The Late Devonian Biota of the Miguasha National Park UNESCO World Heritage Site

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Summary

For the past 168 years, the Late Devonian Miguasha biota from eastern Canada has yielded a diversified aquatic component including 20 species of lower vertebrates (anaspids, osteostracans, placoderms, acanthodians, actinopterygians and sarcopterygians) and a poorly diversified invertebrate assemblage as well as a continental component including plants, scorpions and millipedes. Originally interpreted as a freshwater lacustrine environment, recent paleontological, taphonomic, sedimentological and geochemical evidences corroborate a brackish estuarine setting. More than 18,000 fossil fish have been discovered showing various states of preservation including three-dimensional and soft-tissues 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 and interpretation of different developmental mechanisms. Numerous horizons within the Escuminac Formation are interpreted as either *Konservat* or *Konzentrat Fossil-Lagerstätten*.

Introduction

The Miguasha fossil site from eastern Quebec is one of the first paleontological sites to have been discovered and excavated in North America. The discovery of the first fossils at Miguasha was made in 1842 by Abraham Gesner, a New Brunswick geologist. Between 1879 and 1881, the Geological Survey of Canada organized several expeditions lead by R. W. Ells, A. H. Foord and T. C. Weston. Fossil fishes collected were sent to J. F. Whiteaves, a paleontologist working at the Geological Survey, and plants were given to Sir W. Dawson, a paleobotanist at McGill University. From the late 1880s until the 1940s, American, British, Canadian and Swedish paleontologists came to explore the sandy-shaly cliffs of Miguasha. In 1892, the American vertebrate paleontologist E. D. Cope was the first to recognize that the osteolepiform *Eusthenopteron foordi* from Miguasha had a morphology similar to the first tetrapods. This idea was further developed by Erik Jarvik from the Naturhistoriska Riksmusett in Stockholm who, between 1937 and 1998, wrote some thirty scientific articles on this fish. For more than a century, *Eusthenopteron* was considered as a missing link between fishes and tetrapods, a notion that contributed to Miguasha's fame. Between 1930 and 1970, the Swedish school of paleontology, greatly assisted by the Miguasha fossils, trained tens of scientists from around the world. In 1985, the Government of Quebec designated the area a conservation park. From the 1990s until now, a few Canadian paleoichthyologists have been trained in America and Europe to study different perspectives of the Devonian Miguasha biota. In 1999, the Miguasha National Park was recognized UNESCO World Heritage Site as the fossiliferous site best representing the Devonian period.

Diversity and abundance of the Miguasha biota

The Escuminac Formation owes its scientific reputation largely to its vertebrate fauna. This assemblage includes currently 20 species representative of ten major groups of lower vertebrates: the anaspids (*Endeiolepis aneri* and *Euphanerops longaevus*), osteostracans (*Escuminaspis laticeps* and *Levesquaspis patteni*), placoderms [*Bothriolepis canadensis* (Fig.

1D-E, H, J) and *Plourdosteus canadensis*), acanthodians (*Diplacanthus horridus, D. ellsi, Homalacanthus concinnus* and *Triazeugacanthus affinis*), actinopterygians (*Cheirolepis canadensis*), actinistians (*Miguashaia bureaui*), porolepiforms [*Holoptychius jarviki* (Fig. 1F), *Quebecius quebecensis* and a Porolepiformes indet.], dipnoiforms [*Scaumenacia curta* (Fig. 1E) and *Fleurantia denticulate*], osteolepiforms [*Eusthenopteron foordi* (Fig. 1I) and *Callistiopterus clappi*] and elpistostegids (*Elpistostege watsoni*). More than 18,000 fish specimens have been collected at Miguasha. The four most abundant species are represented by more than 2,000 specimens each (*B. canadensis, T. affinis, S. curta* and *E. foordi*).

Plants [*Archaeopteris* (Fig. 1A)*, Protobarynophyton, Barynophyton* and *Flabellofolium*] are found in several strata, some of which are very abundant. In addition to the macroremains of plants, a wide range of spores (more than 70 species) and marine acritarchs (15 genera) have been attributed to the middle Frasnian [Cloutier et al. 1996]. Invertebrates account for a minor part of the diversity with the presence of nine species including two rare ichnotaxa (Fig. 1C). The aquatic component of the invertebrate fauna included the conchostracan *Asmusia membranacea*, a parastylonurid, an eurypterid, and a scolecodont [Cloutier et al. 1996; Schultze and Cloutier 1996], whereas the continental component includes the millipede *Zanclodesmus willeri* [Wilson et al. 2005], the scorpion *Petaloscorpio bureaui* (Fig. 1B), and a gigantoscorpionid [Schultze and Cloutier 1996].

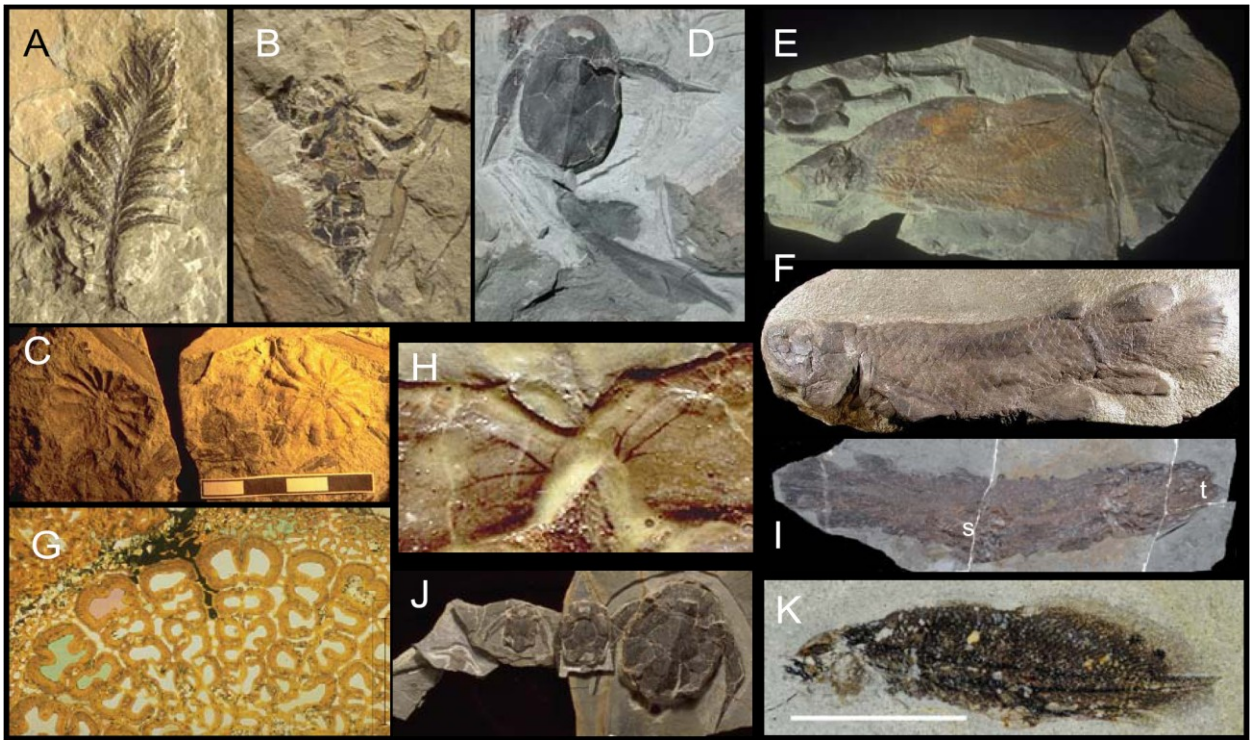

Figure 1: Overview of the Late Devonian Miguasha biota. **A**. Branch system of the progymnosperm *Archaeopteris halliana*. **B**. Articulated terrestrial scorpion, *Petaloscorpio bureaui*. **C**. Part and counterpart of the ichnofossil *Gyrophyllites*. **D**. Complete specimen of the placoderm *Bothriolepis canadensis* with the postcranial soft anatomy. **E**. Slab with two complete *B. canadensis* and two large dipnoan *Scaumenacia curta*. **F**. Complete three-dimensional specimen of the porolepiform *Holoptychius jarviki*. **G**. Cross-section of the osteolepiform *Eusthenopteron foordi* tooth showing perfect microscopic details of dental tissues. **H**. Close-up on blood vessels of the anterior part of the thoracic shield of *B. canadensis*. **I**. Cannibalistic example of *E. foordi*; skull (s) and tail (t) of the ingested juvenile specimen. **J**. Fossilized ontogeny of *B. canadensis*. **K**. Juvenile specimen of *S. curta* (scale bar is 1 cm).

Paleoecology: A dynamic ecosystem

From the base to the top of the Escuminac Formation (129 m thickness), 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. This assemblage might well represent a case of paleoecological statism. Paleobiological information for numerous species are recovered by the presence of coprolites, cololites, ingested preys and larval-juvenile specimens. At least a five-level trophic chain can be inferred based on ingested preys (from bottom to top: *Asmusia, Homalacanthus,* small *Cheirolepis*, large *Cheirolepis*, and *Eusthenopteron*) [Cloutier 2009]. Cannibalism has been reported for *Cheirolepis* [Arratia and Cloutier 1996] and recently observed in *Eusthenopteron* (Fig. 1I). Exceptionally well-preserved larval and juvenile specimens (as small as 6 mm in length) have been identified for 14 out of the 20 species of fishes (Fig. 1K) [Cloutier et al. 2009] that allow us to study fossilized ontogenies (Fig. 1J).

Paleoenvironment: A wave-dominated estuary

The depositional environment of the Escuminac Formation has been alternately considered either as a lacustrine, estuarine, coastal marine or marine environment. An estuarine interpretation is the depositional setting that accommodates best the different lines of evidence provided by the fauna [Schultze and Cloutier 1996], the palynofacies [Cloutier et al. 1996], the trace fossil assemblage [Schultze and Cloutier 1996], the sedimentological and stratigraphic setting of the formation [Hesse and Sawh 1992], and the geochemistry of the sediments and bones [El Albani et al. 2002; Schmitz et al. 1991; Vézina 1991]. Because of the periodicity of daily sedimentation, tidal rhythmites provide a perfect facies for *Konservat* and *Konzentrat Fossil-Lagerstätte* horizons within the Escuminac Formation.

Systematics: An evolutionary milestone

Numerous Escuminac species are recognized for their evolutionary and phylogenetic significance [Cloutier 2009; Schultze and Cloutier 1996]. Among the plants, the progymnosperm *Archaeopteris* (Fig. 1A) is considered the sister group of the gymnosperms and might have constituted the oldest forest of the fossil record. *Spermasporites* is considered one of the oldest seed plants. Among the invertebrates, the scorpion *Petaloscorpio* (Fig. 1B) and the millipede *Zanclodesmus* are among the first continental arthropods. *Endeiolepis* and *Euphanerops* are the last survivors of the anaspids and most likely closely related to living lampreys. *Cheirolepis* is among the most basal actinopterygians, the most diversified group of living vertebrates. *Miguashaia* is among the most primitive coelacanths, a group still represented today by only two living species. *Eusthenopteron* (Fig. 1I) is one of the best-known fossil species and for nearly one hundred years was considered transitional between fishes and the first tetrapods. Finally, *Elpistostege* is one of the fish species closest to tetrapods.

Konservat- and Konzentrat-Lagerstätten

A wide range of preservation and fossilization occur in the Escuminac Formation [Parent and Cloutier 1996]. Well-preserved specimens with no sign of decay (Fig. 1D-K)) down to isolated bony elements have been found. The excellent state of preservation of some fishes is not limited to the gross morphology, the bones show also excellent histological structures preserved. Preservation of hard tissues [e.g., enamel, dentine (Fig 1G), cellular bone, cartilage] as well as cell spaces (e.g., osteocytes, chondrocytes) is most frequent but preservation of soft tissues [e.g., digestive tracks, stomachs, spiral intestines, lungs, gill filaments, blood vessels (Fig. 1H), muscles] is also present [Cloutier 2009; Janvier and Arsenault 2009; Janvier et al. 2007; Janvier et al. 2006]. Concentration of specimens is not limited to fish fragments but mainly to complete specimens (Fig. 1E). Examples of *Konservat-* and *Konzentrat-Lagerstätten* occur throughout the Escuminac Formation.

Conclusions

The distinctiveness of the Miguasha biota to be recognized as a UNESCO World Heritage representative of the Devonian period [Cloutier and Lelièvre 1998] was 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* along with the Cambrian Burgess Shale and Doushantuo, the Carboniferous Mazon Creek and Bear Gulch, the Eocene Messel Shale, and the Cretaceous Jehol biotas.

Acknowledgements

I want to thank many collaborators with whom I am presently working on the Miguasha biota, I. Béchard, F. Charest, J. Kerr, O. Matton, D. Potvin-Leduc, J.-N. Proust, R. Stevenson, and B. Tessier.

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