

Great Canadian Lagerstätten 4. The Devonian Miguasha Biota (Québec): UNESCO World Heritage Site and a Time Capsule in the Early History of Vertebrates

Richard Cloutier

Volume 40, numéro 2, 2013

URI : https://id.erudit.org/iderudit/geocan40_2ser02

[Aller au sommaire du numéro](#)

Éditeur(s)

The Geological Association of Canada

ISSN

0315-0941 (imprimé)

1911-4850 (numérique)

[Découvrir la revue](#)

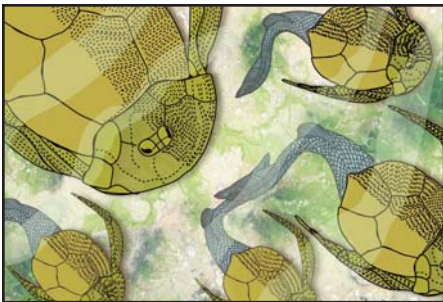
Citer cet article

Cloutier, R. (2013). Great Canadian Lagerstätten 4. The Devonian Miguasha Biota (Québec): UNESCO World Heritage Site and a Time Capsule in the Early History of Vertebrates. *Geoscience Canada*, 40(2), 149–163.

Résumé de l'article

Au cours des 170 dernières années, le biote du Dévonien supérieur de Miguasha de l'Est du Canada a fourni un assemblage aquatique diversifié, comprenant 20 espèces de vertébrés inférieurs (anaspides, ostéostracés, placodermes, acanthodiens, actinoptérygiens et sarcoptérygiens) et un assemblage peu diversifié d'invertébrés ainsi qu'une composante continentale, représentée par des plantes, des scorpions et des mille-pattes. À l'origine interprété comme un milieu lacustre d'eau douce, les dernières preuves paléontologiques, taphonomiques, sédimentologiques et géochimiques confirment un environnement saumâtre rappelant celui d'un estuaire. Plus de 18,000 fossiles de poissons ont été découverts montrant différents états de conservation, notamment en trois dimensions et la préservation de tissus mous. La plupart des vertébrés sont connus par de nombreux spécimens complets et articulés. Des spécimens de larves et de juvéniles, exceptionnellement bien conservés, ont été identifiées pour 14 des 20 espèces de poissons permettant des études détaillées de leur croissance. De nombreux horizons au sein de la Formation d'Escuminac sont interprétés soit comme des *Konservat-* ou *Konzentrat-Lagerstätten*.

SERIES



Great Canadian Lagerstätten 4. The Devonian Miguasha Biota (Québec): UNESCO World Heritage Site and a Time Capsule in the Early History of Vertebrates

Richard Cloutier

Département de Biologie, Chimie et Géographie

Université du Québec à Rimouski

300 allée des Ursulines

Rimouski, QC, Canada, G5L 3A1

Email: richard_cloutier@uqar.ca

SUMMARY

Over the past 170 years, the Late Devonian Miguasha biota from eastern Canada has yielded a diverse aquatic assemblage including 20 species of lower vertebrates (anaspids, osteostracans, placoderms, acanthodians, actinopterygians and sarcopterygians), a more limited invertebrate assemblage, and a continental component including plants, scorpions and millipedes. Originally interpreted as a freshwater lacustrine environment, recent paleontologi-

cal, taphonomic, sedimentological and geochemical evidence corroborates a brackish estuarine setting. Over 18,000 fish specimens have been recovered showing various modes of fossilization, including uncompressed material and soft-tissue preservation. Most vertebrates are known from numerous, complete, articulated specimens.

Exceptionally well-preserved larval and juvenile specimens have been identified for 14 out of the 20 species of fishes, allowing growth studies. Numerous horizons within the Escuminac Formation are now interpreted as either *Konservat-* or *Konzentrat-Lagerstätten*.

SOMMAIRE

Au cours des 170 dernières années, le biote du Dévonien supérieur de Miguasha de l'Est du Canada a fourni un assemblage aquatique diversifié, comprenant 20 espèces de vertébrés inférieurs (anaspides, ostéostracés, placodermes, acanthodiens, actinoptérygiens et sarcoptérygiens) et un assemblage peu diversifié d'invertébrés ainsi qu'une composante continentale, représentée par des plantes, des scorpions et des mille-pattes. À l'origine interprété comme un milieu lacustre d'eau douce, les dernières preuves paléontologiques, taphonomiques, sédimentologiques et géochimiques confirment un environnement saumâtre rappelant celui d'un estuaire. Plus de 18,000 fossiles de poissons ont été découverts montrant différents états de conservation, notamment en trois dimensions et la préservation de tissus mous. La plupart des vertébrés sont connus par de nombreux spécimens complets et articulés. Des spécimens de larves et de juvé-

niles, exceptionnellement bien conservés, ont été identifiées pour 14 des 20 espèces de poissons permettant des études détaillées de leur croissance. De nombreux horizons au sein de la Formation d'Escuminac sont interprétés soit comme des *Konservat-* ou *Konzentrat-Lagerstätten*.

HISTORICAL OVERVIEW

The Miguasha fossil site in eastern Québec was among the first major paleontological localities to have been discovered and excavated in North America. The discovery of the first fossils at Miguasha was made in 1842 by Abraham Gesner, the government geologist in New Brunswick, also known for his work on the distillation of kerosene. While surveying the northern part of New Brunswick for coal, Gesner came to Miguasha and reported "I found the remains of fish, and a small species of tortoise with foot-marks" (Gesner 1843, p. 64). Evidently, this fossil was not a tortoise but rather a placoderm fish, most likely *Bothriolepis canadensis*, one of the most common fish from the Escuminac Formation. Although fossil plants were found, there was no potential in terms of coal mining, and the site was forgotten for more than 30 years.

Between 1879 and 1881, the Geological Survey of Canada organized several expeditions to Miguasha led by R. W. Ells (Fig. 1a), A. H. Foord and T. C. Weston. A few dozens of collected fossils were given to pioneer paleontologists: Joseph F. Whiteaves, a British paleontologist working at the Geological Survey of Canada, who studied the fossil fishes, and Sir J. William Dawson, a Canadian

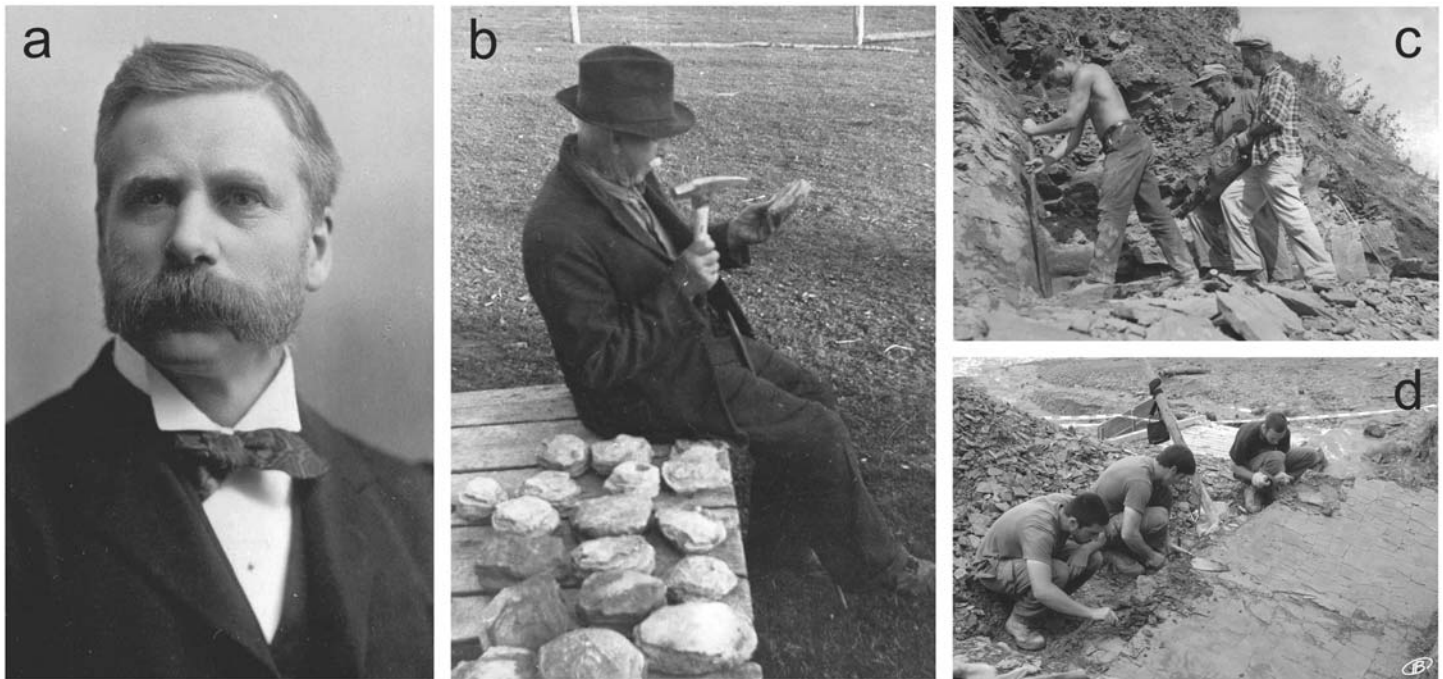


Figure 1. Fossil collecting at the Miguasha site through time. a. Geologist Robert Wheelock Ells, from the Geological Survey of Canada, re-discoverer of the Miguasha fossil site in the summer of 1879 and one of the first fossil collectors in Miguasha (Photograph: Geological Survey of Canada). b. Local collector Joseph Landry in the late 1930s, displaying fossiliferous concretions (Photography: Archive René Bureau, Parc national de Miguasha). c. René Bureau's 1963 expedition in Miguasha, collecting in the cliffs with the help of local collectors Ralph Plourde (son, left) and Euclide Plourde (father, centre) (Photograph: Claude Bureau). d. Recent systematic collecting performed by personnel of the Parc national de Miguasha (Photograph: Johanne Kerr).

paleobotanist working at McGill University, who looked at the fossil plants. These workers were the authors of the first scientific descriptions of the Miguasha fossils (Whiteaves 1880; Dawson 1882). From the late 1880s until the 1940s, British and American paleontologists came to Miguasha (frequently referred to mistakenly as Scaumenac Bay) in order to collect new material for major museums, such as the British Museum of Natural History (London, England), the Royal Scottish Museum of Edinburgh (Scotland) and the American Museum of Natural History (New York, USA). From 1887 to 1892, M. Jex collected an impressive array of fossil fishes in Miguasha, which he sold to different museums in the United Kingdom. As a result, part and counterpart of the same fossils were sold separately to paleontological collections in Edinburgh and London. From this fossil hunting, four fish species were named by two famous British paleontologists, R. H. Traquair and A. S. Woodward.

In 1892, the American vertebrate paleontologist E. D. Cope was the first to recognize that the oste-

olepiform *Eusthenopteron foordi* from Miguasha had a fin anatomy similar to that of the limbs of stegocephalians (Cope 1892), a paraphyletic group acknowledged today to include stem tetrapods. Fossils from Miguasha thereby made their entrance to studies documenting the origin and evolution of major groups of vertebrates, a perspective fairly new at the time, considering the Darwinian revolution. Following Cope's (1892) publication, *Eusthenopteron foordi* was considered a key species in the transition from fishes to tetrapods, thus promoting the focus of numerous studies on the anatomy of its paired fins, vertebral column and nostrils. Between 1905 and 1993, local collectors (Fig. 1b–c) familiar with fossil fish hunting in Miguasha were pivotal in creating reference collections now available around the world (Lemieux 1996). In the early 1920s, Swedish paleontologists started to study in great detail the anatomy of fishes from Miguasha, contributing, in part, to recognition of the famous 'Swedish School' of paleozoology at the Naturhistoriska Riksmuseet in Stockholm (Schultze 2009). Between

1937 and 1998, Erik Jarvik wrote some thirty scientific articles on *Eusthenopteron* (Cloutier 1996c), while Erik Stensiö published on the detailed anatomy of the placoderm *Bothriolepis* (Stensiö 1948).

The history of the Miguasha biota can also be tracked through the sequence of scientific publications and the date of original descriptions for the various vertebrate species (Fig. 2). From 1880 to 1900, half of the known vertebrate diversity had been described on the basis of original collecting in Miguasha. Between 1900 and 1924, most likely as a result of global social instability and World War I, paleontological research, including that on the Miguasha biota, was not a priority in the scientific community. Renewed interest in the fossil material collected in Miguasha by British, Swedish and American paleontologists stimulated a burst of taxonomic descriptions in the mid to late '30s, which eventually faded out with World War II.

Since 1960, a great deal of attention has been given to the evolutionary interpretation of the Miguasha fossil fishes. Reinterpretation of the

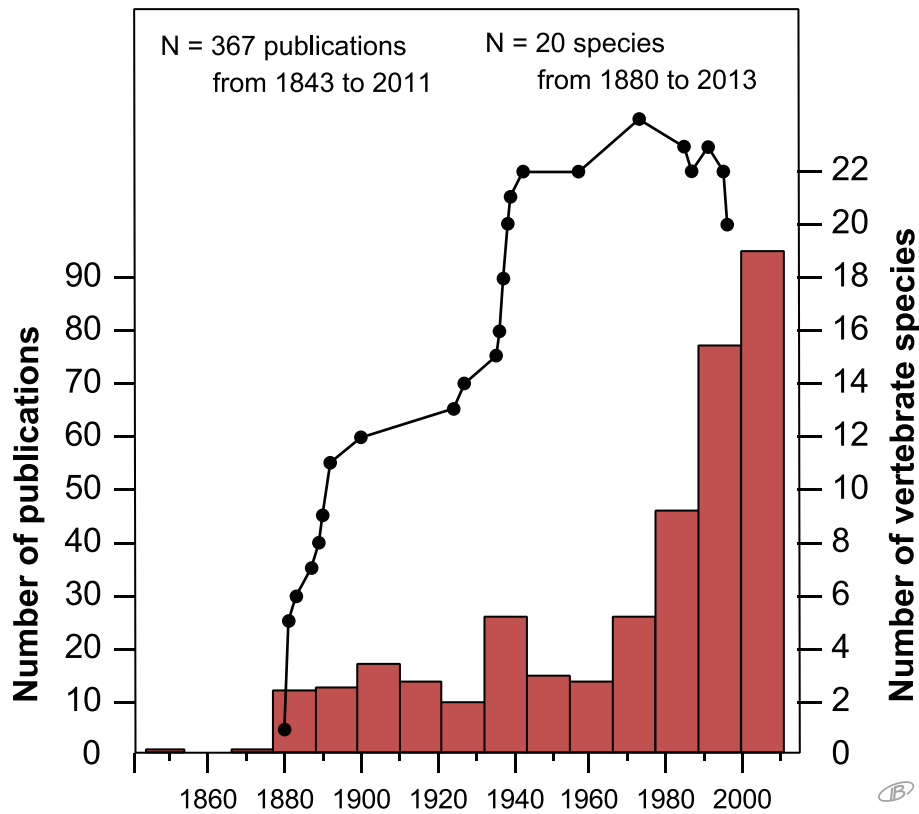


Figure 2. History of the research related to the Escuminac biota. The histogram shows the number of publications related to the Escuminac biota between 1843 and 2011. The point plot represents the discovery curve describing the number of fish species recognized in the Escuminac biota between 1880 and 2013; downward inflexion of the discovery curve corresponds to a reduction in the number of species owing to synonymization of taxa.

fossil material in various collections resulted in the fluctuation of species-level diversity figures until a thorough revision of the Miguasha biota was put together in 1996 (Schultze and Cloutier 1996). Emphasis then shifted from a descriptive perspective to an interpretive one, where the phylogeny, the paleoenvironment, and the taphonomy became important research focuses, and it was at this time that Miguasha was perceived as a *Lagerstätte*. For the past 168 years, fossils from the Miguasha biota have contributed greatly to our understanding of the early evolution of vertebrates. Over the years, at least 367 scientific papers (Fig. 2) have been published by 230 authors from 25 countries. As a modern indicator of interest, more than 200,000 pages on the internet mention fossils from Miguasha.

Aware of the international interest in Miguasha fossils, the Government of Québec created a conser-

vation park in 1978 to protect the Escuminac Formation. Starting in the 1990s, this initiative stimulated renewal of interest in fish paleontology among Canadian researchers who received their Ph.D. training either in Canada (F. Charest), the USA (R. Cloutier) or in France (M. Belles-Isles, P.-Y. Gagnier, D. Vézina), and who studied different perspectives of the Devonian Miguasha biota. In 1999, the Miguasha National Park was confirmed as a UNESCO World Heritage Site in recognition of its global status as the best representation of the Devonian ‘Age of Fishes’ (Cloutier and Lelièvre 1998).

Over the past 20 years, the focus on the biota has shifted from detailed morphological studies, to the phylogenetic positioning of the Miguasha taxa, to the paleoenvironmental reinterpretation of the Escuminac Formation, to studies of exceptional preservation, including

documentation of numerous fossilized ontogenies. In combination, these studies make the Miguasha biota one of the most intensively investigated paleontological sites anywhere.

GEOLOGICAL SETTING

Miguasha National Park is located in eastern Québec on the south coast of the Gaspé Peninsula along the estuary of the Restigouche River (Fig. 3a). The Miguasha biota is contained in the Late Devonian Escuminac Formation (119 m thick), which outcrops primarily as a cliff (from three to 30 m high) along the Restigouche River. Additional satellite outcrops, located between 3 and 40 km away from the main cliffs, have been discovered over the past ten years (Fig. 3c). In 2007, the main Miguasha exposures (Fig. 3b) were named the ‘René Bureau Cliffs’ to honour a self-taught geologist and paleontologist (Fig. 1c) whose work in the 1930s and 1950–1970 was pivotal in establishing this site as a Québec conservation park.

The Escuminac Formation conformably overlies the Fleurant Formation (conglomerate containing sandstone lenses); together, these units constitute the Miguasha Group. Rust et al. (1989) interpreted the Fleurant Formation as proximal alluvium deposits. The Lower Carboniferous Bonaventure Formation (alternating conglomerate and coarse sandstone) rests disconformably on the Escuminac Formation and are interpreted to represent proximal alluvial fan deposition (Rust et al. 1989).

The Escuminac Formation is considered to be middle Frasnian in age, or 385 to 374 Ma according to the timescale of Walker and Geissman (2009), based on miospore content and the fish assemblage (Cloutier et al. 1996; Elliott et al. 2000). Although a precise and absolute dating of the duration of the Escuminac Formation is not possible, the timespan is estimated to lie between 59.5 ka and 2500 ka (Cloutier et al. 2011).

Numerous sedimentological descriptions of the Escuminac Formation show the importance of the alternation between siltstone – sandstone and shale (Alcock 1935; Russell 1939; Dineley and Williams 1968a, b; Carroll et al. 1972; Hesse and Sawh 1982,

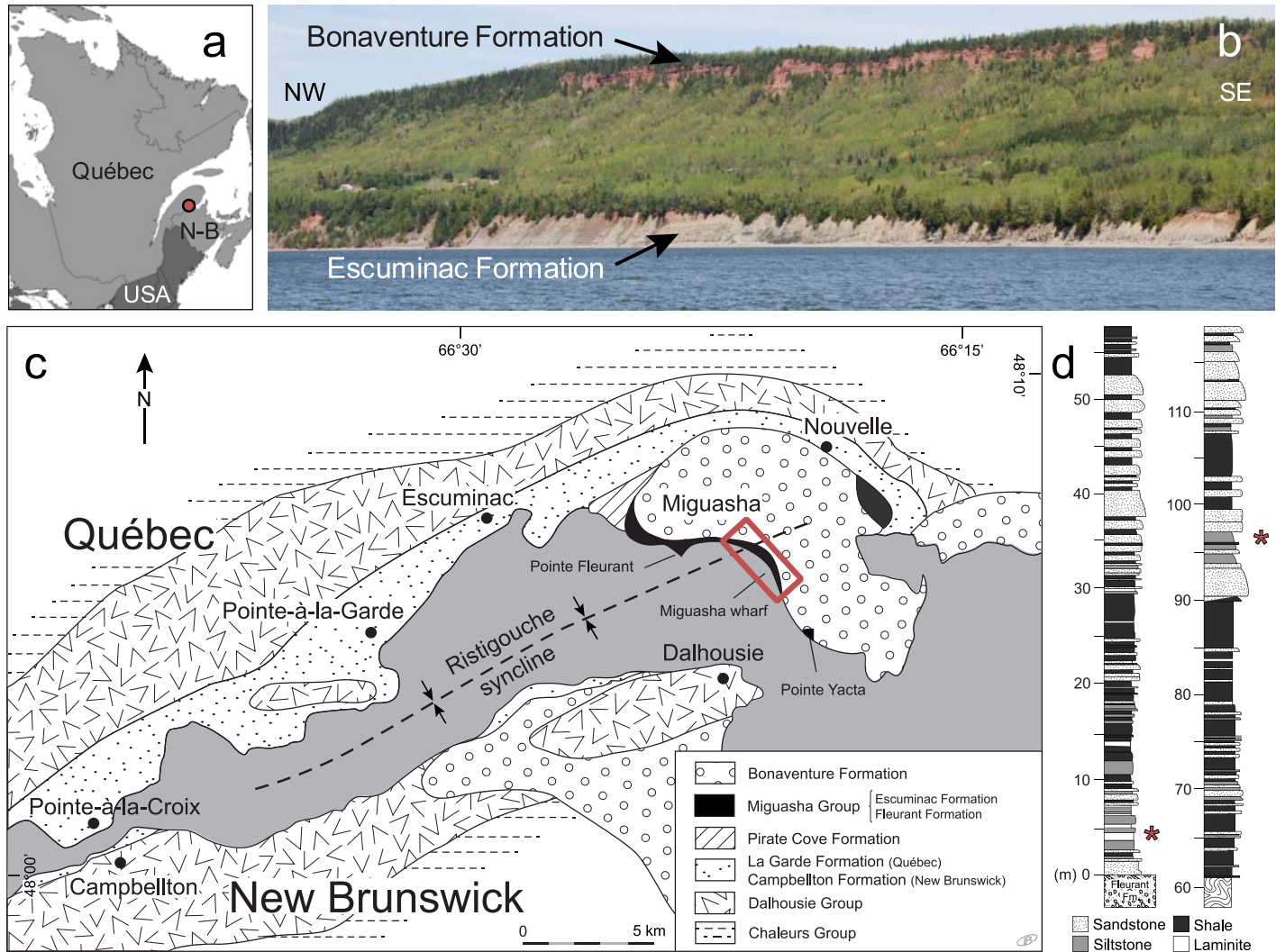


Figure 3. Geographic, geological and stratigraphic contexts of the Escuminac Formation, eastern Québec, Canada. a. Geographic location of Miguasha in eastern Québec. b. Part of René Bureau's Cliff along the Restigouche River showing the east side of the syncline and the overlying red conglomerate of the Carboniferous Bonaventure Formation. c. Geological map modified from Cloutier et al. (2011). d. Stratigraphic section of the Escuminac Formation modified from Cloutier et al. (2011); * corresponds to two exceptional *Konservat-* and *Konzentrat-Lagerstätte* horizons.

1992; Vézina and Cloutier 1991; Prichonnet et al. 1996; Cloutier et al. 2011), and suggest that the sequence comprises lacustrine or estuarine turbidite deposits (Hesse and Sawh 1992; Prichonnet et al. 1996). The clear alternation of lithology allows recognition of 394 individually numbered horizons from the base to the top of the Escuminac Formation at René Bureau's Cliffs (Fig. 3d). As a result of such precise stratigraphic positioning, systematic collecting has enabled documentation of the stratigraphic distribution of various Escuminac species (Cloutier et al. 1996; Cloutier et al. 2011) and of taphonomic modes (Parent and Cloutier 1996; Cloutier et al. 2011).

PALEOBIOLOGY

Diversity of the Miguasha Biota

The diversity of the Miguasha biota includes an allochthonous continental component, composed of plants and invertebrates, and an autochthonous aquatic component, composed of invertebrates and lower vertebrates (Fig. 4). Foliages of various continental plants, e.g. *Archaeopteris* (Fig. 4a), *Spermasporites*, *Protobarynophyton*, *Barynophyton* and *Flabellifolium* (Gensel and Barnett-Lawrence 1996) are found in several strata; some are very abundant (Cloutier et al. 2011). In addition to the plant macrofossils, a wide range of spores (more than 70 species) and marine

acritarchs (15 genera) have been identified (Cloutier et al. 1996). The diverse miospore assemblage could suggest long distance fluvial transport, which is characteristic of equatorial to tropical phytogeographic zones (Cloutier et al. 1996).

Invertebrates are represented by 12 species and account for a minor part of the diversity of the Miguasha biota. The aquatic component of the invertebrate fauna includes the spini-caudatan (or conchostracan) *Asmusia membranacea* (Martens 1996; Fig. 4h), a parastylonurid eurypterid (Jeram 1996), and a scolecodont (Cloutier et al. 1996); the continental component includes the millipede *Zanclodesmus wil-*

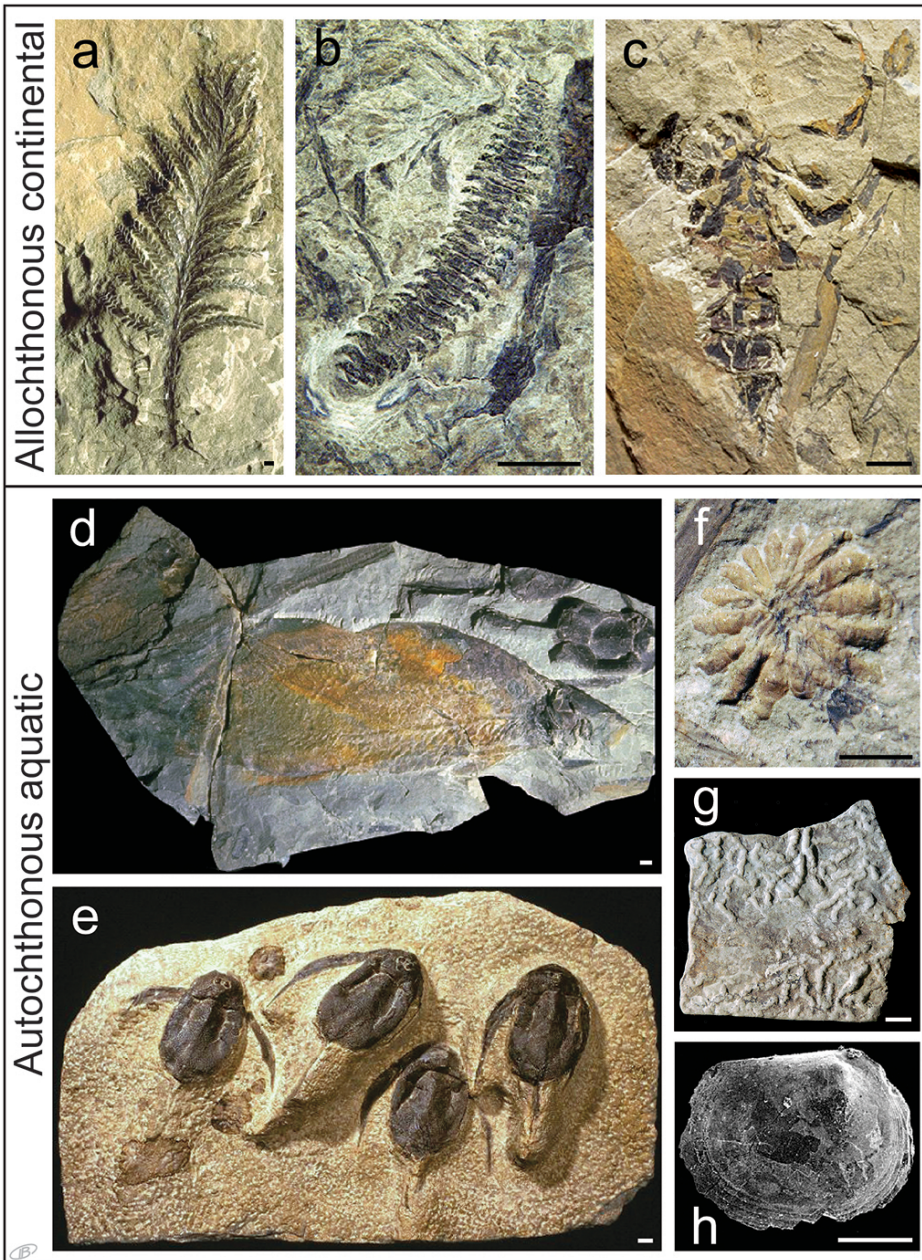


Figure 4. Paleoenvironmental representativity of the allochthonous continental component (a-c) and autochthonous aquatic component (d-h) of the Miguasha biota. a. the lignophyte *Archaeopteris halliana* (MHNM 11-12-13); b. the millipede *Zanclodesmus willetti* (MHNM 27-40A); c. the scorpion *Petaloscorpio bureani* (MHNM 27-31); d. assemblage of the placoderm *Bothriolepis canadensis* (two specimens) and the dipnoan *Scaumenacia curta* (two large specimens) (MHNM 04-426); e. assemblage of gregarious placoderm *Bothriolepis canadensis*, four same-sized specimens oriented in the same direction and with perfect preservation (AMNH 13105); f. the ichnofossil *Gyrophyllites* (MHNM 52-12); g. the ichnofossil *Planolites montanus* (MHNM 52-16); h. the conchostracan *Asmusia membranacea* (MHNM 8-140). Scale bars: 1 cm (a-g), 1 mm (h).

letti (Wilson et al. 2005; Fig. 4b), the scorpion *Petaloscorpio bureani* (Fig. 4c), and a gigantoscorpionid (Jeram 1996). Fragments of arthropod cuticles, some of them likely referable to arachnids or trigonotarbids (Cloutier et al. 2011),

have been found in palynological preparations (Cloutier et al. 1996). Two aquatic ichnotaxa (Fig. 4f-g) have been identified (Maples 1996; Schultze 1999), as well as an additional two types of undescribed traces. Notewor-

thy is the total absence of typical marine invertebrates, a fact which led earlier researchers (Dineley and Williams 1968a, b) to interpret the Miguasha paleoenvironment as fresh-water lakes.

The Escuminac Formation owes its scientific reputation largely to its vertebrate fauna. This assemblage currently includes 20 species representative of ten major groups of lower vertebrates (Table 1). The recent discovery of new specimens of the taxon referred to as holoptychiid sp. indet. (Cloutier and Schultze 1996) or Porolepiformes indet. (Cloutier et al. 2011) confirms that it corresponds to a new species of holoptychiid, which is currently under study. The diversity of Miguasha fishes spans a phylogenetic breadth from some of the most basal vertebrates (the anaspids) to some of the most derived forms (the elpistostegalians). When compared to a survey of 180 Devonian vertebrate assemblages around the world (Cloutier et al. 2011), the richness of the Miguasha biota is significantly above the average of approximately four species (Fig. 5).

Fossil Abundance of the Miguasha Biota

The fossil assemblage is not only fairly diverse, but it is abundant. More than 18,000 specimens of fishes have been found in the Escuminac Formation since its initial discovery. The relative abundance varies greatly among taxa (Fig. 6): some species are known only from a few specimens, whereas others, such as the placoderm *Bothriolepis canadensis*, the acanthodian *Triazengacanthus affinis*, the dipnoan *Scaumenacia curta* and the osteolepiform *Eusthenopteron foordi*, are each known from thousands of specimens. The placoderms, most belonging to *Bothriolepis*, are the most abundant fish group, representing ca. 38% of the specimens, most of them belonging to *Bothriolepis*. Five species are extremely rare: *Callistiopterus clappi* (one specimen), *Elpistostege watsoni* (four specimens including one isolated scale), the new holoptychiid species (four specimens), *Diplacanthus ellsii* (six specimens), and *Levesquaspis patteni* (nine specimens). The taxonomic validity of *C. clappi*, known from a single fairly complete ‘juvenile’ specimen (Thomson and Hahn 1968), has been ques-

Table 1. List of vertebrate species from the Escuminac Formation.

TAXON	Species	Figures
ANASPIDA (OR ANASPID-LIKE)	<i>Euphanerops longaevus</i> <i>Endeiolepis aneri</i>	8j
OSTEOSTRACI	<i>Escuminaspis laticeps</i> <i>Levesquaspis patteni</i>	8l 8k
“PLACODERMI”	<i>Bothriolepis canadensis</i> <i>Plourdosteus canadensis</i>	4d–e, 8c, 9c, 10, 11a
“ACANTHODI”	<i>Diplacanthus horridus</i> <i>Diplacanthus ellsi</i> <i>Triazegacanthus affinis</i> <i>Homalacanthus concinnus</i>	8m 8n, 11e–g
ACTINOPTERYGII	<i>Cheirolepis canadensis</i>	8h
SARCOPTERYGII		
ACTINISTIA	<i>Miguashaia bureaui</i>	8g
DIPNOIFORMES	<i>Scaumenacia curta</i> <i>Fleurantia denticulata</i>	4d, 8d, 11c 8f
POROLEPIFORMES	<i>Holoptychius jarviki</i> <i>Quebecius quebecensis</i> Holoptychiidae nov. sp.	8b 8i
“OSTEOLEPIFORMES”	<i>Eusthenopteron foordi</i> <i>Callistiopterus clappi</i>	8a, 9b, 11d
“ELPISTOSTEGALIA”	<i>Elpistostege watsoni</i>	8e

tioned. Overall, the conchostracan *Asmusia* is the most abundant fossil present, and bedding surfaces at numerous horizons are covered by masses of their tiny (2–4 mm wide) valves.

Evolutionary Significance of the Miguasha Biota

Numerous Escuminac species are recognized for their evolutionary and phylogenetic significance (Schultze and Cloutier 1996; Cloutier 2009). Among the plants, the lignophyte *Archaeopteris* (Fig. 4a; classically identified as a progymnosperm) is considered the sister group of the gymnosperms and might have constituted some of the oldest forests in the fossil record (Meyer-Berthaud et al. 1999). Although extremely rare, *Spermasporites*, only known from megaspores, is thought to represent one of the oldest seed plants

on earth (Marshall and Hemsley 2003). Among the Escuminac invertebrates, the scorpion *Petaloscorpio* (Fig. 4c) and the millipede *Zanclodesmus* (Fig. 4b) are considered to be some of the earliest continental arthropods (Jeram 1996; Wilson et al. 2005).

Most major groups of Devonian aquatic vertebrates are represented in the Miguasha biota with the noticeable exception of chondrichthyans and tetrapods (Fig. 7). The anaspid or anaspid-like *Endeiolepis* and *Euphanerops* (Fig. 8j) are the last survivors of a group that originated in the Silurian (Janvier 1996a, b), and are likely closely related to living lampreys (Gess et al. 2006); however, these two genera are occasionally referred to simply as euphaneropids because of their questionable relationships to either anaspids or lampreys (Janvier and Arsenaault 2007). The actinopterygian *Cheirolepis*

(Fig. 8h) is among the most basal ray-finned fishes (Cloutier and Arratia 2004), the most diverse group of living vertebrates. Sarcopterygians (Fig. 8a–b, d–g, i), or lobe-finned fishes, are well represented at Miguasha; the actinistian *Miguashaia* (Fig. 8g) is a basal coelacanth (Cloutier 1991a, 1996b; Friedman and Coates 2006), a group that today includes only two species (*Latimeria chalumnae* and *L. menadoensis*). The osteolepiform *Eusthenopteron foordi* (Fig. 8a) is one of the best-known Miguasha fossils and for nearly one hundred years was considered transitional between fishes and the first tetrapods. Because of its exceptional state of preservation, anatomical completeness, and the extensive lifelong study by Erik Jarvik, *Eusthenopteron foordi* could to some extent be considered a ‘model organism’. Finally, *Elpistostege watsoni* is now thought to be one of the fish species closest to tetrapods (Schultze 1996). The anatomy of *Elpistostege* is poorly known, based so far on only four fragments (Fig. 8e), but distinctive cranial features, such as the presence of frontal bones, are similar to those of early tetrapods. Daeschler et al. (2006) considered that either *Elpistostege* or *Tiktaalik* from the Canadian Arctic constitute a sister-group to tetrapods.

Because of their significant evolutionary status, some of the Miguasha fish species have been systematically included in the majority of phylogenetic analyses published over the past 20 years: *Euphanerops* in lower vertebrate phylogenies (Donoghue et al. 2000; Gess et al. 2006; Sansom et al. 2010); *Triazegacanthus* and *Homalacanthus* in basal gnathostome phylogenies (Brazeau 2009; Davis et al. 2012); *Cheirolepis* in actinopterygian and osteichthyan phylogenies (Cloutier and Arratia 2004); *Miguashaia* in actinistian, sarcopterygian and osteichthyan phylogenies (Cloutier 1991b; Forey 1998; Zhu et al. 2009); *Scaumenacia* in dipnoan phylogenies (Lloyd et al. 2012); *Eusthenopteron* in osteolepiform, sarcopterygian, and early tetrapod phylogenies (Cloutier and Ahlberg 1996; Ahlberg and Johanson 1998); and *Elpistostege* in early tetrapod phylogenies (Daeschler et al. 2006; Ahlberg et al. 2008).

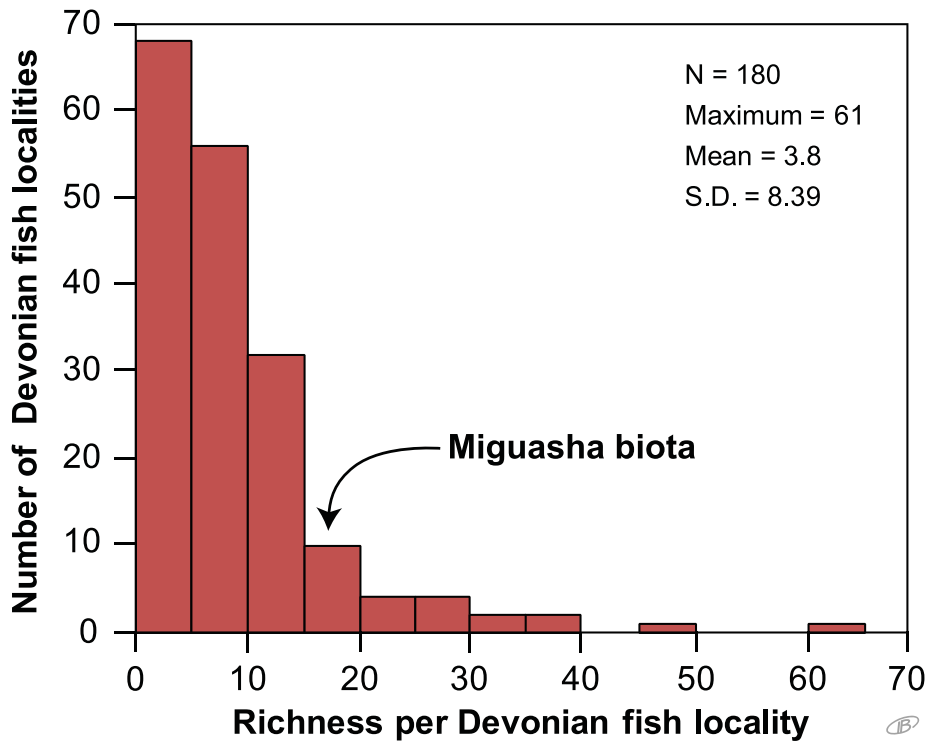


Figure 5. Histogram of fish richness for 180 Devonian fish localities around the world. Only localities with macro-remains have been included. Original data came from various sources (see Cloutier et al. 2011).

prey, regurgitates, cololites (feces still located in intestinal tract), and coprolites (Fig. 9).

The first case of predation reported was an acanthodian, *Homalacanthus*, found in the digestive tract of the osteolepiform *Eusthenopteron* (Arsenault 1982). Subsequently, cannibalism was reported for *Cheirolepis* (Arratia and Cloutier 1996) and recently observed in *Eusthenopteron* (Cloutier et al. 2011; Fig. 9b). In addition to such direct evidence of trophic level partitioning, abundant regurgitates and coprolites have been found with bony inclusions (McAllister 1996). McAllister (1996) identified prey items in coprolites that included acanthodian scales, spines and shoulder elements, actinopterygian scales and bony elements, sarcopterygian scales, and conchostracan valves. Predation scars (bite marks) on a Miguasha fish species are reported here for the first time. A series of small circular bite marks, most likely inflicted by an osteichthyan, have been found on the surface of cephalic shield bones of *Bothriolepis canadensis* (Fig. 9c).

The overall paleoecology and food web of the aquatic Miguasha biota has been inferred from the gross morphology of the organisms and comparisons with closely related forms (Janvier 1996a; Cloutier et al. 2011), as well as from direct evidence of predation. Bacteria and other micro-organisms constitute the decomposers of the Miguasha biota. Evidence of bacterial activity is suggested by the abundance of concretions (see Fig. 1b) containing organic remains (e.g. partial to complete fishes; El Albani et al. 2002); these concretions are thought to have formed as the result of bacterial metabolism. Furthermore, bacterial mats (here reported for the first time) have been observed to cover soft body tissues of Miguasha fishes (Fig. 10c). The paucity of trace fossils and the absence of bioturbation suggest that the bottom was not a particularly hospitable environment. Conchostracans (*Asmusia membranacea*) were the primary consumers of the Miguasha biota. Conchostracans are non-selective algal and detrital feeders (Orr and Briggs 1999), and their valves have been found in the digestive tracts of *Bothriolepis*, *Homalacanthus*, and *Scaumenacia*

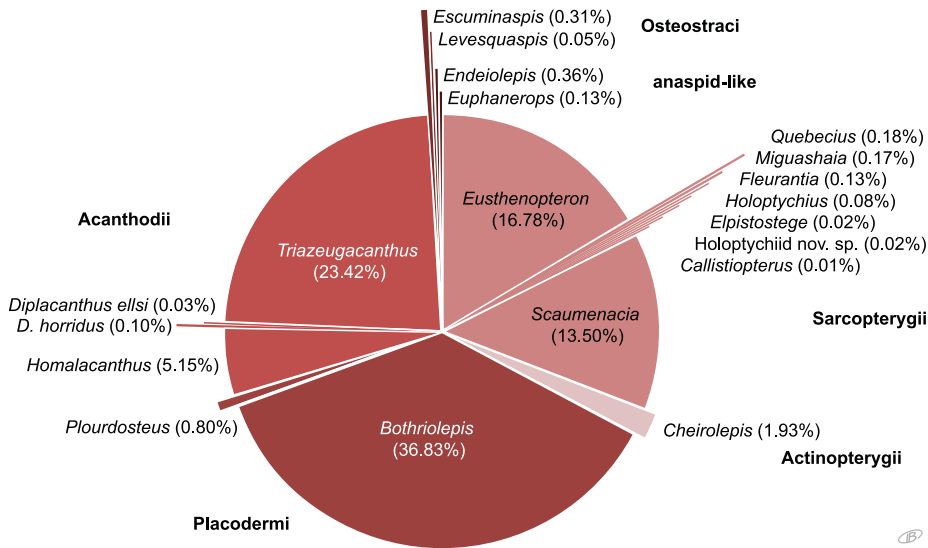


Figure 6. Relative abundance of the Escuminac fish species. The relative abundance (in %) corresponds to the proportion of the total of 18,059 specimens. Original data are provided in Cloutier et al. (2011). *Bothriolepis*, *Triazeugacanthus*, *Eusthenopteron* and *Scaumenacia* are clearly the most abundant taxa.

Paleoecological Significance of the Miguasha Biota

Over the years, an impressive number of paleoecological interactions among the various components of the Devonian Miguasha biota have been recon-

structed, providing the trophic structure of one of the oldest diverse vertebrate assemblages. Paleobiological information for numerous Escuminac species has been recovered based on the presence of bite marks, ingested

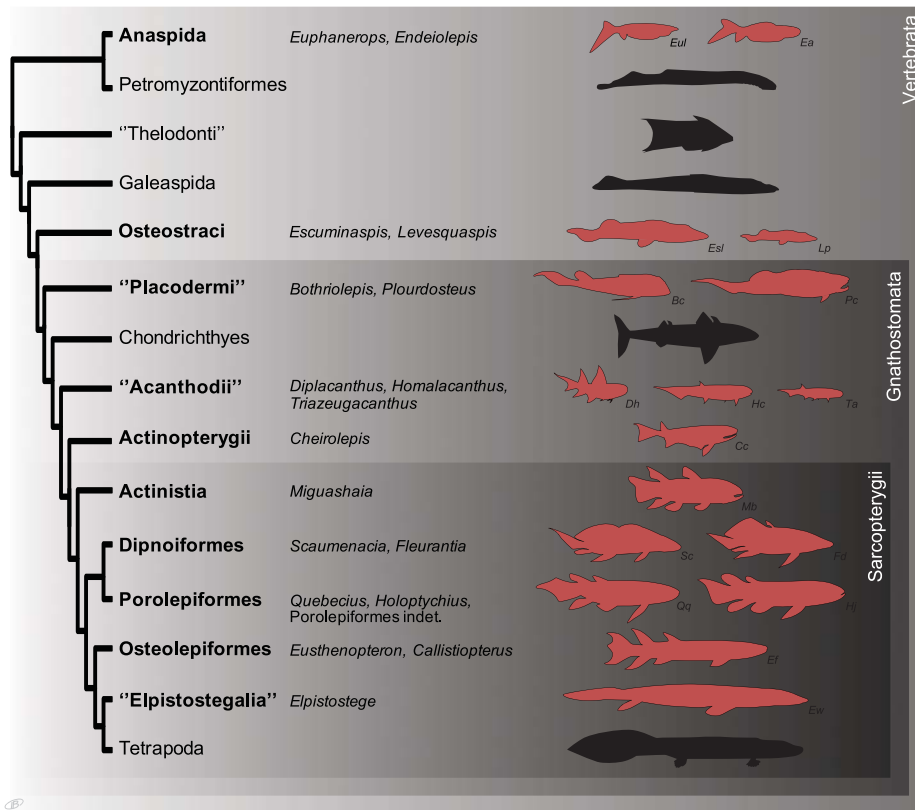


Figure 7. Phylogenetic representativity of the Escuminac vertebrates. The cladogram is not intended as a consensus tree and the phylogenetic position and/or status of certain taxa remain unclear. Tree topology combined from Cloutier and Ahlberg (1996), Brazeau (2009), and Friedman and Sallan (2012). Escuminac vertebrate silhouettes: Bc, *Bothriolepis canadensis*; Cc, *Cheirolepis canadensis*; Dh, *Diplacanthus horridus*; Ef, *Eusthenopteron foordi*; Ea, *Endeiolepis aneri*; Ew, *Elpistostege watsoni*; Esl, *Escuminaspis laticeps*; Eul, *Euphanerops longaevus*; Fd, *Fleurantia denticulata*; Hc, *Homalacanthus concinnus*; Hj, *Holoptychius jarviki*; Lp, *Levesquaspis patteni*; Mb, *Miguashaia bureaui*; Pc, *Plourdosteus canadensis*; Qc, *Quebecius quebecensis*; Sc, *Scaumenacia curta*; Ta, *Triazengacanthus affinis*.

(Cloutier 1996a; Cloutier et al. 2011). The anaspid *Euphanerops* and *Endeiolepis* were most likely microphagous bottom feeders, based on the presence of sediment in a structure interpreted as their stomach (Stensjö 1939; Janvier 1996a; Janvier and Arsenault 2007). The relatively flattened morphology and dorsal eye position of the osteostracan *Escuminaspis* and *Levesquaspis*, and the placoderm *Bothriolepis*, imply that they were also bottom dwellers. *Escuminaspis* and *Levesquaspis* were detritivores, most likely consuming both bottom detritus and particles and organisms suspended in the water column, as suggested for Devonian osteostracans from Russia (Moloshnikov 2008). *Bothriolepis*, *Plourdosteus* and the dipnoans are considered benthivores (Moloshnikov 2008). The four Miguasha acanthodian species were likely planktivores, as suggested

for anatomically similar acanthodians from Scotland (Trewin 1986). Owing to their abundance, their relative small size and their common occurrence in both coprolites (McAllister 1996) and digestive tracts of predators, *Homalacanthus* and to a lesser extent *Triazengacanthus* contributed as forage fish in the aquatic ecosystem. The actinopterygian *Cheirolepis* was a small predator, whereas large predators include the sarcopterygian *Miguashaia*, *Holoptychius*, *Quebecius*, the porolepiform indet., *Eusthenopteron*, and *Elpistostege*. Among predators, *Cheirolepis* (Arratia and Cloutier 1996) and *Eusthenopteron* (Arsenault 1982; Cloutier 1996c; Cloutier et al. 2011) have been found with ingested prey, which includes *Homalacanthus*, *Triazengacanthus*, *Cheirolepis*, and *Eusthenopteron*. Based on numerous observations of ingested

prey, at least a five-level food chain can be inferred (Fig. 9a); from bottom to top: the conchostracan *Asmusia*, *Homalacanthus*, small *Cheirolepis*, large *Cheirolepis*, and *Eusthenopteron* (Cloutier 2009). The trophic network is still incomplete, but is under active study (M. Chevrinai and R. Cloutier).

Exceptional preservation allows studies on specific or group behaviour. Evidence of gregarious behaviour has been suggested for *Bothriolepis* (Fig. 4e), *Triazengacanthus* and *Scaumenacia* (Cloutier et al. 2011). It is likely that the gregarious behaviour of these species is associated with particular periods in their respective life cycles, because groups are generally composed of similar-sized individuals or age classes (Parent and Cloutier 1996; Cloutier et al. 2011). Gregarious behaviour contributes to the high abundance of monospecific assemblages associated with different horizons in the formation.

From the base to the top of the Escuminac Formation, a predominant fish assemblage composed of three species (*B. canadensis*, *S. curta* and *E. foordi*) persists, while the presence of the remaining species fluctuates among the regressive and transgressive phases of the different stratigraphic sequences (Cloutier et al. 2011). This predominant assemblage might well represent a case of paleoecological stasis if we manage to more precisely establish the timespan encompassed by the complete stratigraphic sequence.

PALEOENVIRONMENT OF THE ESCUMINAC FORMATION

The depositional environment of the Escuminac Formation has been variously considered as lacustrine, estuarine, coastal marine or marine. An estuarine interpretation best accommodates the different lines of evidence provided by the fauna (Schultze and Cloutier 1996), the palynofacies (Cloutier et al. 1996), the trace fossil assemblage (Maples 1996), the sedimentological and stratigraphic setting of the formation (Hesse and Sawh 1992; Cloutier et al. 2011), and the geochemistry of the sedimentary rocks and bones (Schmitz et al. 1991; Vézina 1991; El Albani et al. 2002; Matton et al. 2012).

Over the past 15 years, we have accumulated evidence that the

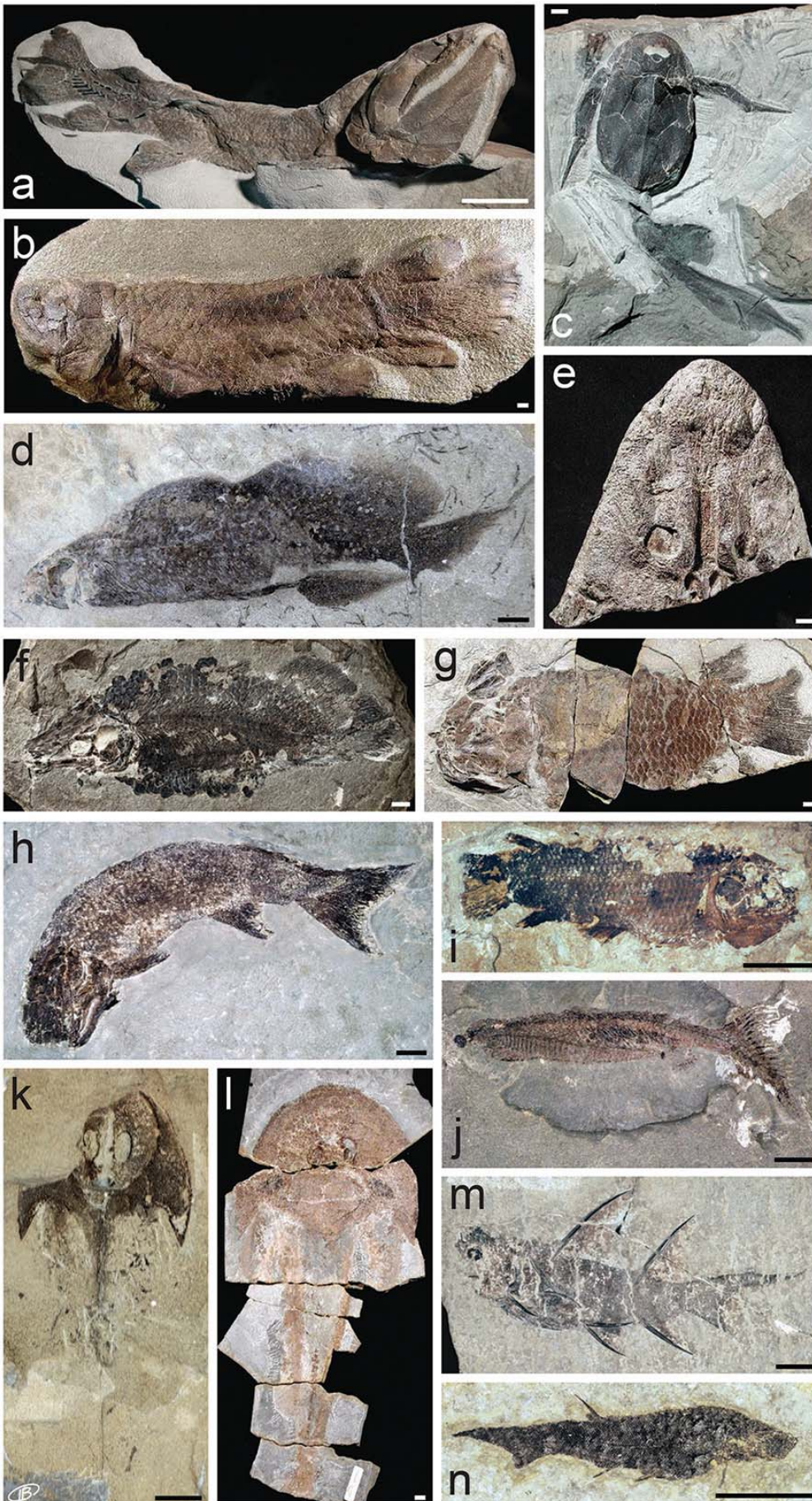


Figure 8. Taxonomic representativity of the vertebrates from the Miguasha biota. a. the osteolepiform *Eusthenopteron foordi* (CMNH 8158); b. the porolepiform *Holoptychius jarviki* (AMNH 11593); c. the placoderm *Bothriolepis canadensis* (MHNM 02-2676); d. the dipnoan *Scaumenacia curta* (MHNM 04-1640A); e. the elpistostegalian *Elpistostege watsoni* (MHNM 06-538); f. the dipnoan *Fleurantia denticulata* (BMNH P24744); g. the actinistian *Miguashaia bureaui* (MHNM 06-494); h. the actinopterygian *Cheirolepis canadensis* (MHNM 05-71); i. the porolepiform *Quebecius quebecensis* (MHNM 06-), juvenile specimen; j. the anaspid *Euphanerops longaevus* (MHNM 01-02); k. the osteostracan *Levesquaspis patteni* (MHNM 01-12-10b); l. the osteostracan *Escuminaspis laticeps* (MHNM 01-09a); m. the acanthodian *Diplacanthus horridus* (MHNM 03-734), n. the acanthodian *Triazengacanthus affinis* (MHNM 03-729). Scale bars: 10 cm (a, l), 1 cm (b-k, m-n).

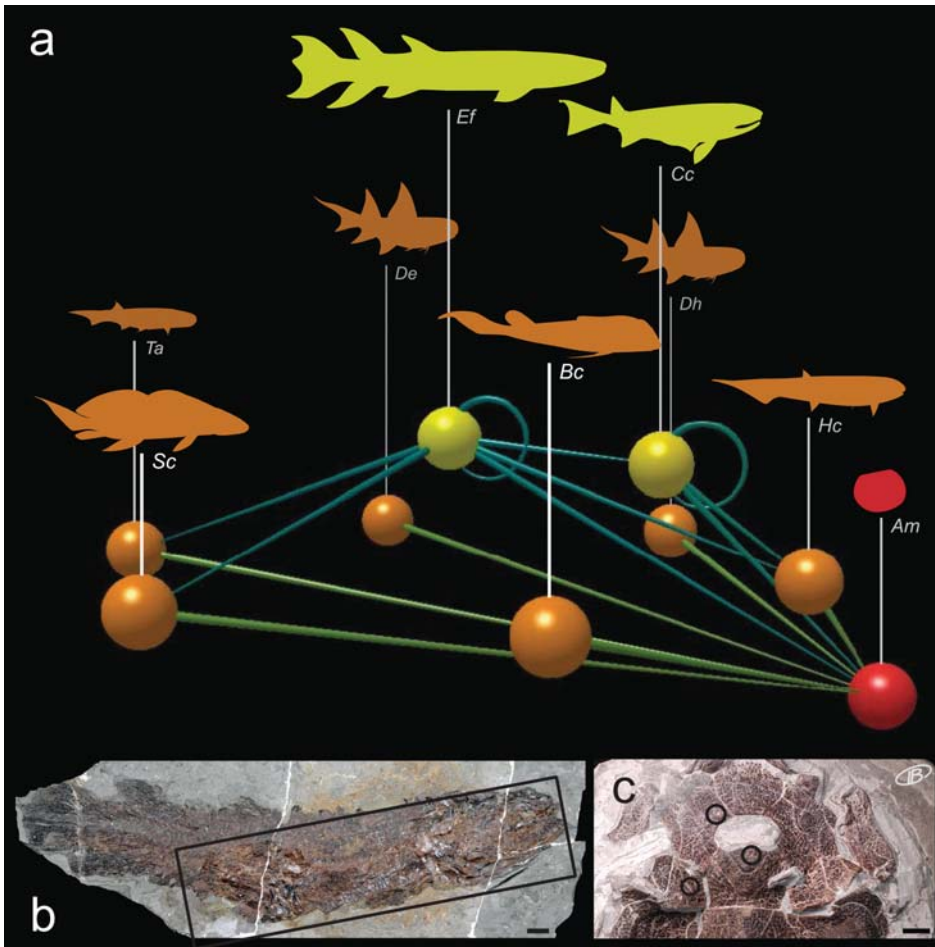


Figure 9. Paleoeological representativity of the Miguasha biota. a. 3D representation of the Miguasha trophic network. b. Cannibalistic osteolepiform *Eusthenopteron foordi* (FMNH PF6021); the ingested smaller *E. foordi* is delimited by the black rectangle. c. The placoderm *Bothriolepis canadensis* with bite marks (three black circles) on the dorsal side of the head and thoracic shields (MHNM 02-3461). Silhouettes: Am, *Asmusia membranacea*; Bc, *Bothriolepis canadensis*; Cc, *Cheirolepis canadensis*; De, *Diplacanthus ellsi*; Dh, *Diplacanthus horridus*; Ef, *Eusthenopteron foordi*; Hc, *Homalacanthus concinnus*; Sc, *Scaumenacia curta*; Ta, *Triæzengacanthus affinis*. Scale bars: 1 cm.

Miguasha biota inhabited an estuarine paleoenvironment, starting with the discovery of acritarchs in association with a large part of the fish assemblage (Cloutier et al. 1996). Furthermore, characterization of the organic matter by kerogen pyrolysis has revealed a predominance of Type II organic matter, which suggests a mixing from continental and marine sources (El Albani et al. 2002). Geochemical analyses of both sediment and bony elements from the Escuminac Formation also suggest a transitional environment. The strontium isotope ratio of Escuminac bony fragments reveals a Frasnian seawater signature, suggesting a slight diagenetic contamination, although fitting within the transitional

range (Matton et al. 2012). Some facies contain evidence of tidal influence, such as thin rhythmites showing daily and lunar cycles (Cloutier et al. 2011). These were originally interpreted as lacustrine varves. Thinning of the rhythmites is associated with neap tides, whereas a thickening is associated with spring tides. Such rapid cyclic deposition, characteristic of the lower part of the Escuminac Formation, facilitated rapid burial of fish carcasses and allowed for the exceptional preservation typical of this facies. Tidal rhythmites provide a perfect host for *Konservat-* and *Konzentrat-Lagerstätte* horizons within the Escuminac Formation.

Five transgressive – regressive

sequences have been recognized in the Escuminac Formation; these sequences are consistent with an inner wave-dominated estuary showing a shift towards continentalization (Cloutier et al. 2011). Throughout the formation, changes in richness, abundance and composition of the fish assemblages show that the transgressive phases are more diverse and better structured in terms of species composition than the regressive phases (Cloutier et al. 2011). In addition, rare and sporadic taxa, such as *Levesquaspis*, *Plourdosteus*, *Miguashaia* and *Elpistostege*, are found solely in the transgressive phases, whereas the most abundant species (Fig. 6) are found in both transgressive and regressive phases (Cloutier et al. 2011).

KONSERVAT- AND KONZENTRAT-LAGERSTÄTTEN

Fossils encountered in the Escuminac Formation show a wide range of preservational modes (Parent and Cloutier 1996; Cloutier et al. 2011), from specimens with no apparent sign of decay down to isolated bony elements. Contrary to popular perception, not all levels qualify as *Lagerstätte* horizons. Where exceptional quality of preservation predominates, the term *Konservat-Lagerstätte* can be applied; where diversity and abundance are outstanding, the horizon represents a *Konzentrat-Lagerstätte*.

The exceptional condition of preservation is indicated by the great number of fish specimens for which completely articulated specimens were found, such as multi-element skeletons of osteostracans and acanthodians (Fig. 8k–n). Although most specimens are compressed laterally, three-dimensional preservation is fairly common (Figs. 4d–e, 8a–c, e, 10a; Parent and Cloutier 1996). Not only is the external morphology well preserved, but detailed bone histology is also present either as hard tissues (e.g. enamel, dentine, cellular bone, cartilage) or as cell spaces (e.g. osteocytes, chondrocytes); examples include cartilages in *Euphanerops* (Janvier and Arsenault 2002), bone tissues in *Bothriolepis* (Downs and Donoghue 2009) and *Eusthenopteron* (Laurin et al. 2007; Zylberberg et al. 2010), and dental tissues of *Scaumenacia* (Thomson 1972; Smith et al. 1987) and *Eusthenopteron* (Schultze

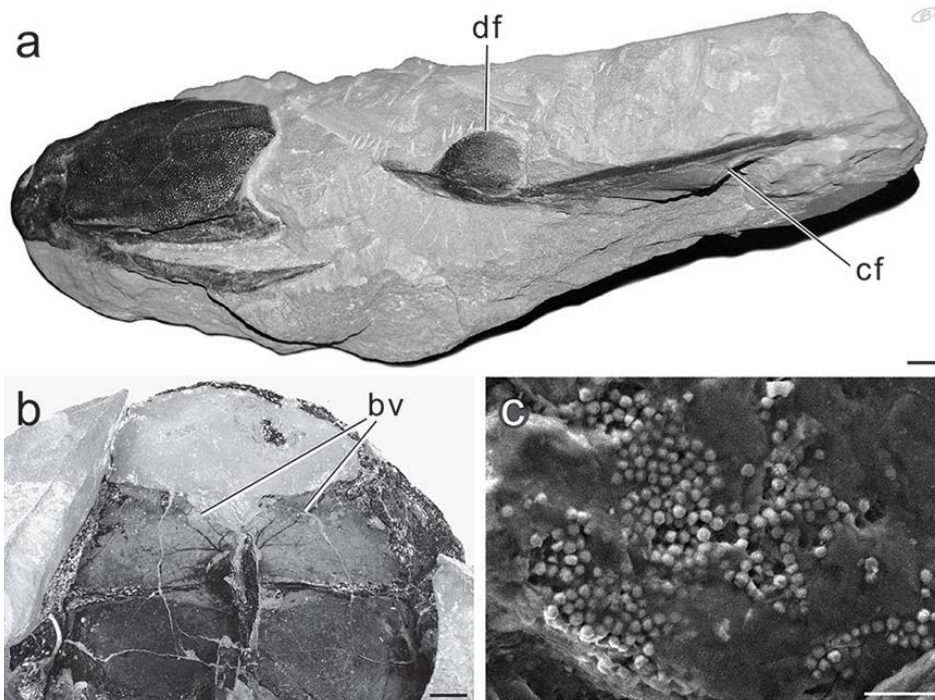


Figure 10. Exceptional preservation in Escuminac fossil fishes. a. 3D specimen of the placoderm *Bothriolepis canadensis* showing anteriorly (left) the bony head and thoracic shields and the non-mineralized trunk and caudal region (dorsal fin, df; caudal fin, cf; MHNM 02-2091). b. Imprint of the blood vessel (bv) located on the ventral side of the anterior part of the thoracic shield of *B. canadensis* (MHNM 02-728a). c. Bacterial mat covering a non-mineralized section of the caudal region of *B. canadensis* seen in scanning electronic microscopy. Scale bars: 1 cm (a, b), 10 μm (c).

1969). Recent investigations have focused on exceptional cases of fossilization where preservation of soft tissues such as digestive tracts, stomachs, spiral intestines, lungs, gill filaments, blood vessels (Fig. 10b) or muscles is involved (Arsenault et al. 2004; Janvier et al. 2006; Janvier et al. 2007; Cloutier 2009; Janvier and Arsenault 2009; Arsenault and Janvier 2010). In addition, preliminary studies on non-mineralized parts of the *Bothriolepis* body suggest that ‘skin preservation’ results from the presence of a bacterial mat outlining the surface of the carcass (Fig. 10a, c); this phenomenon is known as pseudomorphing (Briggs 2003).

Fossilized ontogenies are well represented in the Escuminac Formation. Exceptionally preserved larval and juvenile specimens (as small as 6 mm in total length) have been identified for 14 out of the 20 species of fishes (Cloutier et al. 2009), providing the opportunity to study growth and developmental change (e.g. Fig. 11a, f–g). One of the best examples of a

fossilized growth series is that of the placoderm *Bothriolepis*, where specimens as small as 5 mm long to approximately 22 cm of shield length are known (Cloutier 2010; Fig. 11a). With such material, size and shape changes can be studied (Thomson and Hahn 1968; Schultze 1984; Werdelin and Long 1986; Cloutier 1997; Cloutier et al. 2009), as well as the process of ossification of some of these species (Cote et al. 2002; Cloutier 2010; Béchar and Cloutier 2011). These data can be compared among fossil and living taxa in order to study the evolution of development (Cote et al. 2002; Cloutier et al. 2009; Cloutier 2010).

Concentration of fossils is not limited to fish fragments, but extends to complete specimens. *Konservat-* and *Konzentrat-Lagerstätte* horizons occur throughout the Escuminac Formation. Certain horizons are best considered as *Konzentrat-Lagerstätten* because of their richness and abundance. One of the most outstanding horizons is bed 8 (see lower * in Fig. 3d; Fig. 11e), which

includes 11 species. Many years of systematic collecting in bed 8 (Fig. 1d) provided the opportunity to create a GIS (geographical information system) plot in which more than 700 specimens are mapped within a section of a bed measuring approximately 25 m² in area and 35 cm in thickness. A few years ago, a new *Konzentrat-* and *Konservat-Lagerstätte* (see upper * in Fig. 3d; Fig. 11b) was discovered, most likely corresponding to a fish nursery or an effective juvenile habitat (Béchar and Cloutier 2011). Over 1000 larval and juvenile specimens belonging to at least five species were found (Fig. 11b–d); numerous taphonomic, paleoecological, morphological and developmental aspects of this occurrence are currently under investigation at the Université du Québec à Rimouski.

CONCLUSION

Recognition of the Miguasha fossil locality as an exemplar of the Devonian ‘Age of Fishes’ and its designation as a UNESCO World Heritage Site (Cloutier and Lelièvre 1998) is based on: (1) its faunal representativity of major groups of sarcopterygians, (2) the representativity of vertebrate evolutionary events, (3) the floristic and faunal representativity of aquatic and continental assemblages, (4) the paleobiological representativity (e.g. presence of ingested prey, presence of fossilized ontogenies), (5) the quality of preservation in terms of anatomical completeness, (6) the quality of preservation in terms of exceptional fossilization, and (7) the abundance of specimens. The Devonian Miguasha biota stands as a primary *Fossil-Lagerstätte*, a true time capsule in the early history of vertebrates.

ACKNOWLEDGEMENTS

Over the past 30 years I have had the privilege to collaborate on various aspects of the Miguasha biota with many colleagues, and I would like to especially thank G. Arratia, I. Béchar, A.-M. Candilier, F. Charest, M. Chevrenais, A. El Albani, J. Kerr, J. Leblanc, O. Matton, N. Parent, D. Potvin-Leduc, J.-N. Proust, H.-P. Schultze, R. Stevenson, and B. Tessier. I. Béchar helped with the preparation of the figures. I. Béchar, C. Bureau, M. Chevrenais, and J. Kerr provided some of the photo-

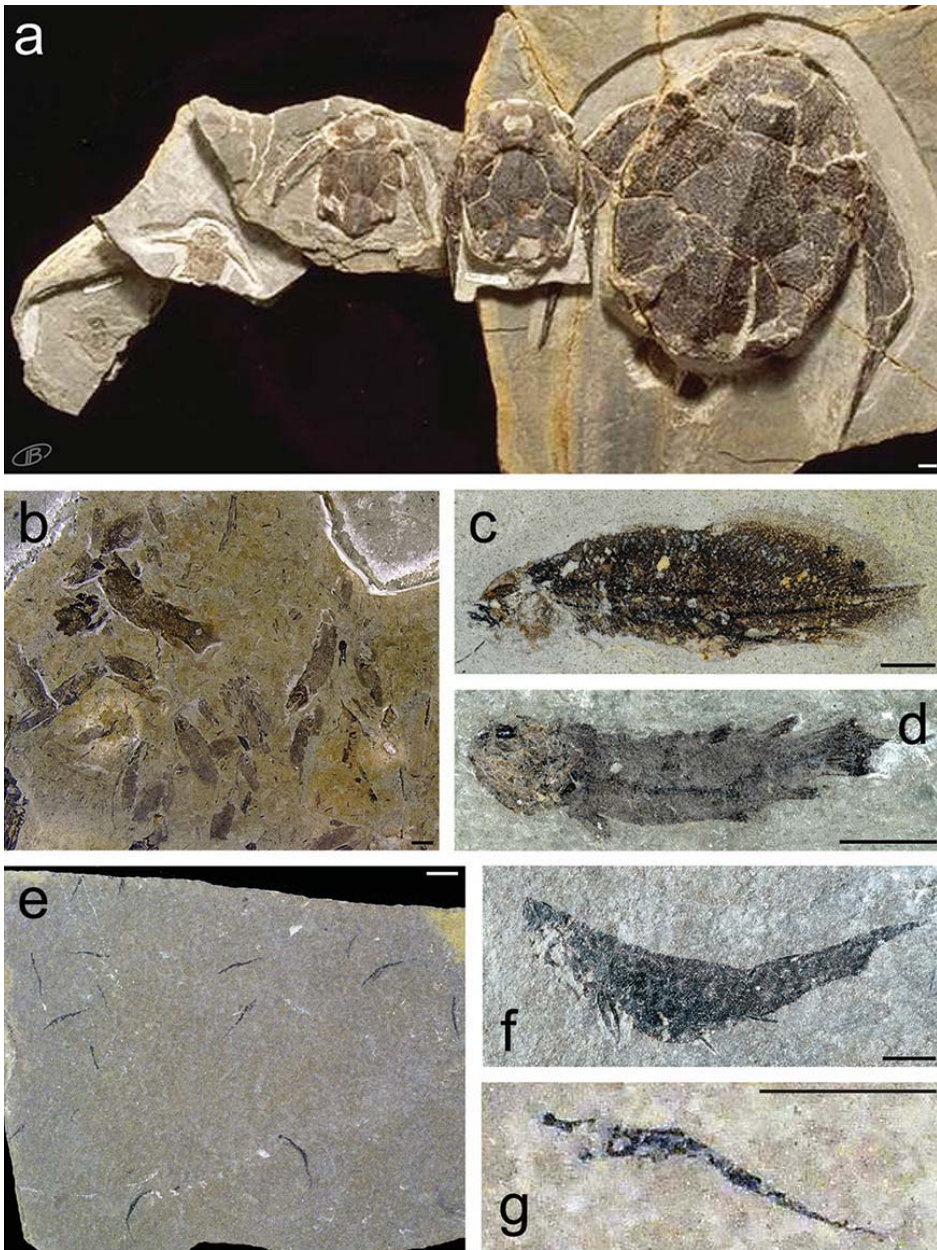


Figure 11. Ontogenies of Escuminac fossil fishes. a. Size series of the placoderm *Bothriolepis canadensis*; the bony shield length of the smallest specimen measures 9 mm (left), whereas the largest one measures 23 cm (right). b. *Konservat*– and *Konzentrat*–*Lagerstätte* horizon (see upper * in Figure 3d) with abundant (>30 individuals solely on this part of the surface) juvenile fishes from multiple species (three species on this part of the surface) (MHNM 04-1293P17b); c. Juvenile specimen of the dipnoan *Scaumenacia curta* (MHNM 04-1379a); d. Juvenile specimen of the osteolepiform *Eusthenopteron foordi* (MHNM 06-535). e. *Konservat*– and *Konzentrat*–*Lagerstätte* horizon (see lower * in Figure 3d) with abundant juvenile – adult fishes of the acanthodian *Triazengacanthus affinis* (MHNM 03-1268); f. adult specimen of *T. affinis*; g. juvenile specimen of *T. affinis* (originally referred to as *Scaumenella*, but see Béland and Arsenaault (1985) and Cloutier et al. (2009)). Scale bars: 1 cm (a, b, d, e), 3 mm (c, f).

graphs. I. Béchar, M. Chevrin, P. Janvier, D. Rudkin, and H.-P. Schultze provided comments on earlier versions of the manuscript. Research carried

out on the Miguasha biota has been financed by the Research Chair in Paleontology and Evolutionary Biology (UQAR-SEPAQ; Power Corporation

Inc.), Natural Sciences and Engineering Research Council (NSERC Discovery Grant), the Parc national de Miguasha (SEPAQ), Ministère de l'Éducation, Loisir et Sport du Québec (Chantier 3 Grant), and the CNRS (USTL1-Lille and Geosciences Rennes).

REFERENCES

- Ahlberg, P.E., and Johanson, Z., 1998, Osteolepiforms and the ancestry of tetrapods: *Nature*, v. 395, p. 792–794, <http://dx.doi.org/10.1038/27421>.
- Ahlberg, P.E., Clack, J.A., Lukševičs, E., Blom, H., and Zupins, I., 2008, *Ventastega curonica* and the origin of tetrapod morphology: *Nature*, v. 453, p. 1199–1204, <http://dx.doi.org/10.1038/nature06991>.
- Alcock, F.J., 1935, *Geology of Chaleur Bay Region*: Geological Survey of Canada, Memoir 183, 146 p.
- Arratia, G., and Cloutier, R., 1996, A reassessment of the morphology of *Cheirolepis canadensis* (Actinopterygii), in Schultze, H.-P. and Cloutier, R., eds., *Devonian Fishes and Plants of Miguasha, Quebec, Canada*: Verlag Dr. Friedrich Pfeil, München, p. 165–197.
- Arsenaault, M., 1982, *Eusthenopteron foordi*, a predator on *Homalacanthus concinnus* from the Escuminac Formation, Miguasha, Quebec: *Canadian Journal of Earth Sciences*, v. 19, p. 2214–2217, <http://dx.doi.org/10.1139/e82-195>.
- Arsenaault, M., and Janvier, P., 2010, Is there a spiral intestine in the anaspid-like jawless vertebrate *Endeiolepis aneri* Stensjö, 1939, from the Upper Devonian Escuminac Formation of Miguasha, Quebec, Canada?, in Elliott, D.K., Maisey, J.G., Yu, X., and D. Miao, eds., *Morphology, Phylogeny and Biogeography of Fossil Fishes*: Dr. Friedrich Pfeil, München, p. 39–43.
- Arsenaault, M., Desbiens, S., Janvier, P., and Kerr, J., 2004, New data on the soft tissues and external morphology of the antiarch *Bothriolepis canadensis* (Whiteaves, 1880), from the Upper Devonian of Miguasha, Quebec, in Arratia, G., Wilson M.V.H., and Cloutier, R., eds., *Recent Advances in the Origin and Early Radiation of Vertebrates*: Verlag Dr. Friedrich Pfeil, München, p. 439–454.
- Béchar, I., and Cloutier, R., 2011, Paedomorphosis and the evolution of the Dipnoi revisited: *Ichthyolith Issues Special Publication*, v. 12, p. 12.
- Béland, P., and Arsenaault, M., 1985, Scauménellisation de l'Acanthodii *Triazengacanthus affinis* (Whiteaves) de la formation d'Escuminac (Dévonien

- supérieur de Miguasha, Québec) : révision du *Scaumenella mesacanthi* Graham-Smith: Canadian Journal of Earth Sciences, v. 22, p. 514–524, <http://dx.doi.org/10.1139/e85-053>.
- Brazeau, M.D., 2009, The braincase and jaws of a Devonian ‘acanthodian’ and modern gnathostome origins: Nature, v. 457, p. 305–308, <http://dx.doi.org/10.1038/nature07436>.
- Briggs, D.E.G., 2003, The role of biofilms in the fossilization of non-biomineralized tissues, in Krumbein, W.E., Pater-son, D.M. and Zavarzin, G.A., eds., Fossil and Recent Biofilms: A Natural History of Life on Earth: Kluwer Academic Publishers, p. 281–290.
- Carroll, R.L., Bell, E.S., Dineley, D.L., Baird, D.S., and McGregor, D.C., 1972, Vertebrate Paleontology of Eastern Canada: International Geological Congress (Montreal 1972), Excursion A59.
- Cloutier, R., 1991a, Interrelationships of Paleozoic actinistians: patterns and trends, in Chang, M.-M., Liu, Y.-H. and Zhang, G.-R., eds., Early Vertebrates and Related Problems of Evolutionary Biology: Science Press, Beijing, p. 379–428.
- Cloutier, R., 1991b, Patterns, trends, and rates of evolution within the Actinistia: Environmental Biology of Fishes, v. 32, p. 23–58, <http://dx.doi.org/10.1007/BF00007444>.
- Cloutier, R., 1996a, Dipnoi (Akinetia: Sarcopterygii), in Schultze, H.-P. and Cloutier, R., eds., Devonian Fishes and Plants of Miguasha, Quebec, Canada: Verlag Dr. Friedrich Pfeil, München, p. 198–226.
- Cloutier, R., 1996b, The primitive actinistian *Miguashaia bureani* Schultze (Sarcopterygii), in Schultze, H.-P. and Cloutier, R., eds., Devonian Fishes and Plants of Miguasha, Quebec, Canada: Verlag Dr. Friedrich Pfeil, München, p. 227–247.
- Cloutier, R., 1996c, Taxonomic review of *Eusthenopteron foordi*, in Schultze, H.-P. and Cloutier, R., eds., Devonian Fishes and Plants of Miguasha, Quebec, Canada: Verlag Dr. Friedrich Pfeil, München, p. 271–284.
- Cloutier, R., 1997, Morphologie et variations du toit crânien du Dipneuste *Scaumenacia curta* (Whiteaves) (Sarcopterygii), du Dévonien supérieur du Québec: Geodiversitas, v. 19, p. 59–105.
- Cloutier, R., 2009, De l’eau à la terre: Parc national de Miguasha, 2nd ed., in situ, Québec.
- Cloutier, R., 2010, The fossil record of fish ontogenies: Insights into developmen-
tal patterns and processes: Seminars in Cell & Developmental Biology, v. 21, p. 400–413, <http://dx.doi.org/10.1016/j.semcdb.2009.11.004>.
- Cloutier, R., and Ahlberg, P.E., 1996, Morphology, characters, and the interrelationships of basal sarcopterygians, in Stiassny, M.L.J., Parenti, L.R., and Johnson, G.D., eds., Interrelationships of Fishes: Academic Press, New York, p. 445–479, <http://dx.doi.org/10.1016/B978-012670950-6/50018-7>.
- Cloutier, R., and Arratia, G., 2004, Origin and early diversification of actinopterygians, in Arratia, G., Wilson, M.V.H., and Cloutier, R., eds., Recent Advances in the Origin and Early Radiation of Vertebrates: Verlag Dr. Friedrich Pfeil, München, p. 217–270.
- Cloutier, R., and Lelièvre, H., 1998, Comparative study of Devonian fossiliferous sites: Ministère Environnement Faune, Gouvernement du Québec, p. 1–86.
- Cloutier, R., and Schultze, H.-P., 1996, Porolepiform fishes (Sarcopterygii), in Schultze, H.-P., and Cloutier, R., eds., Devonian Fishes and Plants of Miguasha, Quebec, Canada: Verlag Dr. Friedrich Pfeil, München, p. 248–270.
- Cloutier, R., Loboziak, S., Candilier, A.-M., and Blicek, A., 1996, Biostratigraphy of the Upper Devonian Escuminac Formation, eastern Québec, Canada: A comparative study based on miospores and fishes: Review of Palaeobotany and Palynology, v. 93, p. 191–215, [http://dx.doi.org/10.1016/0034-6667\(95\)00126-3](http://dx.doi.org/10.1016/0034-6667(95)00126-3).
- Cloutier, R., Béchar, I., Charest, F., and Matton, O., 2009, La contribution des poissons fossiles de Miguasha à la biologie évolutive du développement: Le Naturaliste Canadien, v. 133, p. 84–95.
- Cloutier, R., Proust, J.-N., and Tessier, B., 2011, The Miguasha Fossil-Fish-Lagerstätte: A consequence of the Devonian land–sea interactions: Palaeobiodiversity and Palaeoenvironments, v. 91, p. 293–323, <http://dx.doi.org/10.1007/s12549-011-0058-0>.
- Cope, E.D., 1892, On the phylogeny of the Vertebrata: Proceedings of the American Philosophical Society, v. 30, p. 278–281.
- Cote, S., Carroll, R., Cloutier, R., and Barsagi, L., 2002, Vertebral development in the Devonian Sarcopterygian fish *Eusthenopteron foordi* and the polarity of vertebral evolution in non-amniote tetrapods: Journal of Vertebrate Paleontology, v. 22, p. 487–502, [http://dx.doi.org/10.1671/0272-4634\(2002\)022\[0487:VDITDS\]2.0.CO;2](http://dx.doi.org/10.1671/0272-4634(2002)022[0487:VDITDS]2.0.CO;2).
- Daeschler, E.B., Shubin, N.H., and Jenkins, Jr, F.A., 2006, A Devonian tetrapod-like fish and the evolution of the tetrapod body plan: Nature, v. 440, p. 757–763, <http://dx.doi.org/10.1038/nature04639>.
- Davis, S.P., Finarelli, J.A., and Coates, M.I., 2012, *Acanthodes* and shark-like conditions in the last common ancestor of modern gnathostomes: Nature, v. 486, p. 247–251, <http://dx.doi.org/10.1038/nature11080>.
- Dawson, J.W., 1882, The fossil plants of the Erian (Devonian) and Upper Silurian formations of Canada: Geological Survey of Canada, Part 2, p. 91–142.
- Dineley, D.L., and Williams, B.P.J., 1968a, The Devonian continental rocks of the lower Restigouche River, Quebec: Canadian Journal of Earth Sciences, v. 5, p. 945–953, <http://dx.doi.org/10.1139/e68-091>.
- Dineley, D.L., and Williams, B.P.J., 1968b, Sedimentation and paleoecology of the Devonian Escuminac Formation and related strata, Escuminac Bay, Quebec, in Klein, G. de V., ed., Symposium - Continental Sedimentation in Northeastern North America: Geological Society of America, Special Papers, v. 106, p. 241–264.
- Donoghue, P.C.J., Forey, P.L., and Aldridge, R.J., 2000, Conodont affinity and chordate phylogeny: Biological Reviews, v. 75, p. 191–251, <http://dx.doi.org/10.1111/j.1469-185X.1999.tb00045.x>.
- Downs, J.P., and Donoghue, P.C.J., 2009, Skeletal histology of *Bothriolepis canadensis* (Placodermi, Antiarchi) and evolution of the skeleton at the origin of jawed vertebrates: Journal of Morphology, v. 270, p. 1364–1380, <http://dx.doi.org/10.1002/jmor.10765>.
- El Albani, A., Cloutier, R., and Candilier, A.-M., 2002, Early diagenesis of the Upper Devonian Escuminac Formation in the Gaspé Peninsula, Québec: Sedimentological and geochemical evidence: Sedimentary Geology, v. 146, p. 209–223, [http://dx.doi.org/10.1016/S0037-0738\(01\)00119-1](http://dx.doi.org/10.1016/S0037-0738(01)00119-1).
- Elliott, D.K., Johnson, H.G., Cloutier, R., Carr, R.K., and Daeschler, E.B., 2000, Middle and Late Devonian vertebrates of the western Old Red Sandstone Continent: Courier Forschungs-Institut Senckenberg, v. 223, p. 291–308.
- Forey, P.L., 1998, History of the Coelacanth Fishes: Chapman & Hall, London, 419 p.

- Friedman, M., and Coates, M.I., 2006, A newly recognized fossil coelacanth highlights the early morphological diversification of the clade: *Proceedings of the Royal Society B-Biological Sciences*, v. 273, p. 245–250, <http://dx.doi.org/10.1098/rspb.2005.3316>.
- Friedman, M., and Sallan, L.C., 2012, Five hundred million years of extinction and recovery: A phanerozoic survey of large-scale diversity patterns in fishes: *Palaeontology*, v. 55, p. 707–742, <http://dx.doi.org/10.1111/j.1475-4983.2012.01165.x>.
- Gensel, P.G., and Barnett-Lawrence, M., 1996, Plant megafossils from the Escuminac Formation, *in* Schultzze, H.-P., and Cloutier, R., eds., *Devonian Fishes and Plants of Miguasha, Quebec, Canada*: Verlag Dr. Friedrich Pfeil, München, p. 79–90.
- Gesner, A., 1843, Report on the geological survey of the province of New-Brunswick, with topographical account on the public lands, and the districts explored in 1842, Part 2: Saint John, New Brunswick, 85 p.
- Gess, R.W., Coates, M.I., and Rubidge, B.S., 2006, A lamprey from the Devonian period of South Africa: *Nature*, v. 443, p. 981–984, <http://dx.doi.org/10.1038/nature05150>.
- Hesse, R., and Sawh, H., 1982, Escuminac Formation, *in* Hesse, R., Middleton, G.V., and Rust, B.R., eds., *Paleozoic Continental Margin Sedimentation in the Quebec Appalachians*: 11th International Congress of Sedimentology, Hamilton, Ontario, p. 72–80.
- Hesse, R., and Sawh, H., 1992, Geology and sedimentology of the Upper Devonian Escuminac Formation, Quebec, and evaluation of its paleoenvironment: lacustrine versus estuarine turbidite sequence: *Atlantic Geology*, v. 28, p. 257–275.
- Janvier, P., 1996a, *Early Vertebrates*: Oxford University Press, Oxford, 408 p.
- Janvier, P., 1996b, The Miguasha “Anaspid”, *in* Schultzze, H.-P., and Cloutier, R., eds., *Devonian Fishes and Plants from Miguasha, Québec, Canada*: Verlag Dr. Friedrich Pfeil, München, p. 134–140.
- Janvier, P., and Arsénault, M., 2002, Palaeobiology: Calcification of early vertebrate cartilage: *Nature*, v. 417, p. 609, <http://dx.doi.org/10.1038/417609a>.
- Janvier, P., and Arsénault, M., 2007, The anatomy of *Euphanerops longaeus* Woodward, 1900, an anaspid-like jawless vertebrate from the Upper Devonian of Miguasha, Quebec, Canada: *Geodiversitas*, v. 29, p. 143–216.
- Janvier, P., and Arsénault, M., 2009, La conservation exceptionnelle des fossiles du parc national de Miguasha: *Le Naturaliste Canadien*, v. 133, p. 78–83.
- Janvier, P., Desbiens, S., Willett, J.A., and Arsénault, M., 2006, Lamprey-like gills in a gnathostome-related Devonian jawless vertebrate: *Nature*, v. 440, p. 1183–1185, <http://dx.doi.org/10.1038/nature04471>.
- Janvier, P., Desbiens, S., and Willett, J.A., 2007, New evidence for the controversial “lungs” of the Late Devonian antiarch *Bothriolepis canadensis* (Whiteaves, 1880) (Placodermi: Antiarcha): *Journal of Vertebrate Paleontology*, v. 27, p. 709–710, [http://dx.doi.org/10.1671/0272-4634\(2007\)27\[709:NEFTCL\]2.0.CO;2](http://dx.doi.org/10.1671/0272-4634(2007)27[709:NEFTCL]2.0.CO;2).
- Jeram, A.J., 1996, Chelicerata from the Escuminac Formation, *in* Schultzze, H.-P., and Cloutier, R., eds., *Devonian Fishes and Plants of Miguasha, Quebec, Canada*: Verlag Dr. Friedrich Pfeil, München, p. 103–111.
- Laurin, M., Meunier, F.J., Germain, D., and Lemoine, M., 2007, A microanatomical and histological study of the paired fin skeleton of the Devonian sarcopterygian *Eusthenopteron foordi*: *Journal of Paleontology*, v. 81, p. 143–153, [http://dx.doi.org/10.1666/0022-3360\(2007\)81\[143:AMAHSO\]2.0.CO;2](http://dx.doi.org/10.1666/0022-3360(2007)81[143:AMAHSO]2.0.CO;2).
- Lemieux, P., 1996, The Fossil-Lagerstätte Miguasha: Its past and present history, *in* Schultzze, H.-P., and Cloutier, R., eds., *Devonian Fishes and Plants of Miguasha, Quebec, Canada*: Verlag Dr. Friedrich Pfeil, München, p. 9–22.
- Lloyd, G.T., Wang, S.C., and Brusatte, S.L., 2012, Identifying heterogeneity in rates of morphological evolution: Discrete character change in the evolution of lungfish (Sarcopterygii; Dipnoi): *Evolution*, v. 66, p. 330–348, <http://dx.doi.org/10.1111/j.1558-5646.2011.01460.x>.
- Maples, C.G., 1996, Paleoenvironmental significance of trace fossils in the Escuminac Formation, *in* Schultzze, H.-P., and Cloutier, R., eds., *Devonian Fishes and Plants of Miguasha, Québec, Canada*: Verlag Dr. Friedrich Pfeil, München, p. 114–119.
- Marshall, J.E.A., and Hemsley, A.R., 2003, A Mid Devonian seed-megaspore from East Greenland and the origin of the seed plants: *Palaeontology*, v. 46, p. 647–670, <http://dx.doi.org/10.1111/1475-4983.00314>.
- Martens, T., 1996, Conchostraca (Phyllozoa, Crustacea) from the Escuminac Formation, *in* Schultzze, H.-P., and Cloutier, R., eds., *Devonian Fishes and Plants of Miguasha, Quebec, Canada*: Verlag Dr. Friedrich Pfeil, p. 112–113.
- Matton, O., Cloutier, R., and Stevenson, R., 2012, Apatite for destruction: Isotopic and geochemical analyses of bioapatites and sediments from the Upper Devonian Escuminac Formation (Miguasha, Québec): *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 361–362, p. 73–83, <http://dx.doi.org/10.1016/j.palaeo.2012.08.004>.
- McAllister, J., 1996, Coprolitic remains from the Devonian Escuminac Formation, *in* Schultzze, H.-P., and Cloutier, R., eds., *Devonian Fishes and Plants of Miguasha, Quebec, Canada*: Verlag Dr. Friedrich Pfeil, München, p. 328–347.
- Meyer-Berthaud, B., Scheckler, S.E., and Wendt, J., 1999, *Archaeopteris* is the earliest known modern tree: *Nature*, v. 398, p. 700–701, <http://dx.doi.org/10.1038/19516>.
- Moloshnikov, S.V., 2008, The placoderm *Plourdosteus livonicus* (Eastman) in the Early Frasnian of the Central Devonian Field and the trophic structure of the Mikhailovskii fish assemblage: *Paleontological Journal*, v. 42, p. 607–614.
- Orr, P.J., and Briggs, D.E.G., 1999, Exceptionally preserved conchostracans and other crustaceans from the Upper Carboniferous of Ireland: *Special Papers in Palaeontology Series* 62, p. 5–68.
- Parent, N., and Cloutier, R., 1996, Distribution and preservation of fossils in the Escuminac Formation, *in* Schultzze, H.-P., and Cloutier, R., eds., *Devonian Fishes and Plants of Miguasha, Quebec, Canada*: Verlag Dr. Friedrich Pfeil, München, p. 54–78.
- Prichonnet, G., DiVergilio, M., and Chidiac, Y., 1996, Stratigraphic, sedimentological and paleontological context of the Escuminac Formation: paleoenvironmental hypotheses, *in* Schultzze, H.-P., and Cloutier, R., eds., *Devonian Fishes and Plants of Miguasha, Quebec, Canada*: Verlag Dr. Friedrich Pfeil, München, p. 23–36.
- Russell, L.S., 1939, Notes on the occurrence of fossil fishes in the Upper Devonian of Miguasha, Québec: *Contribution to the Royal Ontario Museum, Palaeontology*, v. 12, p. 1–4.
- Rust, B.R., Lawrence, D.A., and Zaitlin, B.A., 1989, The sedimentation and tectonic significance of Devonian and Carboniferous terrestrial successions in Gaspé, Québec: *Atlantic Geology*, v. 25, p. 1–13.

- Sansom, R.S., Freedman, K., Gabbott, S.E., Aldridge, R.J., and Purnell, M.A., 2010, Taphonomy and affinity of an enigmatic Silurian vertebrate, *Jamoytius kerwoodi* White: *Palaeontology*, v. 53, p. 1393–1409, <http://dx.doi.org/10.1111/j.1475-4983.2010.01019.x>.
- Schmitz, B., Åberg, G., Werdelin, L., Forey, P., and Bendix-Almgreen, S.E., 1991, $^{87}\text{Sr}/^{86}\text{Sr}$, Na, F, Sr, and La in skeletal fish debris as a measure of the paleosalinity of fossil-fish habitats: *Geological Society of America Bulletin*, v. 103, p. 786–794, [http://dx.doi.org/10.1130/0016-7606\(1991\)103<0786:SSNFSA>2.3.CO;2](http://dx.doi.org/10.1130/0016-7606(1991)103<0786:SSNFSA>2.3.CO;2).
- Schultze, H.-P., 1969, Die Faltenzähne der rhipidistiiden Crossopterygier, der Tetrapoden und der Actinopterygier-Gattung *Lepisosteus*; nebst einer Beschreibung der Zahnstruktur von *Onychodus* (strunniiformer Crossopterygier): *Palaeontographica Italica*, v. 65, p. 63–137.
- Schultze, H.-P., 1984, Juvenile specimens of *Eusthenopteron foordi* Whiteaves, 1881 (osteolepiform rhipidistian, Pisces) from the Late Devonian of Miguasha, Quebec, Canada: *Journal of Vertebrate Paleontology*, v. 4, p. 1–16, <http://dx.doi.org/10.1080/02724634.1984.10011982>.
- Schultze, H.-P., 1996, The elpistostegid fish *Elpistostege*, the closest the Miguasha fauna comes to a tetrapod, in Schultze, H.-P., and Cloutier, R., eds., *Devonian Fishes and Plants of Miguasha*, Quebec, Canada: Verlag Dr. F. Pfeil, München, p. 316–327.
- Schultze, H.-P., 1999, The fossil record of the intertidal zone, in Horn, M.H., Martin, K.L.M., and Chotkowski, M.A., eds., *Intertidal Fishes: Life in Two Worlds*: Academic Press, San Diego, p. 373–392.
- Schultze, H.-P., 2009, The international influence of the Stockholm School: *Acta Zoologica*, v. 90, p. 22–37, <http://dx.doi.org/10.1111/j.1463-6395.2008.00354.x>.
- Schultze, H.-P., and Cloutier, R., eds., 1996, *Devonian Fishes and Plants of Miguasha*, Quebec, Canada: Verlag Dr. Friedrich Pfeil, München, 374 p.
- Smith, M.M., Smithson, T.R., and Campbell, K.S.W., 1987, The relationships of *Uronemus*: A Carboniferous dipnoan with highly modified tooth plates: *Philosophical transactions of the Royal Society of London, Series B, Biological Sciences*, v. 317, p. 299–327.
- Stensiö, E.A., 1939, A new anaspid from the Upper Devonian of Scaumenac Bay in Canada, with remark on other anaspids: *Kungliga Svenska VetenskapsAkademiens Handlingar*, v. 18, p. 1–25.
- Stensiö, E.A., 1948, On the Placodermi of the Upper Devonian of East Greenland, II, Antiarchi: subfamily Bothriolepinae, with an attempt at a revision of the previously described species of that family: *Meddelelser om Grønland*, v. 139, p. 1–622.
- Thomson, K.S., 1972, An attempt to reconstruct evolutionary changes in the cellular DNA content of lungfish: *Journal of Experimental Zoology*, v. 182, p. 363–372.
- Thomson, K.S., and Hahn, K.V., 1968, Growth and form in fossil rhipidistian fishes (Crossopterygii): *Journal of Zoology*, v. 156, p. 199–223, <http://dx.doi.org/10.1111/j.1469-7998.1968.tb05929.x>.
- Trewin, N.H., 1986, Palaeoecology and sedimentology of the Achanarras fish bed of the Middle Old Red Sandstone, Scotland: *Transactions of the Royal Society of Edinburgh: Earth Sciences*, v. 77, p. 21–46, <http://dx.doi.org/10.1017/S0263593300010737>.
- Vézina, D., 1991, Nouvelles observations sur l'environnement sédimentaire de la Formation d'Escuminac (Dévonien supérieur, Frasnien), Québec, Canada: *Canadian Journal of Earth Sciences*, v. 28, p. 225–230, <http://dx.doi.org/10.1139/e91-021>.
- Vézina, D., and Cloutier, R., 1991, Guidebook for field trip: 7th International Symposium on the Studies of Early Vertebrates, Parc de Miguasha, Miguasha.
- Walker, J.D., and Geissman, J.W., compilers, 2009, *Geologic Time Scale: Geological Society of America*, <http://dx.doi.org/10.1130/2009.CTS004R2C>.
- Werdelin, L., and Long, J.A., 1986, Allometry in the placoderm *Bothriolepis canadensis* and its significance to antiarch evolution: *Lethaia*, v. 19, p. 161–169, <http://dx.doi.org/10.1111/j.1502-3931.1986.tb00727.x>.
- Whiteaves, J.F., 1880, On a new species of *Pterichthys*, allied to *Bothriolepis ornata*, from the Devonian rocks of the north side of the Baie des Chaleurs: *American Journal of Science*, v. 3, p. 132–136.
- Wilson, H.M., Daeschler, E.B., and Desbiens, S., 2005, New flat-backed archipolypodan millipedes from the Upper Devonian of North America: *Journal of Paleontology*, v. 79, p. 738–744, [http://dx.doi.org/10.1666/0022-3360\(2005\)079\[0738:NFAMFT\]2.0.CO;2](http://dx.doi.org/10.1666/0022-3360(2005)079[0738:NFAMFT]2.0.CO;2).
- Zhu, M., Zhao, W.J., Jia, L.T., Lu, J., Qiao, T., and Qu, Q.M., 2009, The oldest articulated osteichthyan reveals mosaic gnathostome characters: *Nature*, v. 458, p. 469–474, <http://dx.doi.org/10.1038/nature07855>.
- Zylberberg, L., Meunier, F.J., and Laurin, M., 2010, A microanatomical and histological study of the postcranial dermal skeleton in the Devonian sarcopterygian *Eusthenopteron foordi*: *Acta Palaeontologica Polonica*, v. 55, p. 459–470, <http://dx.doi.org/10.4202/app.2009.1109>.

Received May 2013

Accepted May 2013