1; F, cross-section of a spine, NBMG 10739/4. G–H, *Acanthodes* sp.; G, spine in lateral view, NBMG 15174; H, spine in lateral view, NBMG 15852. Line r–s represents the insertion/exsertion boundary (IEB). Line x–y represents a line perpendicular to the leading edge. Scale bar represents 20 mm (B–C); 10 mm (A, G, H); 2 mm (F); 1 mm (D, E). Colour online.

invalid (Carpenter *et al.* 2015), the Minto material merits re-classification. Specimens NBMG 10736, NBMG 15173, NBMG 15826, NBMG 10739/1–11, NBMG 19969 and NBMG 19970 have been removed from the genus *Gyracanthus* based on having spines with ellipsoid cross-sections, open grooved hollows and ornament ridges showing a change in angle from oblique to parallel along the long axis of the pectoral spines. These features are not characteristic of *Gyracanthus*, the spines of which have circular cross-sections and ornament ridges that are consistently oblique, but are characteristic of *Gyracanthides* (Turner *et al.* 2005; Snyder 2011), to which we assign our specimens. Species-level classification of *Gyracanthides* is based on tubercle orientation, ornamentation and arrangement along the ornament ridges (Warren *et al.*

2000; Turner *et al.* 2005). As NBMG 15173 is highly abraded, this specimen cannot be assigned to a species. NBMG 10739/1 and NBMG 10739/2 (Fig. 11B–C) show a much lesser degree of abrasion, yet no striae on the tubercles can be seen, as in *Gyracanthides murrayi* (Warren *et al.* 2000, fig. 8e–f), indicating that these spines still underwent a small degree of abrasion. The en échelon packaging of tubercles on the ornament ridges better fits *Gyracanthides hawkinsi* than the straight ornament ridges of *G. murrayi*, but ornamented ridges in *G. hawkinsi* meet along the leading edge in uneven chevrons, which is not seen in specimen NBMG 10739/1–11, and tubercles have three projections which converge towards the apex, again not seen in this specimen. Therefore we assign all specimens to *Gyracanthides* sp.

Order ACANTHODIDA Berg, 1940
Family ACANTHODIDAE Huxley, 1861

Genus ACANTHODES Agassiz, 1843b

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

Acanthodes sp.
Figure 11G, H

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

Diagnosis. Slender, gently curving spines with a rounded anterior rib; lateral surfaces smooth except for a single longitudinal groove on each side.

Description. Isolated, incomplete spines 10–32.5 mm in length and 0.5–2.5 mm wide, exposed in lateral view. A rounded rib runs along the anterior surface, and is flanked on each side by a prominent longitudinal groove; this is visible as an external mould in the matrix where parts of the spine have been lost, confirming its presence on both sides. The spines are otherwise smooth.

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

Though other acanthodiforms were common in the Maritimes Basin of eastern Canada during the Devonian (Gardiner 1966; Denison 1979; Kennedy *et al.* 2012), the only previously reported occurrence of Acanthodidae is from the Tournaisian Horton Bluff Formation of Nova Scotia (Zidek 1977; Mansky & Lucas 2013, fig. 13A), identified as Acanthodidae indet. Thus, the four isolated spines (NBMG 15174, 15852, 15869, 15913) reported here, are the first Canadian example of *Acanthodes* and extend the known range of the Acanthodidae in Canada by some 35 million years. The acanthodid remains in the

Horton Bluff Formation are tantalising, because if they are in fact referable to *Acanthodes* this would indicate a substantial ghost lineage, and suggest the lack of specimens from this interval is the result of collection failure or taphonomic bias; it is to be hoped that further investigations in the Horton Bluff Formation will provide determinable material which will resolve this issue.

Acanthodidae indet.

Material. Ten specimens containing multiple isolated spines (NBMG 15822, 15835, 15838, 15844, 15873, 16082, 16094, 16095, 20013, 20016).

Diagnosis. Slender, gently curving spines, unornamented except for a single prominent longitudinal groove.

Description. Isolated, incomplete spines 5–25 mm long and 0.5–1.75 mm wide, exposed in various aspects. Several have been crushed and badly damaged, so no further diagnostic features can be discerned.

Class OSTEICHTHYES Huxley, 1880
Subclass SARCOPTERYGII Romer, 1955
Infraclass DIPNOMORPHA Ahlberg, 1991
Order DIPNOI Müller, 1845
Family INCERTAE SEDIS

Genus CTENODUS Agassiz, 1843a

Type species. *Ctenodus cristatus* Agassiz, 1843a.

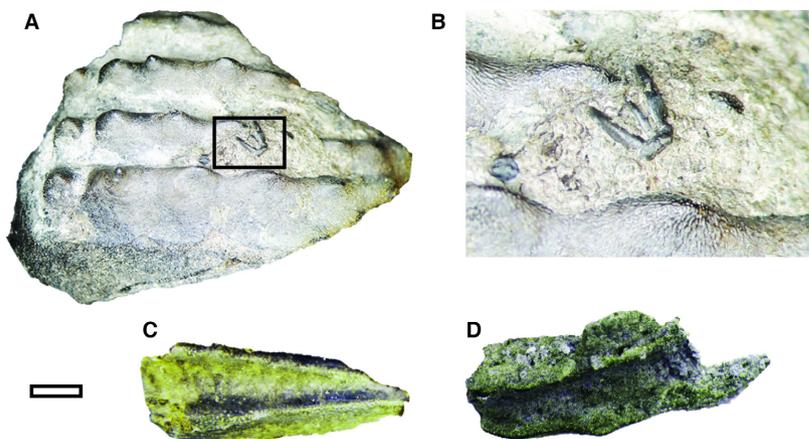
Ctenodus interruptus Barkas, 1869
Figure 12A–B

Material. Two incomplete tooth-plates (NBMG 10740, 15822).

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

Description. NBMG 10740 is a broken fragment of a tooth-plate. Only four near-parallel ridges are present (Fig. 12A) with lengths of 9–31 mm, but these measurements do not represent the original length of the ridges, as they are broken at both ends. There is a space of 5 mm between ridges (measured from between the apices). Individual apex height reduces along each ridge from the centre out in both directions. Ridges are relatively straight.

FIG. 12. Feeding plates of dipnoans from the Minto Formation (Pennsylvanian) of New Brunswick, Canada. A–B, feeding plate of *Ctenodus interruptus*, NBMG 10740; B, enlargement of boxed area in A showing isolated xenacanth teeth sitting on the surface. C–D, fragments of the feeding plates of Dipnoi indet.; C, NBMG 18609 showing convergent ridges; D, NBMG 19699 showing differential apical elongations. Scale bar represents 4 mm (A); 1 mm (B–D). Colour online.



There is a prominent depression between two apices on one side of the specimen (Fig. 12A), seen in three of the ridges (not observable in the fourth ridge as this section of the ridge is not preserved). Apices vary randomly along the ridge between conical and rounded (Fig. 12A); rounded apices are likely to be the result of abrasion. All apices are laterally compressed towards the apex. The basal surface is encased in sediment.

Remarks. Only two species of *Ctenodus* have been reported from the North American continent: *C. cristatus* and *C. interruptus*, with *C. purchisoni* from Nova Scotia being assigned to *Conchodus plicatus* (Baird 1978). NBMG 10740 shows more prominent separated apices than *C. cristatus* (Sharp & Clack 2013, fig. 2) and *C. purchisoni* (Sternberg 1941, figs 1–3). These prominent apices are similar to *C. interruptus* (see Sharp & Clack 2013, figs 5, 14). Therefore NBMG 10740 has been assigned to *C. interruptus*. Ahlberg *et al.* (2006), in their review of the development of lungfish dentitions, convincingly argued that these apices are teeth and not denticles, as described in older literature. The dental plate bears some very small xenacanthid teeth on the occlusal surfaces (Fig. 12B).

Dipnoi indet.
Figure 12C–D

Material. Six specimens, each comprising isolated tooth-plate fragments (NBMG 18609, 19698–19701, 19833).

Diagnosis. Triangular tooth-plates equipped with ridges of teeth.

Description. Fragmentary tooth-plates, each bearing two ridges, converging at an angle of *c.* 20° (Fig. 12C). There is no evidence that any other ridges were originally present. Teeth are laterally

compressed, and this is consistently more pronounced in one ridge than the other (Fig. 12D). Tooth-plates show broken surfaces near the edges.

Remarks. Dipnoan tooth-plates show substantial variation attributed to tooth wear (Schultze & Chorn 1997) and to developmental anomalies (Kemp 1996, 2003), making the identification of isolated specimens difficult. Most diagnostic characters are associated with cranial bones rather than tooth-plates (Sharp & Clack 2013), although isolated tooth-plates can often be identified to species level when complete (Sharp & Clack 2013). Due to the fragmentary nature of the specimens they have been assigned to Dipnoi indet.

Infraclass TETRAPODOMORPHA Ahlberg, 1991
Order RHIZODONTIDA Andrews & Westoll, 1970 emend.
Johanson & Ahlberg, 2001
Family RHIZODONTIDAE Traquair, 1881a emend. Andrews & Westoll, 1970

Genus STREPSODUS Huxley *in* Huxley & Etheridge, 1865

Type species. *Strepsodus sauroides* Binney, 1841.

Strepsodus sauroides Binney, 1841
Figure 13A

Material. Nine isolated teeth (NBMG 9969, 15005, 15007, 15788, 15815, 15820, 15829–15830, 19688).

Diagnosis. Tall, slender teeth that are recurved lingually. Teeth are oval in cross-section. Reversed curvature is present towards the apex of the crown. Raised parallel striae are present on the lingual side and on the lingual

portions of the distal and mesial sides of the teeth. Striae are longitudinal and show minor to no degree of curvature.

Description. Incomplete teeth varying in length from 7 mm in NBMG 9969 to 17 mm in NBMG 15820. Teeth have an oval cross-section. Teeth are recurved and show reverse-curvature

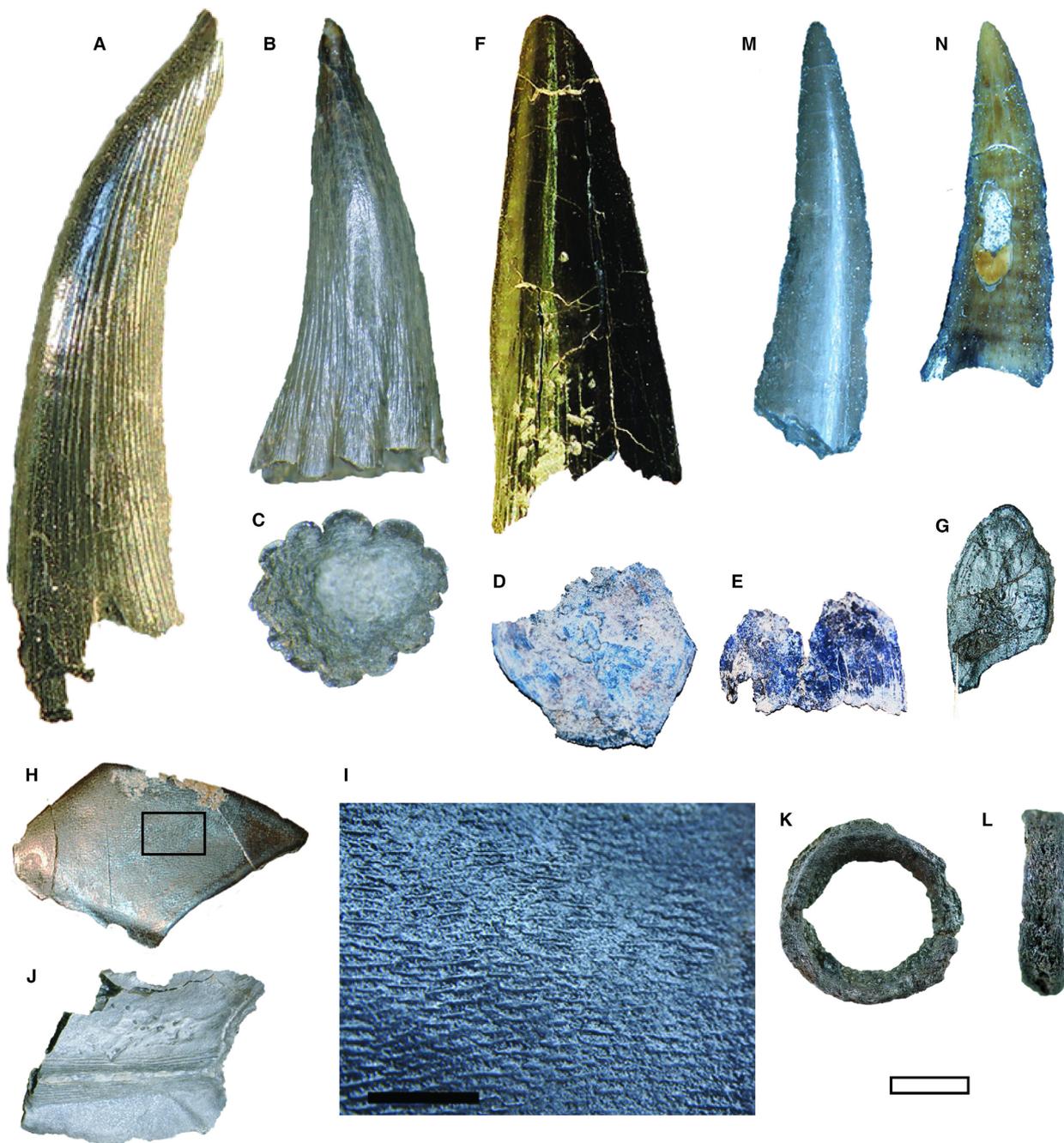


FIG. 13. Teeth and scales of rhizodonts and tetrapodomorphs from the Minto Formation (Pennsylvanian) of New Brunswick, Canada. A, tooth of *Strepsodus sauroides*, NBMG 15820 in lateral view. B–C, tooth of *Archichthys portlocki*, NBMG 19972, showing: B, striations in lateral view; C, plication count on the base. D–E, scales of cf. *Archichthys portlocki*: D, NBMG 19689; E, NBMG 15831. F, tooth of cf. *Rhizodus hibberti* NBMG 15809. G, scale of cf. *Rhizodopsis sauroides* NBMG 15901 showing the attachment side. H–J, scales of *Megalichthys* sp.: H–I, NBMG 10741/1, H, showing the free field; I, close-up image of the cosmine cover of the free field; J, NBMG 19974a, showing the attached surface. K–L, centrum of cf. *Megalichthys* sp. NBMG 19958, in: K, articular; and L, lateral views. M–N, teeth of Tetrapodomorpha indet.: M, NBMG 10776; N, NBMG 10777. Main scale bar represents 2 mm (A–C, M, N); 20 mm (F), 10 mm (D–E, G, K, L), 20 mm (H, J); scale bar in I represents 2 mm. Colour online.

near the apex (Fig. 13A), giving them a sigmoidal shape. Raised striae are longitudinal and some show minor curvature, particularly towards the apex, causing individual striae to cross from the lingual surface to the mesial/distal sides. Striae subside near the apex and are absent on the apex itself. Striae may appear to converge apically as a result of recurvature, yet they never come into direct contact. Instead a stria caught between two converging striae will taper out. Striae show a maximum spacing of 0.1 mm prior to convergence. This distance is consistent irrespective of tooth size; larger teeth simply bear more striae. The base of the crown is absent in all specimens.

Remarks. Reverse curvature seen in NBMG 9969 and possibly present in NBMG 15820 suggests that these may be symphysial tusks, but the small size of NBMG 9969 and the lack of well-preserved *Strepsodus* mandibles makes this uncertain (Jeffery 2003, 2006).

Genus ARCHICHTHYS Hancock & Atthey, 1870

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

Archichthys portlocki Portlock, 1843 ex Agassiz MS Figure 13B–C

Material. Three isolated teeth (NBMG 15799, 15818, 19972).

Diagnosis. Robust, gently curved teeth with 11 plications around the base. A ‘woven’ pattern of striation is present above the plications.

Description. NBMG 19972 is a robust tooth 14 mm long. Teeth show gentle lingual curvature (Fig. 13B) with an oval cross-section, and are equipped with 11 basal plications (Fig. 13C). Striations on the exposed parts of the tooth surface form a ‘woven’ texture; these are most pronounced at the base of the teeth, and become fainter apically, disappearing completely at the apex. Although the labial surface of NBMG 19972 is partially covered in sediment, an exposed part lacks striations.

Remarks. The 11 plications reported from NBMG 19972 are fewer than the 16–18 recorded by Jeffery (2006). This does not rule out assigning NBMG 19972 to *Archichthys portlocki*, as the plication count did not form part of the diagnosis of the species by Jeffery (2006). A plication count of 11 agrees with the estimated 10–12 for *A. portlocki* in Carpenter *et al.* (2015). Although the striations in NBMG 15799, NBMG 15818 and NBMG 19972 are similar to those of *Letognathus* (Brazeau 2005), this assignment has been ruled out because, unlike *Letognathus*, striations are absent from the labial surface of all three teeth, as expected for *A. portlocki* (Jeffery 2006). The teeth of *Letognathus* are long and slender (Brazeau 2005),

unlike the robust teeth of NBMG 15799, NBMG 15818 and NBMG 19972, again supporting our identification.

cf. *Archichthys portlocki* Portlock, 1843 ex Agassiz MS Figure 13D–E

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

Diagnosis. Sub-hexagonal scales with concentric growth lines becoming more prominent towards the periphery of the scale. Median boss on the inner surface.

Description. Two incomplete sub-hexagonal scales with the inner surface exposed. NBMG 19689 has a diameter of 25 mm (Fig. 13D) and NBMG 15831 has a length of 16 mm and a width of 24 mm (Fig. 13E). Concentric growth rings are most prominent at the periphery of the scale and diminish towards the centre. NBMG 19689 has an elongated median boss 4 mm long and 2 mm wide. NBMG 15831 has a pentagon-shaped median boss 1 mm across.

Remarks. NBMG 15831 and NBMG 19689 resemble scales, which formed part of the type series for *Archichthys portlocki* (Portlock 1843, reproduced in Jeffery 2006, fig. 1). Surface detail is partially obscured by a light coating of very fine sediment which proved impossible to remove without damaging the scale.

Genus RHIZODUS Owen, 1840

Type species. *Rhizodus hibberti* Owen, 1840.

Rhizodontidae cf. *Rhizodus hibberti* Owen, 1840 Figure 13F

Material. 15 specimens comprising isolated tusks (NBMG 15787, 15789–15791, 15795, 15798, 15809–15810, 15812–15813, 15816–15817, 15862, 15866, 16074).

Diagnosis. Large tusks with lenticulate cross-section. Approximately 24 plications.

Description. NBMG 15809 is a single robust tusk partially covered in matrix. The exposed portion is 29 mm long. The apex of the crown is either covered in matrix or absent. The exposed surface of the base of the crown is equipped with 12 plications. Recurvature, if any, cannot be observed due to matrix cover. The tusk is slightly compressed which has resulted in longitudinal fractures.

Remarks. Based on the number of plications (12) visible on the exposed portion of NBMG 15809, it is likely that

the tooth bears 22–26 in total. Similar tusk morphotypes from different genera of rhizodont are differentiated based on the number of plications (Jeffery 2003). This tusk cannot be *Archichthys portlocki* or *Letognathus hardingi* because they bear 16–18 and around 14 plications, respectively (Brazeau 2005; Jeffery 2006). *Strepsodus sauroides* is also excluded because it lacks striations. An estimated plication count of 22–26 is consistent with *Rhizodus hibberti* (20–22) and *Barameda decipiens* (20–26) (Jeffery 2003; Holland *et al.* 2007). As *B. decipiens* is known mostly from Australia, whilst *R. hibberti* is found in North American and European localities, this is more likely to be *R. hibberti*. Isolated tusks of *R. hibberti* and *Screbinodus ornatus* are only distinguishable based on size (Jeffery 2003); with a minimum crown height of 26 mm, we assign NBMG 15809 to Rhizodontidae cf. *Rhizodus hibberti*.

Order INCERTAE SEDIS

Family MEGALICHTHYIDAE Hay, 1902

Genus RHIZODOPSIS Young, 1866 ex Huxley MS emend.

Traquair, 1881b

Type species. *Rhizodopsis sauroides* Williamson, 1849.

Tetrapodomorpha indet. cf. *Rhizodopsis sauroides*

Williamson, 1849

Figure 13G

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

Diagnosis. Ovoid scale, divided into four quadrants. Concentric growth lines present in all quadrants. Radial striae present in only the posterior and anterior quadrants. A median boss and concentric growth lines are present on the attachment surface.

Description. Elongated ovoid scale with a length of 26.5 mm and a maximum width of 14 mm. The scale is embedded in the matrix with the attachment surface exposed. The scale is fractured, but almost complete, with only a small section of the outer edge broken off (Fig. 13G). Quadrants can be identified, but with great difficulty, and concentric growth lines can be seen only along the very edges. Radial striae can be seen in parts only along the outer edge. There is a median boss on the attachment surface, elongated along the long axis. The median boss is 4 mm long and 1 mm thick. The scale is marked by punctae, 400 µm in diameter.

Remarks. The placement of *Rhizodopsis* as a sister-taxon to *Megalichthys* (Friedman *et al.* 2007) has led to its transfer from Rhizodontidae Berg (1940) to Megalichthyidae

Hay (1902) and thus it has been referred to as a megalichthyid (Coates *et al.* 2008). Detail on the surface of NBMG 15901 has been lost, seen in the lack of concentric growth lines towards the centre of the scale, making identification uncertain. Overall scale morphology looks similar to that illustrated by Williamson (1837, figs 1, 4), with NBMG 15901 being slightly more ovoid. This less rhombic morphology is seen in other *Rhizodopsis sauroides* scales (e.g. Holland *et al.* 2010, fig. 6f, reproduced from Woodward 1891). The median boss of NBMG 15901 resembles the median boss illustrated by Williamson (1837, figs 1, 4). *Megalichthys* scales with the cosmine removed have been misidentified as the scales of *Rhizodopsis* (Holland *et al.* 2010), but as the scales of *Megalichthys* lack a median boss (Andrews & Westoll 1970) it is certain that NBMG 15901 does not belong to *Megalichthys*. For the present, NBMG 15901 is placed in Tetrapodomorpha indet. cf. *Rhizodopsis sauroides*.

Order SARCOPTERYGII incertae sedis

Family MEGALICHTHYIDAE Hay, 1902

Genus MEGALICHTHYS Agassiz, 1843b

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

Megalichthys sp.

Figure 13H–J

Material. Four specimens (NBMG 10741 in two parts, 15794, 19974). One of these blocks contains up to 11 identifiable fragmented scales (NBMG 10741/1) and seven complete scales in the other part (NBMG 10741/2–7).

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

Description. Fractured rhombic scales c. 25 mm in length where complete (Fig. 13H). Cosmine-covered free field with very low relief ripple-like ornamentation (Fig. 13I). There is a cosmine-free ridge at the margin of the cosmine-covered free field, which gradually thins towards the outer edge of the scale. Where the cosmine covering has been worn away from the scales, the surface is covered by closely spaced punctae. On the attachment surface is a prominent ridge, which follows the line of contact between the cosmine-covered portion and the ridge on the free field. The ridge on the attachment surface does not extend to the margins and tapers off sharply in a stepwise fashion (Fig. 13J). This gives the ridge an elongated rectangular shape.

Remarks. Genus- and species-level identification of megalichthyids is based on cranial characters (Thompson 1964; Andrews 1985, Fox *et al.* 1995), but as *Megalichthys* is

common throughout the Carboniferous Maritimes Basin it is reasonable to associate these rhombic scales with the genus (e.g. Carpenter *et al.* 2015).

cf. *Megalichthys* sp.
Figure 13K–L

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

Diagnosis. Annular centrum with a relatively large notochordal canal.

Description. NBMG 19958 is a single annular centrum with an outer diameter of 27 mm (Fig. 13K) and a thickness of 5.5 mm (Fig. 13L). The inner surface tapers to form a ridge-like structure, and a relatively large notochordal canal (diameter 16 mm) is inferred. Therefore the outer/inner diameter ratio is 1.69. The inner and outer surface is rough and has a worn appearance. There is no evidence of a neural arch or spine.

Remarks. The worn texture of the centrum suggests that smooth or wrinkled periosteal bone is absent, which may be the reason why triangular areas over the posteroventral regions are absent (see Andrews & Westoll 1970, fig. 7d). The outer/inner diameter ratio of NBMG 19958 is slightly larger than the typical ratio seen in *Megalichthys hibberti*, but ratios in excess of 1.6 have been noted (Andrews & Westoll 1970). Based on its size, this centrum would have been from the trunk of the fish. Neural arches are present in some, but not all, megalichthyid trunk vertebrae, meaning that the lack of a neural arch does not exclude this specimen from the trunk (Andrews & Westoll 1970). The higher inner/outer diameter ratio of NBMG 19958 compared to *Megalichthys hibberti*, along with the difficulty of assigning a single isolated worn centrum to a species, means we assign it to cf. *Megalichthys* sp.

Tetrapodomorpha indet.
Figure 13M–N

Material. 13 specimens, comprising incomplete, isolated teeth (NBMG 9968, 10776, 10777, 10783, 10785, 19691–19697) and scales (NBMG 20014).

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

Description. The teeth are conical and very gently curved (Fig. 13M); however, NBMG 10785 has been flattened to such a degree that it is impossible to tell if the tooth was ever recurved. NBMG 19696 has a circular cross-section exposing a sediment-filled pulp cavity. NBMG 10777 (Fig. 13N) has a broken side

exposing part of the pulp cavity that has likewise been filled with sediment. The crown base is absent in all specimens.

Remarks. Apical caps lacking acrodin exclude these teeth from Actinopterygii, so they are identified as sarcopterygians. Sediment-filled pulp cavities suggest that NBMG 19696 and NBMG 10777 had hollow pulp cavities, which are indicative of polyplacodont teeth, such as are present in *Megalichthys*, *Rhizodopsis*, *Rhizodus* and *Strepsodus* (Schultze 1970). Polyplacodont teeth are also present in primitive crown tetrapods, so a tetrapod affinity cannot be ruled out. Without further histological investigation and in the absence of a tooth base, plication folding cannot be determined and these teeth cannot be identified more precisely (Schultze 1970; Vorobyeva 1977; Jeffery 2003). Therefore we identify these teeth as Tetrapodomorpha indet.

Superclass TETRAPODA Goodrich, 1930
Figure 14

Material. Ten specimens, including partial jaws (NBMG 15821, 15853, 15872, 20019, 20020, 20021), vertebrae (NBMG 15783, 15784, 15870) and possible limb bones (NBMG 15915).

Description. NBMG 15821 is the most complete of several jaw bones; it comprises a 14 mm long mandible, with at least 17 elongate, straight, bullet-shaped, pointed teeth that bear faint longitudinal striations confined to the basal one-third of the visible portion of the crown (Fig. 14A). The jaw bone, although somewhat damaged, appears to be narrow, barely as deep as the length of the tooth crowns, and it bears a shallow sculpture of longitudinal ridges. NBMG 15783 is a vertebra comprising a disc-shaped inter- or pleurocentrum, with nearly equidimensional measurements in articular view (Fig. 14B), and anteroposteriorly short (Fig. 14C), and with a central notochordal canal. In lateral view (Fig. 14C), the portion of the lateral surface between the projecting, rolled edges around the articular faces is depressed. NBMG 15915 is one of several small limb bones (Fig. 14D); it is 19 mm long, shows expanded articular ends, 5 mm across, and a narrow shaft, 2 mm wide at its narrowest. The expansions are more or less symmetrical at each end, forming a roller structure on one end and a shallow socket at the adjacent end, as illustrated.

Remarks. The material includes several small jaw bones, vertebrae and limb bones that do not appear to correspond to any of the fishes described above, but more closely resemble those of tetrapods. Jaw material shows similarities to those of stem tetrapods (colosteids) and anthracosaurs (embolomeres) (Carroll 2009); however, neither of these groups of tetrapods have maxillaries or

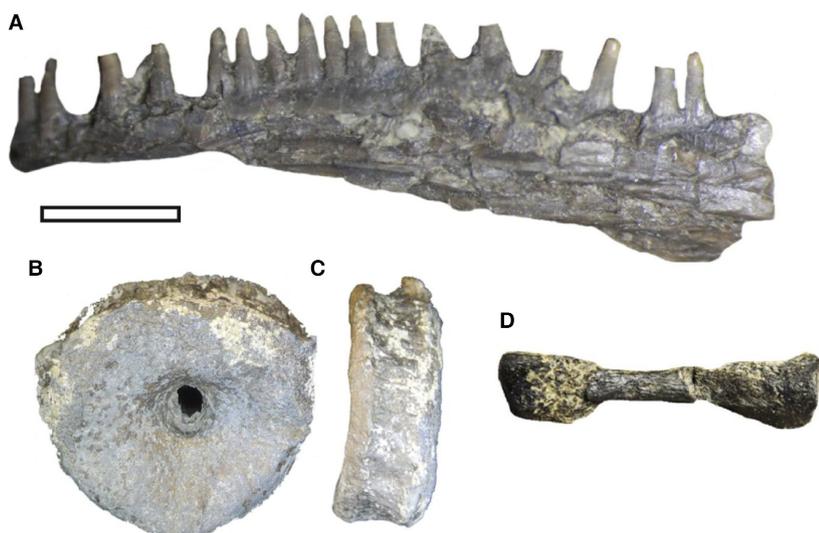


FIG. 14. Tetrapod remains, with provisional identifications. A, small dentary of a possible colosteid, bearing teeth, NBMG 15821. B–C, NBMG 15783, intercentrum of a possible embolomeres anthracosaur vertebra, in: B, ?anterior; and C, lateral views. D, small tetrapod limb bone, NBMG 15915. Scale bar represents 80 mm (A); 10 mm (B–C); 7.5 mm (D). Colour online.

dentary rows with diagnostic features that would allow attribution with confidence (Bolt & Lombard 2010). The vertebral centrum (NBMG 15783) is reminiscent of those of embolomeres anthracosaurs (e.g. ‘rolled up’ projections of the peripheral margins of its anterior and posterior surfaces; markedly arcuate dorsal and ventral profile of vertebral body in lateral view); however, some lungfish have similar disc-shaped centra (e.g. *Griphoganthus* from the Devonian of Australia; Campbell & Barwick 2002) so a dipnoan affinity cannot be entirely discounted. These preliminary remarks do not allow us to make confident interpretations of the tetrapod fauna.

Subclass ACTINOPTERYGII Cope, 1887
Order EURYNOTIFORMES Sallan & Coates, 2013
Eurynotiformes indet.

Material. Incomplete mandible with five attached teeth (NBMG 20021).

Diagnosis. Teeth smooth, bulbous and conical, with apical caps of acrodin.

Description. Isolated mandibular fragment *c.* 2 mm in length. The teeth are bulbous, conical, and unornamented; they are also very small, measuring only *c.* 0.75 mm.

Remarks. Durophagous actinopterygians first appeared during the Tournaisian (Sallan & Coates 2010), and are believed to have undergone at least two significant radiations in Euramerica during the Carboniferous; hence, they are a common component of Pennsylvanian fossil assemblages in North America and Europe (Zidek 1992; Mickle

& Bader 2009; Sallan & Coates 2010). Although their systematic status is yet to be fully resolved, most genera can be placed into either Eurynotiformes Sallan & Coates, 2013 or the likely paraphyletic Bobasatraniaformes Berg, 1940 (Mickle & Bader 2009; Sallan & Coates 2013). The Eurynotiformes possessed a heterognathic dentition consisting of phylloodont tooth plates and a denticulated maxilla; anterior maxillary teeth were tall and conical, while posterior teeth were much more tumid (Sallan & Coates 2013, fig. 14b). In contrast, the Bobasatraniaformes were equipped with similar tooth plates (Johnson & Zidek 1981; Zidek 1992) but otherwise appear to have been generally edentulous (Campbell & Le 1983; Zidek 1992; Mickle & Bader 2009).

Three eurynotiform genera (*Eurynotus*, *Mesolepis* and *Amphicentrum*) are known to have persisted into the Pennsylvanian (Sallan & Coates 2013), but isolated teeth of these taxa cannot be distinguished from one another.

Actinopterygii indet.
Figure 15

Material. Eight specimens containing 25 isolated scales (NBMG 18608, 19678–19683, 20015), ten specimens containing 172 cranial bone fragments (NBMG 19799–19808), one isolated tooth (NBMG 19684), and four isolated centra (NBMG 19834, 19685–19687).

Diagnosis. Rhombic scales with a covering of ganoin, peg-and-socket articulation and asymmetrical serrations. Disc shaped cranial bone fragments with elongated ridges on the outer surface. Conical teeth with a distinct apical cap. Hour-glass shaped centra with concave depressions.

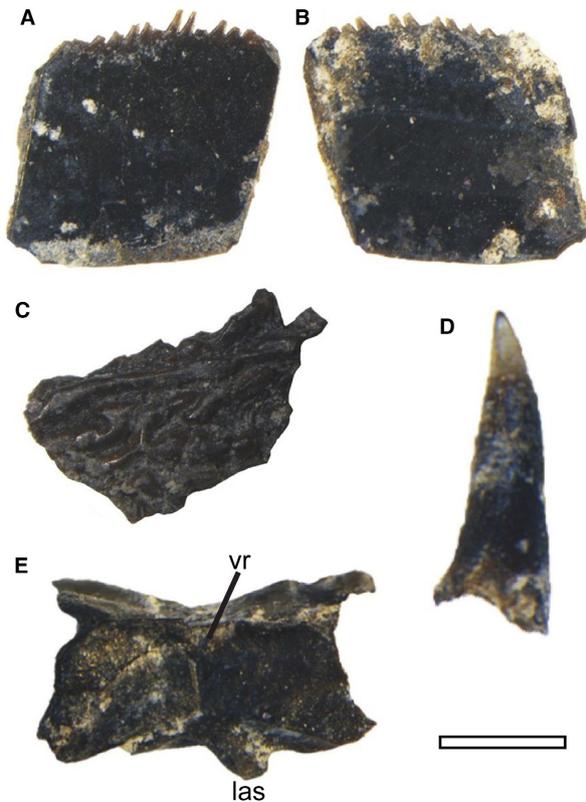


FIG. 15. Actinopterygian remains from the Minto Formation (Pennsylvanian) of New Brunswick, Canada. A–E, indeterminate actinopterygians; A–B, scale, NBMG 19679/1 showing: A, the free field; B, the attachment surface. C, sculptured scale or dermal skull bone, NBMG 19804a. D, tooth, NBMG 19684. E, vertebra, NBMG 19686. *Abbreviations:* las, lateral attachment site; vr, ventral ridge. Scale bar represents 0.5 mm (A–C); 0.2 mm (D); 0.4 mm (E). Colour online.

Description: scales. Rhombic scales 0.5–1 mm in size. Four scales have asymmetrical serrations on the posterior margin (Fig. 15A–B). Dorsal and ventral margins are straight with slight curvature near the anterior and posterior margins. The anterior margins are slightly curved along their entire extent. Sockets from peg-and-socket articulation are present in seven of the scales (Fig. 15B).

Description: cranial bone fragments. Elongated sub-rectangular shaped bone plates with a maximum long axis of 2.5 mm. NBMG 19804 has closely packed, branching ridges present on the outer surface (Fig. 15C), which vary along the surface from longitudinal to curved. The inner surface is smooth lacking a peg-and-socket articulation.

Description: tooth. NBMG 19684 is a slender, recurved conical tooth with translucent apical cap (Fig. 15D).

Description: centra. NBMG 19686 measures 1.22 mm from anterior to posterior margin and 0.5 mm in maximum height, giving a length/height ratio of 2.44. The centrum becomes constricted

towards the centre (Fig. 15E) producing an ‘hour glass-shape’ (Schultze & Chorn 1986). Concave posterior and anterior margins form ‘cup’ shapes on either end that are infilled with sediment. On the dorsal surface there are two sockets elongated along the long axis and separated by a trough. These sockets would have housed the neural arches. A rounded attachment site is present only on one of the lateral sides, which extends laterally (Fig. 15E). On the other lateral side it is likely that an attachment site was present, but has been broken off. A thin ridge runs along the long axis of the ventral surface.

Remarks. The interrelationships of basal Actinopterygii are poorly understood (Patterson 1982; Gardiner 1984; Gardiner & Schaeffer 1989; Sallan 2014), and certain groups, such as the Palaeonisciformes, are certainly paraphyletic (Janvier 1996), making the placement of ichthyoliths in mid-level taxonomic groups problematic. Peg-and-socket articulation in NBMG 19679/1 is similar to that depicted by Schultze (1966, fig. 1a–b) and was previously thought to be characteristic of ganoid fishes, but the discovery of cladistian scales with peg-and-socket articulation suggests that it is plesiomorphic within the Actinopterygii (Schultze 1977; Patterson 1982). The ridge patterns on the cranial bone fragments, from the Minto specimen, resemble to a limited degree the pattern of ridges seen in the rostral and premaxilla of *Gogosardia coatesi* illustrated in Choo *et al.* (2009, fig. 8a–b) suggesting they are of palaeoniscoid-type. Wide variation in the ridges of cranial bones (Choo *et al.* 2009; Choo 2011, 2015) means that identification of fragmented cranial bones is problematic. Likewise, the high variability of scale morphologies in early Actinopterygii means that it is difficult to say whether the Minto Formation scales represent one or more species (Choo 2011). The apical cap of NBMG 19684 is composed of modified dentine called acrodin (Ørving 1978), found only in the teeth of Actinopterygii, including cladistians, some palaeonisciformes, colobodonts and pycnodonts (Ørving 1978; Patterson 1982), though it is absent in pachycormids, *Cheirolepis* and *Severnichthys* (Patterson 1982; Carpenter *et al.* 2014). The centra resemble those of palaeoniscoids illustrated by Schultze & Chorn (1986, fig 3.1–2). The presence of lateral attachment sites, which would have served as attachment points for the ribs, and a length/height ratio of 2.44 suggests that these centra formed part of the abdominal region (Schultze & Chorn 1986), although this is higher than a ratio of 1.5 recorded by Schultze & Chorn (1986).

BROMALITES

Heteropolar microspirial coprolites

Figure 16A–B, E

Material. 33 specimens (NBMG 18789, 19975–19998, 20004–20011).

Diagnosis. Spiral coprolites, with coils concentrated at the posterior end, covering <50% of the total length, and striae parallel to the long-axis at the anterior end.

Description. Spiral coprolites, dark grey to brown in colour, 12–37 mm long and 5–14 mm in diameter (Fig. 16A). Coprolites characterized by 6–12 coils, typically 1–2.5 mm wide, concentrated at the posterior end, and comprising up to 50% of the total length (Coprolite Type F3 of Hunt & Lucas 2012a). The anterior end is characterized by prominent striae, parallel to the long axis, but twisted into a corkscrew. In thin section, posterior coils are recognizable (Fig. 16B), and the bulk of the coprolites comprise amorphous to pelleted phosphatic grains. Abundant fish skeletal material is also present including recognizable bicupid xenacanthid teeth, although their very small size could indicate an origin in a juvenile shark (Fig. 16E).

Remarks. Heteropolar spiral coprolites were produced by fishes with valvular intestines (McAllister 1987), and represent fully evacuated coprolites rather than enterolites preserved *in situ* (Hunt *et al.* 2012; Hunt & Lucas

2012a, b). The phylogenetic distribution of this intestinal structure is not well understood, but it is generally considered to be a primitive feature, most characteristic of elasmobranchs; it is absent in more derived fishes such as actinopterygians and teleosts (Hunt & Lucas 2012a). Various authors have argued that xenacanthiform sharks were the most likely producers of spiral coprolites in the Pennsylvanian–Permian of the USA (Williams 1972; McAllister 1985; Hampe 1988). Johnson (1999) and Hunt *et al.* (2012) described similar coprolites to those reported here from the Pennsylvanian–Permian of the USA and related them to *Orthacanthus* sharks, in particular, based on quantitative co-occurrence data. Given the large size of our coprolites and the abundance of *Orthacanthus* teeth in the Coal Creek assemblages where the heteropolar coprolites co-occur, a biological association is considered very likely. Based on the occurrence of small xenacanthid teeth within the coprolite, *Orthacanthus* may have fed on juvenile sharks amongst other prey.

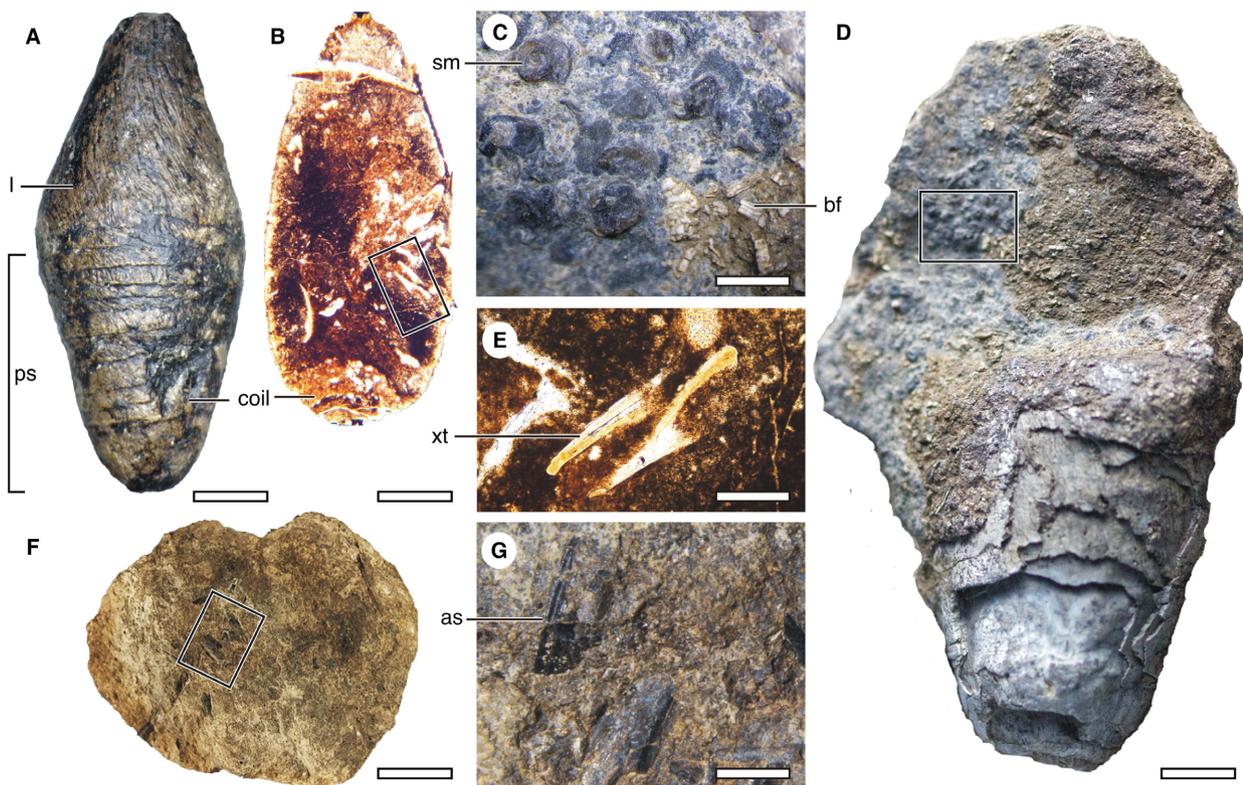


FIG. 16. Fish coprolites (bromalites). A, heteropolar microspiral coprolite, NBMG 19979, showing coils and posterior spire. B, thin section of heteropolar microspiral coprolite containing fish skeletal fragments including probable juvenile xenacanthid tooth (box: E), NBMG 18789. D, large, short cylindrical coprolite composed of calcareous material (box: C), NBMG 20000. F, rounded, bilobed coprolite (box: G), NBMG 19824. C, expanded view of spirorbiform microconchids and bivalve fragments in coprolite shown in D. E, expanded view of xenacanthid tooth in coprolite shown in B. G, expanded view of actinopterygian scale in coprolite shown in F. **Abbreviations:** as, actinopterygian scale; bf, bivalve fragments; ps, posterior spiral; sm, spirorbiform microconchids; xt, xenacanthid tooth. Scale bars represent 4 mm (A–B, D); 6 mm (C); 2 mm (E); 5 mm (F); 1 mm (G). Colour online.

Short cylindrical coprolites
Figure 16C–D

Material. Four specimens (NBMG 19999–20002).

Diagnosis. Short cylindrical coprolites with the posterior end rounded, and the anterior end slightly to strongly tapered.

Description. Light grey, calcareous coprolites, comprising a short cylindrical morphology with two rounded ends or an anterior taper resulting in a tear-drop shape (Copolite Types B1 and B2 of Hunt & Lucas 2012a). Coprolites are 20–60 mm long and 6–20 mm in diameter, and comprise a dense, solid posterior mass and a more diffuse anterior zone (Fig. 16D). Invertebrate fragments, <1 mm in granularity, are abundant, especially at the anterior end and include recognizable microconchids and bivalve fragments, possibly of *Naiadites* type (Fig. 16C).

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

Subspherical coprolite
Figure 16F–G

Material. One specimen (NBMG 19824).

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

Description. The specimen is somewhat nondescript, and can simply be termed ‘round’, or as a subrounded small pellet (Type C1), using the shape scheme of Hunt & Lucas (2012a, b). The coprolite is bilobed, with two equal-sized subspherical portions largely overlapping, and presumably reflecting the original structure. It measures 19 × 22 mm, and is, at most, 7 mm thick. The thickness is probably reduced by compaction and by breakage; one side appears to be external, the other internal (Fig. 16F), showing numerous broken pieces of bone, scales, and teeth preserved. These fish skeletal fragments (Fig. 16G) include a portion of a ridged tooth, preserved shiny and black, possibly from a rhizodont, as well as unidentifiable portions of scales and bones.

Remarks. The coprolite is not especially distinctive; however, based on its size and its contents, it is assignable to a relatively large predatory animal, perhaps a xenacanth shark, rhizodont, or even an aquatic tetrapod.

DOMINANCE–DIVERSITY ANALYSIS

The taxonomic make-up of a total of 722 hand specimens, each containing at least one fish fragment, was analysed quantitatively, at order/class and generic level, with indeterminate material discarded (Table 2). At order/class level, the assemblage (n = 326 identifiable hand specimens) is dominated by chondrichthyans (64.3%), with common sarcopterygians (17.8%) and rare actinopterygians (8.0%), acanthodians (5.2%) and tetrapods (4.6%). At generic level (n = 183 identifiable hand specimens), chondrichthyans are even more dominant with *Ageleodus* (37.0%) and *Orthacanthus* (39.2%) comprising nearly four-fifths of the assemblage, while four sarcopterygians, *Rhizodus* (8.8%), *Strepsodus* (5.0%), *Megalichthys* (2.8%), and *Archichthys* (2.8%) make up most of the rest of the total. Note that these figures represent raw totals, based on the fossils, and they take no account of the differing biology with regards tooth shedding rates between fish taxa. In particular, the dominance of chondrichthyans may reflect, in part, the fact that these taxa, presumably, shed teeth at a relative high rate, throughout their lives, as do modern elasmobranchs. This would inflate the chondrichthyan sample by several multiples. There are no reliable adjustment factors that can be used to relate fossil assemblage data to original fish population pyramids.

In order to examine palaeoecological patterns, specimens were assigned to one of the four sedimentary facies (Ó Gogáin *et al.* 2016, S1) and analysed in a palaeoenvironmental context: shallow marine facies (Lithology 1), brackish embayment facies (Lithology 2), or brackish tidal estuary facies (Lithologies 3 and 4). Fish and tetrapod remains are considered parautochthonous to each facies in which they are found. This is based on the fact that no material shows signs of abrasion, with the exception of abrasion on the distal portions of the spines of *Gyracanthides*, which is attributed to wear during life, suggesting minimal transportation. However, the possibility that fish and tetrapod remains washed in from other environments cannot be entirely ruled out and the disarticulated nature of the material indicates that there was at least some minimal washing.

We note that analysis of the facies distribution of fishes across this offshore to onshore salinity gradient is hampered by the fact that three-quarters of determinate specimens derive from the brackish embayment facies (Lithology 2) whereas fossils in the offshore shallow marine facies (Lithology 1) and onshore tidal estuary facies (Lithologies 3 and 4) are relatively rare. Acknowledging this limitation, genus-level data was analysed using the inverse of the Simpson Index given by the equation:

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

TABLE 2. Quantitative data for the facies distribution of fish specimen ranked at class/order and generic level.

Palaeoenvironment	Number of specimens	Shallow marine	Brackish embayment	Brackish tidal estuary	All facies
Lithology		1	2	3 + 4	
<i>Orthacanthus compressus</i>	71	25.0%	39.2%	53.3%	39.2%
<i>Ageleodus pectinatus</i>	67	18.8%	44.8%	23.3%	37.0%
Chondrichthyes	209	41.9%	65.2%	75.0%	64.3%
<i>Gyracanthides</i> sp.	3	6.3%	1.5%	0.0%	1.6%
<i>Acanthodes</i> sp.	4	0.0%	1.5%	0.0%	1.6%
Acanthodians	17	3.2%	6.4%	0.0%	5.2%
<i>Ctenodus interruptus</i>	2	6.3%	0.8%	0.0%	1.0%
<i>Archichthys portlocki</i>	5	6.3%	1.5%	0.0%	2.8%
<i>Strepsodus sauroides</i>	9	6.3%	5.4%	3.3%	5.0%
cf. <i>Rhizodus hibberti</i>	16	6.3%	5.4%	16.7%	8.8%
cf. <i>Rhizodopsis sauroides</i>	1	0.0%	0.0%	3.3%	0.6%
<i>Megalichthys</i> sp.	5	25.0%	0.8%	0.0%	2.8%
Sarcopterygians	59	48.4%	13.6%	20.5%	17.8%
Actinopterygians	26	6.5%	8.8%	4.5%	8.0%
Tetrapods	15	0%	6.0%	0%	4.6%
1–H for genera		0.805	0.641	0.428	

Note that the number of specimens at class/order level ($n = 326$) is higher than at generic level ($n = 183$) because some specimens can be assigned to class/order but not to genus. Percentage values at class/order and genus level differ because of they are based on these different datasets. The inverse of the Simpson Index (1–H) is calculated for generic level data only.

where n is the total number of specimens of a particular genus and N is the total number of specimens of all genera. This analysis shows that diversity, measured in terms of the total number of taxa and the evenness of the abundance distributions of those taxa, is highest in the shallow marine environment ($D = 0.805$) and progressively declines in the brackish embayment ($D = 0.641$) and tidal estuary ($D = 0.428$). Examining these data qualitatively also reveals patterns. It is noteworthy that both shark genera, *Ageleodus* and *Orthacanthus*, are distributed across the salinity gradient (Lithologies 1–4) in relatively high proportions. Here, the equally high proportions of sharks across all facies may indicate biasing effects of their relative over-abundance because of tooth shedding. In contrast, dipnoans (*Ctenodus*), rhizodonts (*Archichthys*, *Strepsodus*) and *Megalichthys* occur in higher proportions in the marine facies (Lithology 1) while some other rhizodonts (*Rhizodus*) and *Rhizodopsis* are more common in brackish tidal estuaries.

DISCUSSION

In this paper we document a new, diverse assemblage of fish and tetrapods in a facies context from the Pennsylvanian (early Moscovian) Minto Formation of New Brunswick, Canada. Findings improve knowledge of the biodiversity, food webs, and ecology of fish and tetrapod communities during a critical evolutionary phase.

Biodiversity and food webs

Based on specimen counts, the dominant fish were chondrichthyans, comprising 64.3% of the assemblage based on class-level counts. As noted, this value is likely to be inflated by the common shedding of teeth by sharks. Two genera are co-dominant. Most common (39.2%) is *Orthacanthus*, a large predatory shark that reached its acme in Pennsylvanian times. The diet of *Orthacanthus* was catholic, including actinopterygians, acanthodians, dipnoans, xenacanthids and tetrapods, based on analysis of coprolites (Williams 1972; Hampe 1988; Johnson 1999) and gut contents (Kriwet *et al.* 2008). However, the presence of possible juvenile xenacanthid remains in heteropolar microspiral coprolites, reported here, adds another dimension to our understanding of *Orthacanthus* behaviour. It suggests the genus was practising filial cannibalism of juvenile xenacanthids (as postulated at other sites; Hampe 1988; Soler-Gijón 1995; Heidke 1998; Johnson 1999; Beck *et al.* 2014). The ecology of the other abundant shark, *Ageleodus*, remains completely unknown, and it is even uncertain whether skeletal elements represent teeth or specialized branchial denticles (Lebedev 1996; Turner 2013).

The assemblage also contains common (17.8%) sarcopterygians (rhizodontids, megalichthyids, dipnoans) and rare aquatic tetrapods (4.6%), which were similar large predatory animals. Subspherical coprolites containing rhizodont and actinopterygian remains may have been

derived from either of these groups. The dominance of large predators (secondary and tertiary consumers) is inconsistent with a normal trophic pyramid. However, this inverted structure is commonly reported for Pennsylvanian assemblages (e.g. Carpenter *et al.* 2015), and may simply reflect a much lower preservation potential of, mostly soft-bodied, producers and primary consumers.

Within the fish assemblage, the acanthodians (5.2%) had differing feeding habitats. *Acanthodes* was likely to have been a suspension feeder (Brazeau & Winter 2015) filtering planktonic organisms, while *Gyracanthides*, which based upon abrasion on pelvic and pectoral spines (Denison 1979) occupied a partial benthic habitat and possibly fed on small benthos. Also present were eurynotiforms and the dipnoan, *Ctenodus*, whose crushing/grinding dentition suggests a durophagous mode of life. Based on their size, dipnoans were the most likely producer of the short ellipsoid coprolites that contain fragmentary invertebrate remains (microconchids, bivalves) and rare fish fragments. Non-eurynotiform actinopterygians may have fed on a variety of organisms including zooplankton, arthropods or other fish but, due to the fragmentary nature of the associated material, this cannot be deduced with any certainty.

Euryhaline tolerances

The fish and tetrapod assemblages date from the early Moscovian acme of a major diversification event within brackish/freshwater environments (Falcon-Lang *et al.* 2015a).

Acquisition of a euryhaline habitat within Carboniferous fish groups occurred prior to the diversification event (Sallan & Coates 2010, 2014; Friedman & Sallan 2012). However, there is considerable disagreement as to whether Carboniferous fish communities documented from continental facies were adapted for a euryhaline habitat. Some authors agree that fish communities were, indeed, temporary visitors from adjacent marine environments because their cosmopolitan distribution implies dispersal via marine seaways (Schultze 2009; Carpenter *et al.* 2011, 2014, 2015). In contrast, others have maintained that they comprised elements of an endemic freshwater ecosystem because the strontium isotope ratio ($^{87}\text{Sr}/^{86}\text{Sr}$) of apatite tooth enamel (0.70824–0.71216) suggests substantial contact with continental-influenced water bodies (Masson & Rust 1984; Stamberg & Zajíc 2008; Fischer *et al.* 2011, 2013; Montañez & Cecil 2013).

Quantitative analysis of fish remains in a facies context, reported here, indicate that some fish taxa at least were euryhaline, but also reveals previously unsuspected ecological heterogeneity. Chondrichthyans appear to have been particularly successful in colonising the full salinity

gradient, and both *Orthacanthus* and *Ageleodus* have been found in apparently freshwater fluviolacustrine facies upstream of the marine coast at other sites (Schneider *et al.* 2000; Hampe 2002; Carpenter *et al.* 2014). This is also the case for *Acanthodes*, which been reported from a variety of lacustrine, fluvial, estuarine/deltaic, and fully marine settings (Zidek 1976; Beznosov 2009; Burrow *et al.* 2010; Sallan & Coates 2010). In contrast, while also probably euryhaline, dipnoans (*Ctenodus*), rhizodonts (*Archichthys*, *Strepsodus*) and *Megalichthys* appear to have been better adapted to marine environments, while some other fishes (*Rhizodus*, *Rhizodopsis*) appear to be better suited to life in brackish tidal estuaries based on facies distribution data (Table 2). This heterogeneity is reflected by the Simpson Index, which shows that fish diversity declines from open marine environments towards more variably saline estuaries, suggesting that not all taxa were equally successful at infiltrating brackish water coastal tracts.

By contrast, aquatic tetrapod remains (embolomeres, colosteids) are found only in brackish-water facies and were probably euryhaline, hunting within coastal brackish bays. This hypothesis has been raised, periodically, based on anecdotal facies associations across Euramerica (Milner 1987; Laurin & Soler-Gijón 2001; Schultze 2009), and is here supported, based on analysis of parautochthonous assemblages associated with a brackish water fauna. Embolomeres and colosteids have always been identified as primarily aquatic forms. The embolomeres, typically 1–4 m long, with their short limbs, elongate, laterally flexible trunks, and long flat-sided tails, have always been interpreted as largely aquatic predators on fishes of all sizes (Milner 1987). Likewise, colosteids were long-bodied, flat-headed predators up to 1 m in length, with reduced limbs and prominent lateral line systems, both indicators of a primarily aquatic lifestyle (Milner 1987). Further, Milner (1987) noted the prevalence of a tetrapod association comprising embolomeres, keraterpetontid neotrideans, lysorophians and trimerorachoid temnospondyls in Pennsylvanian assemblages throughout Europe and North America; these have been interpreted as salinity-tolerant organisms, indicating brackish conditions (Schultze 2009). Our findings suggest that early tetrapods, either retained the osmoregulatory systems of their sarcopterygian ancestors, or independently diversified back into brackish settings.

The inferred widespread euryhalinity of Carboniferous fish and tetrapods in the Minto Formation contributes to the long-running debate regarding ecology. If taxa were freely migrating between marine and freshwater settings, or even occupying brackish coastal settings, it is possible for them to have a marine-based dispersal pattern, explaining the cosmopolitan nature of assemblages (Sahney *et al.* 2010; Carpenter *et al.* 2015). However, a

euryhaline habit would also explain how such fishes and tetrapods could show enriched strontium isotope values indicative of continental or freshwater influences (Fischer *et al.* 2011, 2013; Montañez & Cecil 2013).

Evolutionary implications

The Maritimes Basin of Canada is a particularly informative area for studying the evolution of fish populations within brackish coastal waters. This depocentre is positioned near the continental interior of Pangaea (Falcon-Lang *et al.* 2006) but was intermittently connected to marine water bodies in the course of glacio-eustatic and tectonic fluctuations (Gibling *et al.* 2008). Fully marine incursions occurred during only three brief intervals, during part of the Visean (Windsor Group), the Bashkirian (Joggins and Tynemouth Creek formations; Grey *et al.* 2011; Falcon-Lang *et al.* 2015*b*) and early Moscovian stages (Minto Formation; this paper). However, brackish incursions were far more common, spanning the entire Carboniferous interval (Archer *et al.* 1995; Tibert & Scott 1999; Falcon-Lang *et al.* 2006; McIlroy & Falcon-Lang 2006; Gibling *et al.* 2008), and reflecting the periodic development of a brackish epicontinental sea, in some ways, analogous to the present-day Baltic Sea (Calder 1998; Falcon-Lang 2005). These brackish-marine incursions contain rich but fragmentary fish faunas (summarized in Fig. 17; see references in figure caption). A remarkable feature of these faunas is their conservative composition, with a consistent collection of taxa assembled by Serpukhovian times (Pomquet Formation) and persisting for 20 million years, with minimal variation, until late Moscovian times (Sydney Mines Formation). Conservative composition was probably maintained by euryhalinity, which kept populations well mixed, and suppressed allopatric speciation.

CONCLUSIONS

1. We describe a new fish and tetrapod assemblage from the Carboniferous (Pennsylvanian; early Moscovian) Minto Formation of New Brunswick, Canada.
2. The fish fauna includes chondrichthyans (xenacanthids and the enigmatic *Ageleodus*), acanthodians (gyracanthids and acanthodiforms), sarcopterygians (rhizodontids, megalichthyids, rhizodopsids, dipnoans) and actinopterygians (eurynotiforms).
3. The tetrapod fauna includes small to medium-sized, and largely aquatic, forms of stem tetrapods (colosteids) and anthracosaurs (embolomeres).
4. Facies analysis of taxa across a brackish-marine palaeosalinity gradient demonstrates that almost all

fish and tetrapod taxa were euryhaline, with chondrichthyans especially well equipped to traverse into non-marine environments.

5. Documentation of widespread euryhalinity in fish may explain how strontium isotope analyses of tooth enamel indicate continental influence when other data point to marine dispersal.
6. In the context of other rich Carboniferous fish faunas of the Maritimes Basin of Atlantic Canada, fossils show the assembly of a conservative range of euryhaline taxa over the 20 million year period coinciding with the mid-Carboniferous diversification.

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DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.nc3f2>

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