Université de Montréal

An Upper Ordovician faunal assemblage from the Neuville Formation of Québec, including an exceptionally preserved soft bodied sea anemone, *Paleocerianthus neuvillii* n. sp.

Par
Huda Alghaled

Départment de sciences biologiques
Faculté des Arts et des Sciences

Mémoire présenté à la faculté des études supérieures
en vue de l'obtention du grade de M.Sc.
en sciences biologiques

juillet 2019

Université de Montréal
Faculté des études supérieures

Université de Montréal

Faculté des études supérieures et postdoctorales

Ce mémoire intitulé :

An Upper Ordovician faunal assemblage from the Neuville Formation of Québec, including an exceptionally preserved soft bodied sea anemone, *Paleocerianthus neuvillii* n. sp.

Présenté par :

Huda Alghaled

A été évalué par un jury composé des personnes suivantes :

Dr. Jesse Shapiro, président-rapporteur

Dr. Christopher B. Cameron, directeur de recherche

Dr. Hans Larsson, membre du jury

ABSTRACT

Fossils are the primary source of information on ancient life and its biodiversity. Fossils are attributed to geological periods, and the Ordovician is the most significant, having yielded valuable information on the origins, paleoecology and the biodiversity of today's taxa. Some Ordovician fossil deposits are distinguished by their diversity and exceptionally preserved soft bodied fossils – the two criteria for defining a Konservat-Lägerstatte. Konservat-Lägerstatten are rare and created under specific taphanomic factors that lead to exceptional preservation. Here we demonstrate a new Ordovician Period Konservat-Lägerstatte from the Upper Ordovician of the Neuville Formation, Québec based on high diversity and the preservation of tube-dwelling anemones *Paleocerianthus neuvillii* n. sp. (Anthozoa: Ceriantharia). This is a benthic organism, with tentacles and a long soft column projecting from the tube. The mouth is surrounded by the crown of tentacles. The tubes often share a base with two, three or more additional tubes. The total length of the tubes varied from 24.9 mm to 51.0 mm (± 36.9 mm) with small change in width, representing allometric growth. *P. neuvillii* lived in fine sediment associated with brachiopods, trilobites and echinoderms. The specimens were buried rapidly by a sedimentary flow. *Paleocerianthus neuvillii,* is the oldest record of a fossil tube anemone.

Current phylogenies of the Anthozoa based on morphology and 18S rDNA sequence data place the Ceriantharia as a monophyletic group among Ceriantipatharia, and as a basal group of the Anthozoa. *P. neuvillii* is the oldest tube anemone fossil and therefore the best proximate ancestor for the Anthozoa.

Key words: Ordovician Period, Trenton Group, Neuville Formation, Sea Anemone, Cerianthus, Great Ordovician Biodiversity Event (GOBE)

RÉSUMÉ

Les fossiles constituent la principale source d'informations sur la vie ancienne et sa biodiversité. Les fossiles sont attribués à des périodes géologiques et l'ordovicien est le plus significatif, il a fourni des informations précieuses sur les origines, la paléoécologie et la biodiversité des taxons actuels. Certains gisements de fossiles de l'Ordovicien se distinguent par leur diversité et par la préservation exceptionnelle des fossiles à corps mous - les deux critères permettant de définir un Konservat-Lägerstatte. Les Konservat-Lägerstatten sont rares et créés sous des facteurs taphanomiques spécifiques qui conduisent à une conservation exceptionnelle. Nous présentons ici une nouvelle période de l'Ordovicien Konservat-Lägerstatte de l'Ordovicien supérieur de la Formation de Neuville, au Québec, fondée sur une grande diversité et la préservation des anémones tubulaires *Paleocerianthus neuvillii* n. sp. (Anthozoa: Ceriantharia). C'est un organisme benthique, avec des tentacules et une longue colonne molle faisant saillie du tube. La bouche est entourée par la couronne de tentacules. Les tubes partagent souvent une base avec deux, trois tubes supplémentaires ou plus. La longueur totale des tubes variait de 24.9 mm à 51.0 mm (± 36.9 mm) avec une faible variation de largeur, représentant une croissance allométrique. *P. neuvillii* vivait dans les sédiments fins associés aux brachiopodes, aux trilobites et aux échinodermes. Les spécimens ont été enterrés rapidement par un flux sédimentaire.

Les phylogénies actuelles des anthozoaires basées sur la morphologie et les données de séquences d'ADNr 18S placent le Ceriantharia en tant que groupe monophylétique parmi les Ceriantipatharia et en tant que groupe de base des Anthozoaires. *P. neuvillii* est le plus ancien fossile d'anémone tubulaire et, par conséquent, le meilleur ancêtre proche des Anthozoaires.

Mots clés: période ordovicien, groupe de Trenton, formation de Neuville, anémone de mer, Cerianthus, Grand événement de biodiversification ordovicien (GOBE)

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENTS

I would like to take this opportunity to extend my appreciation to the many people without whom the completion of this thesis would not have been possible. Indeed, I must acknowledge that there are other people that either contributed directly or indirectly to enable the completion of this thesis. While I salute all, I find it imperative to mention a few directly.

Firstly, I would like to specially mention my supervisor, Dr. Christopher B. Cameron. Writing this thesis has been a remarkable and engaging exercise that I could not have undertaken without the able supervision of Dr. Cameron. Other than always creating time to attend to my questions and to offer guidance on how to proceed, Dr. Cameron has gone out of his way many times to provide additional resources that helped me complete this thesis project. Further, he unwaveringly reviewed my work in progress and ensured that I did not deviate from the main aim of the research. For these contributions, I salute Dr. Cameron and I greatly appreciate both his professional and personal help, as they played an essential role in this thesis's completion. I hugely appreciate Dr. Cameron, especially for sharing his expertise so willingly, and for being so dedicated to his role as my supervisor.

I would also like to thank Mario Cournoyer and Jean-Bernard Caron. They played a major part in completion of this thesis, as both consistently offered their help from the onset of this project to its completion. A special thank you to Mr. Kevin Lagacé, of Les Entreprises LT (Québec) for providing access to the Saint-Joachim quarry, and to John Iellamo, who discovered and prepared the numerous fossils. Also, thanks to Daniel Lavoie for assistance with the general geological setting of the Québec City area. To all of them, I extend my immense appreciation.

Most importantly, my acknowledgement would be incomplete without mentioning my father and my sisters, all of whom not only encouraged me to pursue further studies but also offered advice and encouragement that helped me through the difficult times in writing this thesis. Without them, it would have been a tedious and an entirely discouraging task. Sadly, to my mother's and sister's soul– you waited for me and encouraged me to finish my thesis and go back home, but I was not able to see you one last time before you left us. You will forever be in my heart.

I cannot fail to mention my loving daughters, Omhani, Leen and Yomna. Completing a research like this not only takes time but also consumes an immense amount of resources, even when Mummy was far away and working on the thesis, they were always a source of support.

Finally, my appreciation goes to the entire Department of Biology, University of Montreal, which offered me the chance to complete this study, and to the University of Sirt, Libya, which honored me with this scholarship to pursue my academic studies and gave me this valuable opportunity to achieve my career and make my dreams come true.

CHAPTER 1 - GENERAL INTRODUCTION

1.1 The Importance of fossils

Most of our knowledge about the evolution of plants and animals has been learned from fossils (Seilacher, 1967). Fossils have been used to determine the earth's history through two essentially different types of evidence: chronological and spatial. The chronological evidence is biostratigraphical, meaning that fossils are one of the most significant way, offering the relative ages of strata and making it possible to understand the sequences of geological events (Rosen, 1988). Studies and investigations of fossils are always of special interest. They display uncommon or exceptional preservation, and they may suggest the ecology of an ancient community. One of the purposes for studying fossils is that they preserve characters lost in the living taxa, recommended as a crucial role for fossils in many current and pending studies (Novacek, 1992). The fossil data can be used to offer a more detailed reconstruction of the sequences of evolutionary variations that led to new traits, determine the polarity of specific traits or to identify the root of an unrooted tree, and finally, to re-estimate primary hypotheses of homology or homoplasy (Grantham, 2004). Some of the most important, exceptionally preserved fossils are found in the Ordovician period.

1.2 The Ordovician Period

The Ordovician Period was a time of special environments and events which influenced the global biota. It was characterized by wide epeiric seas, paleocontinent spreading, periods of strong volcanism and black shale deposition, a greenhouse climate state deteriorating to a brief icehouse state, strong faunal territories, and deep changes to the biota including the changeover from the Cambrian fauna to the Paleozoic fauna. This period represents one of the largest major turnovers in the history of life on earth and marks the appearance of groups that came to characterize marine ecosystems for the next 250 million years (Barnes et al., 1996). The International sub-commission on stratigraphy has classified the Ordovician into three epochs, the Low, Middle and the Upper Epochs, and seven stages (Bergstroem et al., 2009). In the Low and Middle Ordovician, the Great Ordovician Biodiversification Event (GOBE) or radiation occurred, causing a remarkable increase in marine biodiversity at all taxonomic levels, in phyla established during the Cambrian Explosion (Munnecke et al., 2010).

1.3 Known Ordovician Lägerstatte

Fossils that present almost exceptional preservation and provide more evidence about the Ordovician period biodiversity are called Lägerstatte fossils (German: from *Lager* 'storage, lair' and *Stätte* 'place'; plural *Lägerstatten*). The exceptionally preserved fossils from Konservat-Lägerstatte sediments are significant because they provide more detail than normal fossils, relating to, for example, fine animal structures, the living environment (paleoecology), and taphonomic information. The occurrence of Konservat-Lägerstatte is due to combinations of physical and chemical conditions that are rare, especially during the Ordovician Period. The best identified and most important Ordovician Konservat-Lägerstatten are those of the Fezouata Shale in Morocco (Lower Ordovician), Beecher's Trilobite Bed located within the Frankfort Shale in Cleveland's Glen, Oneida County, New York (Upper Ordovician), the Soom Shale in South Africa (Upper Ordovician), the William Lake and Airport Cove, Manitoba, Canada (Upper Ordovician) (Young et al., 2007) and the Winneshiek Konservat-Lägerstatte (Middle Ordovician) in northeast Iowa (Liu et al., 2006). Each of these deposits exemplifies an uncommon preservation of soft tissues. This preservation is attributed to a mixture of favorable depositional, environmental and/or early diagenetic circumstances for the mineral replication of soft tissue (Vaucher et al., 2016). Ordovician Lägerstatten are scarce and most of them are from the Upper Ordovician, long after the initial stages of the GOBE. Moreover, they typically contain low-diversity faunas that lived in limited marine environments (Martin, 2016). Examples of soft bodied fossils from Ordovician Lägerstatten are the Fezouata biota, which seems to exhibit 'Burgess Shale-type' fossils, includes sponges, annelid worms, and a great variety of superbly preserved arthropods, along with graptolites, conulariids, hyolithids and other molluscs, brachiopods, bryozoans, and echinoderms (Nowak et al., 2016).

Beecher's Trilobite Bed in the Upper Ordovician strata of New York State is an exception. It is a typical locality for trilobites having appendages and other soft tissues preserved in pyrite. One of the rare examples where pyrite formed early enough to contribute to the preservation of soft tissues, this layer is dominated by trilobites, graptolites and brachiopods (Briggs et al., 1991).

The Upper Ordovician Soom Shale of South Africa contains rare naraoiid arthropods, eurypterids, straight-shelled ‘nautiloid’ cephalopods, conodont animals, and anaspid-like ‘fishes (Young et al., 2012). The William Lake and Airport Cove Upper Ordovician Lägerstatten in Manitoba, Canada include dasycladacean algae, eurypterids, xiphosurids, conodonts, linguloid brachiopods, gastropods, cephalopods, and large phosphatic or chitinophosphatic problematic tubes happen at both locations with diverse relative abundances (Young et al., 2007).

The Winneshiek Konservat- Lägerstatte in northeast Iowa is particularly important because it is from the Middle Ordovician, an empty space where non-shelly fossils are poorly represented in the fossil record (Liu et al., 2005). Assemblages from the Winneshiek Konservat- Lägerstatte show conodonts, linguloid brachiopods, large fragments of eurypterid cuticles, a basal chelicerate and phyllocarid crustaceans. Conspicuously absent from the Ordovician Period are soft-bodied members of the phylum Cnidaria, including jellyfish, siphonophores and sea anemones.

The major objectives of this thesis are i) to describe the exceptionally preserved fossils of the soft bodied tubicolous sea anemone, *Paleocerianthus neuvillii* n. sp., and ii) to introduce the Upper Ordovician fossils from the Neuville Formation, Québec, Canada and argue that this formation comprises a Lägerstatte.

1.4 Tube Anemone Morphology

Tube-dwelling anemones (Anthozoa: Ceriantharia) are organisms that live in benthic marine sediment from shallow waters to the deep sea. These animals live with their tentacles and a little of their long, soft column projecting from the tube. The mouth is generally hidden by a crown of short oral tentacles that are surrounded by longer outer marginal tentacles. The tentacles have large pores that are often positioned in the direction of water flow (Zapata, 2015). Individuals produce a tube that may be up to a meter long. Most feed at night, withdrawing (at least partially) into their tubes by day. Other animals, including lophophorates, may dwell inside of the tube (Wallace, 2008) for substratum, protection or to capture food (Stampar et al., 2010). Invertebrates such as phoronids, polychaetes, sipunculoids, bivalves, crustaceans etc., have also been considered as tube substrata (Molodtsova, 2007). The tubes produced by these animals differ from those of Ceriantharia groups according to the various adaptations to different environments. Some significant differences in tube lengths between species have also been identified, related to the habitat of the species. These tough tubes are mostly vertically-orientated and unbranched (Stampar et al., 2015). The production of the tube is originated shortly after larval settlement (metamorphosis), when ectodermal glandular cells of the larvae begin to secrete mucus that is considered the main mechanism of tube construction. In the Cerianthidae ptychocyst family, tubules build flat adhesive tapes organized in overlapping layers, creating an arrangement like manufactured fabric, a process that requires a small amount of sediment (Mariscal et al., 1977). The walls of the tube help the animals to control their internal body pressure, as without it, the body wall may swell, particularly in the aboral region. If the animals are kept in water without sand in which to burrow, the tentacles' pressures vary in relaxation and undergo partial atrophy, and then the aboral region becomes distorted and often ruptures because it cannot resist the pressure (Child, 1908). Cerianthids are unique among anemones in having only complete mesenteries; new mesenteries arise from a single part called the multiplication chamber located inside of the oral end of the body cavity (Tiffon, 1987). Little is known about their behavior, regeneration, nutrition and physiology (Stampar et al., 2016).

1.5 Tube Anemone Life Habits and Ecology

Ceriantharia distribution is related to latitude, depth, temperature, and sediments. Ceriantharia environments show a strict range in bottom water temperature (summer maximum minus winter minimum) and are found in all types of sediment except for 100% gravel and coarse moving sand. Geographic and bathymetric distribution is attributed firstly to temperature and secondarily to food source and substrate type. They typically live in groups of animals that are commonly referred to as cerianthid tube forests. These tubes alter water velocities and sedimentation, and may improve local species diversity and richness by (1) attracting and protecting motile species looking for cover, and (2) working as a stable, high substrate for tubiculous and suspension-feeding macrofauna (Shepard et al., 1986).

The subclass Ceriantharia is separated into the clades Penicilaria and Spirularia. The most unusual group within Spirularia is the family Cerianthidae (Milne-Edwards, 1851), that is defined by lacking specialized nematocyst-bearing internal structures called acontioids or cnidorages. This family is comprised of some genera that are known as adults, and others as larvae (Stampar et al., 2016). Ceriantharia are protandry hermaphrodites; gametes are formed in the mesenteries and the fertilization is external. The larvae are pelagic, and the period of the planktonic stage is adjustable and can last for a long time, which may expand to months. Adults are able to realize oral disc regeneration by budding (Shepard et al., 1986). Ceriantharia are solitary animals. These aclonal species can reach a large body size (up to one meter) that will need to alter their hydroskeleton and behavior to respond to water flow, or retract into the tube in response to predation (Geller et al., 2005). They are predated upon primarily by gastropods and nudibranches. Gastropoda are suggested to be predators. Wentletraps are predators that eat small (juvenile) anemones and swallow these whole. Field and laboratory experiments have shown that this method of hunting indeed still occurs, as a Wentletrap feeds on the tentacles of sea anemones by enclosing the tip of a tentacle with its proboscis and then eats it (Kokshoorn et al., 2007). Ceriantharia is a clade whose taxonomic position is currently argued; a situation attributed to the missing data on their fossil record.

1.6 Anemone Evolution

Molecular phylogenetic investigation has revealed that the division of the phylum Cnidaria into Anthozoa and Medusozoa possibly occurred in deep time, as early as the Cryogenian–Ediacaran (720–635 Ma) (Han et al., 2016) . The systematics and evolution of the cnidarian classes indicate that the Scyphozoa symbolize the basal class, while the Cubozoa take the middle position (Fig. 1.1). The Anthozoa are seemingly an early offspring of the common ancestors (Werner, 1973). The phylogeny of the cnidarian class Anthozoa (including tube anemones), is debatable; although anthozoans, Ceriantharia is a clade whose taxonomic position is currently debated, it is sometimes placed into clades of the Hexacorallia and sometimes estimated as an ancestral clade of all other Anthozoa clades. There are three phylogenetic hypotheses for the Anthozoa. First, based on mesenteric arrangements, (Wells & Hill, 1956) recommended three subclasses Ceriantipatharia, which are branched off first with Alcyonaria and then with Zoantharia (Fig. 1.2.A). Second, based on nematocysts, (Schmidt, 1974) divided the Anthozoan into two subclasses: Alcyonaria and Zoantharia, and suggested that the order Ceriantharia in the subclass Zoantharia is primitive and that the Antipatharia has a shared ancestor with the order Zoantharia (Fig. 1.2.B). Finally, based on the consensus of morphological and 18S rDNA sequence data (Won et al., 2001), the parsimony trees derived from the morphological data did not correspond strictly with the molecular data, the composite analysis using total evidence offers a more resolved and highly supported topology, as is indicated by higher bootstrap values and decay indices than either analysis alone, a tree was built from the molecular data, using neighbor-joining and maximum-likelihood methods, and which is similar to the results from earlier evidence. According to these results, Anthozoa is divided into three subclasses: Alcyonaria (Octocorallia), Zoantharia (Hexacorallia), and Ceriantipatharia. Ceriantipatharia now includes only one order, Ceriantharia, since the order Antipatharia is more strictly related to orders inside the Zoantharia. The Alcyonaria subclass is a monophyletic group, in which the order Pennatulacea is basal, and orders Alcyonacea and Telestacea appear later. The order Gorgonacea is divided into two suborders, Holaxonia and Scleraxonia. *Bellonela* is more related to order Stolonifera, making a monophyletic group. In Zoantharia, the order Zoanthinaria is basal, and the residual taxa are separated into two clades: one includes the order Actiniaria and the other contains orders Antipatharia, Corallimorpharia, and Scleractinia, the latter two orders making a monophyletic group (Won et al., 2001) (Fig. 1.2.C).

Ceriantharia show some detailed features such as labial tentacles and continuously forming coupled, not arranged, complete mesenteries in the intermesenterial box that is located on the opposite (ventral) side of the siphonoglyph. These specific characteristics suggest that the order Ceriantharia branches basally to Hexacorallia and is regarded as a sister group of other lineages of Hexacorallians (J. K. Han, Shin Uchida, Hiro-omi Stanley Jr, George D Yao, Xiaoyong Shu, Degan Li, Yong Yasui, Kinya, 2010); (Rodríguez, 2014).

1.7 Anemone Paleontology

Five cnidarian classes (Anthozoa, Hydrozoa, Cubozoa, Scyphozoa and Staurozoa) have been identified in the Cambrian fossil record; Cubozoa, Scyphozoa and Staurozoa are medusae. Hydrozoan include both medusa and polyp stages, but the basic part of the Anthozoan's adult stage is the polyp. Polyps are categorized by a terminal holdfast, and look like living peers in that they possess strong tentacles, oral and anal openings, and an oral disc. The tentacles lack cilia, which are recognized in the Chengjiang fossil *Xianguangia* (Fu et al., 2019). To date there are no fossil tube anemones, but there are sea anemone fossils, and one anemone-like problematic fossil. Here I will discuss only those soft-bodied anemone, or anemone-like fossils. The small sea anemone *Eolympia pedunculata* range from 500 to 670 μm in diameter and from 300 to 625 μm in height with or without pedicle from the Lower Cambrian of China, which is preserved in three dimensions

(Han et al., 2010), *Archisaccophyllia* (Hou et al., 2005), *Xianguangia* (Chen, 1991), and *Mackenzia* (Morris, 1993), which are all known to be from the Early or Middle Cambrian and have been identified with the Cnidaria based on their external appearance. They exhibit confident features such as siphonoglyphs, mouth shape and the expression of internal mesenteries through the body wall in *Archisaccophyllia* that defend this assignment. Traces attributed to the burrowing activities of anemones have also been found from the Early Cambrian (Mata et al., 2012), which would be consistent with body fossils from as early as the Lower Cambrian of *Eolympia pediculate,* a Cambrian sea anemone, regarded as a stem group of the Hexacorallia, from which the Ceriantharia may have diverged before the appearance of *Eolympia pediculate* (Han et al., 2010).

CHAPTER 2 - ARTICLE

An Upper Ordovician faunal assemblage from the Neuville Formation of Québec, including an exceptionally preserved soft bodied sea anemone, *Paleocerianthus neuvillii* n. sp.

HUDA ALGHALID, MARIO COURNOYER, JEAN-BERNARD CARON, and CHRISTOPHER B. CAMERON

Article in preparation.

2.1 Abstract

We studied exceptionally preserved fossils of the Upper Ordovician period from the Neuville Formation in the St. Lawrence platform of Québec. A significant aspect of this finding is that the locality and the fossil represent a new fossil deposit in the Ordovician period with Burgess Shale-type preservation, curated at the Musée de Paléontologie et de l'Évolution, Montréal. The collection is comprised of a trace fossil and 22 genera, including algae, cnidarians, bryozoans, brachiopods, mollusks, arthropods, and echinoderms. From these we describe an exceptionally preserved soft bodied cerianthid tubicolous sea anemone *Paleocerianthus neuvillii* n. sp. Fifteen slabs of limestone containing approximately 135 *P. neuvillii* fossil specimens were examined. *P. neuvillii* were tubicolous, and the tubes often shared a base with two, three or more additional tubes. The total length of the tubes varied from 24,9 mm to 51,0 mm (+ 36.9 mm) with little change in their widths, demonstrating allometric growth. These lived in fine sediment associated with brachiopods, trilobites and echinoderms. Individuals appear to have been buried rapidly by a sedimentary flow. This is the oldest record of a fossil tube anemone. Its soft-bodied preservation and the diversity of the Neuville Formation suggest it is a Konservat-Lägerstatte of the Great Ordovician Biodiversification Event (GOBE).

Key words: Ordovician Period, Trenton Group, Neuville Formation, sea anemone, *Cerianthus*, Great Ordovician Biodiversification Event (GOBE).

2.2 Introduction

The Ordovician Period (485–443 Ma) is characterized by an increase in the abundance and diversity of hard bodied invertebrates, including those with carapaces, shells and tubes. The Lower Ordovician was a time of extreme continental separation and the time when faunal evidence can be used to evaluate paleogeography in a decisive way (Fortey et al., 1989). The Lower- to Middle-Ordovician cooling phase shows a significant change in Early Paleozoic climate, which played an important role in defining marine biodiversity patterns (Trotter et al., 2008). The end of the Upper Ordovician marks the first major extinction event, when about 85% of marine species went extinct (Munnecke et al., 2010). Drivers of this large-scale global extinction include chemical and physical processes that occurred in the atmosphere and oceans, including sea-level changes, caused by major glaciations. The main sign of extinction near the Katian/Hirnantian-Age boundary is correlated with the rapid growth of south polar ice sheets on Gondwana. Development of continental ice sheets was accompanied by significant cooling of the tropical oceans, a major perturbation of the global carbon cycle which drained the vast cratonic seaways that characterized the Upper Ordovician world (Sutcliffe et al., 2000). In the Ordovician, the fossil record is especially rich with shelly invertebrates, which characterized and provided understanding for both the fossilization process or taphonomy, and the paleoecology (Holland et al., 2009).

Despite the abundance of Ordovician fossils, Lägerstatte are rare. A Lägerstatte is a sedimentary deposit that exhibits a diversity of extraordinary fossils with exceptional preservation and often includes preserved soft tissues. Soft-tissue fossils are rare because they deform, decay and disappear before fossilization. Preservation of soft tissues has only occurred in rare circumstances where non-mineralized body parts resisted decay processes long enough to be transformed into recalcitrant carbonaceous ingredients or become secondarily replicated by minerals, which preserved them over geologic periods (Briggs, 2003). Some examples of exceptionally preserved fossil localities in the Ordovician include the Fezouata and Tafilalt Biota of Morocco (Van Roy et al., 2015). The Fezouata Biota is a Lägerstatte from the Lower Ordovician (Tremadocian–late Floian) in the central Anti-Atlas mountains of Morocco (Lefebvre et al., 2016). It is considered to have exceptionally well-preserved fossils (EPFs) that can even be interpreted as original assemblages buried by storm sediments, similar to storm wave-bases (Vaucher et al., 2016). The rapid burial in fine grained sediment, early suppression of microbial activity, low concentrations of both sulfate (in the global ocean) and oxygen (in the bottom waters) contribute to the flat aspect of fossils; all of these conditions are considered as Ordovician Burgess Shale type (BST) (Gaines, 2012). The Tafilalt biota includes sponges, annelid worms, a great variety of superbly-preserved arthropods, graptolites, conulariids, hyolithids and other molluscs, brachiopods, bryozoans, and echinoderms (Young et al., 2012).

Beecher's Trilobite Bed, Upper Ordovician of New York State, is best known for its trilobites, notably *Triarthrus* and *Cryptolithus*, with limbs preserved in pyrite. Pyrite forms generally in fine-grained marine shales. It is formed through the activity of sulphate-reducing bacteria and regularly occurs throughout the sediment (Briggs & Edgecombe, 1993). Soft tissues are preserved by pyrite replacement, which occurred in the presence of suboxic and iron rich pore waters (Raiswell et al., 2008). Such fossils are rarely regarded as BST, as they only occur by rapid depositional mudstones

(Farrell et al., 2009). In addition to trilobites, this location includes other taxa such as graptolites, branching algae, brachiopods, and problematica (Hagadorn, 2004).

The Soom Shale Lägerstatte, of Upper Ordovician age, crops out in the Cedarberg mountain range, to the north of Cape Town, South Africa. This unique Ordovician Lägerstatte preserves both completely soft-bodied organisms and some animals which have biomineralized parts. This deposit includes conodonts, naraoiid arthropods, eurypterids, chitinozoans, orthocones with encrusting brachiopods, cornulitids and myodocopid ostracodes (Aldridge et al., 2006). The low-variety community lived in an uncommon cold-water setting, dominated by anoxic bottom waters, in the immediate result of the Hirnantian glaciation (Gabbott et al., 2016).

The William Lake and Airport Cove Upper Ordovician Lägerstatten are near Manitoba, Canada. The fossils and rocks at these sites show rapid burial under anoxic and/or hypersaline circumstances. Wave and current energy were possibly higher at Airport Cove than at William Lake. Both sites contain 16 order or class-level groups. Soft tissue residues and articulated arthropod sclerites are found in William Lake, and arthropods are the best-preserved specimens from the Airport Cove fossils (Young et al., 2007).

The Winneshiek Lägerstatte, a mid-Ordovician (Darriwilian) site in northeast Iowa, includes a non-shelly fauna of a special marine environment. It is characterized by unusual fossils and extraordinary fossil preservation including tissue and soft bodies. Its unusual geologic setting is preserved within the 5.6 km diameter and ~200 m deep Decorah structure originated by meteorite impact (French et al., 2018). Assemblages from this locality have yielded conodonts, linguloid brachiopods, large fragments of eurypterid cuticles and phyllocarid crustaceans (Liu et al., 2005).

Next, we showcase a diversity of fossil taxa from some localities in Québec and review the fossil record from the Cambrian to the Ordovician Periods.

2.3 The fossils in Québec

Fossils from Québec extend from the Lower Cambrian to the Upper Ordovician Periods. The lower Ordovician limestone mixture is exposed at several localities on the south shore of the St. Lawrence, from Lévis to Grosses Roches -- a distance of about 270 miles -- have yielded large assemblages, in which Lower, Middle and Upper Cambrian fossils are represented. Rocks of different ages (Lower, Middle and Upper Cambrian) often lie close together in the same bed, and, being identical lithologically, can be divided based only on the origin of the enclosed fossils. (Rasetti, 1948a). The Lower and Middle Cambrian are known for their trilobites, in which forty species are described from the limestone rocks characterized by an excellent state of preservation (Rasetti, 1948b). The best known soft-bodied fossils in Québec are scyphozoan medusa and rare unmineralized arthropods. These Cambrian medusae and soft-bodied arthropods are the oldest soft-bodied animals described from Québec (Lacelle et al., 2008). On the other hand, the best-known Ordovician fossils in Québec are shelly fossils. The Lower Ordovician at the deep water layers of the Lévis Formation (Middle Cambrian-lower Middle Ordovician) showing in and around the Lévis-Lauzon area of southern Québec (eastern Canada) comprise a well preserved ichnofauna dominated by simple horizontal burrows of *Planolites* Nicholson, *Alcyonidiopsis* Massalongo and the fecal pellet *Tomaculum* Groom (Pickerill & Narbonne, 1995). The Trenton Limestone (Middle Ordovician), also known by its graptolites zone, also contains large numbers of brachiopods, ostracods, bryozoa, trilobites, gastropods, crinoids, cephalspods, coelenterates sponges and algae. (Belt et al., 1979). It is in part comprised of soft-bodied organisms or soft-parts, including an errant polychaete, a lingulid brachiopod pedicle, and the appendages of several species of trilobite (Morris et al., 1982). At the Laval formation of the Chazy Group (Middle Ordovician) near Montreal, bryozoan, algae and sponges, which control the cavity biota, have been found (Kobluk, 1981). The Nicolet River Valley, in the St. Lawrence platform (Upper Ordovician), is an exceptional setting to discover successional regularities in the incidence of invertebrate fossils (Bretsky & Bretsky, 1975). Graptolites provide the only biostratigraphical zonation of the Nicolet River formation (Walters et al., 1982).

Far from the Saint Lawrence River valley is another formation, the Upper Ordovician Whitehead formation of Percé that is comprised of fauna from thirteen recognized areas, including twenty-six trilobite species and eighteen brachiopod species (Cooper & Kindle, 1936) and twenty-three cephalopod species (Foerste, 1936). This assemblage contains six genera that are unique to North America, but that are known in Europe (Cooper & Kindle, 1936).

This study outlines a diverse fossil fauna from a new geological locality in southern Québec, the Saint-Joachim quarry, where Upper Ordovician marine clastic rocks of the Neuville formation of the Trenton Group contain exceptionally preserved fossils including algae, cnidarians, bryozoans, brachiopods, mollusks, arthropods, echinoderms, and trace fossils. Significantly, it also includes a species of soft bodied tubicolous anemone, which we describe here as Konservat Lägerstatten.

2.4 Fossil Fauna of The Saint-Joachim Quarry

The Saint-Joaquim quarry fossil fauna is diverse and abundant, meeting the criteria for its designation as a Konservat-Lägerstatte (Table 1). The Ordovician deposits are distinctive, notably for their abundance of well-preserved fossils found in limestones and shales, which were deposited as sediments on the sea floor. These include invertebrates such as trilobites, bryozoans, brachiopods, Mollusca, echinoderms, and graptolites. Their excellent preservation is attributed to these deposit's fine sediment matrix, environment and the nature of deep water in low energy and muddy bays. These features allowed for very little diagenesis and no metamorphic change of the fossil's burial. All of these conditions are necessary for the creation of Konservat-Lägerstatten.

Konservat-Lägerstatten only form when there has been obrution (sudden burial) by the rapid deposition of fine-grained sediment (mud) and the rapid removal of oxygen (Holland et al., 2009). Moreover, Konservat-Lägerstatten have preserved soft bodied, lightly sclerotized organisms, and/or the soft composition of forms otherwise known only from their mineralized or decay-resistant anatomy. Such sediments are rare in the fossil record because unmineralized tissues are usually broken down completely by post-mortem scavenging and decomposition. Konservat-Lägerstatten are key to understanding the origins and the evolutionary histories of organisms and offer exceptional evidence of extinct biological communities (Young et al., 2013).

2.5 Location, Stratigraphy and Geological Setting

The material studied for this memoir was collected from a small quarry located at Saint-Joachim, approximately 43 km northeast of Québec City, Québec, Canada (Fig. 2.1. B). The stratigraphy of the Saint-Joachim quarry has not been formally described, nor for that matter has that of any of the other limestone quarries located east of Québec City. For the area east of Quebec City, the quarry at Château-Richer is the best understood geological setting (Harper & Pickerill, 1996; Plckerill & Forbes, 1979). The rocks from the Château-Richer quarry are comprised of Upper Ordovician limestones and shale interbeds, which are interpreted to be included within the uppermost Neuville Formation (and in the youngest Grondines Member) of the Trenton Group (Harper & Pickerill, 1996). The Trenton Group of Québec represents a transgressive continental

(Laurentian), platformal margin succession deposited on a carbonate ramp that primarily developed in warm-water tropical and later in temperate conditions (Lavoie, 1995).

The Neuville Formation, a geological formation of the Trenton Group (Clark, 1995) extends from Grondines (its westernmost part) to Saint-Joachim (its easternmost part) (Fig. 2.1. A). It is divided into two geological members: The Saint-Casimir Member (oldest) and the Grondines Member (youngest). The richness of fossils is variable in the Grondines section (the upper 52 meters of the Grondines Limestone Member include graptolites). Two biozones are found in the Grondines Member: the *Cryptolitus lorettensis* zone at the base, and the *Rafinesquina deltoidea* zone above (Globensky, 1987; Globensky & Jauffred, 1971). The Neuville Formation consists of beds of limestone of 1 to 15 cm divided by thin beds of clay shale. The limestone, usually compressed, is semi-lithographic in the lower part, with only a few beds with crystalline texture. The Saint-Casimir Member (lower and older) is characterized by a larger percentage of semi-lithographic limestone, and the Grondines Member (upper and younger) by a higher percentage of shale intervals (Globensky, 1993).

The rocks at the Saint-Joachim Quarry are somewhat similar to those of the Château-Richer quarry, which are regarded as belonging to the Grondines Member. However, an abundant and diverse echinoderm fossil fauna, new trilobites species, and soft bodied fossils, suggests that these rocks may belong to: i) a new geological member, or ii) a new rock formation. For the purpose of this study the limestones rocks at the Saint-Joachim Quarry will be considered here as belonging to the Grondines Member of the Neuville Formation of the Trenton group.

2.6 Materials and Methods

All of the fossil specimens that form the basis of this study are deposited in the collections of the Musée de paléontologie et de l'Évolution, Montréal, Québec, Canada. Reflected light photographs were made with an Olympus D80 camera, under a Lowel 1000W tungsten light, and paired polarized lenses. These photos were used in the morphological and elemental analysis.

Other photos were used for measurements with ImageJ software (NIH). Each specimen was photographed by a Nikon D3100, with two lenses, one for general view SIGMA DC 17-10 MM 1:2.8-4.5 Macro, HSM, and the other an AF-S Micro Nikkor 85 mm 1:3.5 GED for individual group views. Additionally, a Macro extension tube (20 mm-12 mm. N-AF Digital) was used to take more precise closeup pictures under three different conditions: i) with two soft-white halogen lightbulbs: 23 w, 120 v, 60 Hz mA. CF23 EL/ Micro 6500K, lighting in two positions (vertical and horizontal), located on the right side of the camera (Nikon D3100); ii) in polarized light, using an optical filter to enhance contrast and reveal features of the gut; and iii) submerged in water or ethanol to reveal details not seen with the other methods. The specimens are flat in relief and did not need preparation before photography. Photographs of thirty-nine *Paleocerianthus neuvillii,* specimens were measured using ImageJ. The width and height of each specimen was measured. These traits were then graphed using Excel (Microsoft).

An electron microscopic analysis was conducted on *Paleocerianthus neuvillii,* specimen MPEP713.3 using an SEM, FEI environmental scanning electron microscope (ESEM) with a Field Emission Gun (FEG) Quanta 200 model. The EDS mapping and point elemental analyses were done in a low vacuum pressure chamber of 70 Pa.

EDS: The EDS detector is an energy dispersive X-ray spectroscopic (EDAX) Octane Plus SDD detector, running on TEAM software.

The EDS map settings for the multi-field map of the tip of one specimen were: Individual Field of View Magnification: 150X, voltage: 12 kV. Spot size (arbitrary number with no units): 5. Aperture on column: 5 (40 µm aperture). Working distance: 10.1 mm. Amplification time: 1.92 s. Dead time: 11.2 s. X-ray counts per second (cps): 28,000-30,000. Map resolution: 512x400. # Frames: (Number of times it scanned each field of view to compile the data): 8. Dwell time: (time spent at each pixel): 500 µs. Map matrix: 6 x 8 fields of view (final image is composed of 48 fields of view stitched together: 6 columns, 8 rows). Total mapping time: 12 hours.

EDS multi-field map of matrix outside the fossil area: Individual Field of View Magnification: 100x. Voltage: 12 kV. Spot size: 5. Aperture on column: 5 (40 µm). Working Distance: 9.7. Amp time: 1.92 s. Dead time: 12.3 s. X-ray counts per second (cps): 33,000-35,000. Map resolution: 512x400. # Frames (Number of times it scanned each field of view to compile the data): 8. Dwell time: 200 µs. Map matrix: 3 x 4 (final image is composed of 12 fields of view stitched together: 3 columns, 4 rows).

Any quantitative data is ZAF-corrected (corrected for Atomic number (Z), Absorbance of x-rays (A), and Fluorescence (F).

2.7 Systematics

Phylum Cnidaria (Hatschek, 1888)

Class Anthozoa (Ehrenberg, 1834)

Subclass Ceriantipatharia (Van Beneden, 1898)

Order Ceriantharia (Perrier, 1893)

Family Cerianthidae (Milne-Edwards, 1851)

Diagnosis: Long, solitary, anemone-like forms, without pedal disk, with numerous simple tentacles in two whirls, oral and marginal; septa numerous, single, complete; siphonoglyph single dorsal (Hyman, 1940). Life cycles of ceriantharian species have only been described from this family, based on individuals which have two general types: long-term larvae and short-term larvae. Most of these family species have plankton larvae in their life cycle (Stampar et al., 2015).

Genus *Cerianthus* (Chiaje, 1841)

Diagnosis: Cylindrical body with an anterior conical hole, surrounded by a twofold series of long tentacles exterior or marginal, and short tentacles interior or buccal, back attenuated and provided with a circular terminal orifice, acontiferae living implanted in mud or sand provided with a casing containing felted nemoatocysts and mucus. Mesesnteries and tentacles usually numerous, so that the quartette system of the deuterocnemes is distinct.

Anthoactis (Leloup, 1932)

Diagnosis: Marginal tentacles 3.5 mm. long. The circular body supports very long marginal tentacles, the aboral pole rounded has no evidence of aboral pore. The peristome is raised into a buccal cone spread out and divided by oval actinostoma.

Nautanthus (Leloup, 1964)

Diagnosis: Yellowish-white in the preservative liquid. Tubular shape, two circles of tentacles, 24 marginals, 24 labials, close together, forming a crown rejected outside.

Pachycerianthus (Roule, 1904)

Diagnosis: The second group of the protocnemes are short, antiseptic and provided with an extremely well-developed region of the cnido-glandular tract.

Ceriantheopsis (Carlgren, 1912)

Diagnosis: The second group of the protocnemes are long, fertile and provided with a very small region of the cnido-glandular tract.

Ceriantheomorphe (Carlgren, 1931)

Diagnosis: Cerianthidae, the mesenteries of which, except the directives, are all fertile. The second couple of protocnemes are long and provided with a small plectocraspedon. Arrangement of the metacnemes in each quartette MBmb are more or less distinct. M. is diminishing in length towards the multiplication chamber with some breaks. Siphonoglyph probably always small, hyposulcus small or well developed. Large forms with numerous tentacles.

2.8 Results

Paleocerianthus neuvillii n. genus.n. sp. (Figs: 2.2, 2.3, 2.4, 2.5)

2.8.1 Diagnosis

Ordovician Period fossils. Simple tubular body with blind gut. One or more rows of tentacles.

2.8.2 Material examined

Holotype: MPEP713.4. Approximately 135 specimens, on 15 rock slabs –MPEP713.1. through to MPEP713.15. Of these 135 specimens, 39 were sufficiently complete that they were measured for total length and maximum width. One specimen was sufficiently complete (MPEP713.4) that the number of tentacles was estimated.

2.8.3 Etymology

Genus: *Paleocerianthus*. Paleo for *'palaios'*, old, ancient, cerianthus for the genus *Cerianthus*. Species: '*neuvillii'* after the Neuville Formation of the St. Lawrence platform of Québec, Canada.

2.8.4 Occurrence

Neuville Formation of the Saint Lawrence Lowlands of Québec, Canada.

2.8.6 Description

Paleocerianthus neuvillii, n. sp. is a tubicolous sea anemone (order Ceriantharia). The approximately 135 individuals were small, their average length was 36.9 mm (± 39) and their average width was 6.0 mm (± 39, N=39). About three specimens show slight details of the tentacles, some specimens show details of the gut and the tubes (Fig. 2.2. A, B, C). The basal ends of the tubes were dark black, and 5 specimens showed some annular rings at the base of the tube (Fig. 2.2. C). An interpretive drawing of *Paleocerianthus neuvillii* as a living animal is provided (Fig. 2.3. A, B). Some individuals were attached, resulting in 35 clusters, indicating a facultative semi-colonial existence (Fig. 2.4). There is no indication that the tubes were inside of burrows, as with living cerianthids. Instead, the tubes appear to have been epibenthic, most probably perpendicular to the sea floor. In modern forms, an individual can rapidly withdraw into the tube, in response, for example, to a predator. All 135 fossils appeared to extend from the mouth of the tube. This may be because *P. neuvillii* could not withdraw into the tube or may have extended from the tube in response to low oxygen conditions that followed a rapid burial. There was no evidence of contractile or connective tissues.

Some fossils show details of the gut and of crowns of tentacles. The guts appear clearly in the middle of the tube and were blind (Fig. 2.5). The gut showed no evidence of a siphonoglyph. The mid-gut was about 1.388 mm (± 4) wide, and the posterior gut was 2.309 mm (± 3) wide. The tentacles were numerous and hollow (Fig. 2.2. A). We estimated that there were 8 or more tentacles in the best-preserved specimen (MPEP713-04) in a single corona. No individual crown of tentacles was found in the open, relaxed, feeding position. Instead, the crowns of tentacles were tightly packed, intertwined, and extending anteriorly from the body (Fig. 2.2A). Although no mouth was seen, it is presumed to be at the center of the crown of tentacles. Body septa were not found.

Growth was allometric, varying little in width with an increase in length (Fig. 2.6), the data should be taken with caution because i) anemones are soft bodied and ii) the fossilization process likely changed the actual biological measurements. Despite these problems, allometric growth is characteristic of most animals including anemone, indicating the most common form of development and suggesting that this type of development evolved at least 480 million years ago.

2.8.7 Remarks

P. neuvillii is a new genus. It is the only fossil in the family Cerianthidae, and its morphology is unlike the living genera. Moreover, the following genera are known only from the larvae: *Synarachnactis* (Carlgren, 1924), *Sacculactis* (Leloup, 1964), *Syndactylactis* (Carlgren, 1924), *Apiactis* (van Beneden, 1897), *Peponactis* (Van Beneden, 1897), *Paradactylactis* (Carlgren, 1924), *Isodactylactis* (Carlgren, 1924), *Trichactis* (Leloup, 1964), *Engodactylactis* (Leloup, 1942), *Plesidoactylactis* (Leloup, 1942), *Parovactis* (Leloup, 1964), *Bursanthus* (Leloup, 1968) and *Solasteractis* (van Beneden, 1897). *Paleocerianthus* is unusual in that it possesses a single corona of tentacles, unlike living genera, which always have two rows of tentacles.

2.8.8 Paleontology

P. neuvillii lived in dark, fine sediment, indicating an abundance of organics and a low energy environment, akin to the Cambrian Period Burgess Shale (Figs. 2.2 and 2.4). Individuals were oriented in the same direction, suggesting a rapid burial by a mud-slide (Fig. 2.4). The sediments appear to originate in a relatively deep-water, outer shelf location where bottom currents were not found. Though some specimens are exceptionally well preserved, others showed evidence of decay, suggesting a low, but variable presence of oxygen following burial. (Fig. 2.2.A) shows excellent preservation whereas (Fig. 2.2.B) shows evidence of decay.

2.8.9 Preservation

Elemental analysis of specimen MPEP 713.3 revealed that it is mostly carbon, but slightly enriched in calcium or magnesium. The matrix is richer in aluminum and potassium. None of these elements may be original, except for carbon (Fig. 2.7). This is similar to the Cambrian Period Burgess Shale and confirm Burgess Shale-type preservation. This type of preservation that encapsulated soft-bodied specimens is rare in the Ordovician, perhaps because of the closure of the taphonomic window that favored Burgess Shale-type preservation (Gaines, 2012).

2.9 The Sympatric species at Saint-Joachim Quarry

The Saint-Joachim quarry fossil fauna contains a putative branching algae, consisting of a single specimen (MPEP706.83) (Fig. 2.8) (Table 1). There are two Cnidarians, in addition to the one described here; there is a Cnidaria, Scyphozoa, Conulariida, Conulatidae. *Conularia* sp. Paleoecology: Stationary epifaunal suspension feeders, rare, specimen (MPEP706.79) (Fig. 2.9). There are two Bryozoans, one is a branching form which is a stationary epifaunal suspension feeder

(MPEP706.22) (Fig. 2.10), and a Bryozoa, Stenolaemata, Cryptostomata, Arthrostyliidae, *Arthroclema* cf. *billingsi*. Paleoecology: Stationary epifaunal suspension feeder, extremely rare (one specimen found), specimen (MPEP706.75) (Fig. 2.11).

There are four Brachiopoda. The first is Brachiopoda, Lingulata, Lingulida, Trematidae, *Schizocrania* sp. Paleoecology: Stationary low-level epifaunal suspension feeder, rare, specimen (MPEP706.77) (Fig. 2.12). The second is Brachiopoda, Lingulata, Lingulida, Pseudolingulidae, *Pseudolingula* sp. Paleoecology: Stationary low-level epifaunal suspension feeder, rare, specimen (MPEP706.78) (Fig. 2.13). The third is Brachiopoda, Rhynchonellata, Orthida, Dalmanellidae, *Paucicrura* sp. Paleoecology: Stationary epifaunal suspension feeder, somewhat common, uncatalogued specimen. (Fig. 2.14), and the fourth one is Brachiopoda, Strophomenata, Strophomenida, Strophomenidae, *Strophomena* sp. Paleoecology: Stationary epifaunal suspension feeder, rare, specimen (MPEP706.76) (Fig. 2.15).

Three Mollusca are identified: Gastropoda Cyrtolites. sp. Paleoecology: Slow-moving low-level epifaunal grazer, not common, specimen (MPEP706.70) (Fig. 2.16), Mollusca, Cephalopoda, Trocholites. sp. Paleoecology: Slow-moving low-level epifaunal grazer, not common, specimen (MPEP706.80) (Fig. 2.17), and Mollusca, Cephalopoda, Orthocerida, Orthoceratidae, cf. *Orthoceras* sp. Paleoecology: Nektonic carnivore, rare, specimen (MPEP706.81) (Fig. 2.18).

There are nine Echinodermata. One is Crinoidea, Cladida, Dendrocinidae, *Dendrocrinus* n. sp. Paleoecology: Stationary intermediate-level epifaunal suspension feeder extremely rare, a new species denoted by Jim Brower, specimen (MPEP706.57) (Fig. 2.19). Three specimens of Echinodermata, Crinoidea, Disparida the first is Iocrinidae, *Iocrinus trentonensis*. Paleoecology: Stationary intermediate-level epifaunal suspension feeder, extremely rare, specimen (MPEP706.73) (Fig. 2.20), second is Homocrinidae, *Ectenocrinus simplex.* Paleoecology: Stationary intermediate-level epifaunal suspension feeder, shows directional flow, Pyritised, somewhat common on certain levels, specimen (MPEP706.61) (Fig. 2.21), and the third is Cincinnaticrinidae, *Cincinnaticrinus varibrachialus.* Paleoecology: Stationary intermediate-level epifaunal suspension feeder, rare, specimen (MPEP706.43) (Fig. 2.22). Echinodermata, Paracrinoidea, an unidentified new species. Paleoecology: Stationary epifaunal suspension feeder, extremely rare (only one specimen found) (MPEP706.69) (Fig. 2.23). Echinodermata, Rhombifera, Glyptocystida, Cheirocrinidae, *Cheirocystis* cf. *anatiformis.* Paleoecology:

Stationary intermediate-level epifaunal suspension feeder, somewhat common on certain levels, specimen (MPEP706.23) (Fig. 2.24). There are specimens of two Echinodermata, Soluta and one Asteroidea, the solutes are *Syringocrinus* cf. *paradoxicus.* Paleoecology: Unknown, rare, specimen (MPEP706.46) (Fig. 2.25), and the undet. n. sp. Paleoecology: Unknown, somewhat common on certain levels, specimen (MPEP388.1-a) (Fig. 2.26). The Asteroidea is an unidentified new species that is an epifaunal detritivore, extremely rare, only one specimen (MPEP706.3-f) (Fig. 2.27).

Of the Arthropoda there are two trilobite specimens, the first is an unidentified new species Odontopleurida, Odontopleuridae. Paleoecology: Fast-moving low-level epifaunal carnivore, somewhat common on certain levels (MPEP687.1) (Fig. 2.28). The second trilobite specimen, Phacopida, Calymenidae, *Flexicalymene.* cf. *multituberculata.* Paleoecology: Nektobenthic carnivore and rare (MPEP706.20) (Fig. 2.29). One trace fossil, common specimen (MPEP706.23-c) (Fig. 2.30).

The most common specimens in the biota at Saint Joachim quarry are the Echinodermata, which are much more abundant than the others. The Soluta undet. n. sp. is the most common, with about 155 individuals. Less common is *Cheirocystis* cf. *anatiformis*, at about 87 individuals. *Ectenocrinus simplex,* of the same phylum, is the third most-common species, with about 18 individuals. *Syringocrinus* cf. *paradoxicus*, three individuals. *Cincinnaticrinus varibrachialus, Dendrocrinus* n. sp. and paracrinoidea undet. n. sp. All have two individuals of each species. Finally, there is one *Iocrinus trentonensis,* and one asteroidea n. sp.

Trilobita, with 71 individuals, are the second most-common specimens at the Saint Joachim quarry, with two species, cf. *Meadowtownella* n. sp. containing 66 individuals, and *Flexicalymene*. cf. *multituberculata*, which has five individuals.

Brachiopoda are a close third, with about 70 individuals. These are composed of *schizocrania,* the most common at 36 individuals, *Paucicrura,* with about 32 individuals, and finally *Strophomena* and *Pseudolingula,* each with a single individual.

Eighteen trace fossils were recognized. Five Mollusca, gastropoda of cf. *Cyrtolites.* Three bryozoa were found; one *Arthroclema,* and two of undet. Two Mollusca, cephalopoda, one is cf. *Orthoceras,* and one is cf. *Trocholites*. Two undetermined algae, one Echinodermata new sp. and one Cnidaria *Conularia.*

2.9.1 Orientation and preservation

The orientation and quality of this fossil collection reflects the burial conditions and clues to the taphonomy of these animals just before death. In specimen (MPEP706.3), we can identify that the burial was from the top (partial directional flow) (Fig. 2.31. A). With specimen (MPEP 706.2), we were able to determine that the ground was hard in this rock type, which means there was no mud accumulation with clear and calm water, and so the species in this rock are well-preserved (Fig. 2.31. B). In (MPEP706.10), the three trilobite tails are pointed in the same orientation (Fig. 2.31. C). Specimen (MPEP706.61) indicates an orientational flow in the same direction. (Fig. 2.31. D). In specimen (MPEP 706.70), the Soluta undet. n. sp, have the same orientation (Fig. 2.31. E). In (MPEP706.71) the *Cheirocystis* cf. *anatiformis*, all have the same orientation (Fig. 2.31. F). In (MPEP706.75) the colony of the Bryzoan *Arthroclema,* is very fragile, but it is clearly visible with no fragments, an indication of its excellent preservation (Fig. 2.31. G). Specimen (MPEP706.77) shows approximately 36 individual *Schizocrania,* a high concentration of animals (Fig. 2.31. H). Only one soft bodied fossil is identified in specimen (MPEP706.83), a branching form of Algae (Fig. 2.31. I). (MPEP 388.8) the Solutans, undet. n. sp. this slab has four animals, one that is oriented in a different direction; the fact that three of them are pointing in the same direction shows the direction of the water flow (Fig. 2.31. J).

2.10 Discussion

Paleocerianthus neuvillii, n. sp, is an Upper Ordovician tubicolous sea anemone from Saint-Joachim, Québec, found in the Neuville Formation. *P. neuvillii*, n. sp. is morphologically similar to the living species of the order Ceriantharia. It has a tube-shaped body and a crown of tentacles around the mouth. The average length of the fossil individuals is 36.9 mm (± 39) and the average width is 6.0 mm (± 39). The modern Ceriantharia vary in size, with the largest tube individuals reaching up to a meter (Wallace, 2008).

Fossil records of the cnidarian sea anemone are abundant for the Cambrian period. In the 100 years since Walcott's first discovery of the Burgess Shale, exceptionally preserved fossil collections have been reported from Cambrian strata. The early Cambrian Chengjiang biota of Yunnan Province has matched the Burgess Shale in total diversity of soft-bodied taxa and accuracy of preservation. Along with the Qingjiang biota from South China, these localities are considered as BST thanks to their ecological, environmental and taphonomic grades and to their high abundance of soft-bodied animals such as cnidarians, including both medusoid and polypoid forms (Fu et al., 2019).

Some of the known cnidarian sea anemone which are not tubiculous include a polyp that is roughly cylindrical with its aboral end attached to the substrate by means of a disc-like holdfast called the pedal disc, while in colonies polyps are attached to each other's ends, either directly or indirectly. The oral end contains the mouth and it is surrounded by a circlet of tentacles (Fu et al., 2019). The Lower Cambrian specimens of *Bergaueria* is the earliest known occurrence of a sea anemone from the fossil record (Alpert, 1973). Soft-bodied fossils from the Lower or Middle Cambrian strata, such as *Archisaccophyllia kunmingensis*, appear to have twelve tentacles with six or seven longitudinal ridges (Hou et al., 2005), and *Xianguanagia sinica* has feather-like tentacles that have many long branches spreading alternately from the tentacle axis (Chen, 1991).

The genus *Bergaueria* has left cylindrical traces of a protuberance in the Ordovician sandstone beds of Bohemia (Prantl, 1945). These assemblies are also attributed to similar living anthozoans such as *Cerianthus.* Later work has shown that the genus seems to be probably actinian, compared to the burrows of living anthozoans, and so it is now considered as actinian and not as cerianthid dwelling sea anemones.

As mentioned earlier, for the exceptional preservation of soft tissues, the time between the death and the removal of oxygen from the decaying organism should be short. The preservation quality is significantly improved by rapid burial in fine-grained sediment in low turbulence conditions (Selden & Nudds, 2012). Elemental analysis of our fossil's rock indicates that most of the specimens are pure carbon, but part of it seems to be slightly enriched in calcium or magnesium, and the matrix is even richer in aluminum and potassium. None of these elements may be original, except the carbon. This composition is somewhat similar to the Burgess Shale type.

The fossil rock's precise composition is one of the reasons why it is proposed to be as significant as the Burgess Shale-type (BST) fossilization. It is a sediment composition with clay mineralogy. The siliciclastic deposits that preserve BST fossils have high clay-to-organic ratios, and clay minerals have been suggested to facilitate exceptional preservation by binding to autolytic enzymes, making them inactive and slowing the rate of decay (Anderson et al., 2018). Studies have also revealed the important taphonomic role that authigenic clay minerals play in exceptional preservation, specifically the preservation of non-biomineralized tissues and especially in carbonaceous compressions widely referred to as Burgess Shale-type (BST) in lower Phanerozoic marine deposits (Meyer et al., 2012). The elemental analysis maps confirm a Burgess Shale-type preservation quite clearly (Fig. 2.7).

Finding these fossils in a black shale indicates that their preservation occurred in a deep water, organic-rich and anoxic condition, which is very favorable to the conservation of organic matter. While the exact association between clay minerals and exceptional preservation is still being studied, as stated above, clay minerals play an important role in soft tissue conservation by preventing autolytic decay. However, new evidence indicates metamorphism also plays a role in creating and altering clays within fossils (Meyer et al., 2018). The preservation of BST fossils can be credited to pervasive clay-organic interactions as the organisms were transported in a moving sediment cloud and buried with all hollows and spaces filled with fine-grained clays (Butterfield, 1990).

The taphonomic procedures responsible for Burgess Shale-type fossils have been discussed at length, with explanations ranging from the simple absence of bioturbation, to the mechanical features of embedding clays, early aluminosilicate diagenesis, inhibition of decay due to enzyme adsorption on and within clay minerals, and inhibition of decay due to Fe^{2+} adsorption on structural biopolymers (Allison & Briggs, 1993; Butterfield, 2003; Wollanke & Zimmerle, 1990). Our specimens therefore meet all the Konservat- Lägerstatten conditions, including their location in a dark fine sediment, presentation of BST, the abundance of organics, a low-energy environment, and anoxic conditions. Their orientations suggest rapid burial by mud, and they present well-preserved images of soft tissue, in which some features such as the gut and the tentacles are visible (Fig. 2.2 A, B).

GENERAL CONCLUSION

Paleocerianthus neuvillii, n. sp. is a tubicolous sea anemone. The average length of the individuals is 36.9 mm (± 39) and the width is 6.0 mm (± 39). The *P. neuvillii* fossils show details of the tentacles, gut, and tubes. The basal ends of the tubes are dark, and some specimens show a few annular rings. Some individuals were attached at a shared base, resulting in 35 clusters, indicating a semi-coloniality trend. The tubes appear to have been epibenthic, unlike the tubes of living cerianthids which project from burrows in the sediment. There are approximately 135 specimens, and individuals on any one rock slab were oriented in the same direction, indicating a rapid burial by a mud-flow. This, and the lack of sedimentary ripples, suggests a subtidal habitat, rather than a calm, shallow, muddy bay. While some specimens are exceptionally well preserved, others show some evidence of decay.

Morphological (Schmidt, 1974; Wells & Hill, 1956) and 18s rDNA sequence analysis place Ceriantharia as monophyletic among the Ceriantipatharia, and basal in the class Anthozoa. *P. neuvillii* is the oldest known tube anemone and therefore may represent the plesoimorphic Anthozoan body plan (Fig. 3.1).

The fine preservation of this soft bodied anemone, including details of its adult development, paleoecology, and taphonomy support the argument that the Neuville Formation is a Konservat-Lägerstatte. The second line of evidence is the extraordinary diversity and abundance of other marine invertebrate fossils and an algae, representing 24 species. These include an unidentified algae, two Cnidaria, two Bryozoa, four Brachiopoda, two Mollusca, two Arthropoda, nine Echinodermata and a trace fossil.

These numbers are comparable to those of the Lower Ordovician Fezouata and Tafilalt Biota Lägerstatten of Morocco that have shelly fossils, including conulariids, a variety of trilobites (asaphids, harpetids, odontopleurids, phacopids, proetids, ptychopariids and agnostids), articulated hyolithoids and other molluscs (helcionelloids, bivalves, gastropods, nautiloids), brachiopods, occasional bryozoans, and echinoderms (homalozoans, asterozoans, various eocrinoids, cystoids, rare crinoids), planktic and benthic graptolites (Van Roy et al., 2010).

Beecher’s Trilobite Bed in the Upper Ordovician strata of New York State is a special Lägerstatte containing a typical locality for trilobites with appendages and other soft tissues preserved in pyrite. This location also contains brachiopods and graptolites (Rabano et al., 2008).

The Upper Ordovician Soom Shale Lägerstatte, in the Western Cape Province of South Africa includes conodonts myodocopid ostracodes, eurypterids and naraoiids, as well as chitinozoans, marine phytoplankton, brachiopods, orthoconic cephalopods and trilobites, organism’s indicative of a marine setting. The soft tissues of several taxa are preserved by their replacement by illite, often with alunite group minerals, and frequently to a high degree of fidelity. Most unique is the preservation of conodont myomeres, eye muscles, muscle tissue and gill tracts in eurypterid specimens (Whittle et al., 2007).

The William Lake and Airport Cove Upper Ordovician Lägerstatten biotas in Manitoba, Canada include dasycladacean algae, eurypterids, xiphosurids, conodonts, linguloid brachiopods, gastropods, cephalopods, and large phosphatic or chitinophosphatic problematic tubes happen at both locations with diverse relative abundances. These sites provided exceptional preservation (Young et al., 2007).

The biota of the Winneshiek Konservat-Lägerstatte in northeast Iowa is from the Middle Ordovician and includes the earliest eurypterid, as well as a new basal chelicerate and the earliest ceratiocarid phyllocarid, conodonts, bromalites and rarer elements, including a linguloid brachiopod and a probable jawless fish. Arthropod appendages and filamentous algae are also present (Briggs et al., 2018).

The Saint-Joachim site represents a snapshot of Ordovician Period fauna based on the sympatric species it yielded and the BST of their exceptional preservation, we described in chapter 2. By comparing its fossils with those of other Ordovician fossil sites such as the Lower Ordovician Fezouata and Tafilalt biota of Morocco, Beecher’s Upper Ordovician Trilobite Bed of New York State, the Upper Ordovician Soom Shale Lägerstatte in Western Cape Province, South Africa, the William Lake and Airport Cove Upper Ordovician, Manitoba, Canada and the Middle Ordovician of the Winneshiek Shale in northeast Iowa, we can argue that our site shares some of the most important features common to those sites, such as soft-bodied fossil preservation, taphonomy, BST, the nature of the sediments, the dark fine sediment, abundance of organics, low energy environment, anoxic conditions and the orientations. This unique combination of features supports the idea that this site should be regarded as a Lägerstatte. The variation of the sympatric species found in the Neuville Formation is also one of the best characteristics of the Ordovician Lägerstatte. This variation is composed of soft-bodied fossils, fragile fossils, hard fossils and a trace fossil.

We look forward to pursuing our studies analyzing and delving deeper into this unique collection of sympatric species from the Saint-Joachim quarry. Having this Ordovician Lägerstatte recognized in Québec would bring it broader attention. Further work on this unique collection will broaden our understanding of the Great Ordovician Biodiversification Event.

TABLES

Table 1. Faunal list of Saint-Joachim quarry, Québec, Canada

Algae?

- branching form
  - \- undet. n. sp.? *

Cnidaria

- Anthozoa, Spirularia, Cerianthidae?
  - \- *Paleocerianthus neuvillii* n. sp. *
- Scyphozoa, Conulariida, Conulatidae
  - \- *Conularia* sp.

Bryozoa

- Stenolaemata, Cryptostomata, Arthrostyliidae
  - \- *Arthroclema* cf. *billingsi*
  - \- branching form

Brachiopoda,

- Lingulata, Lingulida, Trematidae
  - \- *Schizocrania* sp.
- Lingulata, Lingulida, Pseudolingulidae
  - \- *Pseudolingula* sp.
- Rhynchonellata, Orthida, Dalmanellidae
  - \- *Paucicrura* sp.
- Strophomenata, Strophomenida, Strophomenidae
  - \- *Strophomena* sp.

Mollusca

- Gastropoda
  - \- cf. *Cyrtolites*. sp.
- Cephalopoda, Orthocerida, Orthoceratidae
  - \- cf. *Orthoceras* sp.
- Cephalopoda
  - *Trochlites*. sp.

Arthropoda

- Trilobita, Odontopleurida, Odontopleudidae
  - \- undet. n. sp. *
- Trilobita, Phacopida, Calymenidae
  - \- *Flexicalymene multituberculata* †

Echinodermata

- Crinoidea, Cladida, Dendrocinidae

- *Dendrocrinus* n. sp. *

Crinoidea, Disparida, Iocrinidae
- *Iocrinus trentonensis*

Crinoidea, Disparida, Homocrinidae
- *Ectenocrinus simplex*

Crinoidea, Disparida, Cincinnaticrinidae
- *Cincinnaticrinus varibrachialus*

Paracrinoidea
- undet. n, sp. *

Rhombifera, Glyptocystida, Cheirocystidae
- *Cheirocystis* cf. *anatiformis*

Soluta
- Undet. n. sp.*
- *Syringocrinus* cf. *paradoxicus*

Asteroidea
- undet. n, sp. *

Trace fossils

* - new species

† - new occurrence

FIGURES

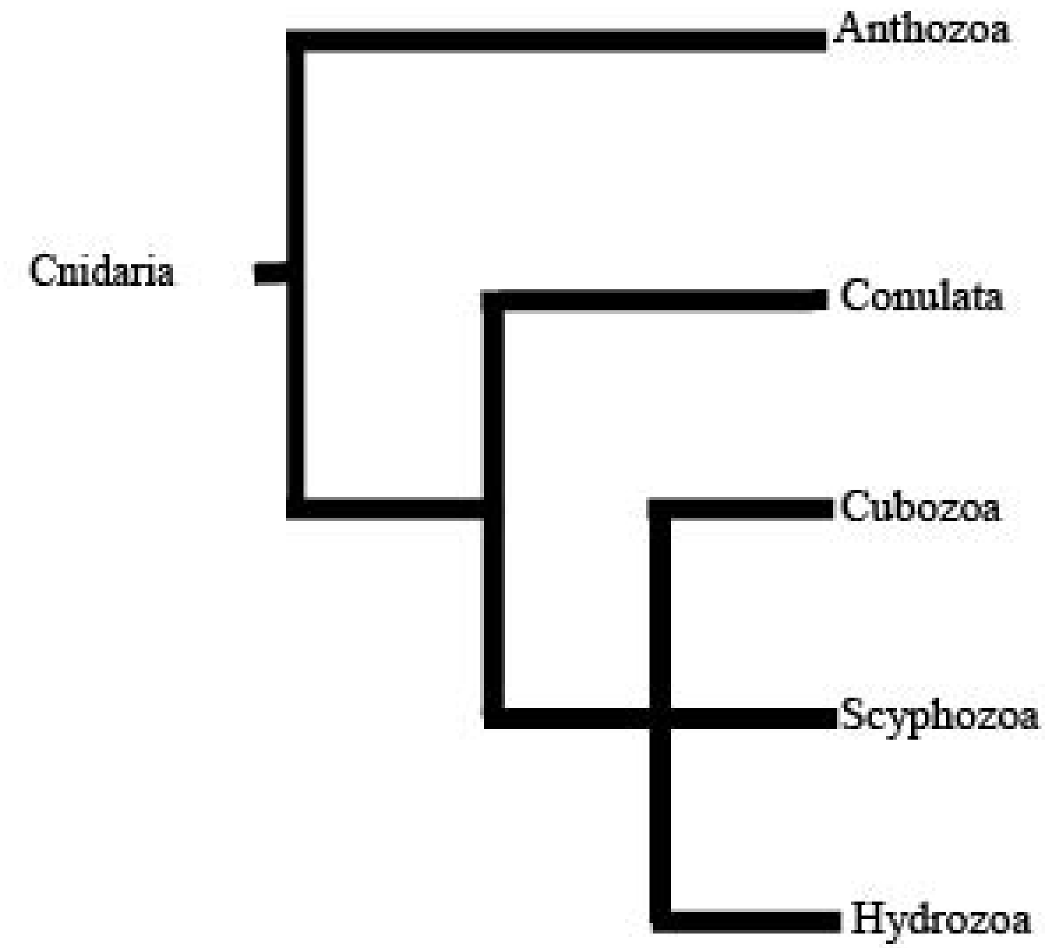

Figure1.1. The phylogenetic tree of Cnidaria.

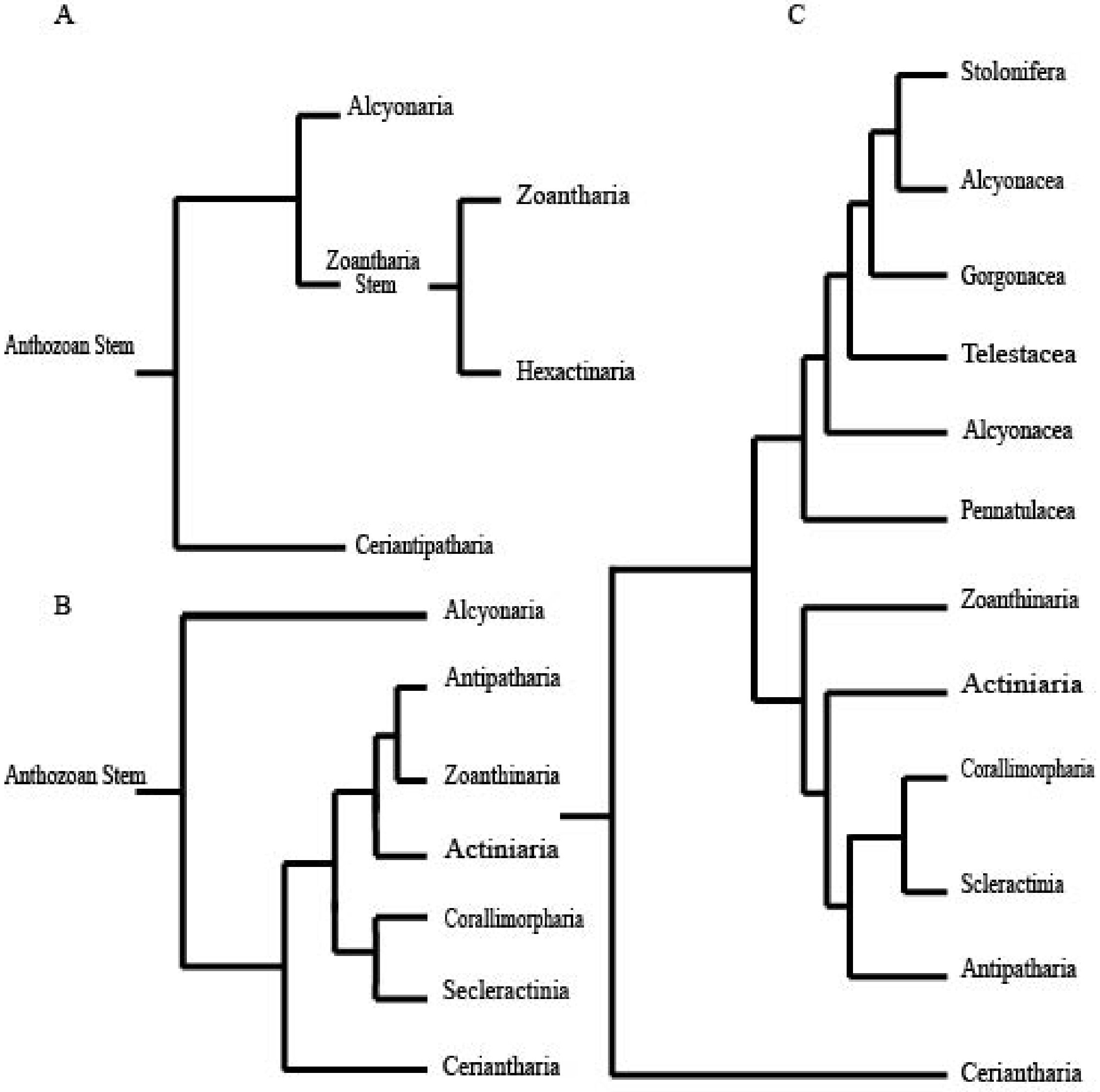

Figure 1.2. Phylogenetic trees of the anemones. A) based on mesenteric morphology, B) based on cnidocyte morphology, and C) based on morphology and an 18S rDNA tree.

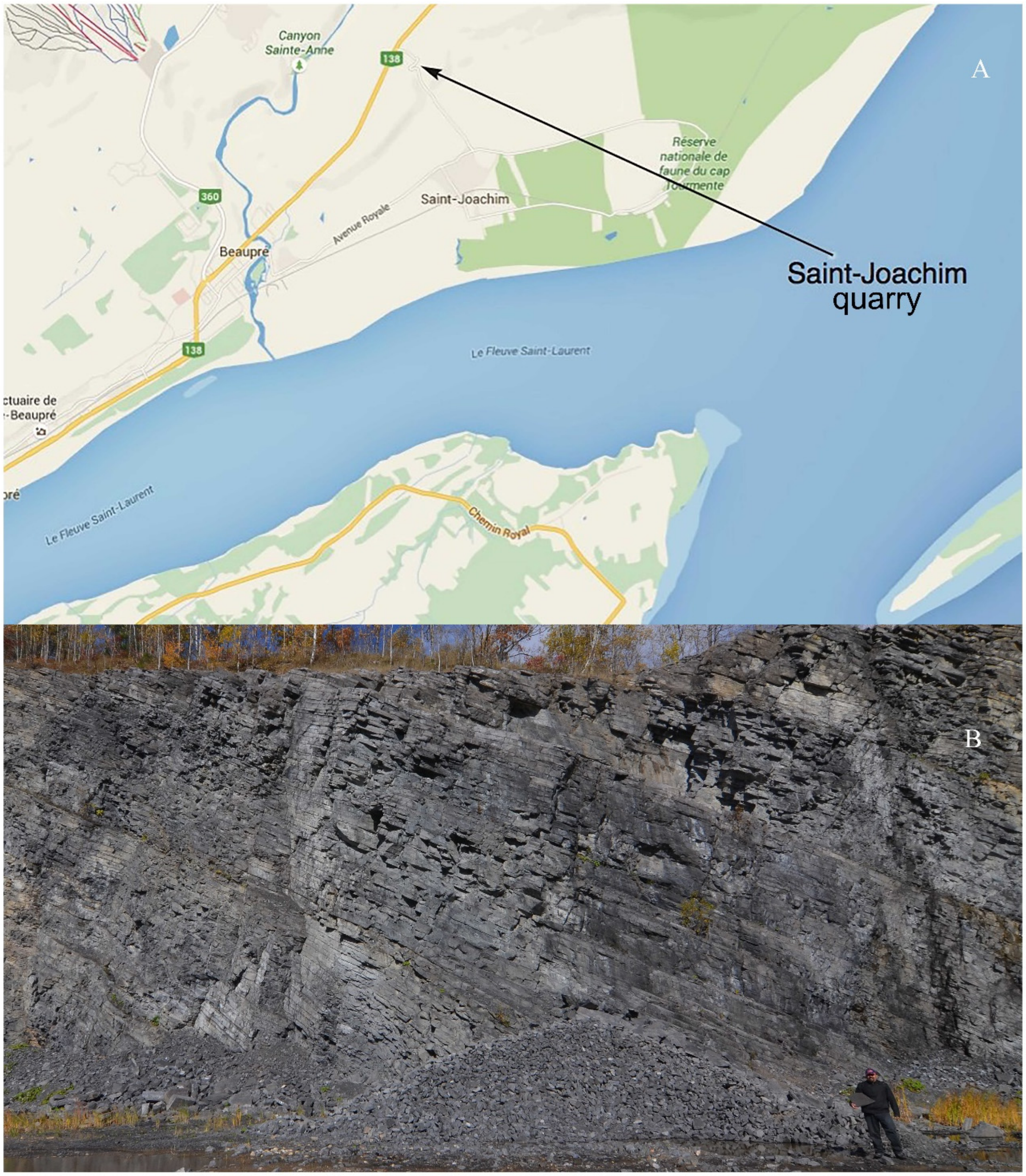

Figure 2.1. The Saint-Joachim quarry, Québec, Canada is part of the Upper Ordovician (N.A) (460.9 - 451 ma) Neuville Formation, a formation of the Trenton Group (Clark 1959). The Neuville Formation extends from Grondines (westernmost part) to Saint-Joachim (easternmost part) and consists of two geological members: The Saint-Casimir Member (oldest) and the Grondines Member (youngest).

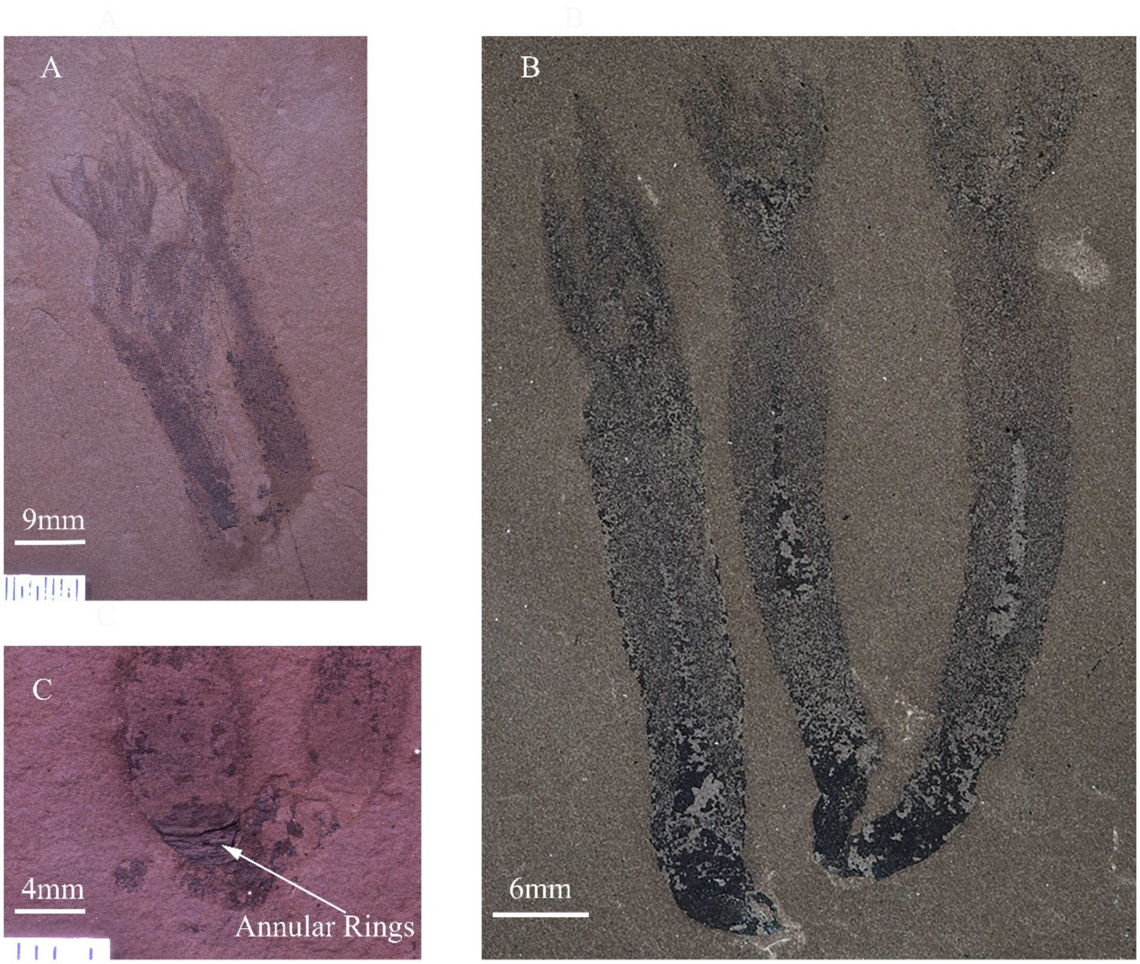

Figure 2.2. A, B, C. These three specimens show some specific details of preservation: A) shows the hollow tentacles, estimated to be more than 8 MPEP.713.04; B) shows the simple gut that stretches the length of the body MPEP.713.06; and C) exposes the annular rings at the end of the tube MPEP.713.07.

Figure 2.3. Our interpretations of the morphology of *Paleocerianthus neuvillii,* A) with closed tentacles, which may be an artifact of burial, and B) with tentacles extended open in the feeding position, characteristic of living species.

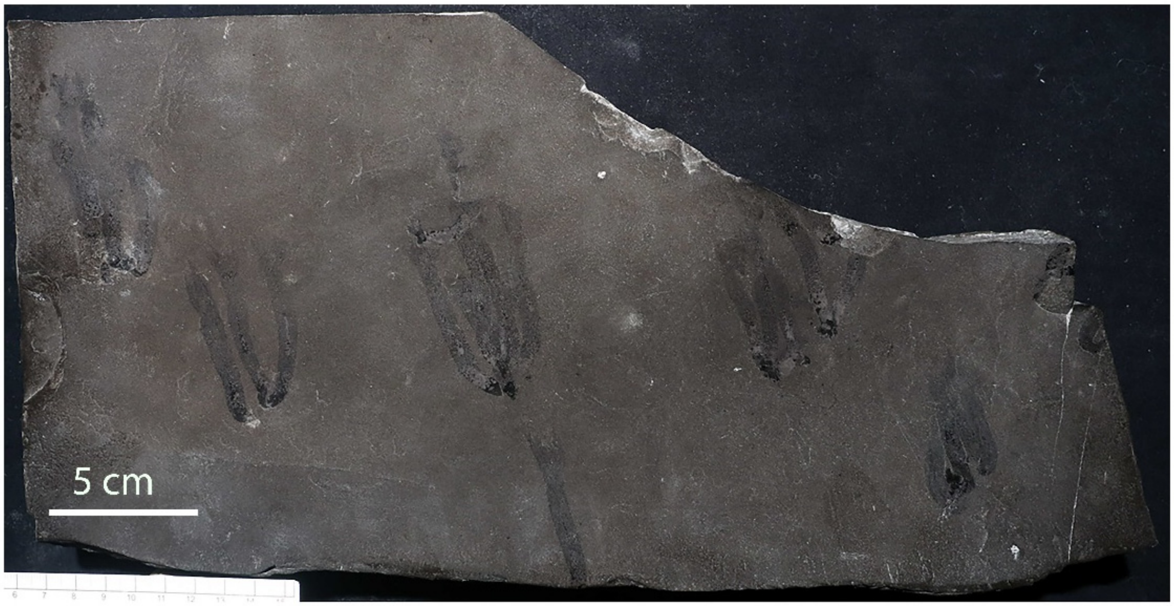

Figure 2.4. *Paleocerianthus neuvillii*. Notice that some individuals are attached at a common base, indicating 35 semi-colonial clusters. All of the specimens are oriented in the same direction, suggesting burial by a unidirectional mud MPEP.713.06.

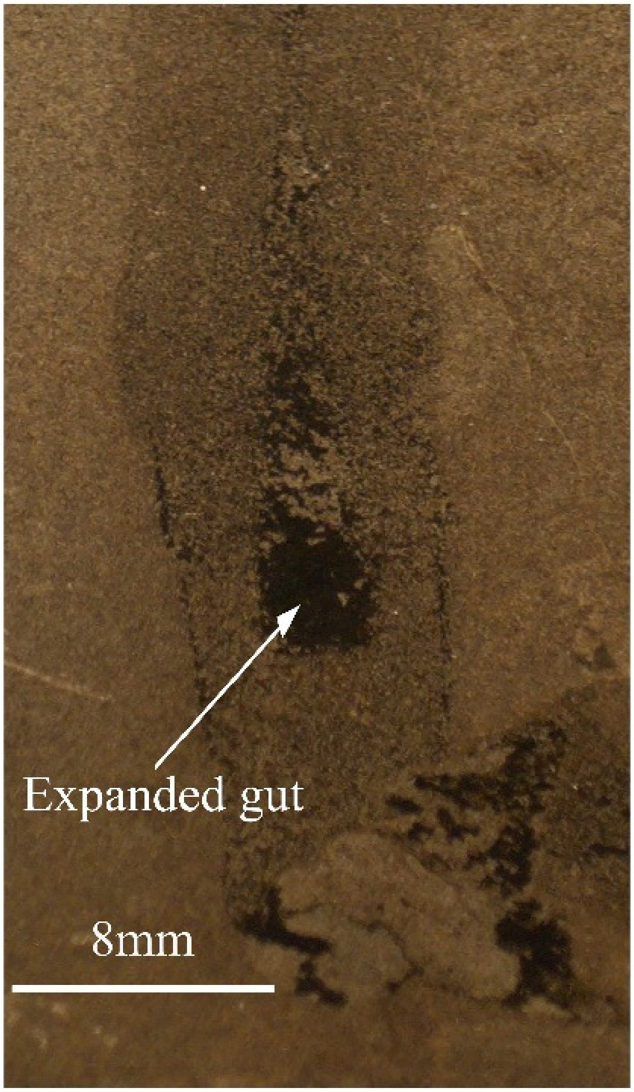

Figure 2.5. *P. neuvillii* had a blind gut, the widened from the mid- to the posterior gut. There was no evidence of a siphonoglyph in the gut or of a septal in the body cavity. The mid-gut is 1.388 mm (N=4) wide and the hindgut is 2.309 mm (N=3) wide MPEP.713.01.

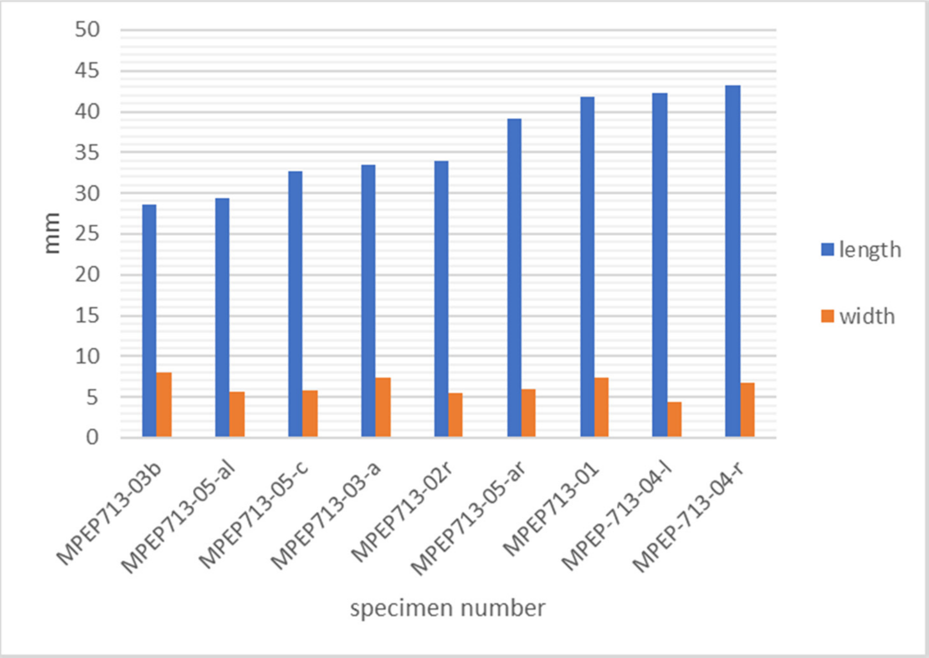

Figure 2.6. The width of *P*. *neuvilli* fossils show little change with an increase in length, suggesting allometric growth. The specimen number of each of these nine fossil specimens is indicated below each pair of lines.

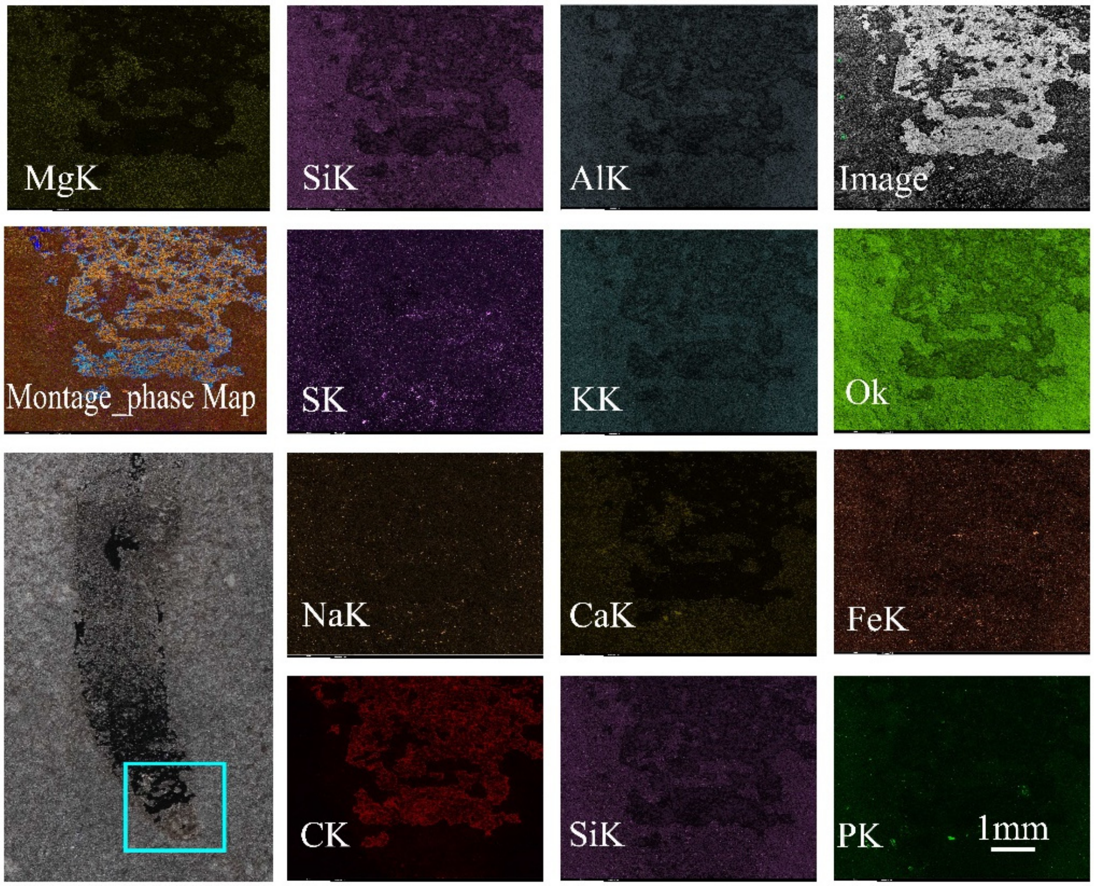

Figure 2.7. Elemental analysis of *P. neuvillii* fossil surface indicates that most of the specimens are pure carbon, but part of it seems to be slightly enriched in calcium or magnesium, and the matrix is richer in aluminum and potassium. None of these elements may be original, except for the carbon. This is similar to the Burgess Shale-type rock composition MPEP 713.03.

Figure 2.8. A branch algae form is another example of soft tissue preservation. Specimen (MPEP706.83).

Figure 2.9. The Cnidaria, *Conularia* sp was a stationary, epifaunal suspension feeders, rare. Specimen (MPEP706.79)

Figure 2.10. Branching form of Bryozoa, which are stationary epifaunal suspension feeders, (MPEP706.22).

Figure 2.11. The bryozoa, Stenolaemata, *Arthroclema* cf. *billingsi* was a stationary epifaunal suspension feeder, extremely rare. A single specimen was found (MPEP706.75).

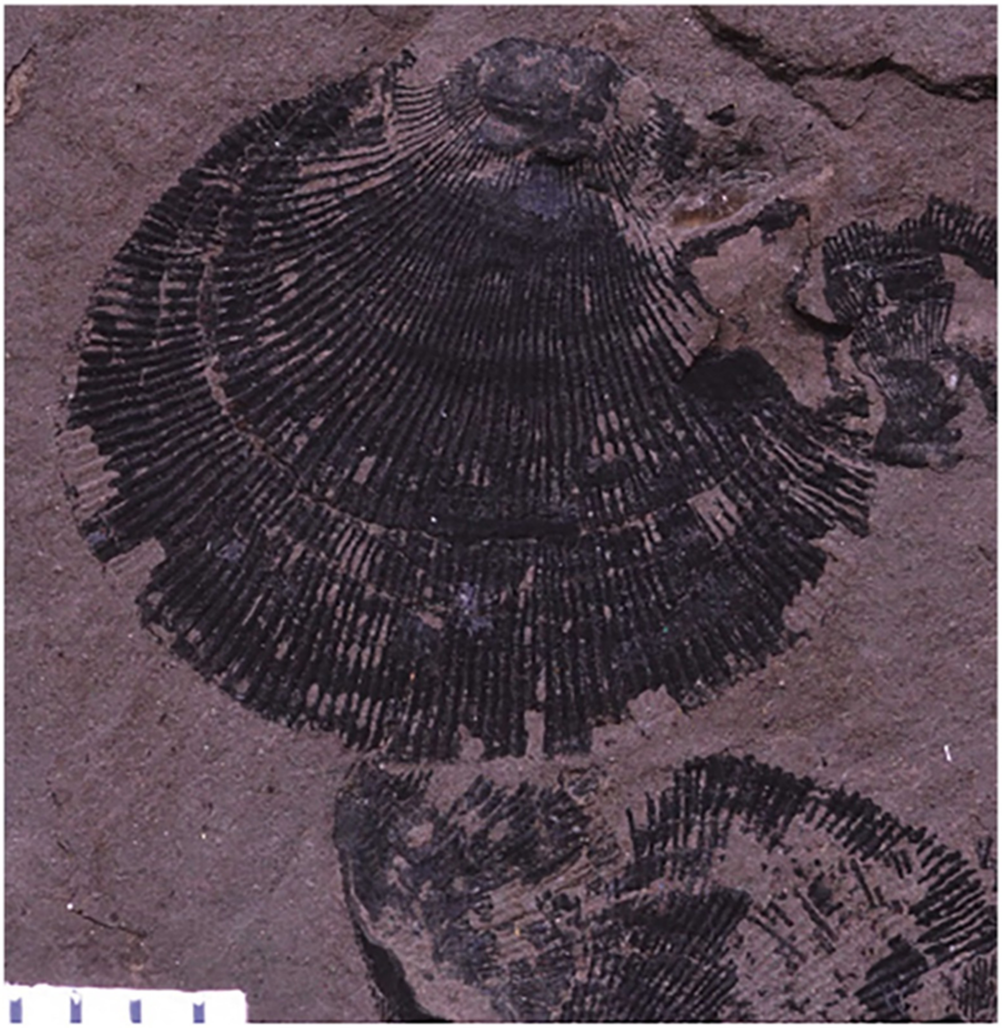

Figure 2.12. The Brachipoda, Lingulata, *Schizocrania* sp. was a stationary low-level epifaunal suspension feeder, rare. Specimen (MPEP706.77).

Figure 2.13. The Brachipoda, Lingulata, *Pseudolingula* sp. was a stationary low-level epifaunal suspension feeder, rare. Specimen (MPEP706.78).

Figure 2.14. The Brachipoda, Rhynchonellata, *Paucicrura* sp. was a stationary epifaunal suspension feeder, somewhat common, uncatalogued specimen.

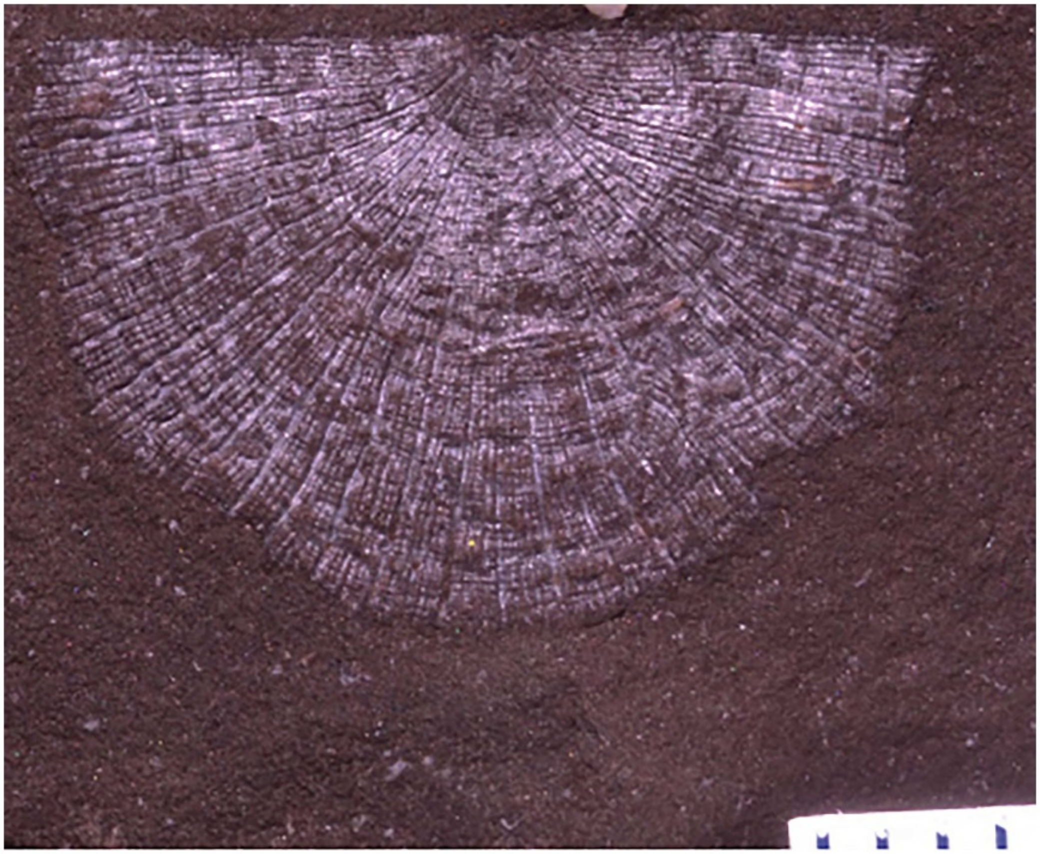

Figure 2.15. The Brachipoda, Strophomenata, *Strophomena,* sp. was a stationary epifaunal suspension feeder, rare. Specimen (MPEP706.76).

Figure 2.16. The Mollusca, Gastropoda, Cyrtolites. sp. was a slow-moving low-level epifaunal grazer, not common. Specimen (MPEP706.70).

Figure 2.17. The Mollusca, Cephalopoda, Trocholites. sp. was a slow-moving low-level epifaunal grazer, not common. Specimen (MPEP706.80).

Figure 2.18. The Mollusca, Cephalopoda, Orthoceratidae, cf. *Orthoceras* sp. was nektonic carnivore, rare. Specimen (MPEP706.81).

Figure 2.19. The Echinodermata, Crinoidea, *Dendrocrinus* n. sp. was a stationary intermediate-level epifaunal suspension feeder, extremely rare. Specimen (MPEP706.57).

Figure 2.20. The Echinodermata, Crinoidea, *Iocrinus trentonensis* was a stationary intermediate-level epifaunal suspension feeder, extremely rare. Specimen (MPEP706.73).

Figure 2.21. The Echinodermata, Crinoidea, *Ectenocrinus simplex* was a stationary intermediate-level epifaunal suspension feeder. The orientation of these specimens indicate directional flow, pyritised. Somewhat common on certain strata (MPEP706.61).

Figure 2.22. The Echinodermata, Crinoidea, *Cincinnaticrinus varibrachialus* was a stationary intermediate-level epifaunal suspension feeder, rare. Specimen (MPEP706.43).

Figure 2.23. The Echinodermata, an unidentified new species of Paracrinoidea. It was a stationary, epifaunal suspension feeder, extremely rare. Only one specimen found (MPEP706.69).

Figure 2.24. The Echinodermata, Rhombifera, *Cheirocystis* cf. *anatiformis* was a stationary intermediate-level epifaunal suspension feeder, somewhat common on certain levels. Specimen (MPEP706.23).

Figure 2.25. The Echinodermata, Soluta, *Syringocrinus* cf. *paradoxicus.* Its paleoecology is unknown, rare. Specimen (MPEP706.46.).

Figure 2.26. The Echinodermata, new species of Soluta, undet. n. sp. Its paleoecology is unknown, somewhat common on certain levels. Specimen (MPEP388.1-a.).

Figure 2.27. The Echinodermata, asteroidea, an unidentified new species. An epifaunal detritivore, extremely rare. Only one specimen found (MPEP706.3-f).

Figure 2.28. The Arthroboda, an unidentified new species of trilobite. Odontopleurida, Odontopleuridae. It was a fast-moving, low-level epifaunal carnivore, somewhat common on certain levels. Specimen (MPEP687.1).

Figure 2.29. The Arthroboda, trilobite, *Flexicalymene.* cf. *multituberculata* was a nektobenthic carnivore, rare. Specimen (MPEP706.20).

Figure 2.30. This trace fossil is common. Specimen (MPEP706.23-c).

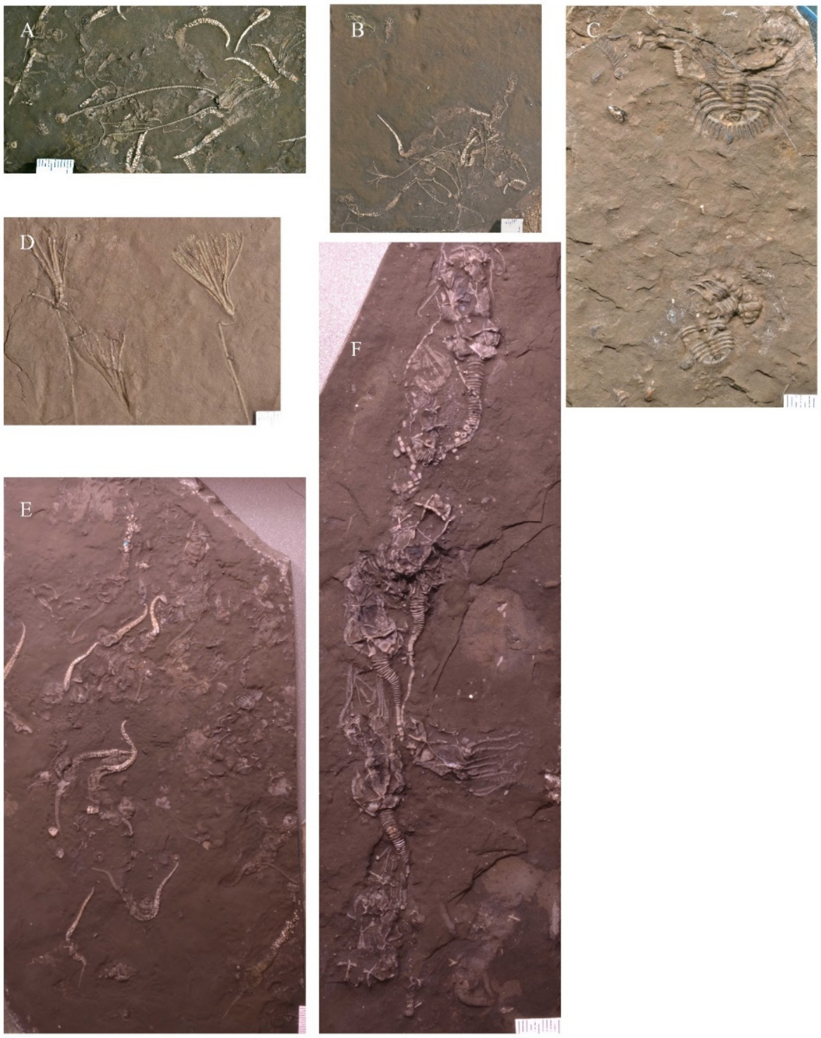

Figure 2.31. A, B, C, D, E, F. Remarkable orientation and preservation of some Upper Ordovician faunal assemblage from the Neuville Formation of Québec, curated at the Musée de Paléontologie et de l'Evolution, Montreal, Quebec, Canada that show the role of burial, and clues to the taphanomy. A) Specimen (MPEP706.3) shows partial direction flow. B) Specimen (MPEP 706.2) is an example of exceptional preservation. C) The orientation of these trilobite specimen (MPEP706.10) and D) crinoid specimens (MPEP706.61) indicate that the burial flow was in the same direction. E) *Quebecarpos* n. sp. specimen (MPEP 706.70) have the same orientation. F) *Cheirocystis* cf. *anatiformis* (MPEP706.71) have the same orientation.

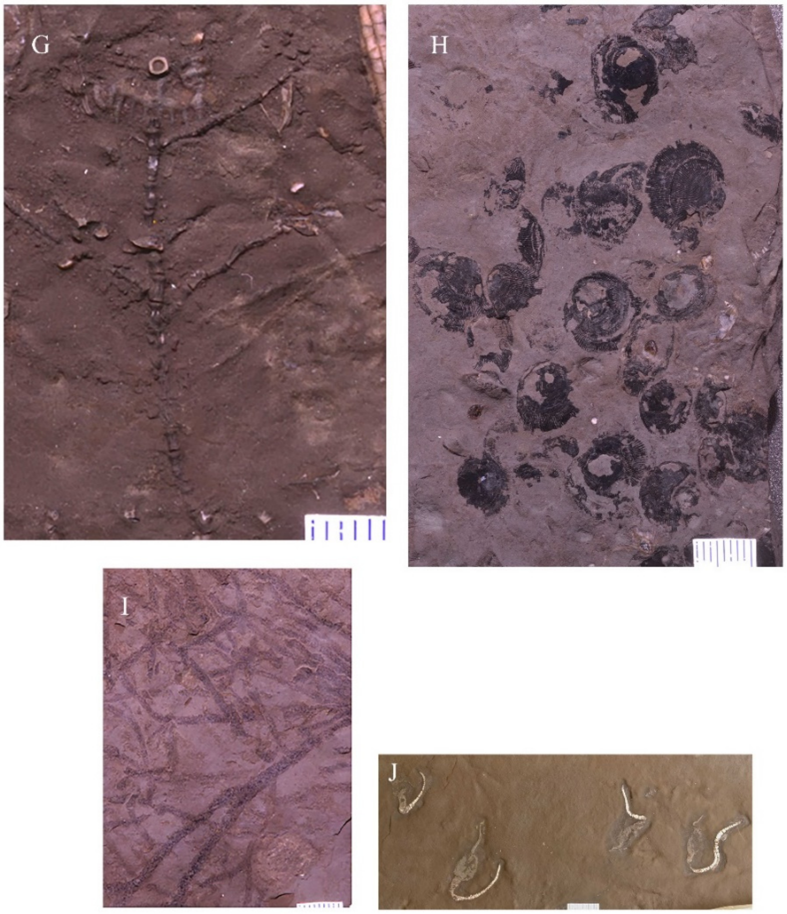

Figure. 2.31 *(suite)*. G, H, I, J. G) The Bryozoan colony *Arthroclema*, specimen (MPEP706.75) is very fragile, proof of its excellent preservation. H) Specimen (MPEP706.77) shows a high concentration of *Schizocrania*, approximately 36 individuals. I) The soft tissue of a branching algea (MPEP706.83). J) Four specimens of an unidentified new species of Solutan echinoderm, specimen (MPEP 388.8) shows three of four in the same orientation.

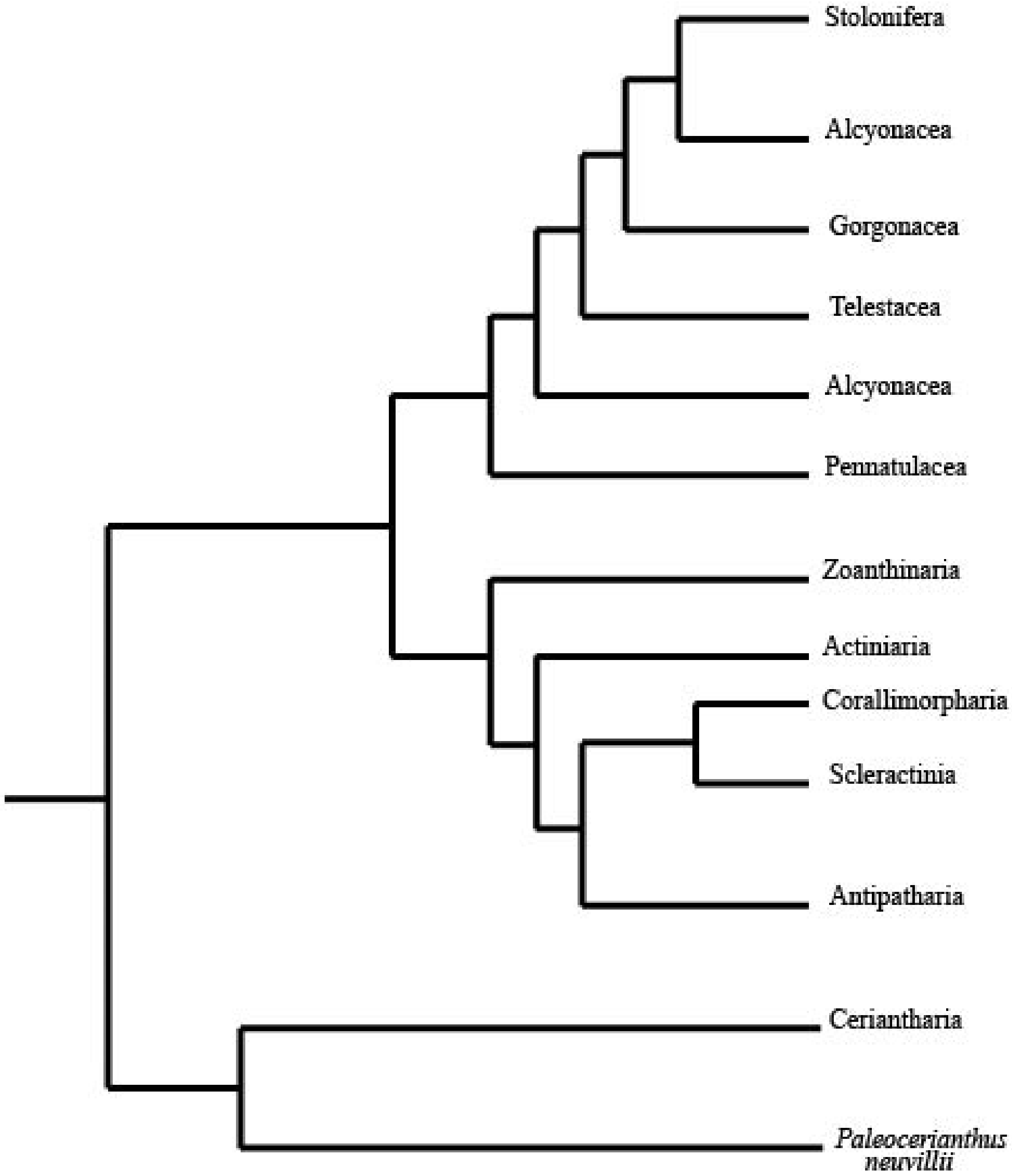

Figure 3.1. Phylogenetic tree of Anthozoa based on morphology and 18SrDNA sequence data. This tree has been modified from (Won et al., 2001) to show the position of *Paleocerianthus neuvillii.*

REFERENCES

Aldridge, R. J., Gabbott, S. E., Siveter, L. J., & Theron, J. N. (2006). Bromalites from the Soom Shale Lagerstätte (Upper Ordovician) of South Africa: palaeoecological and palaeobiological implications. *Palaeontology, 49*(4), 857-871.

Allison, P. A., & Briggs, D. E. (1993). Exceptional fossil record: distribution of soft-tissue preservation through the Phanerozoic. *Geology, 21*(6), 527-530.

Alpert, S. P. (1973). Bergaueria Prantl (Cambrian and Ordovician), a probable actinian trace fossil. *Journal of Paleontology*, 919-924.

Anderson, R. P., Tosca, N. J., Gaines, R. R., Mongiardino Koch, N., & Briggs, D. E. (2018). A mineralogical signature for Burgess Shale–type fossilization. *Geology, 46*(4), 347-350.

Barnes, C. R., Fortey, R. A., & Williams, S. H. (1996). The Pattern of Global Bio-Events During the Ordovician Period. In O. H. Walliser (Ed.). In *Global Events and Event Stratigraphy in the Phanerozoic: Results of the International Interdisciplinary Cooperation in the IGCP-Project 216 "Global Biological Events in Earth History"*. Berlin, Heidelberg: Springer Berlin Heidelberg, 139-172.

Belt, E. S., Riva, J., & Bussières, L. (1979). Revision and correlation of late Middle Ordovician stratigraphy northeast of Quebec City. *Canadian Journal of Earth Sciences, 16*(7), 1467-1483.

Bergstroem, S. M., Chen, X., Gutiérrez-Marco, J. C., & Dronov, A. (2009). The new chronostratigraphic classification of the Ordovician System and its relations to major regional series and stages and to δ13C chemostratigraphy. *Lethaia, 42*(1), 97-107.

Bretsky, P. W., & Bretsky, S. S. (1975). Succession and repetition of Late Ordovician fossil assemblages from the Nicolet River Valley, Quebec. *Paleobiology, 1*(3), 225-237.

Briggs, D. E. (2003). The role of decay and mineralization in the preservation of soft-bodied fossils. *Annual Review of Earth and Planetary Sciences, 31*(1), 275-301.

Briggs, D. E., Bottrell, S. H., & Raiswell, R. (1991). Pyritization of soft-bodied fossils: Beecher's trilobite bed, Upper Ordovician, New York State. *Geology, 19*(12), 1221-1224.

Briggs, D. E., & Edgecombe, G. D. (1993). Beecher's trilobite bed. *Geology Today, 9*(3), 97-102.

Briggs, D. E., Liu, H. P., McKay, R. M., & Witzke, B. J. (2018). The Winneshiek biota: exceptionally well-preserved fossils in a Middle Ordovician impact crater. *Journal of the Geological Society*, jgs2018-2101.

Butterfield, N. J. (1990). Organic preservation of non-mineralizing organisms and the taphonomy of the Burgess Shale. *Paleobiology, 16*(3), 272-286.

Butterfield, N. J. (2003). Exceptional fossil preservation and the Cambrian explosion. *Integrative and comparative biology, 43*(1), 166-177.

Carlgren, O. (1912). Ceriantharia. *Danish Ingolf-Expedition, 5A*(3), 1-79.

Carlgren, O. (1924). Die Larven der Ceriantharien, Zoantharien und Actiniarien. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer" Valdivia" 1898-1899, 9*(8), 341-488.

Carlgren, O. (1931). On some Ceriantharia. *Arkiv För Zoologi A, 23*, 1-10.

Chen, J.-Y. (1991). Lower Cambrian fossil Lagerstatte from Chengjiang, Yunnan, China: insights for reconstructing early metazoan life. *The early evolution of Metazoa and the significance of problematic taxa*, 57-76.

Chiaje, S. d. (1841). *Descrizione e notomia degli animali invertebrati della Sicilia citeriore osservati vivi negli anni 1822-1830*. Naples: C. Batelli.

Child, C. (1908). Form regulation in Cerianthus aestuarii. *The Biological Bulletin, 15*(1), 27-53.

Clark, T. (1959). Stratigraphy of the Trenton Group, St. *Lawrence Lowlands, Quebec: Geological Association of Canada Proceedings, 11*, 13-21.

Cooper, G. A., & Kindle, C. H. (1936). New brachiopods and trilobites from the Upper Ordovician of Perce, Quebec. *Journal of Paleontology*, 348-372.

Ehrenberg, C. (1834). Die Corallenthiere des rothen Meeres physiologisch Untersucht und systematisch Verzeichnet. Beiträge zur physiologischen Kenntniss der Corallenthiere im allegemeinen, und besonders des rothen Meeres, nebst einem Versuche zur physiologischen Systematik derselben. *Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin, 1832*, 225-380.

Farrell, Ú. C., Martin, M. J., Hagadorn, J. W., Whiteley, T., & Briggs, D. E. (2009). Beyond Beecher's Trilobite Bed: Widespread pyritization of soft tissues in the Late Ordovician Taconic foreland basin. *Geology, 37*(10), 907-910.

Foerste, A. F. (1936). Cephalopods from the Upper Ordovician of Percé, Quebec. *Journal of Paleontology*, 373-384.

Fortey, R., Owens, R., & Rushton, A. (1989). The palaeogeographic position of the Lake District in the Early Ordovician. *Geological Magazine, 126*(1), 9-17.

French, B. M., McKay, R. M., Liu, H. P., Briggs, D. E., & Witzke, B. J. (2018). The Decorah structure, northeastern Iowa: Geology and evidence for formation by meteorite impact. *GSA Bulletin, 130*(11-12), 2062-2086. doi:https://doi.org/10.1130/B31925.1

Fu, D. T., Guanghui Dai, Tao Liu, Wei Yang, Yuning Zhang, Yuan Cui, Linhao Li, Luoyang Yun, Hao Wu, Yu Sun, Ao Liu, Cong Pei, Wenrui Gaines, Robert R. Zhang, Xingliang. (2019). The Qingjiang biota—A Burgess Shale–type fossil Lagerstätte from the early Cambrian of South China. *Science, 363*(6433), 1338-1342. doi:10.1126/science.aau8800

Gabbott, S. E., Browning, C., Theron, J. N., & Whittle, R. J. (2016). The late Ordovician Soom Shale Lagerstätte: an extraordinary post-glacial fossil and sedimentary record. *Journal of the Geological Society, 174*(1), 1-9.

Gaines, R. R. H., Emma U Hou, Xianguang Qi, Changshi Gabbott, Sarah E Zhao, Yuanlong Peng, Jin Canfield, Donald E. (2012). Mechanism for Burgess Shale-type preservation. *Proceedings of the National Academy of Sciences, 109*(14), 5180-5184.

Geller, J. B., Fitzgerald, L. J., & King, C. E. (2005). Fission in sea anemones: integrative studies of life cycle evolution. *Integrative and comparative biology, 45*(4), 615-622.

Globensky, Y. (1987). *Géologie des Basses-Terres du Saint-Laurent,* Rapport MM 85-02: Québec Ministère de l'énergie et des ressources, Direction générale de l'exploration géologique et minérale. 63.

Globensky, Y. (1993). Lexique stratigraphique canadien–volume VB–Région des Appalaches, des Basses-Terres du Saint-Laurent et des Îles-de-la-Madeleine. *Ministère des Ressources naturelles, Québec*, 91-23.

Globensky, Y., & Jauffred, J.-C. (1971). Upper Trenton Conodonts from the Grondines Section of Quebec. *Canadian Journal of Earth Sciences, 8*(11), 1473-1479.

Grantham, T. (2004). The role of fossils in phylogeny reconstruction: Why is it so difficult to integrate paleobiological and neontological evolutionary biology? *Biology and Philosophy, 19*(5), 687-720.

Hagadorn, J. W. (2004). Digital Paleobiology And Taphonomy Of an Ordovician Lagerstätte: Beecher's Trilobite Bed. *Geological Society of America Abstracts with Programs, 36*(5), 383.

Han, J., Zhang, X., & Komiya, T (2016). Integrated Evolution of Cnidarians and Oceanic Geochemistry Before and During the Cambrian Explosion. In S. Goffredo & Z. Dubinsky (Éd.). In *The Cnidaria, Past, Present and Future: The world of Medusa and her sisters*. Cham: Springer International Publishing. 15-29.

Han, J. K., Shin Uchida, Hiro-omi Stanley Jr, George D Yao, Xiaoyong Shu, Degan Li, Yong Yasui, Kinya. (2010). Tiny sea anemone from the Lower Cambrian of China. *PLoS One, 5*(10), e13276.

Harper, D. A., & Pickerill, R. K. (1996). Mid Ordovician commensal relationships between articulate brachiopods and a trepostome bryozoan from eastern Canada. *Atlantic Geology, 32*(3). doi:https://doi.org/10.4138/2087

Hatschek, B. (1888). *Lehrbuch der Zoologie: eine morphologische Übersicht des Thierreiches zur Einführung in das Studium dieser Wissenschaft* (Vol. Lieferung 1-3): Gustav Fischer, Jena.

Holland, S. M., Davis, R. A., & Meyer, D. L. (2009). *A sea without fish: life in the Ordovician sea of the Cincinnati region*: Indiana University Press, Bloomington, Indiana.

Hou, X. g., Stanley, G., Zhao, J., & Ma, X. y. (2005). Cambrian anemones with preserved soft tissue from the Chengjiang biota, China. *Lethaia, 38*(3), 193-203.

Hyman, L. H. (1940). *The invertebrates: Protozoa through Ctenophora vol. 1*: The McGraw-Hill Companies.

Kobluk, D. R. (1981). Cavity-dwelling biota in Middle Ordovician (Chazy) bryozoan mounds from Quebec. *Canadian Journal of Earth Sciences, 18*(1), 42-54.

Kokshoorn, B., Goud, J., Gittenberger, E., & Gittenberger, A. (2007). Epitoniid parasites (Gastropoda, Caenogastropoda, Epitoniidae) and their host sea anemones (Cnidaria, Actiniaria, Ceriantharia) in the Spermonde archipelago, Sulawesi, Indonesia. *Basteria, 71*(1/3), 33-56.

Lacelle, M., Hagadorn, J. W., & Groulx, P. (2008). The widespread distribution of Cambrian medusae: Scyphomedusa strandings in the Potsdam Group of southwestern Quebec. *Geological Society of America Annual Meeting Abstracts with Programs, 40*(6), 369.

Lavoie, D. (1995). A Late Ordovician high-energy temperate-water carbonate ramp, southern Quebec, Canada: implications for Late Ordovician oceanography. *Sedimentology, 42*(1), 95-116.

Lefebvre, B., El Hariri, K., Lerosey-Aubril, R., Servais, T., & Van Roy, P. (2016). The Fezouata Shale (Lower Ordovician, Anti-Atlas, Morocco): a historical review. *Palaeogeography, Palaeoclimatology, Palaeoecology, 460*, 7-23.

Leloup, E. (1932). Cérianthaires de l'Océan Atlantique. *Bulletin du Musée Royal d'Histoire Naturelle de Belgique - Mededeelingen van het Koninklijk Natuurhistorisch Museum van België, 8*(4), 1-19.

Leloup, E. (1942). Larves de Cérianthaires appartenant à trois espèces nouvelles. *Bulletin du Musée Royal d'Histoire Naturelle de Belgique - Mededeelingen van het Koninklijk Natuurhistorisch Museum van België, 18*(34), 1-16.

Leloup, E. (1964). Larves de Cérianthaires. *Discovery reports, 33*, 251–307.

Leloup, E. (1968). Larves de Cérianthaires du Golfe de Guinée. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique - Bulletin van het Koninklijk Belgisch Instituut voor Natuurwetenschappen, 44*(7), 1-22.

Liu, H. P., Mckay, R. M., Young, J. N., Witzke, B. J., Mcvey, K. J., & Liu, X. (2005). A new soft-bodied Middle Ordovician fauna from the St. Peter Sandstone in northeast Iowa. *Geological Society of America Abstracts with Programs, 37*(7), 116.

Liu, H. P., McKay, R. M., Young, J. N., Witzke, B. J., McVey, K. J., & Liu, X. (2006). A new Lagerstatte from the Middle Ordovician St. Peter Formation in northeast Iowa, USA. *Geology, 34*(11), 969-972.

Mariscal, R. N., Conklin, E. J., & Bigger, C. H. (1977). The ptychocyst, a major new category of cnida used in tube construction by a cerianthid anemone. *The Biological Bulletin, 152*(3), 392-405.

Martin, E. L. P., Bernard Gutiérrez-Marco, Juan-Carlos Vannier, Jean El Hariri, Khadija Lerosey-Aubril, Rudy Masrour, Moussa Nowak, Hendrik Servais, Thomas Vandenbroucke, Thijs RA. (2016). The Lower Ordovician Fezouata Konservat-Lagerstätte from Morocco: age, environment and evolutionary perspectives. *Gondwana Research, 34*, 274-283.

Mata, S. A., Corsetti, C. L., Corsetti, F. A., Awramik, S. M., & Bottjer, D. J. (2012). Lower Cambrian anemone burrows from the upper member of the Wood Canyon Formation, Death Valley region, United States: Paleoecological and Paleoenvironmental significance. *PALAIOS, 27*(9), 594-606.

Meyer, M., Schiffbauer, J. D., Xiao, S., Cai, Y., & Hua, H. (2012). Taphonomy of the upper Ediacaran enigmatic ribbonlike fossil Shaanxilithes. *PALAIOS, 27*(5), 354-372.

Meyer, M. B., Ganis, G. R., Wittmer, J. M., Zalasiewicz, J. A., & De Baets, K. (2018). A late ordovician planktic assemblage with exceptionally preserved soft-bodied problematica from the Martinsburg Formation, Pennsylvania. *PALAIOS, 33*(1), 36-46. doi:10.2110/palo.2017.036

Milne-Edwards, H. (1851). Monographie des polypiers fossiles des terrains paléozoques. *Archives du Muséum d'histoire Naturelle, 5*, 1-502.

Molodtsova, T. (2007). Tube anemones (Ceriantharia Anthozoa) of New Caledonia. *Compendium of marine species of New Caledonia. Documents scientifiques et techniques, IRD Nouméa, II7 (volume spécial, deuxième édition)*, 133.

Morris, S. C. (1993). Ediacaran-like fossils in Cambrian Burgess Shale-type faunas of North America. *Palaeontology, 36*(3), 593-635.

Morris, S. C., Pickerill, R. K., & Harland, T. (1982). A possible annelid from the Trenton Limestone (Ordovician) of Quebec, with a review of fossil oligochaetes and other annulate worms. *Canadian Journal of Earth Sciences, 19*(11), 2150-2157.

Munnecke, A., Calner, M., Harper, D. A., & Servais, T. (2010). Ordovician and Silurian sea–water chemistry, sea level, and climate: a synopsis. *Palaeogeography, Palaeoclimatology, Palaeoecology, 296*(3-4), 389-413.

Novacek, M. J. (1992). Fossils, topologies, missing data, and the higher level phylogeny of eutherian mammals. *Systematic Biology, 41*(1), 58-73.

Nowak, H., Servais, T., Pittet, B., Vaucher, R., Akodad, M., Gaines, R. R., & Vandenbroucke, T. R. (2016). Palynomorphs of the Fezouata Shale (Lower Ordovician, Morocco): age and environmental constraints of the Fezouata Biota. *Palaeogeography, Palaeoclimatology, Palaeoecology, 460*, 62-74.

Perrier, E. (1893). *in Traité de Zoologie. Fascicule I, Zoologie Générale*. Masson, Paris. 8-413.

Pickerill, R. K., & Narbonne, G. M. (1995). Composite and compound ichnotaxa: a case example from the Ordovician of Quebec, eastern Canada. *Ichnos: An International Journal of Plant & Animal, 4*(1), 53-69.

Plckerill, R., & Forbes, W. (1979). Ichnology of the Trenton Group in the Quebec City area. *Canadian Journal of Earth Sciences, 16*(10), 2022-2039.

Prantl, F. (1945). Two new problematic trails from the Ordovician of Bohemia. *Académie tchéque des sciences, Bulletin international, Classe des sciences mathematiques et naturelles et de la médecine, 46*, 49-59.

Rabano, I., Gozalo, R., & Garcia-Bellido, D. (2008). Pyritized trilobite faunas from the Ordovician of New York State: Beecher's Trilobite Bed and the Whetstone Gulf Formation near Lowville. *Advances in trilobite research,*(9), 109.

Raiswell, R., Newton, R., Bottrell, S. H., Coburn, P. M., Briggs, D. E., Bond, D. P., & Poulton, S. W. (2008). Turbidite depositional influences on the diagenesis of Beecher's Trilobite Bed and the Hunsrück Slate; sites of soft tissue pyritization. *American Journal of Science, 308*(2), 105-129.

Rasetti, F. (1948a). Lower Cambrian trilobites from the conglomerates of Quebec (exclusive of the Ptychopariidea). *Journal of Paleontology*, 1-24.

Rasetti, F. (1948b). Middle Cambrian trilobites from the conglomerates of Quebec (exclusive of the Ptychopariidea). *Journal of Paleontology*, 315-339.

Rodríguez, E. B., Marcos S Brugler, Mercer R Crowley, Louise M Grajales, Alejandro Gusmão, Luciana Häussermann, Verena Reft, Abigail Daly, Marymegan. (2014). Hidden among sea anemones: the first comprehensive phylogenetic reconstruction of the order Actiniaria (Cnidaria, Anthozoa, Hexacorallia) reveals a novel group of hexacorals. *PLoS One, 9*(5), e96998.

Rosen, B. R. (1988). From fossils to earth history: applied historical biogeography. In *Analytical biogeography*: Springer, 437-481.

Roule, L. (1904). Note préliminaire sur quelques formes nouvelles de Cerianthaires. *Compte Rendu de la Association Française pour l'Avancement des Sciences, 32*, 791-793.

Schmidt, H. (1974). On evolution in the Anthozoa. *Proceedings of the Second International Coral Reef Symposium, 1974, 1*, 533-560. Great Barrier Reef Committee.

Seilacher, A. (1967). Fossil behavior. *Scientific American, 217*(2), 72-83.

Selden, P., & Nudds, J. (2012). *Evolution of fossil ecosystems*: CRC Press, https://doi.org/10.1201/b15128.

Shepard, A. N., Theroux, R. B., Cooper, R. A., & Uzmann, J. (1986). Ecology of ceriantharia (coelenterata, anthozoa) of the northwest Atlantic from Cape Hatteras to Nova Scotia. *Fishery Bulletin,.;(United States), 84*(3).

Stampar, S. N., Beneti, J. S., Acuña, F. H., & Morandini, A. C. (2015). Ultrastructure and tube formation in Ceriantharia (Cnidaria, Anthozoa). *Zoologischer Anzeiger-A Journal of Comparative Zoology, 254*, 67-71.

Stampar, S. N., Emig, C. C., Morandini, A. C., Kodja, G., Balboni, A. P., & Lang Da Silveira, F. (2010). Is there any risk in a symbiotic species associating with an endangered one? A case of a phoronid worm growing on a Ceriantheomorphe tube. *Cahiers de Biologie Marine, 51*(2), 205.

Stampar, S. N., Morandini, A. C., Branco, L. C., Da Silveira, F. L., & Migotto, A. E. (2015). Drifting in the oceans: Isarachnanthus nocturnus (Cnidaria, Ceriantharia, Arachnactidae), an anthozoan with an extended planktonic stage. *Marine biology, 162*(11), 2161-2169.

Stampar, S. N., Scarabino, F., Pastorino, G., & Morandini, A. C. (2016). A new species of tube-dwelling anemone (Cnidaria, Anthozoa, Ceriantharia, Ceriantheopsis) from the Warm Temperate South-western Atlantic. *Journal of the Marine Biological Association of the United Kingdom, 96*(7), 1475-1481.

Sutcliffe, O. E., Dowdeswell, J. A., Whittington, R. J., Theron, J. N., & Craig, J. (2000). Calibrating the Late Ordovician glaciation and mass extinction by the eccentricity cycles of Earth's orbit. *Geology, 28*(11), 967-970.

Tiffon, Y. (1987). Ordre des cérianthaires. *Traité de zoologie, 3*, 211-256.

Trotter, J. A., Williams, I. S., Barnes, C. R., Lécuyer, C., & Nicoll, R. S. (2008). Did cooling oceans trigger Ordovician biodiversification? Evidence from conodont thermometry. *Science, 321*(5888), 550-554.

Van Beneden, É. (1897). *Les Anthozoaires de la « Plankton-Expedition » : avec 16 planches, une carte et 59 figures dans le texte. Kiel; Liepzig*. Germany: Lipsius & Tischer.

Van Beneden, É. (1898). Die Anthozoen der Plankton-Expedition : Les anthozoaires de la "Plankton-Expedition". *Ergebnisse der Plankton-Expedition der Humboldt-Stiftung, 2 K. e*.

Van Roy, P., Briggs, D. E., & Gaines, R. R. (2015). The Fezouata fossils of Morocco; an extraordinary record of marine life in the Early Ordovician. *Journal of the Geological Society, 172*(5), 541-549.

Van Roy, P. O., Patrick J Botting, Joseph P Muir, Lucy A Vinther, Jakob Lefebvre, Bertrand El Hariri, Khadija Briggs, Derek EG. (2010). Ordovician faunas of Burgess Shale type. *Nature, 465*(7295), 215.

Vaucher, R., Martin, E. L., Hormière, H., & Pittet, B. (2016). A genetic link between Konzentrat- and Konservat-Lagerstätten in the Fezouata Shale (lower Ordovician, Morocco). *Palaeogeography, Palaeoclimatology, Palaeoecology, 460*, 24-34.

Wallace, C. C. (2008). 19. Hexacorals 1: Sea Anemones and Anemone-like Animals (Actiniaria, Zoanthidea, Corallimorpharia, Ceriantharia and Antipatharia). In O. Hutchings P.A. Kingsford M and Hoegh-Guldberg (Ed.), *The Great Barrier Reef: Biology, environment, and management* Collingwood, Australia: CSIRO Publishing, 199-208.

Walters, M., Lespérance, P. J., & Hubert, C. (1982). The biostratigraphy of the Nicolet River Formation in Quebec and intra-North American correlations in Middle and Upper Ordovician strata. *Canadian Journal of Earth Sciences, 19*(3), 571-588.

Wells, J., & Hill, D. (1956). Anthozoa—general features. *Treatise on Invertebrate Paleontology Part F: Coelenterata. Geological Society of America and University of Kansas Press, Lawrence*, F161-F166.

Werner, B. (1973). New investigations on systematics and evolution of the class Scyphozoa and the phylum Cnidaria. *Publications of the Seto Marine Biological Laboratory, 20*, 35-61.

Whittle, R. J., Gabbott, S. E., Aldridge, R. J., & Theron, J. N. (2007). Taphonomy and palaeoecology of a Late Ordovician caryocaridid from the Soom Shale Lagerstätte, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology, 251*(3-4), 383-397.

Wollanke, G., & Zimmerle, W. (1990). Petrographic and geochemical aspects of fossil embedding in exceptionally well preserved fossil deposits. *Mitteilungen Geologisch-Paläontologischen Institut der Universitat Hamburg, 69*, 57-74.

Won, J., Rho, B., & Song, J. (2001). A phylogenetic study of the Anthozoa (phylum Cnidaria) based on morphological and molecular characters. *Coral Reefs, 20*(1), 39-50.

Young, G. A., Rudkin, D. M., Dobrzanski, E. P., Robson, S. P., Cuggy, M. B., Demski, M. W., & Thompson, D. P. (2012). Great Canadian Lagerstätten 3. Late Ordovician Konservat-Lagerstätten in Manitoba. *Geoscience Canada, 39*(4).

Young, G. A., Rudkin, D. M., Dobrzanski, E. P., Robson, S. P., Cuggy, M. B., Demski, M. W., & Thompson, D. P. (2013). Great Canadian Lagerstätten 3. Late Ordovician Konservat-Lagerstätten in Manitoba. *Geoscience Canada, 39*(4).

Young, G. A., Rudkin, D. M., Dobrzanski, E. P., Robson, S. P., & Nowlan, G. S. (2007). Exceptionally preserved Late Ordovician biotas from Manitoba, Canada. *Geology, 35*(10), 883-886.

Zapata, F. G., Freya E Smith, Stephen A Howison, Mark Siebert, Stefan Church, Samuel H Sanders, Steven M Ames, Cheryl Lewis McFadden, Catherine S France, Scott C. (2015). Phylogenomic analyses support traditional relationships within Cnidaria. *PLoS One, 10*(10), e0139068.