

EARLY PENNSYLVANIAN (LANGSETTIAN) FISH ASSEMBLAGES FROM THE JOGGINS FORMATION, CANADA, AND THEIR IMPLICATIONS FOR PALAEOECOLOGY AND PALAEOGEOGRAPHY

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Abstract: A review of all available specimens of fossil fishes from the classic Pennsylvanian Joggins locality of Nova Scotia, Canada, reveals the existence of a diverse community of chondrichthyans (xenacanthids, ctenacanthids and the enigmatic *Ageleodus*), acanthodians (gyracanthids), sarcopterygians (rhizodontids, megalichthyids, rhizodopsids and dipnoans) and actinopterygians (haplolepidids). Reassessment of supposed endemic species (*Ctenopterychi* *cristatus*, *Sagenodus* *plicatus*, *Gyracanthus* *duplicatus*) indicates they are invalid, and overall, the assemblage comprises cosmopolitan taxa that were widespread around the coasts of tropical Pangaea. Strontium isotope analysis of fish remains and a critical study of their facies context suggest that these fish communities occupied bodies of water with salinities across the marine–freshwater spectrum. This preponderance of euryhaline forms implies a community structure quite distinct from

that of today and might represent a transitory phase prior to the establishment of fully freshwater fish communities. Interpretation of fish ecology provides further evidence that the Joggins Formation was deposited in a paralic setting, and the recognition of one previously undetected brackish incursion strengthens the link between sedimentary cycles at Joggins and Milankovitch-induced glacio-eustatic change. Furthermore, interregional correlation of these marine transgressions supports palynostratigraphical arguments for an early Langsettian age for the Joggins Formation. This places tighter constraints on the age of the earliest known crown amniote, *Hylonomus lyelli*, an important calibration point used in phylogenomic studies.

Key words: Carboniferous, Nova Scotia, strontium isotope analysis, euryhaline community, endemism, palaeosalinity.

JOGGINS, Nova Scotia, Canada, is a UNESCO World Heritage Site famous for its Pennsylvanian coal measures and associated tropical biota (Falcon-Lang and Calder 2004; Falcon-Lang *et al.* 2010). These towering sea-cliffs, hewn by the world's highest tides in the Bay of Fundy, were one of the first places in North America where coal was mined (Falcon-Lang 2009; Quann *et al.* 2010) and have been continuously studied by geologists for nearly two centuries (Calder 2006; Falcon-Lang 2006; Grey and Finkel 2011). An early visitor in 1842 was Charles Lyell, who documented many horizons with lycopsid trees preserved in growth position, which demonstrated that most Pennsylvanian coal seams originated as peats beneath tropical forests (Lyell 1843; Scott 1998). Returning a decade later in the company of William Dawson, Lyell

unearthed amphibian remains within the broken casts of some of these fossil trees (Lyell and Dawson 1853). This discovery so fired the young Dawson's interest in the site that he spent the next 47 years documenting the rich fossil biota of Joggins (Dawson 1901). Largely as a result of Dawson's meticulous, bed-by-bed collections (Dawson, 1854, 1865, 1868) – which comprised rich faunas of tetrapods (including the oldest known reptile, *Hylonomus lyelli*), myriapods, arthropleurids, arachnids, annelids and gastropods, as well as plant remains (e.g. Dawson 1860, 1861, 1863, 1877, 1880, 1882, 1896) – Joggins has long been regarded as the key site for understanding the terrestrial ecosystems of tropical Pangaea (Falcon-Lang *et al.* 2006). The cliffs at Joggins continue to yield important fossil material today (e.g. Falcon-Lang 1999; Falcon-Lang

et al. 2004; Calder *et al.* 2006; Prescott *et al.* 2014), and a new museum, the Joggins Fossil Centre, has recently been built on-site as a permanent repository (Grey and Skilliter 2011).

One prominent lithology at Joggins comprises thick beds of bituminous limestone, which were interpreted until relatively recently as the deposits of deep freshwater lakes, based on the absence of unequivocal marine fauna and on isotopic studies (Brand 1994). However, later discoveries of ichnofaunas, agglutinated foraminifera, brachiopods and echinoderms in these beds (Archer *et al.* 1995; Grey *et al.* 2011; Prescott *et al.* 2014), together with re-evaluations of the palaeoenvironmental implications of associated bivalves, ostracodes, microconchids, eurypterids, carideans, limulids and fish (Calder 1998; Tibert and Dewey 2006; Falcon-Lang *et al.* 2006; Grey *et al.* 2012; Zaton *et al.* 2014), now favour an origin in extensive brackish bodies of water partly analogous to the Baltic Sea today (Falcon-Lang 2005), corroborating much earlier suspicions of marine influence (Dawson 1868; Bell 1913; Calver 1968; Duff and Walton 1973). The 'brackish seas' of Joggins probably represent the distal extension of the marine bands that characterize coal measure successions in north-west Europe (Davies *et al.* 2005). Based on alluvial drainage patterns, which give an indication of basin topography (Gibling *et al.* 1992), shallow seas probably transgressed westward from the Tethys Ocean, through a hypothetical 'mid-Euramerican seaway' (Calder 1998), before eventually flooding of the inland continental reaches of the Maritime Basin of eastern Canada at high-stand (Fig. 1; Falcon-Lang 2005). Sea-level fluctuations were probably glacio-eustatic, being driven by Milankovitch-scale orbital cycles (Waters and Davies 2006).

Least studied of the aquatic communities that occupied the brackish seas at Joggins are the fish assemblages, which form the focus of this paper. These fragmentary remains are moderately rare, and for most historic collections (Dawson 1854, 1865, 1868; Copeland 1957, 1958; Baird 1962, 1978; Carroll *et al.* 1972; Calder 1998), systematic revision is long overdue. The primary aim of this study was to describe systematically all available collections of fish from Joggins and to document the dominance–diversity characteristics of the assemblage. A secondary aim was to assess the salinity tolerance of the fish through strontium isotope analysis and an evaluation of the facies distribution of taxa at sites worldwide (Carpenter *et al.* 2011, 2014). Our findings improve knowledge of the palaeogeographical setting of the Joggins locality and demonstrate that Pennsylvanian fish communities were unusually cosmopolitan as a result of their dominantly euryhaline mode of life.

GEOLOGICAL CONTEXT

The 'classic' Joggins section is located between Lower Cove and the old Joggins Wharf (latitude 45°42' N; longitude 64°26' W) on Chignecto Bay, Bay of Fundy, Nova Scotia, Canada (Fig. 2A). Here, the Pennsylvanian Joggins Formation is exposed in its entirety, in its type section (Davies and Gibling 2003; Davies *et al.* 2005; Rygel *et al.* 2014). Although patchy exposures along streams, and in former coal mines, indicate the inland extension of this formation for more than 35 km to the east (Copeland 1958), all the fish specimens described in the paper, with one exception, originated from the coastal section.

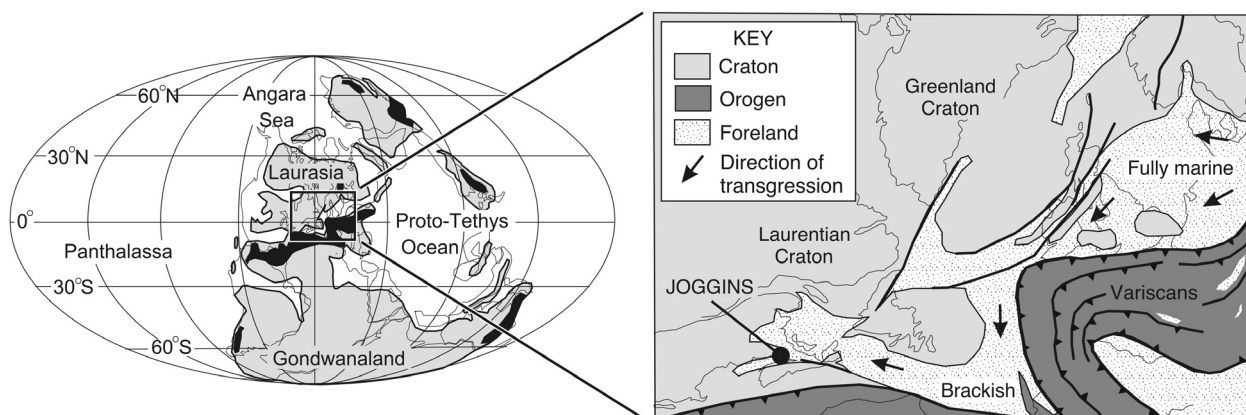


FIG. 1. Palaeogeographical setting of the 'brackish seas' (OWFA; open water facies association) developed at Joggins, Nova Scotia. A, global palaeogeography (after Scotese and McKerrow 1990) showing putative connection of Maritimes Basin to the Tethys Ocean during marine maximum flooding (partly after Calder 1998). B, reconstruction of central tropical Pangaea at maximum sea level, showing an extensive brackish embayment within the Maritimes Basin (modified from Ziegler 1988). Transgression direction inferred from the inverse of fluvial palaeocurrents (Gibling *et al.* 1992).

Age of the Joggins Formation

Marine index fossils (conodonts, goniatites) have not been found in the Joggins Formation because, as noted above, transgressions were brackish by the time they entered the Maritimes Basin, and precise correlation with global marine-based biostratigraphical systems remains uncertain (Calder 1998; Falcon-Lang 2005). Nonetheless, palynoflora and megaflores indicate a Langsettian age, close to the Namurian–Westphalian boundary (Calder 1998; Utting and Wagner 2005; Utting *et al.* 2005). Falcon-Lang *et al.* (2006) inferred a mid- to late Langsettian age based on megaflores assemblages, while Utting *et al.* (2010) suggested placement in the early Langsettian based on palynology. Within the limits of these uncertainties, the Joggins Formation is correlative with the late Morrowan regional stage in North America, and the mid-Bashkirian global stage in the IUGS system (Fig. 2B; Heckel *et al.* 2008).

Stratigraphical and sedimentological framework

The ‘classic’ Joggins section was first logged at a reconnaissance level, in 1843, by William Logan, and assigned to his stratigraphic Division 4 (Logan 1845), which is almost exactly equivalent to the Joggins Formation as recognized in present stratigraphical nomenclature (Davies *et al.* 2005; revised by Rygel *et al.* 2014). Subsequently, the section was remeasured, bed by bed, in much greater detail (Dawson 1854, 1865, 1868). Both authors utilized the same system of numbering coal-bearing intervals from top to base as Coal Group 1 to 45 (Fig. 2C; Rygel and Shipley 2005).

A new, high-resolution sedimentological log of the 932.4-m-thick type section is correlated with Logan and Dawson’s Coal Group numbers (Davies and Gibling 2003; Davies *et al.* 2005; position of the top of the formation revised upwards by Rygel *et al.* 2014). This log is divided into 15 sedimentary cycles (Cycles 1–15) based on major flooding surfaces (Davies *et al.* 2005; Fig. 2C). An idealized Joggins cycle comprises a retrogradational, poorly drained floodplain facies association (rPDFA), overlain by an open water facies association (OWFA), which together record basinwide flooding by a ‘brackish sea’. This is succeeded by a progradational, poorly drained floodplain facies association (pPDFA), which represents bay-fill deposits formed by wetland deltas, and capping the cycle there is typically a well-drained floodplain facies association (WDFA) deposited following floodplain aggradation above base level (Davies and Gibling 2003; Davies *et al.* 2005; Falcon-Lang *et al.* 2006). This cyclic pattern of sedimentation represents the complex interplay of tectonism, climate and glacio-eustasy (Davies *et al.* 2005).

Stratigraphical context of fish fossils

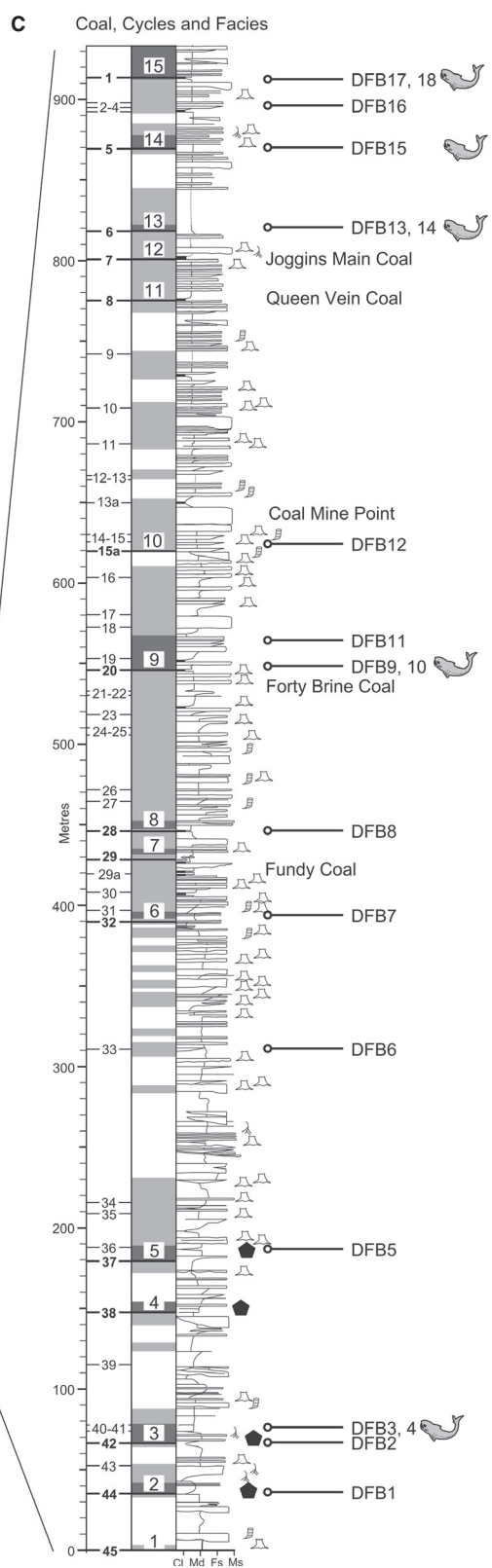
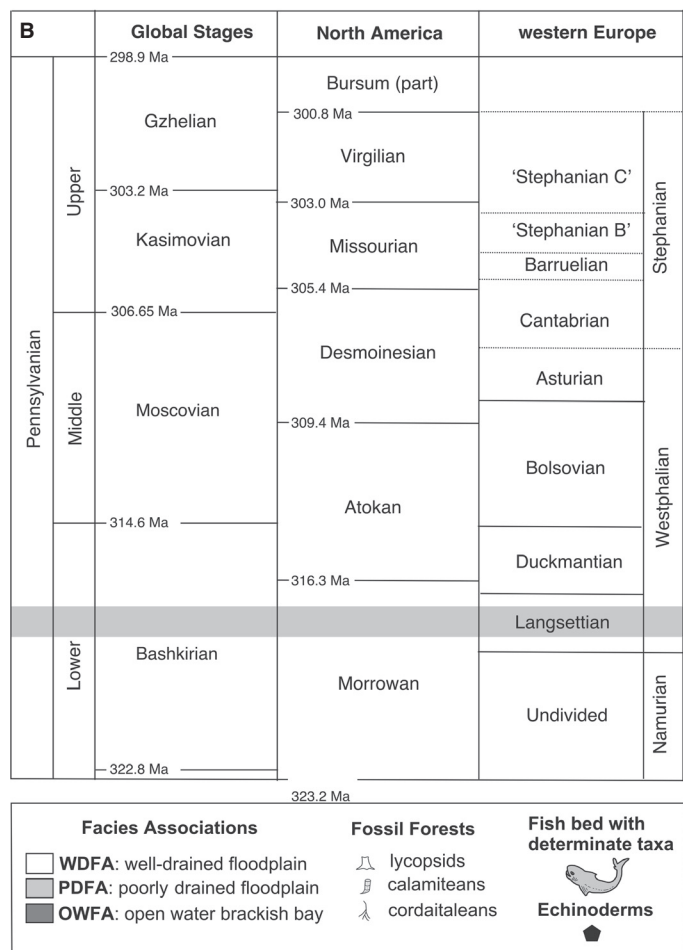
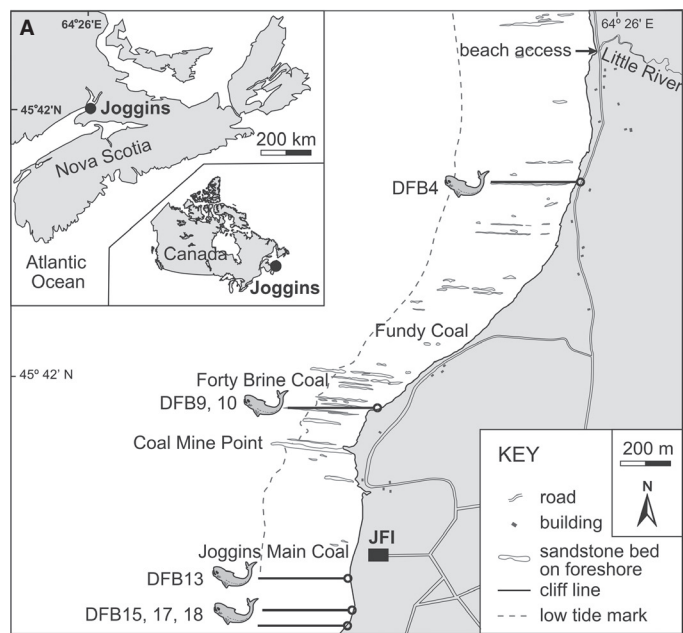
Dawson (1854, 1865, 1868) undertook the first and most comprehensive study of fossil fish distribution in the Joggins Formation, identifying eighteen productive beds, herein referred to as Dawson’s fish beds (DFBs) 1–18 (Fig. 2C). However, only four of these beds produced determinate material: DFB4 positioned at 76 m (*Gyracanthus duplicatus*), DFB13 at 820 m (*Ctenoptychius cristatus*, *Diplodus*, *Palaeoniscus* and *Rhizodus*), DFB17 at 910 m (*Rhizodus*) and DFB18 at 915 m (*Rhizodus*). In the late twentieth century, additional determinate material was located by Carroll *et al.* (1972), Baird (1978) and Skilliter (2001) in two of Dawson’s other beds: DFB9 at 547 m (*Haplolepis*) and, most fossil-rich of all, DFB10 at 555 m (*Callopristodus pectinatus*, *Ctenacanthus*, *Xenacanthus*, *Sagenodus*, *Rhizodopsis*, *Megalichthys* and *Haplolepis*).

Other determinate material was reported without sufficient stratigraphical data for assignment to a particular bed. Dawson (1868) recorded *Conchodus plicatus* and *Psammodus*, while Duff and Walton (1973) reported specimens of *Rhabdoderma* and *Rhizodopsis*, but neither gave their bed of origin within the Joggins Formation. Baird (in Yale Peabody Museum archives) also reported a specimen of *Strepsodus* from ‘south of Joggins wharf’, which would place it in the uppermost part of the formation (equivalent to the interval containing DFB15–18). Finally, Copeland (1958) reported a specimen of *Gyracanthus* in River Hebert coal mine (11 km east of Joggins), the only specimen described from outside the type section. Although inland correlation is uncertain, this specimen probably derived from above the Forty Brine Coal (equivalent to the interval containing DFB9 and 10).

Facies context of fish fossils

Among Dawson’s 18 fish beds, only seven have yielded determinate material over the past 175 years. Five of these seven beds (DFB4, 9, 10, 15 and 18) occur in bituminous limestone units, 0.2–1.8 m thick, in the lower part of OWFA intervals that mark the base of sedimentary cycles (Davies and Gibling 2003). Based on the very high sulphur content of underlying coals (up to 13%; Hower *et al.* 2000) and various aspects of the lithology and palaeontology of the limestone beds (reviewed in the introduction), fish-bearing concentrates were deposited in extensive, shallow, aerobic to dysaerobic, brackish seas (Gibling and Kalkreuth 1991; Archer *et al.* 1995; Grey *et al.* 2011, 2012; Zaton *et al.* 2014). The near absence of siliciclastic grains in the bituminous limestone confirms that these were very extensive bodies of water.

The richest of these fish-bearing limestone assemblages occurs in the interval above the Forty Brine Coal, which



includes DFB9 and DFB10 (Fig. 3). This interval is interpreted as the most pronounced and long-lived 'brackish-marine' transgression into the basin in the Joggins section, based on the unusually great thickness (23 m) of the OWFA interval and the thickness of individual bituminous limestone beds (up to 1.8 m) (Gibling and Kalkreuth 1991; Hower *et al.* 2000). The upper part of this particular OWFA interval shows planar sandstone beds with wave ripples, cross-ripple lamination with paired mud drapes, and large-scale mounded forms, capped by a channelized sandstone unit, interpreted as delta mouth bar and distributary channel deposits developed on the tidal coast of these brackish seas (Archer *et al.* 1995; Wells *et al.* 2005; M.R. Gibling, pers. comm. 2014).

One other fish bed with determinate material (DFB13), from a different facies context, occurs within a thin (30 mm), laminated, clastic-rich coaly shale, which is rich in impressions of *Cordaite* leaves and pteridosperm axes (Dawson 1868, p. 164). Although this fish bed is directly overlain by a bituminous limestone (the lithology that normally contains fish in the Joggins section), Dawson was very specific that the fish fossils were found directly within the coal. This coal forms part of an rPDFa interval, and its laminated, clastic-rich nature, fossil content and proximity to a bituminous limestone are all consistent with formation as a coastal *Cordaite* mangrove environment rather than a freshwater peat (Falcon-Lang 2005; Falcon-Lang and Miller 2007; Stull *et al.* 2012). Possibly, as Dawson (1868) suggested, this record is of fish swimming from open brackish seas into coastal mangroves populated by *Cordaite* and pteridosperm trees (cf. Carpenter *et al.* 2011).

A final fish bed with determinate material (DFB17) occurs in a channelized sandstone within an rPDFa interval, which is notable in that it contains plant remains encrusted with microconchids (referred to as 'spirorbids' in Dawson 1868, p. 163). This deposit probably formed within a distributary channel and is a record of fish swimming within a fluvial channel. The microconchid-encrusted plants indicate that the channel may have comprised part of an estuary that existed on the margins of the brackish seas (Zaton *et al.* 2014), and a similar channel lower in the succession has yielded microbial mats and ichnofauna characteristic of fluvial-tidal deposits (Prescott *et al.* 2014).

Therefore, in summary, all the determinate fish occurrences in the Joggins Formation occur either within the

deposits of brackish epeiric seas, or in the coastal mangroves and estuaries that fringed them.

MATERIALS AND METHODS

A comprehensive review of all Joggins fish fossils available in museum collections was undertaken (see Carpenter *et al.* 2015 for a full list of 281 specimens).

Museum repositories. Fossil material is accessioned as follows: FGM, Fundy Geological Museum, Parrsboro, Nova Scotia, Canada; GLAHM, Glasgow Hunterian Museum, Glasgow, Scotland; JFC, Joggins Fossil Centre, Joggins, Nova Scotia, Canada; MCZ, Museum of Comparative Zoology, Cambridge, Massachusetts, USA; NSM, Nova Scotia Museum of Natural History, Halifax, Nova Scotia, Canada; RM, Peter Redpath Museum, Montreal, Canada; VPPU, Vertebrate Paleontology Collection, Princeton University, Princeton, New Jersey, USA; YPM VPPU, Yale Peabody Museum of Natural History, New Haven, Connecticut, USA (specimens formerly housed at VPPU). The type material of Dawson (1868) is in the Peter Redpath Museum, although not all illustrated specimens were located.

Sample preparation

We chemically prepared selected, unpublished specimens from the JFC by immersion in a 5% acetic acid solution, buffered with calcium acetate following the approach of Jeppsson *et al.* (1985). Fossil material was lightly coated with a weak, ethanol-based contact adhesive ('Mowital') before acid digestion; this reduced the risk that fractured material might disintegrate after the supporting matrix had been removed, and also provided an added barrier against acid attack. Prepared specimens were photographed with a Nikon D700 digital SLR camera with a Nikon 60 mm macro lens; remaining specimens were photographed using a Panasonic Lumix DMC-ZS3 digital camera.

Strontium isotope analysis

One xenacanthid tooth and one sarcopterygian scale were submitted for destructive $^{87}\text{Sr}/^{86}\text{Sr}$ analysis to assess palaeosalinity, based on methods of Schmitz *et al.* (1991). As there was insufficient material to separate enamel from

FIG. 2. Geological context. A, map of classic Joggins section, showing the position of the most important fossil fish localities (inset shows location of site in Nova Scotia and Canada). B, stratigraphical context of the Joggins Formation (highlighted as a grey horizontal bar) in the revised Pennsylvanian stratigraphical system (after Falcon-Lang *et al.* 2012). C, summary sedimentological log of the 932.4-m-thick Joggins Formation (after Davies *et al.* 2005; revised Rygel *et al.* 2014) showing Dawson's fish beds (DFB1–18) and other key coals and fossils (Dawson 1868).

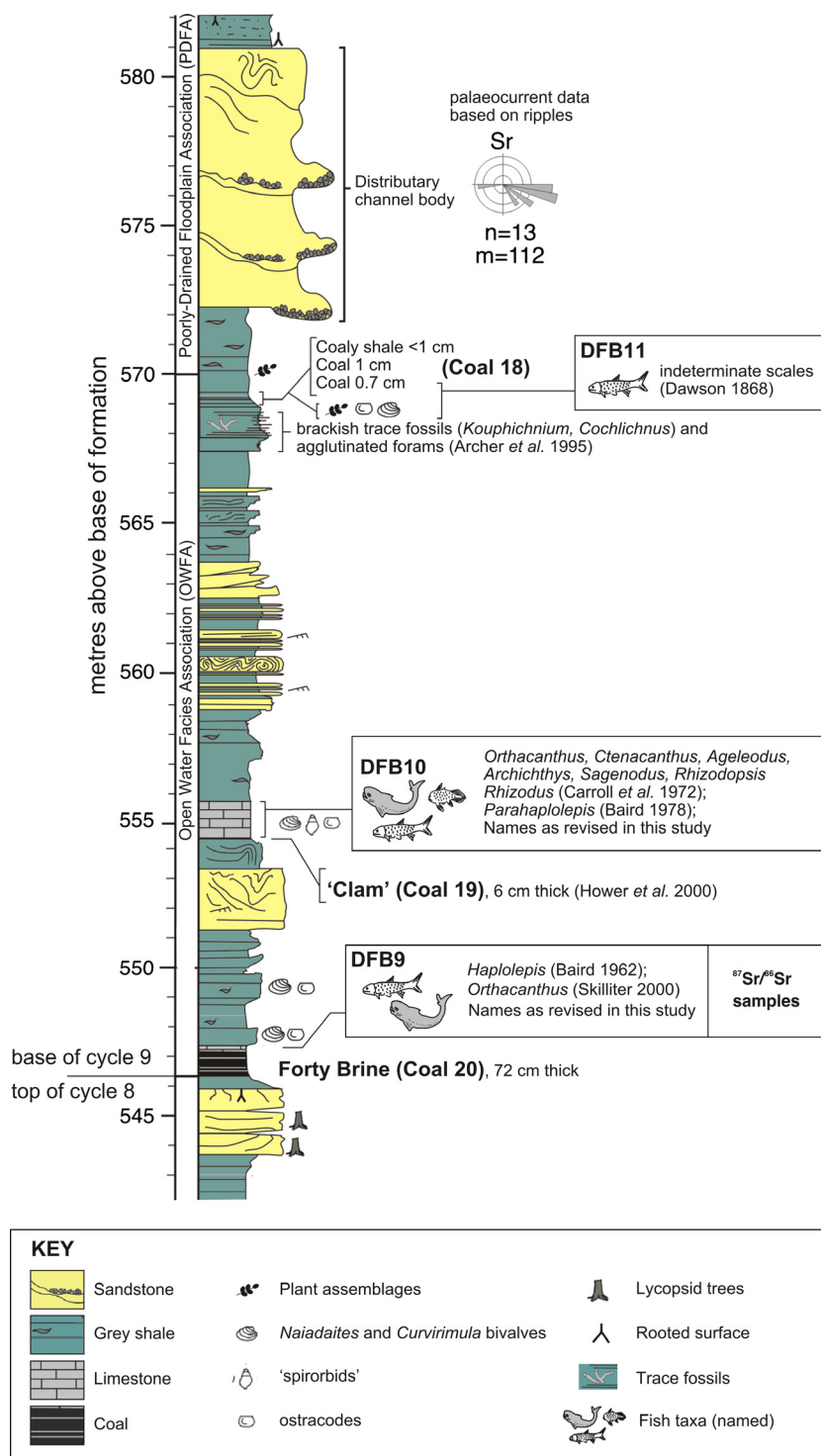


FIG. 3. Detailed sedimentological log of the Forty Brine interval of the Joggins Formation, which represents the most long-lived brackish sea deposit (OWFA; open water facies association) in the formation, and contains the richest and most abundant fish fauna in DFB9 and DFB10 (modified from Davies *et al.* 2005). Colour online.

dentine and apatite, bulk samples were used. Samples were prepared using standard protocols (Carpenter *et al.* 2011). The isotopic analysis was conducted with a VG 354 multicollector mass spectrometer, using multi-dynamic routines. Values were corrected to 0.710248 for the SRM 987 standard.

HISTORICAL REVIEW OF DAWSON'S SPECIES

Three fish taxa unique to the Joggins Formation were described by Dawson (1868): *Ctenoptychius cristatus*, *Gyracanthus duplicatus* and *Conchodus plicatus* (Fig. 4A–C);

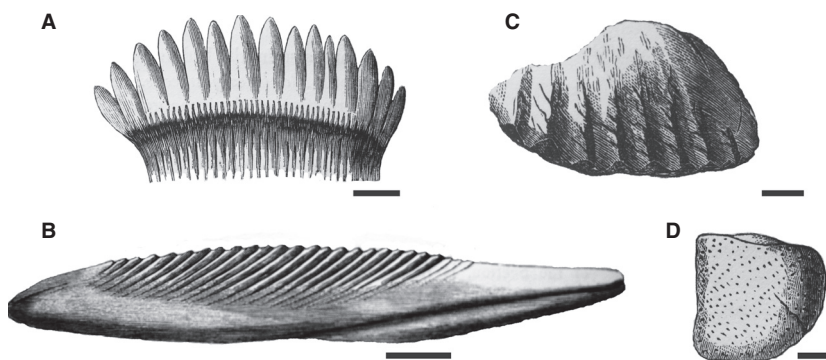


FIG. 4. Fossil fish remains from the Joggins Formation, as illustrated in Dawson (1868, pp. 209–210). A, holotype of Dawson's *Ctenoptychius cristatus* (= *Ageleodus pectinatus*), RM 3070; scale bar represents 1 mm. B, holotype of Dawson's *Gyracanthus duplicatus* (= *Gyracanthidae* indet. cf. *Gyracanthides* sp.), RM3074; scale bar represents 10 mm. C, holotype of Dawson's *Conchodus plicatus* (= *Sagenodus* indet.), RM3073; scale bar represents 5 mm. D, specimen that Dawson referred to *Psammodus* (megachthyid?), specimen presumed lost; scale bar represents 5 mm.

he also illustrated, but did not describe, a specimen referred to *Psammodus* (Fig. 4D). Before presenting a full systematic study of all Joggins fish material, we first provide a historical and nomenclatural review of Dawson's three supposedly novel taxa.

Ctenoptychius cristatus Dawson, 1868

The petalodontid genus *Ctenoptychius* has had a complex nomenclatural history (see Downs and Daeschler (2001) for a detailed account), and only those salient points relevant to the Joggins type material are summarized here. Agassiz (1843a) originally described three species of *Ctenoptychius*, of which two (*C. pectinatus* and *C. denticulatus*) were subsequently synonymized and promoted to generic status as *Ageleodus pectinatus* (Barkas 1874; Zangerl 1981), and ultimately removed from Petalodontida altogether (Hansen 1985).

Dawson's novel species, *Ctenoptychius cristatus*, was based on a single isolated tooth (Dawson 1868). Although its similarity to *C. pectinatus* was noted (Woodward 1889, p. 56), it continued to be treated as a distinct (but rarely discussed) species.

Gardiner (1966) erroneously transferred *C. cristatus* without explanation to the lungfish genus *Sagenodus*. Presumably he had confused *Ctenoptychius cristatus* with *Ctenodus cristatus* Agassiz (1843a), which was identified by Sternberg (1941) as a junior synonym of *Sagenodus cristatus*. To complicate matters further, *Conchodus plicatus* (= *Ctenodus* or *Sagenodus*; Schultze and Chorn 1997; see also below) from Joggins was also discussed in those papers. In addition, Gardiner (1966) only included references to Dawson's *Ctenoptychius cristatus* in his synonymy list and therefore gave the impression that he himself was the authority for *Sagenodus cristatus*. He also noted the similarity of *Ctenoptychius cristatus* to *Callopristodus*

pectinatus (= *Ageleodus pectinatus*), although it is unclear whether he actually examined either holotype.

Whatever the cause of Gardiner's (1966) error, the effect was that Dawson's *Ctenoptychius cristatus* largely dropped out of sight for the next 50 years. The species did not appear in Hansen's (1985) otherwise comprehensive review of the petalodonts, nor in more general reviews of the chondrichthyans as a whole (Zangerl 1981; Ginter *et al.* 2010); however, it did continue to feature in taxonomic lists for the Joggins Formation (Calder 1998; Falcon-Lang *et al.* 2006).

Gyracanthus duplicatus Dawson, 1868

This species was erected by Dawson (1868) based on a single isolated spine. The generalized nature of Dawson's illustration (Fig. 4B) at an early stage led to doubts over the validity of the species and, indeed, whether the specimen was an acanthodian at all (Newberry 1889; Baird 1962); this uncertainty was seemingly justified by the fact that for 94 years, it was the only acanthodian known from the Pennsylvanian of North America (Baird 1962). It was nonetheless listed as a valid species in various catalogues (e.g. Woodward 1891; Gardiner 1966) and a redescription by Baird (1978) confirmed its gyracanthid affinities. It appeared also in the synopsis of acanthodians by Denison (1979).

The most recent consideration of *G. duplicatus* was by Turner *et al.* (2005), who suggested, based on examination of Dawson's illustration (but not his type material), that the specimen might in fact belong to the closely related genus *Gyracanthides*, identifying it as a pelvic spine of that genus. The assertion by Turner *et al.* (2005), citing Baird (1978), that *G. duplicatus* is known elsewhere from shoulder girdle remains appears to be incorrect (no mention is made of this by Baird). Four further spines possibly belonging to this species have been subsequently

reported from Joggins, and other sites nearby (Calder 1998 fig. 6a; Miller 1999 fig. 2) under the name *Gyracanthus* cf. *duplicatus*.

Conchodus plicatus Dawson, 1868

This species was erected for a single isolated element, in this case a dipnoan tooth plate. Although figured under the name *Conchodus plicatus*, Dawson (1868) offered no justification for placing it in a new species, merely stating that it 'appears to belong to M'Coy's genus *Conchodus*' (p. 209). Dawson's specimen was transferred to *Ctenodus* by Woodward (1891) and then to *Sagenodus* by Sternberg (1941), in each case retaining the *plicatus* species epithet. Baird (1978) argued that the specimen was too fragmentary for species-level identification, and dismissed *Sagenodus plicatus* as a *nomen vanum*. This was also the position of Schultze and Chorn (1997), although neither author provided a redescription. Therefore, the most recent detailed description of the specimen is Sternberg (1941), who considered it to be similar to *Sagenodus periprion* Cope (1878). So far as we are aware, no other material has been, even tentatively, assigned to this species.

SYSTEMATIC PALAEONTOLOGY

The fish community at Joggins was found to comprise a rich fish fauna of sarcopterygians (rhizodontids, megalichthyids, rhizodopsids and dipnoans), chondrichthyans (xenacanthids, ctenacanthids and the enigmatic *Ageleodus*), acanthodians (gyracanthids) and actinopterygians (haplolepidids) (Fig. 5).

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Order EUSELACHIDAE Hay, 1902
Superfamily CTENACANTHOIDEA Zangerl, 1981
Family CTENACANTHIDAE Dean, 1909

Genus CTENACANTHUS Agassiz, 1843a

Type species. *Ctenacanthus major* Agassiz, 1843a.

Ctenacanthus sp.
Figure 6

Material. One isolated spine, exposed in lateral view, comprising part and counterpart preserved as cast and external mould (YPM VPPU 019341).

Class CHONDRICHTHYES
Subclass ELASMOBRANCHII
Order EUSELACHIDAE
Superfamily CTENACANTHOIDEA
Family CTENACANTHIDAE
Genus CTENACANTHUS
Ctenacanthus sp.
Order XENACANTHIFORMES
Family DIPLODOSELACHIDAE
Diplodoselachidae indet.
Genus ORTHACANTHUS
Orthacanthus cf. *denticulatus*
Family XENACANTHIDAE
Genus XENACANTHUS
Xenacanthus sp.
ELASMOBRANCHII *incertae sedis*
Genus AGELEODUS
Ageleodus pectinatus
Class ACANTHODII
ACANTHODII *incertae sedis*
Family GYRACANTHIDAE
Gyracanthidae indet. cf. *Gyracanthides* sp.
Genus GYRACANTHIDES
Gyracanthides sp.
Class OSTEICHTHYES
Subclass SARCOPTERYGII
Infraclass DIPNOMORPHA
Order DIPNOI
Family SAGENODONTIDAE
Genus SAGENODUS
Sagenodus cf. *serratus*
Sagenodus sp.
Infraclass TETRAPODOMORPHA
Order RHIZODONTIDA
Family RHIZODONTIDAE
Genus STREPSODUS
Strepsodus sauroides
Genus ARCHICHTHYS
Archichthys portlocki
Genus RHIZODUS
?Rhizodus hibberti
Family RHIZODOPSIDAE
Genus RHIZODOPSIS
Rhizodopsis sauroides
SARCOPTERYGII *Incertae sedis*
Family MEGALICHTHYIDAE
Genus MEGALICHTHYS
Megalichthys sp.
Subclass ACTINOPTERYGII
ACTINOPTERYGII *Incertae sedis*
Family HAPLOLEPIDAE
Genus PARAHAPLOLEPIS
Parahaplolepis cf. *canadensis*
Genus HAPLOLEPIS
Haplolepis cf. *corrugata*

FIG. 5. Summary list of fish taxa from the Lower Pennsylvanian Joggins Formation of Nova Scotia, Canada.

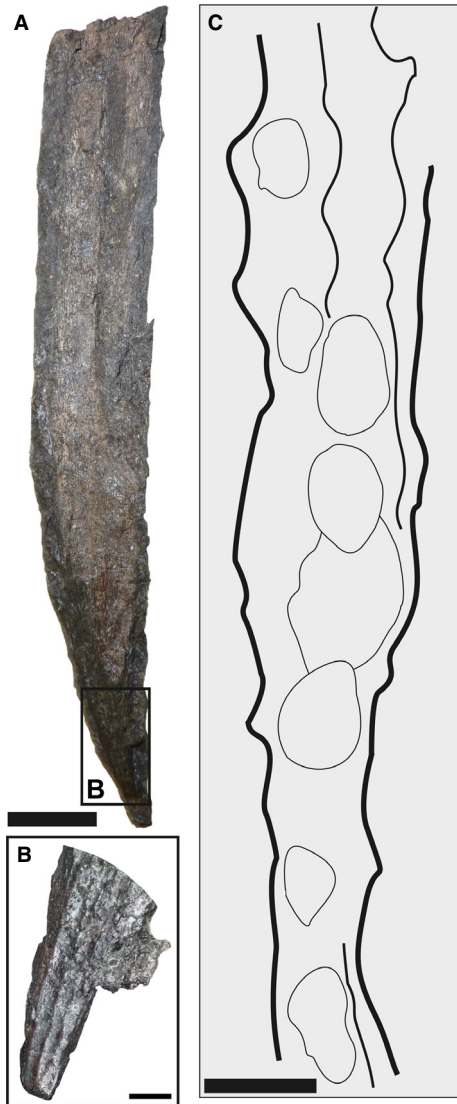


FIG. 6. Photographs of YPM YPPU 19341 *Ctenacanthus* indet. dorsal fin spine. A, lateral view. B, expanded view showing tuberculated longitudinal costae. C, interpretative line drawing showing detail of tubercles. Scale bars represent 2 cm (A), 5 mm (B) and 2 mm (C). Colour online.

Diagnosis. Tapering spine, gently recurved posteriorly, 180 mm long, bearing tuberculated, coarse longitudinal costae; tubercles closely spaced. Posterior face appears slightly concave; no evidence of denticulated postero-lateral margins.

Description. The cast is broken longitudinally at an oblique angle such that only the distal tip (c. 50 mm) is intact. The heavily abraded external surface bears longitudinal costae (Fig. 6B), regularly spaced c. 1.5 mm apart and following the curve of the spine. The external mould, although also somewhat damaged, preserves the external ornamentation with greater fidelity; tubercles are clearly visible, arrayed in longitudinal rows that correspond to the intercostae of the cast. These tubercles

are typically ellipsoid, c. 1 mm in length, and closely spaced such that their bases are contiguous longitudinally (Fig. 6C).

Remarks. The generic diagnosis for *Ctenacanthus* includes the presence of a pronounced proximal median ridge/convexity on the posterior surface (Maisey 1981). However, this diminishes apically, making the posterior face flat or concave distally; thus, the concave posterior surface observed in YPM VPPU 019341 is consistent with our identification and argues against a hybodont affinity (the entire posterior surface is convex in hybodontids). The apparent lack of posterolateral marginal denticles, although initially included as a diagnostic character by Maisey (1981), was subsequently found not to have been universally present in other ctenacanth-like genera (e.g. *Amelacanthus*) and therefore might not in fact be a useful diagnostic criterion (Maisey 1982). Two other genera erected by Maisey (1982) for 'ctenacanth' of uncertain affinity, *Bythiacanthus* and *Amelacanthus*, are distinguished from *Ctenacanthus* by the shape of the spine in lateral view (rhomboidal in *Bythiacanthus*), the lack of a shiny enameloid layer over the spine ornament (present in *Amelacanthus*) and the presence of tubercles on the lateral surfaces (absent in *Amelacanthus*). Although the size and configuration of the tubercles are typical of *Ctenacanthus*, their simple ovoid shape is not; they would typically be expected to exhibit vertical striations and raised lateral projections (Maisey 1981, fig. 1E). This is most likely explained by the abraded nature of the specimen.

Order XENACANTHIFORMES Berg, 1937

Type genus. *Xenacanthus* Agassiz, 1843a.

Xenacanthiformes indet.

Material. Two isolated teeth (NSM008GF031.589 and NSM010GF031.003).

Diagnosis. Tricuspid teeth, crown consisting of two divergent lateral cusps of approximately equal size and a smaller, central cusp.

Description. NSM008GF031.589 is an isolated tooth largely obscured by matrix; only the labial surfaces of the lateral cusps and the basal tubercle are exposed. NSM010GF031.003 is a block containing several scattered elements of which one, an isolated tooth, is referred to *Xenacanthiformes* indet. The tooth retains only a single lateral cusp, 5 mm in length, and the tip of the smaller central cusp; the remaining cusps are preserved in impression, and the base is not preserved. The central cusp is approximately half the size of the lateral cusps; all cusps are non-serrated. The remaining material in the block is referred to

Diplodoselachidae indet. and Chondrichthyes indet. (see below and Carpenter *et al.* 2015).

Family DIPLODOSELACHIDAE Dick, 1981

Type genus. *Diplodoselache* Dick, 1981.

Diplodoselachidae indet. Figure 7A–B

Material. One isolated tooth. (NSM010GF031.003), and one isolated spine, preserved as an external mould (YPM VPPU 021153).

Diagnosis. NSM010GF031.003: tricuspid tooth, lateral cusps serrated; YPM VPPU 021153: tapering spine bearing longitudinal striae.

Description. Tricuspid tooth with lateral cusps approximately twice the size of the central cusp, preserved as an impression only and lacking a base. Serrations are visible on the margins of the lateral cusps, which are 4 mm in length. YPM VPPU 021153: Isolated spine 113 mm in length and with a maximum

width of 9 mm, preserved as an external mould. Fine longitudinal striae are present along the entire length of the spine; these are smooth (i.e. not tuberculated) and only rarely merge or bifurcate. No curvature of the spine is apparent, and no denticulation is visible. Maximum width/length ratio is 1:12.5.

Remarks. NSM010GF031.003 contains several scattered elements including a second isolated tooth referred to *Xenacanthiformes* indet., but only one is identifiable as belonging to the Diplodoselachidae, diagnosed by the serrated margins of its cusps. For YPM VPPU 021153, the absence of denticulation indicates either that denticles were never present, or that they were posteriorly oriented (which would place the specimen within the family Diplodoselachidae) and not visible because the specimen is an external mould of the anterior surface; this is consistent with the presence of longitudinal striae, which are often more prominent on the anterior surface (Hampe 2003) and are widely distributed in Diplodoselachidae, seen in *Orthacanthus* and *Lebachacanthus* (Heidke 1998, figs 2, 5–7), *Diplodoselache* (Lebedev 1996, fig. 9 g–h) and *Dicentrodus* (Hampe 2003, fig. 13d). The maximum width/length ratio of 1:12.5 falls between the ranges established (Hampe 2003) for the robust spines of *Dicentrodus* and *Diplodoselache*, and the slender spines of *Orthacanthus*.

Genus ORTHACANTHUS Agassiz, 1843a

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

Orthacanthus denticulatus Davis, 1880 Figure 8

Material. One complete (YPM VPPU 023513) and two incomplete (YPM VPPU 023480, NSM012GF013.001) isolated cephalic spines.



FIG. 7. Photographs of xenacanthid material. A, photograph of YPM VPPU 021153 Diplodoselachidae indet. spine; B, expanded view showing longitudinal striae. C, photomicrograph of NSM012GF013.002 *Xenacanthus* sp. tooth, occlusal view. Scale bars represent 25 mm (A) and 1 mm (B–C). Colour online.



FIG. 8. Photomicrographs of NSM012GF013.001 *Orthacanthus denticulatus* cephalic spine. A, ventral view. B–C, lateral view. Scale bar represents 10 mm. Colour online.

Diagnosis. Gently curved, slender spines equipped with two denticle rows situated ventrally and of near-parallel orientation. Denticles recurved, slender and sharply pointed with a distinct bend in the proximal margin. No median ventral ridge; lateral and dorsal surface bears longitudinal striae. Maximum width/length ratio 1:16 to 1:18.

Description. Slender and gently curving spines with a flattened ventral surface in cross section; two near-parallel denticle rows are situated ventrally. The denticles are slender and recurved anteriorly, with a conspicuous bend in the concave proximal margin; the tips frequently missing, but 1.0–1.5 mm long and equipped with sharp points where complete. Median ridge absent on the ventral surface, but the lateral and dorsal surfaces have longitudinal striae. YPM VPPU 23513 is 108 mm long, with a maximum width of c. 6 mm, narrowing to 1 mm distally; YPM VPPU 23480, although incomplete, preserves the gross morphology as an impression; original length was 160 mm, with a maximum width of c. 10 mm. Width/length ratios for these two specimens are therefore approximately 1:18 and 1:16, respectively. NSM012GF013.001 is 34 mm long as preserved, but is broken at both ends; the maximum width of the preserved portion is 3 mm. The central pulp cavity comprises approximately 50% of the cross section of the spine.

Remarks. The denticles of the spines are extremely similar in form and disposition to those of *Orthacanthus denticulatus*, a spine-based species which occurs in the Langsettian – early Bolsovian (= Bashkirian) of northern England; in particular, the bent proximal margin is considered characteristic of this species (Hampe 2003, fig. 10 h). In gross morphology, the spines are also comparable; they differ from their European counterparts only in attaining a somewhat greater maximum length. The term ‘slender’ is used here in the sense of Soler-Gijón (1997) to indicate a maximum width/total length ratio of $\geq 1:12$. Note also that Hampe (2003) refers to the bent margin as the *posterior* margin, although in fact it faces anteriorly relative to the body of the shark; we have adopted the term proximal to indicate its orientation relative to the spine.

Family XENACANTHIDAE Fritsch, 1889

Genus XENACANTHUS Beyrich, 1848

Type species. *Xenacanthus decheni* Goldfuss, 1847.

Xenacanthus sp. Figure 7C

Material. Two isolated teeth (NSM012GF013.002i and NSM012GF013.002ii).

Diagnosis. Tricuspid teeth with lanceolate, non-serrated lateral cusps; median cusp approximately 75% of the length of the lateral cusps.

Description. Tricuspid teeth with divergent lateral cusps separated by a smaller central cusp, 75% as long as the laterals. The lateral cusps are smooth and lanceolate in cross section. Matrix obscures the basal tubercle, median foramen and nutritive foramina. A circular coronal button circular is present, but lacks a lingual shaft.

Remarks. The presence of a large median cusp combined with the lack of serrations and lanceolate cross section of the lateral cusps excludes these specimens from the family Diplodosselachidae. The smooth surface (i.e. lacking carinae) excludes the teeth from any other known genus within the Xenacanthidae.

Order and Family *incertae sedis*

Genus AGELEODUS Owen, 1867

Type species. *Ageleodus pectinatus* (Agassiz, 1843a).

Remarks. As the teeth of *Ageleodus* are known only in isolation, their order- and family-level affinity is unknown. Also, unknown is their configuration within the jaw, although it is reasonable to assume the curvature is lingual as this would facilitate prey capture; the descriptive terminology used here follows that of Downs and Daeschler (2001).

Ageleodus pectinatus (Agassiz, 1843a)

Figure 9

- 1843a *Ctenoptychius pectinatus* Agassiz, p. 100, tab. 19, figs B–C (non fig. D).
- 1843a *Ctenoptychius denticulatus* Agassiz, p. 101, tab. 19, figs E–G.
- 1867 *Ageleodus diadema* Owen, p. 20, pl. 4, figs 1–3.



FIG. 9. Photomicrograph of RM 3070 *Ctenoptychius* ‘*cristatus*’ holotype. Scale bar represents 2.5 mm. Colour online.

- 1868 *Ctenoptychius cristatus* Dawson, p. 209, fig. 52.
 1888 *Callopristodus pectinatus* Traquair, p. 85.
 1891 *Ctenoptychius cristatus* Dawson, p. 209, fig. 52.
 1966 *Sagenodus cristatus* Gardiner, p. 95.
 1972 *Callopristodus pectinatus* Carroll *et al.*, p. 74.

Material. Dawson's type specimen for the invalid *Ctenoptychius cristatus* (RM 3070), and eight further isolated teeth (NSM008GF031.234, NSM008GF031.243, NSM008GF031.322, NSM008GF031.461, NSM008GF031.540, NSM008GF039.390, NSM008GF039.556 and YPM VPPU 019340).

Diagnosis. Mesio-distally elongated tooth bearing multiple conical cusps in a pectinate configuration. Crown mesio-distally wider than base, which lacks imbrication.

Description of Dawson's RM 3070. A mesio-distally elongated, labio-lingually compressed tooth with bulbous basal ridge and a denticulated, pectinate crown bearing 15 conical cusps. The cusps are blunt-tipped, smooth and recurved, presumably lingually. Mesio-distal width is 6 mm; total height (root and crown) is 6 mm. The base bears longitudinal depressions aligned with the gaps between cusps; longitudinal furrows also occur in the root, and these broadly correspond with the longitudinal depressions seen in the base. The base curves lingually at the mesial and distal margins, in contrast to Dawson's illustration, which depicts curvature along its entire width. The original description also quotes the number of cusps as 14, when in fact there are 15.

Description of new material. The remaining specimens resemble RM 3070 in most respects. NSM008GF031.461, NSM008GF039.390, NSM008GF039.556 and YPM VPPU 019340 are exposed in labial view, indicated by the more bulbous shape of the crown, while NSM008GF031.234 and NSM008GF031.322 are exposed in lingual view (the latter as an impression). The remaining specimens, NSM008GF031.243 and NSM008GF031.540, are too incomplete for the aspect to be determined. The number of cusps ranges from 12 to 19; width and height of the teeth varies from five to seven and four to six mm, respectively.

Remarks. Intraspecific variation of *A. pectinatus* based on a large number of specimens from the Upper Devonian Catskill Formation at Red Hill, Pennsylvania (Downs and Daeschler 2001) includes attributes such as the shape, configuration (i.e. pectinate versus digitate) and number of cusps. The specimens described here fall comfortably within the established ranges for this species. They closely resemble specimens described from the Tournaisian of Bute, Scotland, by Carpenter *et al.* (2014, fig. 4). Thus, we conclude that Dawson's *Ctenoptychius cristatus* is a junior synonym of *Ageleodus pectinatus* (Agassiz, 1843a).

Note. Dawson (1868, p. 162) also reported a specimen (presumed lost) of *Ageleodus pectinatus* that originated

5.5 m above the top of the Joggins Formation within Coal Group 22 of the overlying Springhill Mines Formation (Rygel *et al.* 2014).

Class ACANTHODII Owen, 1846

Order *incertae sedis*

Family GYRACANTHIDAE Woodward, 1906 emend.

Warren *et al.* 2000

Type genus. *Gyracanthus* Agassiz, 1843a.

Remarks. Although the Gyracanthidae have long been placed within the Order Climatiformes (e.g. Denison 1979; Janvier 1996; Sullivan *et al.* 1999; Warren *et al.* 2000), more recent work suggests the order is actually paraphyletic (Hanke and Wilson 2002; Brazeau 2009) and the higher-level systematics of the Acanthodii have yet to be resolved; therefore, we cannot at present confidently place Gyracanthidae in any order.

Gyracanthidae indet.

Figure 10G–H

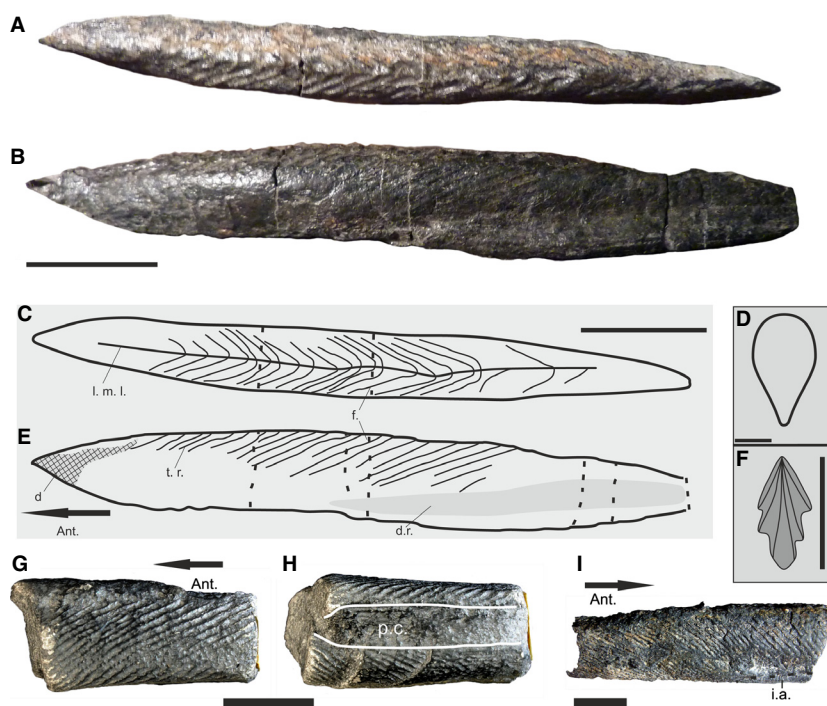
Material. Cast of one isolated pelvic spine (GLAHM V2556).

Diagnosis. Slightly curving, spine-bearing tubercles arranged in oblique ridges.

Description. Tapering acanthodian spine 47.5 mm in length; maximum anteroposterior depth is 20 mm, falling to 16 mm distally. Specimen is incomplete, broken at both ends and shows slight curvature. Surface ornamented with oblique ridges equipped with tubercles; ridges spaced approximately 1.5 mm apart. Ridge angle varies from 25 to 29° but with no directional trend. A longitudinal internal cavity extends along the posterior (trailing) edge; cross-sectional shape is ovoid, exhibiting lateral compression. Some abrasion is apparent on the anterior (leading) edge. The tubercles are heavily abraded and no informative detail can be seen.

Remarks. The lack of insertion area indicates that this fragment is from a distal portion of the spine; however, the open cavity along the posterior surface would normally suggest a more proximal position. This extensive cavity is typical of one of the two *G. hawkinsi* pelvic spine morphotypes, in which the trailing edge is open along the entire length of the spine (Turner *et al.* 2005); descriptions of *G. murrayi* and *G. warreni* did not specify the extent of this cavity, or even if it is present (Warren *et al.* 2000). It is also unclear whether such a cavity is common in *Gyracanthus*; Snyder (2011) indicated that a 'canoe'

FIG. 10. A–F, photographs and interpretative drawings of RM 3074 *Gyracanthus* ‘*duplicatus*’ holotype; A, C, dorsal view; B, E, lateral view; D, spine seen in cross section; F, expanded view of tubercle. G–H, photographs of GLAHM V2556 *Gyracanthidae* indet. replica; G, lateral view; H, posterior view. I, photograph of NSM012GF013.006, lateral view. *Abbreviations:* Ant., anterior; d., damage; d.r., deformed region; f., fractures; i. a., insertion area; l.m.l., longitudinal mesial line; p.c., posterior cavity; t.r., transverse ridges. Scale bars represent 25 mm (A–C, E), 5 mm (D), 0.75 mm (F) and 20 mm (G–I). Colour online.



morphology is also present in the pectoral spines of *Gyracanthus filius* Snyder, 2011. In the absence of clearly defined tubercles, the pelvic spines of *Gyracanthus* and *Gyracanthides* cannot be reliably distinguished, and we therefore assign this specimen to *Gyracanthidae* indet. GLAHM V2556 is a reproduction; the original is believed to be the specimen listed by Copeland (1958) and identified by him as *Gyracanthus duplicatus*, but the location of this original is unknown. Information attached to the GLAHM reproduction indicating the original is housed in the New Brunswick Museum of Geology is incorrect (R.F. Miller, pers. comm. 2014).

Note. This is the only fish specimen that did not originate from the type section of the Joggins Formation but was collected from a coal mine at River Hebert, at a level probably equivalent to DFB9 or DFB10.

Gyracanthidae indet. cf. *Gyracanthides* sp.
Figure 10A–F

- 1868 *Gyracanthus duplicatus* Dawson, p. 210, fig. 55.
- 1891 *Gyracanthus duplicatus*; Woodward, p. 144.
- 1966 *Gyracanthus duplicatus*; Gardiner, p. 52.
- 1978 *Gyracanthus duplicatus*; Baird, p. 12, fig. 7.
- 1979 *Gyracanthus duplicatus*; Dennison, p. 34.
- 2005 *Gyracanthides duplicatus*; Turner *et al.*, p. 998.

Material. Dawson's type specimen of the invalid *Gyracanthus duplicatus*, comprising one isolated dorsal spine (RM 3074).

Diagnosis. Laterally compressed spine bearing oblique rows of tubercles; dorsal surface equipped with chevron pattern and prominent longitudinal mesial line. Ridge angle relative to the long axis decreases distally.

Description of Dawson's RM 3074. Laterally compressed incomplete straight spine missing its distal tip of length 104 mm; original size c. 116 mm based on imprint of missing portion. A total of 22 oblique ridges spaced at approximately three per centimetre are visible, the remainder having been obscured by abrasion and breakage. Ridge angle relative to the long axis decreases from approximately 27 to 18° distally (Fig. 10C). Cross-sectional shape is difficult to judge as the spine is partially embedded and deformed, but appears to have formed a rounded V shape (Fig. 10D); the maximum depth is 14 mm, but this is likely to be exaggerated by compression. Dorsal surface exhibits a chevron pattern where ridges meet, and a prominent longitudinal mesial line (Fig. 10C). Close examination of the ridges reveals heavily abraded remnants of elongate tubercles, ornamented with anteriorly converging ridges (Fig. 10F). These are 0.5–1.0 mm long and variably spaced, 4–20 per centimetre; abrasion has rendered them almost flat. The extent of the insertion area is difficult to judge, as there is no sharp insertion/exsertion boundary; there is no evidence of striations in the assumed insertion area, but these may have been lost to abrasion.

Remarks. Following a review of *Gyracanthides* by Warren *et al.* (2000), Turner *et al.* (2005) demonstrated that *Gyracanthides* species could be separated based on the configuration of ridges and shape/distribution of tubercles. More generally, they found that the laterally compressed cross-sectional shape of *Gyracanthides* pectoral spines (subtriangular or V-shaped) was quite distinct from the

rounded shape of the *Gyracanthus* type species, *G. formosus*, and that the distal decrease in ridge angle was also characteristic of this genus. On this basis, they suggested that many of the North American 'Gyracanthus' species, which also exhibit lateral compression, should be referred to *Gyracanthides*. Unfortunately, the spines have not been described in detail for most species. As a result, we currently cannot confidently separate the non-pectoral spines of *Gyracanthus* and *Gyracanthides* based on either tubercle shape and distribution or ridge configuration. A longitudinal change in ridge angle has thus far only been reported in the pectoral and dorsal spines of *Gyracanthides* (Warren *et al.* 2000; Turner *et al.* 2005), and the absence of curvature clearly demonstrates that RM 3074 is not a pectoral spine. The 9° change in ridge angle of the Joggins specimen is somewhat less than the change of 15° reported in the dorsal fin spines of *G. hawkinsi* (Turner *et al.* 2005), and the tubercles more closely resemble in form those figured for the pectoral spine of *Gyracanthides murrayi* (Warren *et al.* 2000, fig. 10); however, the two dorsal *G. murrayi* fin spines described therein lacked tubercles, and the configuration of the ridges was not discussed in detail. The ridges of *G. warreni* were described with reference to those of *G. murrayi* (the ridges of the former are straighter, narrower and more numerous), but this description was not quantified. The situation regarding tubercle spacing is similar – these were described as 'more numerous' but, again, without quantification. Considering these difficulties, and given the deformed and incompletely exposed state of the *G. duplicatus* holotype, we assign Dawson's holotype to *Gyracanthidae* indet. cf. *Gyracanthides* sp.

Genus GYRACANTHIDES Woodward, 1906 emend.

Turner *et al.* 2005

Gyracanthides sp.

Figure 10I

Material. One isolated pectoral spine (NSM012GF013.006, figured in Calder (1998, fig. 6a) as FGM.998.GF.1).

Diagnosis. Laterally compressed, curving spine bearing oblique rows of tubercles forming ridges; ridge angle relative to the long axis decreases distally.

Description. Incomplete, gently curving spine truncated at both ends, 101 mm in length and 25–30 mm in depth, narrowing distally; a further 25 mm of length is preserved in impression at the proximal end. Some lateral compression is apparent, although it is difficult to determine if this resulted from post-mortem compression. The spine is ornamented with oblique, parallel ridges equipped with tubercles; these are quite heavily abraded over most of the exposed lateral surface of the spine,

but are more distinct towards the anterior and, particularly, posterior margin. Where it can be determined, the spacing between tubercles is approximately 1 mm, whereas the spacing between ridges is 1.5–2 mm, again decreasing distally. A small part of the insertion area is also preserved and appears to be unornamented, although this may also be due to abrasion. The angle of the ridges relative to the long axis decreases from 49° at the proximal end to 27° at the distal end.

Remarks. Species-level identification of *Gyracanthides* spines rests on the shape and distribution of tubercles; unfortunately, the tubercles of NSM012GF013.006 are heavily abraded, and although their spacing (approximately 10/cm) is within the range reported for *G. murrayi* (Warren *et al.* 2000), this attribute has not been reported for all species. Given the overlap between *G. murrayi* (8–10/cm) and *G. hawkinsoni* (5–9/cm), this may not be a reliable diagnostic character.

Class OSTEICHTHYES Huxley, 1880

Subclass SARCOPTERYGII Romer, 1955

Infraclass DIPNOMORPHA Ahlberg, 1991

Order DIPNOI Müller, 1845

Family SAGENODONTIDAE Woodward, 1891

Genus SAGENODUS Owen, 1867

Type species. *Sagenodus inaequalis* Owen, 1867.

Sagenodus sp.

Figure 11A–B

1865 *Conchodus plicatus* Dawson, p. 209, fig. 53.

1891 *Ctenodus plicatus* Woodward, p. 255.

1934 *Ctenodus plicatus*; Romer and Smith, p. 702.

1941 *Sagenodus plicatus* Sternberg, p. 837, pl. 1, fig. 4.

1978 *Sagenodus* indet. Baird, p. 8.

1997 *Sagenodus* indet. Schulze and Chorn, p. 2.

Material. Dawson's holotype of the invalid *Conchodus plicatus*, comprising isolated tooth plate (RM 3073) and one other specimen (NSM008GF031.070).

Diagnosis. Subtriangular tooth plate bearing seven divergent ridges.

Description of Dawson's RM 3073. Incomplete dipnoan tooth plate with seven ridges; length (as measured perpendicular to ridges) 38 mm; width (parallel to ridges) 17 mm, giving a length/width ratio of ≤ 2.2 . The ridges are divergent, with a projected angle between the first and last ridge of approximately 40° (Fig. 11B). The tooth plate is subtriangular and appears to be

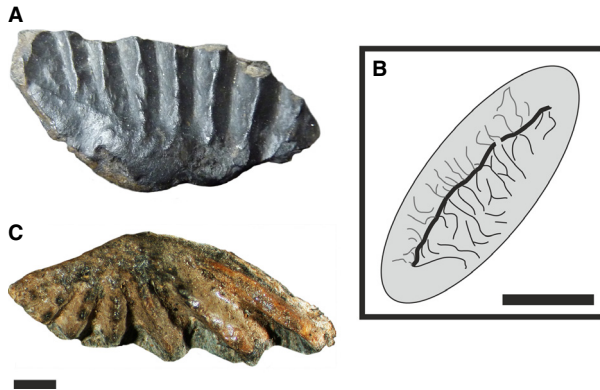


FIG. 11. Photographs of RM 3073 *Sagenodus plicatus* holotype and NSM012GF013.008 *Sagenodus* cf. *serratus* tooth plate. A–B, RM 3073; A, occlusal view; B, expanded view showing undulating ridge crest and attrition marks. C, NSM012GF013.008, occlusal view. Scale bars represent 5 mm (A, C) and 1 mm (B). Colour online.

flat; no concavity or convexity is evident. No denticles are visible, but the ridges undulate gently, suggesting denticles may once have been present; the apical surface also bears attrition marks (Fig. 11C). Terminology for length/width follows that of Kemp (1996).

Remarks. Dawson's type specimen (RM 3073) was considered by Sternberg (1941) to be 'close to *S. periprion* in form', presumably based on the low angulation of the ridges; the attrition marks were ascribed to the presence of tubercles on the opposing plate. However, the number of ridges (seven) lies outside of the range established by Schultze and Chorn (1997) for that species, instead falling within that of *Sagenodus serratus*; the true length/width ratio can only be estimated but cannot have been greater than 2.2, which also suggests a closer affinity with *S. serratus* than *S. periprion* (Fig. 12). Sternberg's photograph and drawing of the holotype (Sternberg 1941, figs 1, 4) are inverted; the drawing, which is an attempted restoration, exaggerates the angle of divergence of the ridges to about 60°, although the figure quoted by Sternberg actually refers to the angle of the ridges from the vertical as seen in his figure. Although Schultze and Chorn (1997) did not include angulation measurements in their data, they did note that although angulation in *S. periprion* is typically lower than in other species, there is considerable overlap. Examination of their images for *S. periprion* (op. cit. figs 43–44) suggests a typical angle of around 60° for both pterygoids and prearticulars, in contrast with 40° as seen in the *S. plicatus* holotype. Until more is known about the distribution of angulation values in *Sagenodus*, it is impossible to say whether this feature alone is sufficient to retain *Sagenodus plicatus* as a valid species. Given that over 150 years of collecting has not yielded a

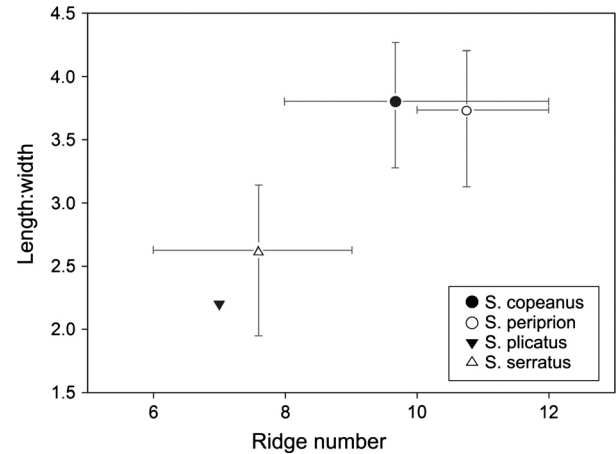


FIG. 12. Comparison plot of length:width ratio and ridge number for *Sagenodus copeanus*, *S. serratus*, *S. periprion* and *S. plicatus*.

single additional specimen, for the moment it seems best to treat RM 3073 as *Sagenodus* indet.

Sagenodus cf. *serratus* (Newberry, 1875)

Figure 11C

Material. One isolated tooth plate (NSM012GF013.008).

Diagnosis. Tooth plate bearing nine radiating, denticulated ridges; angulation high, length/width ratio of tooth plate 2.6.

Description. Subtriangular tooth plate 16 mm in length and 6 mm wide, bearing nine radiating tooth ridges. Ridges equipped with 4–8 cusps, laterally compressed and with confluent bases. The maximum ridge angle is 122°.

Remarks. Neither the number of tooth ridges present nor the length/width ratio of the tooth plates are wholly reliable in diagnosing *Sagenodus* species; although Schultze and Chorn (1997) were able to show via discriminant function analysis that three of the four *Sagenodus* species which they examined (*S. copeanus*, *S. periprion*, *S. serratus*) were statistically distinct, there is nevertheless a partial overlap between them (the fourth species, *S. ohioensis*, is known only from a single skull roof and so is not suitable for analysis). The number of tooth ridges in NSM012GF013.008 (nine) is the modal value for *S. copeanus*, at the upper limit for *S. serratus*, and below the lower range for *S. periprion* (based on values reported by Schultze and Chorn 1997). The widely radiating tooth rows in NSM012GF013.008 are typical of *S. copeanus* and *S. serratus*, but not *S. periprion*. The

length/width ratio is 2.6 in NSM012GF013.008, which is low enough to fall outside the range reported by Schultze and Chorn (1997) for *S. copeanus*; 2.6 is, however, the mean value indicated by them for the upper jaw of *S. serratus*. In combination, these observations are most consistent with *S. serratus*.

Infraclass TETRAPODOMORPHA Ahlberg, 1991

Order RHIZODONTIDA Andrews and Westoll, 1970

Family RHIZODONTIDAE Traquair, 1881a *sensu* Andrews and Westoll, 1970

Genus STREPSODUS Huxley, *in* Huxley and Etheridge 1865

Type species. *Strepsodus sauroides* Binney, 1841.

Strepsodus sauroides Binney, 1841

Figure 13

Material. Seven isolated teeth (NSM008GF031.377, NSM008GF031.434, NSM008GF031.580, NSM008GF039.343, NSM008GF039.369, NSM009GF025.002 and RM 14.366).

Diagnosis. Slender, gently sigmoid teeth equipped with prominent longitudinal striations covering the exposed lateral tooth surface. Curvature of striations lower than that of tooth, hence parallel to long axis basally and oblique apically; teeth oval in cross section.

Description. Length 5–15 mm. The striations occasionally appear to merge apically, although they do not in fact come into contact; instead, one will typically disappear within 10–50 µm of the other. Striae are typically *c.* 60 µm thick, and density is 5–10 per mm. Where it can be determined, cross-sectional shape is oval; basal plications are retained in one specimen (NSM009GF025.002) although only two are visible, the remainder being obscured by the matrix.



FIG. 13. Photomicrograph of NSM009 GF025.002 *Strepsodus sauroides* tooth, mesio-distal view. Scale bar represents 5 mm. Colour online.

Remarks. The teeth described here closely resemble those figured by Jeffery (2006, fig. 2C–D) as *Strepsodus sauroides*.

Genus ARCHICHTHYS Hancock and Atthey, 1870

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

Archichthys portlocki Portlock, 1843 ex Agassiz MS

Figure 14A–B

Material. Two isolated teeth (YPM VPPU 019334 and NSM008GF040.063).

Diagnosis. Moderately stout, recurved teeth 40–45 mm in length, equipped with basal plications and ovoid in cross section. Lingual and lateral faces bear raised striations in a ‘woven’ texture.

Description. Six plications are visible around the exposed portion of the base of the more complete specimen, YPM VPPU 019334, giving an estimated total number of 10–12. The basal 75% of the lingual and lateral faces are equipped with raised striations in a ‘woven’ texture (Fig. 14B); these are most prominent on the lingual surface, fading labially and apically, and they regularly branch and merge. NSM008GF040.063 is preserved mainly as an impression, showing the same woven texture and at least four plications; the shape in this case is slightly sigmoid.

Remarks. This ‘woven’ surface texture is only seen in *Archichthys portlocki* *sensu* Jeffery (2006, text-fig. 2A–B) and *Letognathus hardingi* Brazeau (2005). While the teeth of *Letognathus* are typically quite slender, those of *Archichthys* are more robust and similar in their proportions to

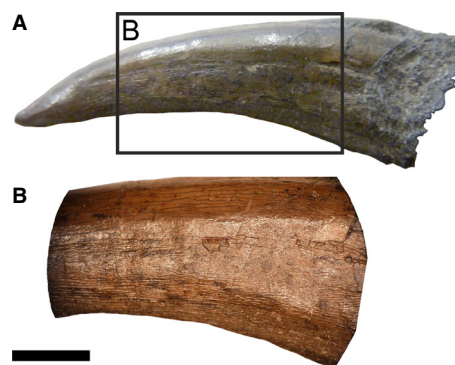


FIG. 14. Photomicrographs of YPM VPPU 19334, *Archichthys portlocki*. A, tooth, mesio-distal view; B, expanded view showing striae exhibiting ‘woven’ texture. Scale bar represents 1 cm (A) and 5 mm (B). Colour online.

those of *Rhizodus* (Brazeau 2005; Jeffery 2006), as is the case with YPM VPPU 19334; Jeffery (2006) also reported that the characteristic striations of *Archichthys* are absent from the labial surface, whereas in *Letognathus* they are present on all surfaces (Brazeau 2005), again as seen in YPM VPPU 19334.

Order *incertae sedis*
Family RHIZODOPSIDAE Berg, 1940

Genus RHIZODOPSIS Young, 1866 ex Huxley MS

Type species. *Rhizodopsis sauroides* Williamson, 1849.

Rhizodopsis sauroides Williamson, 1849
Figure 15C–D

Material. Seven isolated scales (NSM008GF031.408, NSM008GF031.533, NSM008GF039.271, NSM008GF039.487, NSM008GF039.535, YPM VPPU 019337).

Diagnosis. Scales with outer surface ornament clearly divided into four quadrants (Fig. 16); posterior quadrant equipped with concentric growth lines and radial striae; anterior quadrant similarly equipped but with less prominence; ‘lateral’ quadrants equipped with concentric growth lines only. Inner surface equipped with median boss and prominent concentric growth lines; anterior quadrant surface bears puncta arranged in a radiating pattern.

Description. Rhomboid or ovoid scales with surface clearly divided into four quadrants, ornamented as described above. Radial striae of the anterior quadrant combine with concentric growth lines to form a mesh-like pattern. Puncta irregularly spaced but of consistent size.

Remarks. Despite the availability of partial cranial and near-complete postcranial material (Young, 1866; Traquair, 1881b; Woodward, 1891; Säve-Söderbergh, 1936; Andrews and Westoll, 1970), the original diagnosis (based on a type series of isolated scales from northern England, now lost) has not been emended since Traquair (1881b). Several additional species of questionable validity have been erected (e.g. *R. robusta* Woodward, 1891; *R. dispersa* Koenen, 1895; *R. savenkovi* Obruchev, 1955) based on isolated scales which differ only slightly from the *R. sauroides* type series and appear to fall well within the variation in form observed by Williamson (1837, 1849). For that reason, we refer all Joggin specimens to *R. sauroides*. The position of Rhizodopsidae within Tetrapodomorpha is unclear, but it seems likely that this

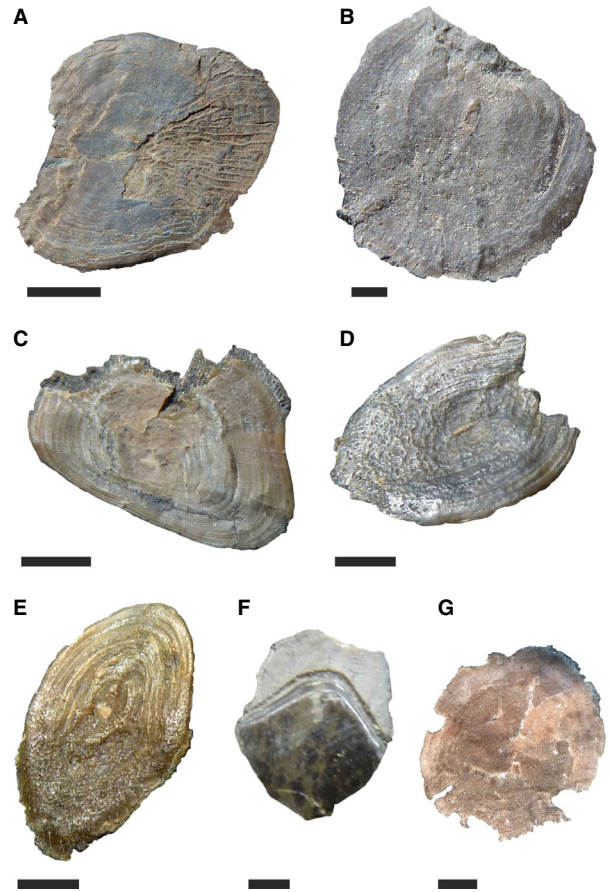


FIG. 15. Photographs of sarcopterygian scales. A, NSM008GF031.592 Tetrapodomorpha indet. cf. *Strepsodus sauroides*. B, NSM008GF039.515 Tetrapodomorpha indet. cf. *Strepsodus sauroides*. C, NSM008GF039.535 *Rhizodopsis sauroides* D, NSM008GF039.487 *Rhizodopsis sauroides* E, NSM008GF031.408 *Rhizodopsis* sp. F, YPM VPPU 21745 *Megalichthys* sp. scale, external surface. G, YPM VPPU 019336, *Rhizodus hiberni*. Scale bars represent 1 cm (A), 5 mm (B), 2 mm (C, E–G), 2.5 mm (D). Colour online.

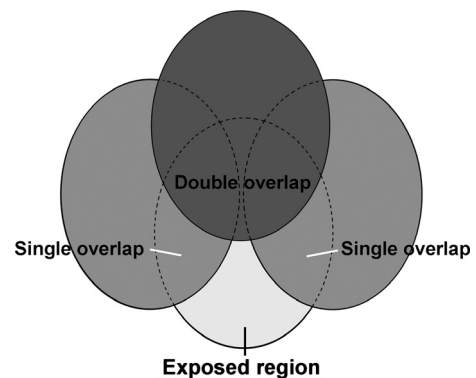


FIG. 16. Line drawing showing generalized rhizodont and rhizodopsid scale arrangement.

family is allied more closely with the megalichthyids than the rhizodonts, falling somewhere within the 'osteolepid' group (Andrews and Westoll 1970; Friedman *et al.* 2007; Holland *et al.* 2010).

SARCOPTERYGII *incertae sedis*
Family MEGALICHTHYIDAE Hay, 1902
MEGALICHTHYIDAE indet. cf. *Megalichthys* sp.
Figures 15F, 17

Material. Three blocks containing multiple disarticulated scales (YPM VPPU 021745, NSM008GF031.306 and NSM008GF031.499), five isolated scales (NSM008GF031.388, NSM008GF031.490, NSM008GF031.587, NSM008GF039.542 and NSM008GF031.615), one isolated dentary (NSM009GF37.5), one incomplete right mandibular ramus (NSM008GF031.533) and assorted indeterminate dermoskeletal material (NSM008GF031.481, NSM008GF031.498, NSM008GF031.586).

Diagnosis. Subrhombic scales with a cosmine-covered free field; isolated dentary equipped with cosmine.

Description. Scales: rhombic to rectangular, 4–10 mm in size, with a coating of cosmine on the free field; prominent ridge separating this from the rest of the scale; no other ornamentation visible. Dentary: left dentary 50 mm in length and 12 mm in height, equipped with a superficial cosmine layer, and a horizontal pit line near the ventral margin comprising 38 sensory pits. Ramus: incomplete lower jaw comprising part of dentary, surangular, angular and postsplenial, of length 11 mm and height 3 mm. 21 sensory pores are visible, along with prominent horizontal and vertical pit lines. An oblique line that bisects the specimen vertically is interpreted as a fracture.

Remarks. Although widely distributed among Devonian sarcopterygians, by the Pennsylvanian, cosmine was restricted to the Megalichthyidae. Generic- and species-level identification of megalichthyids rests on cranial

characters, which do not apply to isolated bones of the mandible (Thompson 1964; Fox *et al.* 1995); in their review of Megalichthyidae, Fox *et al.* (1995) maintained that the configuration of pit lines on the mandible is not helpful in separating megalichthyid genera. However, the only megalichthyid genus currently recorded from the Pennsylvanian of Euramerica is *Megalichthys* itself, and this genus is reportedly common at several Pennsylvanian sites in Nova Scotia, including Joggins (Calder 1998). It is therefore not unreasonable to provisionally attribute the material to this genus. The small size of NSM008GF031.533 most likely indicates that this is a juvenile specimen.

Tetrapodomorpha indet. cf. *Strepsodus sauroides* Binney,
1841
Figure 15A–B

Material. Four isolated scales (NSM008GF031.088, NSM008GF031.592, NSM008GF039.515 and NSM008GF040.083).

Diagnosis. Internal surface bearing median boss and concentric growth lines; posterior quadrant equipped with faint radial striae, and anterior quadrant bearing tubercles. External surface also bears concentric growth lines, anastomosing radial striae on the anterior quadrant, and tubercles or puncta on the opposing posterior quadrant. Scales thick and robust.

Description. Two rhomboid and two circular scales, of diameter/long axis 45, 35, 15 and 25 mm, respectively. Smaller circular scale (Fig. 15B) represents the inner surface and therefore bears a median boss that is elongated along the anterior/posterior axis; the concentric growth lines are most prominent towards the rim, and fade away completely towards the centre. Most of the posterior quadrant is lost, but radial striae are visible around the broken edge. The portion of the scale occupied by the anterior quadrant is approximately 20%. The two rhomboid scales (NSM008GF031.592 and NSM008GF031.088; Fig 15A), which represent the outer surface, have lost much of the surface layer of the posterior quadrant, revealing a prominent network of radiating lateralis canaliculae. The small part of the surface layer that is preserved in this region is equipped with puncta.

Remarks. Order Rhizodontida *sensu* Johanson and Ahlberg (2001) is not diagnosed by scale characters, nor with the exception of *Barameda* (Holland *et al.* 2007) are any rhizodontid genera diagnosed in this way (Owen 1840; Johanson and Ahlberg 1998, 2001; Brazeau 2005; Jeffery 2006). In their emended diagnosis of the family Rhizodontidae, Andrews and Westoll (1970) did include scale characters, but two of these (the presence of a median boss and cycloid shape) are shared by many tetrapodomorphs (Holland *et al.* 2010), and the third, the



FIG. 17. A, NSM009GF27.5 *Megalichthys* sp. left dentary. B, NSM008GF031.533, *Megalichthys* sp. incomplete mandibular ramus. Scale bar represents 5 mm (A) and 1 mm (B). Colour online.

presence of granular tubercles on the posterior exposed quadrant of the external surface, is frequently destroyed by abrasion. Jeffery (1999) also noted that the scales of *Barameda* and *Strepsodus* are indistinguishable in isolation, and suggested that much of the apparent variation between specimens was the result of differing methods of preparation (i.e. acid vs mechanical). Nevertheless, NSM008GF031.592 does closely resemble scale NHMUK P40533, *Strepsodus sauroides* (Woodward 1891, pl. 16, fig. 1). Although there is often little to distinguish the inner surfaces of rhizodont scales, the relatively low proportion of the scale's surface occupied by the tuberculated anterior quadrant is more typical of rhizodontids than of rhizodopsids (pers. obs.) and, given that nearly all identifiable material from Joggin recovered thus far is attributable to that genus, we provisionally assign NSM008GF039.515 to *Strepsodus sauroides* as well. The vascular channels visible in the damaged portion of the scale most likely correspond to part of the lateral line system, although it should be noted that among recent groups (such as the family Esocidae), this is not always the case (Jeffery 1999). Traquair (1890) described but did not figure similar structures in the scales of *Strepsodus 'minor'* (= *S. sauroides*; Jeffery, 2006) from Fife, Scotland.

Tetrapodomorpha indet. cf. *Rhizodus hibberti* Owen, 1840
Figure 15G

Material. Two blocks containing three isolated scales (YPM VPPU 019336, NSM009GF025.004).

Diagnosis. Thin, subcircular scales equipped with concentric growth lines, anastomosing radial striae, and puncta/tubercles on the outer surface; median boss present on inner surface.

Description. Blocks containing very thin, circular scales 10–45 mm in diameter; where the outer surface is exposed (NSM009GF025.004, YPM VPPU 019336; Fig. 15G) anastomosing radial striae occupy approximately one-half of the scale surface, and faint concentric growth lines are also visible, producing a mesh-like pattern where they overlap. Spacing between successive growth lines and radial striae is c. 60 µm at the outer edge. No cosmine present.

Remarks. Some seemingly consistent features of the scales of *Rhizodus* as compared to those of other rhizodonts are their comparative thinness and cycloid shape (Andrews and Westoll 1970; Andrews 1985; Jeffery 1999). We have also observed that in *Rhizodopsis*, the radial striae are invariably straight, whereas they are frequently anastomosing for rhizodont genera such as *Rhizodus* and *Strepsodus*.

Subclass ACTINOPTERYGII Cope, 1887
ACTINOPTERYGII *incertae sedis*
Family HAPLOLEPIDAE Westoll, 1944

Genus PARAHAPLOLEPIS Westoll, 1944 emend. Lowney 1980

Type species. *Parahaplolepis tuberculata* Newberry, 1856.

Parahaplolepis cf. *canadensis* Baird, 1978
Figure 18

Material. One skull roof (YPM VPPU 021708).

Remarks. The specimen was accurately described by Baird (1978) and assigned with caution to his new species *Haplolepis (Parahaplolepis) canadensis*, erected for a skull roof from Parrsboro, Cumberland county, Nova Scotia. The subgenus *Parahaplolepis* was subsequently raised to generic status by Lowney (1980). The slightly more angular profile of this specimen compared to the holotype, noted by Baird (see Baird 1978, fig. 1 for a comparison), raises the possibility that it represents a distinct species, but this minor difference could just as easily be an example of intraspecific or ontogenetic variation; as no further examples of *P. canadensis* have been reported thus far, the question remains open.

Genus HAPLOLEPIS Westoll, 1944 emend. Lowney 1980

Type species. *Haplolepis corrugata* Newberry, 1856.

Haplolepis cf. *corrugata* Baird, 1962

Material. Postcranium (MCZ 8867).



FIG. 18. Photograph of YPM VPPU 021708 ?*Parahaplolepis canadensis* skull roof, dorsal view. Scale bar represents 2 mm. Colour online.

Remarks. We have not been able to personally examine this specimen, but include it here to ensure that this account is comprehensive. Material was described by Baird (1962, p. 29) as follows: ‘The fish, unfortunately headless, is somewhat macerated and compressed so that the fins cannot be made out; the calcareous matrix does not permit the fractured bones and scales to be removed by etching. Such diagnostic parts as are visible – the cleithra and the anterolateral scales – appear nearly identical to those of *Haplolepis* (*H.*) *corrugata* (Newberry) from Linton, Ohio’.

ERRONEOUS RECORDS

The following taxa have also been reported from the Joggins Formation: the holocephalians, *Psammodus* and *Helodus*, the coelacanth, *Rhabdoderma*, and other indeterminate coelacanth material (Dawson 1868, fig. 53; Duff and Walton 1973; Calder 1998; Falcon-Lang 2006). Based on re-examination of material in the JFC, all these records are considered erroneous.

Dawson (1868, fig. 53) figured but did not describe a tooth that he attributed to the holocephalian genus *Psammodus* and his single indirect reference to the specimen suggests that it was not unique. Although it has featured in numerous taxonomic lists (e.g. Lesley 1889; Hay 1902; Lambe 1904; Copeland 1958; Gardiner 1966), it appears never to have been redescribed, and we have been unable to locate the figured specimen in the RM collection. Based on Dawson’s illustration, Whiteaves (1881, p. 36) considered it to be ‘most nearly allied’ to his new species *P. bretonensis*, which was subsequently placed in synonymy with *Megalichthys hibberti* (Hay 1902). Whiteaves apparently having mistaken megalichthyid scales for the crushing dentition of *Psammodus*. Given that no further occurrences have been identified, we speculate that Dawson, like Whiteaves, mistook megalichthyid scales for psammodontid teeth and that the specimen depicted in fig. 53 should be identified as *Megalichthys*. The *Helodus* record has only appeared as part of taxonomic lists (Calder 1998; Falcon-Lang 2006) and so probably was based on Dawson’s ‘*Psammodus*’ specimen.

The *Rhabdoderma* record relied on Duff and Walton’s (1973) lost specimen, but other material, attributed to coelacanths in the JFC, comprises ?*Strepsodus sauroides* and other indeterminate sarcopterygian scales.

DOMINANCE–DIVERSITY MEASURES

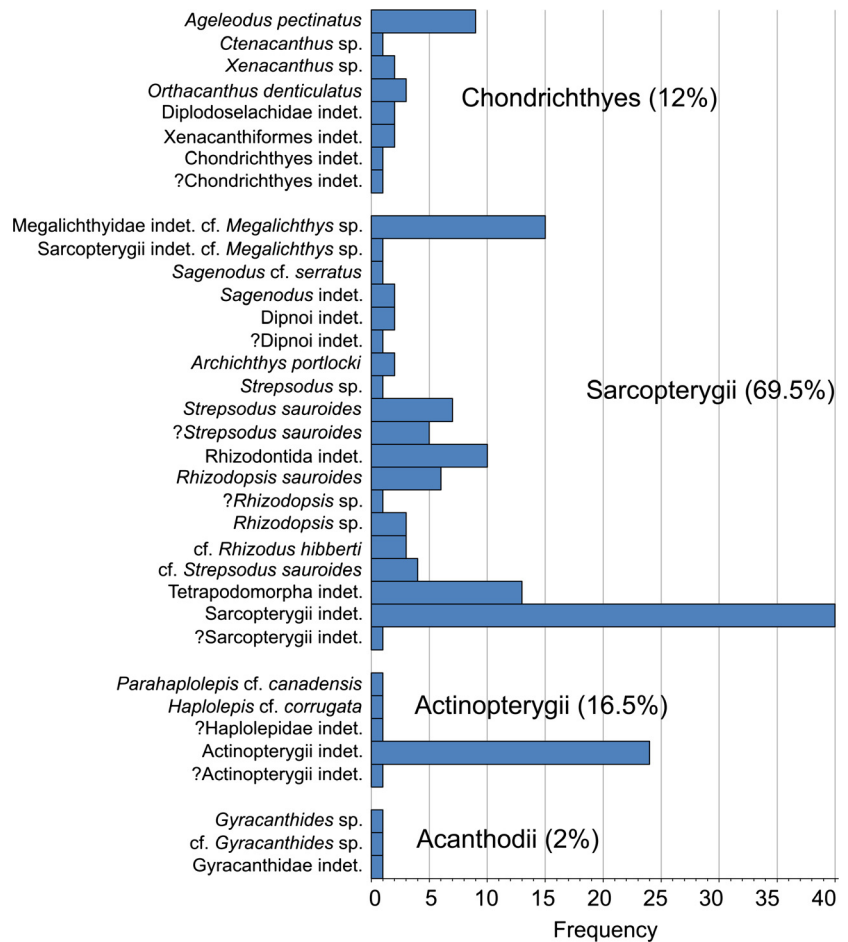
Although fish fossils are relatively common in the Joggins Formation, of the several hundred specimens found over the past 175 years, only a few dozen are determinate at

ordinal level or better. To investigate the composition of the Joggins fish assemblage, diversity was studied at class/subclass and ordinal level. Of the 281 specimens examined in this study, only 170 are determinable to any meaningful (class/subclass) level, as follows: chondrichthyans ($n = 21$; 12%), acanthodians ($n = 3$; 2%), sarcopterygians ($n = 118$; 69.5%) and actinopterygians ($n = 28$; 16.5%). At ordinal level or lower, there are only 81 determinable specimens (Fig. 19), as follows: chondrichthyans are mostly represented by the enigmatic *Ageleodus* ($n = 9$; 5%) and xenacanthids ($n = 9$; 5%; including *Orthacanthus* and *Xenacanthus*), together with rare ctenacanthids ($n = 1$; 0.6%; comprising *Ctenacanthus*). Acanthodians are represented only by gyracanthids ($n = 3$; 1.8%). Sarcopterygian material is dominated by rhizodonts ($n = 32$; 18%, including *Archichthys*, ?*Rhizodus*, *Strepsodus* and other indeterminate rhizodontid remains) and also includes megalichthyids ($n = 16$; 9%), a few dipnoans ($n = 6$; 3.5%, of which half are *Sagenodus*), and *Rhizodopsis* ($n = 10$; 6%). The actinopterygians are, also, mostly indeterminate, but where rarely determinable comprise haplolepidids only ($n = 3$; 2%; including both *Parahaplolepis* and *Haplolepis*).

STRONTIUM ISOTOPE ANALYSES

Results of the strontium isotope analysis were 0.710338 ± 83 (cf. *Xenacanthus*) and 0.7097772 ± 300 (cf. *Rhizodopsis*). These values are similar to those obtained from bivalves (clustered around 0.7094) that co-occur in the OWFA (Brand 1994) and significantly exceed those of Pennsylvanian seawater (typically ≤ 0.7083), although higher values (>0.710) have been reported for some sites (Woodward *et al.* 2013). The values of the two Joggins samples are similar to those of fish assemblages including sharks recently reported from other North American (Carpenter *et al.* 2011) and European (Fischer *et al.* 2013) basins of Pennsylvanian age. However, there is no consensus on how to interpret these data in terms of palaeosalinity (Brand 1994; Calder 1998), the former study inferring estuarine salinities and a euryhaline habit (Carpenter *et al.* 2011), and the latter inferring a freshwater mode of life (Fischer *et al.* 2013). The problem is that, although $^{87}\text{Sr}/^{86}\text{Sr}$ ratios offer a good way of positively identifying well-mixed open marine waters, the basins in all the studies cited above are highly restricted, being surrounded by enriched basement complexes. In analogous settings like the present-day Baltic Sea, $^{87}\text{Sr}/^{86}\text{Sr}$ ratios are dominated by meteoric sources, but nonetheless salinity is brackish and elevated well above freshwater values (Andersson *et al.* 1992, 1994). Furthermore, studies have shown that otoliths of diadromous fishes have $^{87}\text{Sr}/^{86}\text{Sr}$ ratios that strongly reflect the varied water composition

FIG. 19. Histogram showing absolute and relative abundances of Joggins fish taxa. Colour online.



of inland basins rather than the open marine environments occupied for a significant part of their life cycle (Hughes *et al.* 2014). Therefore, the results of $^{87}\text{Sr}/^{86}\text{Sr}$ ratios are equivocal, merely indicating that the environment was unlikely to have been fully marine. However, we highlight that the findings are based on two specimens only, and we recommend that future work targets more diverse remains than those at our disposal.

DISCUSSION

The fossil fish assemblage at Joggins includes a diverse community of chondrichthyans (*Ageleodus*, *Ctenacanthus*, *Orthacanthus*, *Xenacanthus*), acanthodians (gyracanthids), dipnoans (*Sagenodus*), rhizodonts (*Archichthys*, ?*Rhizodus*, *Strepsodus*), megalichthyids (*Megalichthys*), rhizodopsids (*Rhizodopsis*) and actinopterygians (*Parahaplolepis*, *Haplolepis*). As noted above, sarcopterygians (rhizodonts, rhizodopsids, dipnoans and megalichthyids) are the overwhelmingly dominant group comprising 69.5% of all determinate specimens. This fossil record allows new insights into: (1) food webs; (2) euryhaline tolerances; (3)

evolutionary dynamics; and (4) sequence stratigraphy and the age of the Joggins Formation.

Food webs

Living fishes use various feeding strategies including deposit feeding, suction and ram feeding, durophagy (crushing mineralized invertebrate exoskeletons), piscivory and carnivory; one strategy may be used exclusively, or several in combination. Reconstruction of ancient food webs requires inferences based on dentition and body shape (Sahney *et al.* 2010), tooth marks of predators or scavengers on the mineralized skeletons of prey, direct observations of gut contents and coprolites (Hauff 1953; Falcon-Lang *et al.* 2015) or indirect evidence of association (Soler-Gijón 1995). Notable examples relevant to this study include the tetrapod–fish food web reconstructed for the Pennsylvanian site at Nýřany, Czech Republic (Milner 1980) and a Permian case study demonstrating three trophic tiers based on remarkable preservation of xenacanth gut contents containing amphibians, which in turn contained acanthodian remains (Kriwet *et al.* 2008).

As the Joggins fish material is fragmentary, reconstruction of food webs must be partly based on inferences from better-preserved material at other sites. Primary consumers included haplolepidids (Westoll 1944) and gyracanthids (Daeschler and Cressler 2011), which fed on plankton and small soft-bodied macroinvertebrates. Other fish near the base of the consumer chain include *Sagenodus*, whose tooth plates suggest durophagous feeding on extensive mollusc banks that covered the shallow brackish seafloors at Joggins (Dawson 1868), an inference supported by the crushed and processed nature of many of these shells (Falcon-Lang *et al.* 2006). However, by far the largest number and diversity of fishes, including chondrichthyans, rhizodonts, rhizodopsids and megalichthyids, were evidently secondary and tertiary consumers. These fishes show tooth morphologies, body sizes and body shapes indicative of active predators, adapted to feeding on smaller fish and tetrapods (Dick 1981; Jeffery 1999, 2006). The absence of microwear on these teeth is consistent with a predatory mode of life because modern sharks shed similarly pristine teeth by rapid replacement (Daeschler and Cressler 2011). The inverted trophic pyramid, with a predominance of top predators and just a few primary consumers, probably suggests that preserved numbers of each taxon are strongly taphonomically biased and do not represent original population structure. Alternatively, there may have been many soft-bodied, or unpreserved, primary consumers in the ecosystem that were not fish, such as arthropods (Falcon-Lang *et al.* 2006) as indicated by trace fossil assemblages (Prescott *et al.* 2014).

Dawson (1882) recorded fish fragments (not described sufficiently for identification) associated with reptile and amphibian 'dens' within standing trees at Joggins, suggesting that tetrapods may also have consumed fish. Some of the Joggins tetrapods were partly aquatic (*Dendropteron*) or fully aquatic (baphetids) and must have hunted in open coastal waters (Prescott *et al.* 2014), where their remains are sometimes found in bituminous limestone beds. However, these tetrapods were probably not the top predators in the Joggins ecosystem (Calder 1998; Calder *et al.* 2006). Based on their facies distribution, large predatory xenacanthids and rhizodonts, up to several metres long, hunted among coastal mangroves and estuaries and are likely to have preyed upon semiaquatic tetrapods, which were generally an order of magnitude smaller (cf. Kriwet *et al.* 2008).

Euryhaline tolerances

The same unusual lithology of bituminous limestone, which contains most of the fish assemblages at Joggins, also occurs throughout the Pennsylvanian (Westphalian) fill of the Maritimes Basin of Atlantic Canada (Gibling

and Kalkreuth 1991), suggesting that brackish seas were widespread and persistently re-occurred during eustatic highstands throughout *c.* 10 million years of basin evolution (Gibling *et al.* 2008). These brackish sea deposits contain near-identical fish faunas at more than thirty sites within the Cumberland and Morien groups of Nova Scotia and New Brunswick, including the Joggins, Parrsboro, Stellarton, Port Hood, Mabou Mines, Minto and Sydney Mines formations (Dawson 1868; Baird 1962, 1978; Carroll *et al.* 1972; Masson and Rust 1984; Calder 1998; Miller 1999). However, remarkably, many of the fish taxa are also known from fully marine basins in the Pennsylvanian of Europe and North America (Hansen 1985; Schultze 1985; Schultze and Chorn 1997), although, where their stratigraphical distribution is well constrained in the British Coal Measures, some taxa (e.g. *Orthacanthus denticulatus*) notably disappear from the basin fill exactly coincident with the last (mid-Bolsovian) marine incursion (Hampe 2003). These taxa also show very widespread occurrence around tropical Pangaea across different basins, apparently unconstrained by orogenic belts or major seaways (e.g. North Variscan Basin, Pennine Basin, Midland Valley Basin, Maritimes Basin, Illinois Basin, Appalachian Basin; Hampe 2003; Falcon-Lang *et al.* 2006; Carpenter *et al.* 2011). This combination of apparent cosmopolitan biogeographical distribution and restriction to marine-influenced successions is consistent with fish populations centred in open marine waters; however, as these taxa also occur in brackish and near-freshwater bodies at Joggins and other sites, they cannot represent stenohaline marine fishes but rather are in our view best interpreted as having a distinctly euryhaline or diadromous mode of life. The traditionally held (opposing) view is that some of these fishes (e.g. xenacanthids; Masson and Rust 1984) must have been obligate freshwater animals, as argued by Fischer *et al.* (2013) based on new isotopic inferences. If correct, the fish fossil record should show a high degree of endemism with every isolated lacustrine basin containing different taxa (Leithwick *et al.* 2008). Given the large size of the brackish seas at Joggins (Falcon-Lang 2005), a steep salinity gradient is considered unlikely. Therefore, neither temporary penetration by stenohaline taxa nor long-distance post-mortem transport seems plausible. Although reworking cannot be ruled out entirely, this would not be consistent with our strontium isotope data, which indicate a probable brackish habitat for the specimens analysed.

Although the data presented here are consistent with a cosmopolitan biogeographical distribution and euryhaline mode of life, alternative interpretations cannot be ruled out. Chief among these is that the fragmentary nature of assemblages at Joggins and across tropical Pangaea precludes unequivocal recognition of endemism, because many taxa cannot be identified to species level. However,

where species-level revision is possible (as for Dawson's putative species), it has been found that species previously believed to be unique are actually rather broadly distributed throughout tropical Pangaea. Thus, while the current sample cannot wholly address this issue, it can dispel the notion that the faunal composition at Joggins provides any evidence of endemism, and does demonstrate that many taxa were cosmopolitan at genus level.

Evolutionary implications

With their largely cosmopolitan distribution and euryhaline mode of life, Pennsylvanian fish communities in tropical Pangaea appear to have been remarkably different from modern fish ecosystems, where most taxa are stenohaline (i.e. restricted either to freshwater or marine salinities). Only 3–5% of fishes are euryhaline today (McCormick *et al.* 2013), and of those, only a small proportion (e.g. sturgeon, salmon) freely migrate between the fully marine oceans and lower-salinity settings inland in the same way as envisaged for many Pennsylvanian fishes. An unusually widespread adoption of a euryhaline mode of life by fishes in Pennsylvanian times, as exemplified by the Joggins fish fauna, probably represents a key evolutionary stage in the invasion of freshwater. Freshwater colonization began in the Silurian–Devonian, triggered by the rise of land plants that provided a rich source of organic detritus in continental basins for the first time (Buatois *et al.* 1998). Migrating across the marine–freshwater divide would have required the development of sophisticated osmoregulatory systems (Miller and Labandeira 2002), and the predominance of euryhaline adaptation probably reflects a temporary transition phase towards developing specialist stenohaline freshwater ecosystems. Pennsylvanian times were characterized by dramatic glacio-eustatic fluctuations, which would have resulted in the unusually widespread development of brackish estuaries and epeiric seaways as continental coasts and interiors were repeatedly flooded during transgressions (Waters and Condon 2012).

Implications for Joggins sequence stratigraphy and age

The largely euryhaline ecology of Joggins fishes, migrating between open seas and restricted estuaries, strengthens the concept that the Joggins Formation was deposited in a paralic setting (Dawson 1868; Duff and Walton 1973; Falcon-Lang 2005), and improves knowledge of sequence stratigraphy by providing a tool for the recognition of cryptic flooding surfaces (Davies and Gibling 2003). As noted above, the 15 sedimentary cycles recognized in the formation, each of which begins with a brackish incursion

(OWFA; Davies *et al.* 2005), were probably mediated by Milankovitch-driven glacio-eustatic fluctuations and therefore might be expected to have been of similar duration. Although cycle duration and sedimentary thickness are not necessarily directly correlated, it is noteworthy that one Joggins cycle is anomalously thick (210 m) compared to the average cycle thickness of 50 m (Davies *et al.* 2005). This Cycle 5 spans 180–390 m in the Joggins section; however, within this 'thick cycle', Dawson (1868) noted a fish bed (DFB5) at c. 308–316 m, which was associated with the typical range of invertebrate faunas seen in other fish beds, but lacked prominent bituminous limestone beds (Davies *et al.* 2005). This fish bed probably represents a previously undetected brackish incursion (OWFA), and on this basis, we propose dividing Cycle 5 into Cycle 5a whose base occurs at 180 m and Cycle 5b whose base occurs at 308 m. Although still thicker than average, this subdivision of sedimentary cycles into more uniformly thick units makes an orbital driver for the observed cyclicity more likely.

The age of the Joggins Formation has proved elusive because the section lacks the marine index faunas required to correlate it with global stratotypes. Determining the age of this section is important, because the Joggins Formation includes the oldest crown amniote (*Hylonomus lyelli*), widely used to calibrate the bird–mammal split, and so is widely debated and cited in phylogenomic studies (Benton 1990; Reisz and Müller 2004; Benton and Donoghue 2007; Benton *et al.* 2015). Although palynostratigraphy indicates a general Langsettian age close to the Namurian–Westphalian boundary (Falcon-Lang *et al.* 2006; Utting *et al.* 2010), a means of improving the precision of dating of the Joggins Formation is to use globally synchronous marine transgressions as a tool for interregional correlation.

According to Utting *et al.* (2010), the Boss Point and Little River formations in the lower Cumberland Group span the Namurian–Westphalian boundary (Yeadonian–Langsettian), whereas the overlying Joggins, Springhill Mines and Ragged Reef formations of the upper Cumberland Group are of general Langsettian age. Within the Cumberland Group, only the Joggins Formation shows evidence for pronounced high-amplitude marine incursions (Grey *et al.* 2011; Zaton *et al.* 2014; Prescott *et al.* 2014; this paper). Based on compilations of marine bands in the well-studied British Coal Measures, the most prominent episode of high-amplitude marine cycles occurs in the early Langsettian, whereas the late Langsettian, above the Listeri Marine Band, shows subdued cycles only (Waters and Condon 2012). If these episodes of high-amplitude sea-level fluctuations can be correlated, then the Joggins Formation would be of early Langsettian age, as also indicated by recent studies of palynostratigraphy (Utting *et al.* 2010).

CONCLUSIONS

The Pennsylvanian fish community at Joggins was more cosmopolitan than previously thought, with all supposedly endemic taxa (*Ctenoptychius cristatus*, *Sagenodus plicatus* and *Gyracanthus duplicatus*) found to be invalid. The assemblage is dominated by geographically widespread euryhaline forms, suggesting a community structure quite different from that of modern-day ecosystems, in which such species are relatively rare. Strontium isotope analysis, although unable to distinguish brackish from fully freshwater environments, does strongly suggest the taxa studied (*Xenacanthus* and *Rhizodopsis*) did not reside permanently in a normal marine environment. This analysis was limited by the small number of samples available, and it is hoped that a more comprehensive isotope study will be possible in the future. We speculate that the Joggins community represents a transitional phase in the colonization of freshwater environments, before specialized, obligate freshwater ecosystems had been fully established. The identification of a previously undetected flooding surface within the Joggins Formation supports the assumption that sedimentary cycles at Joggins are Milankovitch driven. If correct, interregional correlation of marine transgressions suggests an early Langsettian age for the Joggins Formation and hence for the earliest crown amniote, *Hylonomus lyelli*.

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Data for this study are available in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.b0551>.

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