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Evolution, Paleoecology, and Paleobiogeography of the Late Ordovician Brachiopod Fauna of Laurentia

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Graduate Program in Geology

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Abstract

During the early Katian (Late Ordovician), the North American craton was being inundated due to a major eustatic sea level rise and regional subsidence associated with the ongoing Taconic orogeny. The Trentonian brachiopod fauna, as a dominant group of the marine shelly benthos at that time, evolved and invaded the expanding epicontinental seas.

Three Trentonian brachiopod lineages were studied to trace their evolution. The Rostricellula-Rhynchotrema-Hiscobeccus lineage was characterized by an increase in shell size, globosity, and frilled lamellae, with Hiscobeccus becoming a prominent component of the Late Ordovician epicontinental brachiopod fauna.

Parastrophina is a widely reported but non-dominant taxon of the Trentonian brachiopod fauna in eastern North America. This study clarified details of the internal structures of the type species, P. hemiplicata, and quantified the high degree of intraspecific variability, particularly the development of ribs, fold, and sulcus. This has led to the recognition of Parastrophina tarimensis from northwest China as a new species.

Plectorthis is another key taxa of the Trentonian fauna, previously reported from several tectonic paleoplates. By examining the type species, P. plicatella, from the Cincinnati area in this study, the diagnostic characters of the genus were defined, which provided a basis for evaluating the North American and global distribution and diversity of this genus and a more accurate paleobiogeographic analysis.

Multivariate analyses of the Trentonian brachiopod collections from Manitoulin Island and the Lake Simcoe area in Ontario, in conjunction with other Trentonian faunas from North America, demonstrated that during the early stage of the Late Ordovician (early Katian) sea level rise and marine inundation of the continental interior, the epicontinental sea brachiopod fauna began to separate from the older pericratonic faunas. In Ontario, this is reflected by the brachiopod fauna of Lake Simcoe being more closely related to the Scoto-Appalachian fauna, and that of Manitoulin Island most similar to those in the intracratonic basins (e.g. Minnesota).

Key words: Brachiopoda, Late Ordovician, Trentonian, early Katian, Chatfieldian, evolution, paleobiodiversity, paleogeography
Co-Authorship Statement

**Chapter 4** — A version of Chapter 4 was published in the Memoirs of the Australasian Association of Palaeontologist as:


Sohrabi provided systematic information, photos and figures of *Hiscobecus arcticus* and wrote some of the systematic paleontology section for this species. Jin contributed to the project design, field work, and fossil collection, and provided editorial assistance and proofread the article prior to publishing.

**Chapter 5** — A version of Chapter 5 was published in Palaeoworld as:


Jin contributed to the project design, field work, and fossil collection in Ontario and northwest China, and provided editorial assistance and proofread the article prior to publishing. Zhan contributed to field work and fossil collections in northwest China and Ontario, provided the basis for the description of the Lianglitag Formation in northwest China and provided the locality information for the *Parastrophina tarimensis* specimens. Rudkin helped collect the material from Ontario and provided editorial assistance.

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Jin contributed to the project design, field work, and fossil collection, and provided editorial assistance and proofread the article prior to publishing.
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Chapter 1 — Introduction

1.1 Introduction

During the Ordovician Period (445–483 Ma), marine biota underwent a transition from the Cambrian Evolutionary Fauna to the Paleozoic Evolutionary Fauna that would dominate the marine realm until the Permian extinction event (Figure 1.1; Sepkoski 1981; Sheehan 2001a). The Cambrian Evolutionary Fauna was dominated by trilobites, early echinoderms (eocrinoids), and lingulate brachiopods while the evolution of the Paleozoic Evolutionary Fauna marked the rise of articulate brachiopods, bryozoans, tabulate and rugose corals, stromatoporoid sponges, nautiloids, and graptolites (Sepkoski 1984). This transition increased morphological and ecological diversity creating more complex food webs — the Cambrian fauna was dominated by deposit feeders while the Paleozoic fauna marked the rise of filter feeders that could filter food particles out of the water and were capable of symbiotic relationships with simple unicellular algae to supplement their energy intake.

The rapid diversification of this fauna has been termed the Great Ordovician Biodiversification Event (GOBE) (Webby et al. 2004). The GOBE is marked by evolutionary radiation of the shelly benthos at the ordinal, familial, and generic level following the Cambrian explosion that established much of the higher level invertebrate taxa (e.g. phylum level) and marked the first appearance of many of the invertebrate forms that we still see today (Webby 2004). This may have been related to a diversification, and presumed increase in abundance, of the plankton on which these filter feeders were feeding on (Servais et al. 2008, 2010 fig. 4).

Brachiopods, together with the filter feeding phoronids and bryozoans, form the informal taxonomic group of the lophophorates. Although superficially similar in appearance to bivalves, brachiopods are not mollusks, but rather form a separate phylum. The phylum consists of three subphylums (the Linguliformea, Craniiformea, and Rhynchonelliformea), which in turn comprise 8 classes (Williams et al. 1997).
Figure 1.1: Familial diversity levels of the Cambrian, Paleozoic, and Modern evolutionary faunas over the Phanerozoic (after Sepkoski 1984). The Ordovician (highlighted) marks the rise of the primarily filter feeding Paleozoic fauna (middle) and the beginning of the decline of the less complex, primarily deposit feeding, Cambrian fauna.
The brachiopod bauplan consists of two dissimilar valves that enclose a relatively small soft body in the posterior of the shell. The bulk of the mantle cavity contains the lophophore, a ciliated loop used for filter feeding and gas exchange. A small fleshy stalk at the posterior of the organism, known as the pedicle, is used to anchor the brachiopod to the seafloor.

Brachiopods are not as abundant or diverse today as they were during the Paleozoic. They were a dominant constituent of the Paleozoic Evolutionary Fauna that diversified during the GOBE (Harper et al. 2004; Harper 2006). Brachiopods occupied most marine settings in the Paleozoic, but were especially abundant in tropical shelf/platform environments. Since the Mesozoic, however, their habitats have shifted to temperate- to cold-water environments (e.g. coasts of New Zealand, South Australia, and Antarctica) and deep ocean ridges (Richardson 1997). Their hard calcitic shell preserves well in normal marine environments and is resistant to shallow-burial diagenesis, making them ideal proxies for studying the evolution of the marine fauna and determining paleoecological factors that influenced the GOBE.

The GOBE occurred at a time when global atmospheric conditions differed greatly from those of the present day. The world was in a supergreenhouse state due to elevated atmospheric carbon dioxide concentrations (Berner 1994, 2006; Tobin and Bergström 2002; Tobin et al. 2005). Although the Late Ordovician experienced relative cooling leading to the terminal Ordovician (Hirnantian) glaciation (Trotter et al. 2008), a relatively stable warm period in pre-Hirnantian time, known as the Boda Event (Fortey and Cocks 2005), marked a biodiversification peak during the Katian in the Late Ordovician. The warm climate likely contributed to high eustatic sea levels (Haq and Schutter 2008), that may have been the highest of the Phanerozoic. Global temperatures and sea levels remained high until glaciation in the southern hemisphere at the end of the period caused a significant drop in sea level, triggering the End Ordovician Mass Extinction Event (Sheehan 2001b).

By the Late Ordovician, the GOBE was well underway on the tectonic plate of Laurentia, a plate that included North America, Greenland, and peri-Laurentian terranes (e.g. Scotland and the northeastern part of Ireland). The paleoequator ran through the middle of Laurentia at this
Figure 1.2: Paleogeographic map of Laurentia during the Late Ordovician with the locations of the main collections used in this thesis. Base map modified from Cocks and Torsvik 2011 to reflect a more accurate land-water distribution using information on structural elements from Sloss (1988), Cecile and Norford (1993), and Sanford and Grant (2000). Extent of flooding is only an approximation due to erosion in the rock record. Localities: 1) Silliman’s Fossil Mount on Baffin Island, 2) Manitoulin Island, 3) Lake Simcoe, 4) Ottawa Valley, and 5) Cincinnati type area.
time (Figure 1.2; Cocks and Torsvik 2011; Jin et al. 2013). The Taconic orogeny, the first episode of mountain building that created the Appalachian Mountains in eastern North America, was underway on the eastern margin of the continent (then southern margin) (van Staal 2007; Ganis and Wise 2008; Wise and Ganis 2009). The downward warping of the margin of Laurentia associated with tectonic loading (Coakley and Gurnis 1995) combined with the extremely high eustatic sea levels (Haq and Schutter 2008) led to a regional marine transgression, flooding the edge of the craton and several pericratonic sedimentary basins.

The “Trentonian” brachiopod fauna of Ontario is part of an early Late Ordovician (Mohawkian, early Katian) benthic fauna that inhabited the Late Ordovician shallow marine continental shelf of eastern North America. The brachiopod fauna is of relatively low diversity but widespread in its distribution in the pericratonic basins and platforms in eastern North America at this time. The fauna has long been recognized in the eastern United States, where classic early studies focussed on areas of New York (Hall 1847; Raymond 1905, 1910; Titus 1982, 1986), Tennessee and Virginia (Raymond 1928, Willard 1928, Cooper 1956), Cincinnati region (Meek 1872, 1873; Foerste 1910; Davis 1985), and Minnesota (Winchell and Schuchert 1893, Weiss 1955, Rice 1987). Time-equivalent occurrences in Canada, however, have not been as well-studied. Wilson (1946a) contributed an extensive systematic study of the brachiopods in the Ottawa Valley, but never expanded her study to the neighboring area of south-central Ontario. Liberty (1969) incorporated biostratigraphic lists in his lithographic overview of the rocks of central Ontario, but no systematic descriptions were provided. Recently, Sohrabi (2013) began the systematic work necessary to properly describe the fossil fauna, studying the evolution of *Rhynchotrema-Hiscobecus* lineage, but continued work is needed to document the great richness, diversity, and widespread paleogeographic distribution of the fauna as a whole. This thesis aims to continue to systematically describe the fossil brachiopod fauna, focusing on Manitoulin Island and the area east of Lake Simcoe but also incorporating species from other regions, for the purpose of interpreting the evolution and paleoecology of this important taxonomic group.
1.2 Great Ordovician Biodiversification Event

The Trentonian brachiopod fauna emerged during a period of global rapid evolution known as the Great Ordovician Biodiversification Event that lasted for about 25 million years (485–460 Mya; Servais et al. 2010). The GOBE was the second major biodiversification event of the Phanerozoic after the Cambrian Explosion, although some authors see the two events as parts of a single event, with the Ordovician event rooted in the Cambrian — e.g. Droser and Finnegan 2003; Harper 2006). Unlike the Cambrian Explosion, which marked the first appearance of most metazoan phyla and the widespread evolution of biomineralization, the GOBE was a radiation at lower taxonomic levels (species, genus, family, and order) with less radical morphological innovation (Webby 2004).

1.2.1 Environmental contributors to the GOBE

The ultimate physical causes of the GOBE remains controversial. Global cooling (Saltzman and Young 2005; Trotter et al. 2008), or warming (Fortey and Cocks 2005) may have caused an ecological shift, inducing diversification. The largest pulse of biodiversification has been linked to orogenic events and the development of foreland basins (Miller and Mao 1995), indicating that changes in tectonic setting may have contributed to the GOBE indirectly, either through the expansion of shallow marine habitats through creation of shallow foreland basins that were ideal for the expansion of the shelly benthos that inhabited the shallow marine realm, or an increased influx of inorganic nutrients into the sea as a consequence of enhanced rates of weathering and erosion in rising highlands. A superplume during the Middle Ordovician may have increased mantle convection, driving these tectonic processes while also adding heat and nutrients like iron and phosphorous to the oceans (Barnes 2004). The biodiversification has also been linked to rapid fluctuations in sea levels, volcanic events, and climate change (see Achab and Paris 2007). The event may even be linked to extraterrestrial events, such as the break-up of an asteroid and increased meteor impacts on the Earth during this interval (Paris 2008; Schmitz et al. 2008), though the connection between these events is not well understood.
1.2.2 Paleoecological diversification during the GOBE

Several major ecological revolutions also occurred during the GOBE in addition to the biodiversification. The GOBE marked the first extensive development of ecological tiering in the suspension feeders, with organisms occupying different heights above and below the sea floor, opening new niches for colonization in the marine ecosystem (Ausich and Bottjer 1982; Bottjer and Ausich 1986). The evolution of crinoids, in particular, enabled organisms to feed within the water column up to about 50 centimetres above the substrate by the end of the Ordovician (Figure 1.3). Burrowing also became more widespread and intense during the Ordovician, but would only later intensify to modern levels by Carboniferous time when the rise of infaunal bivalve clades led to significantly deeper levels of bioturbation and increased burrow complexity (Bottjer and Ausich 1986). Even so, however, vertical burrows up to 30 cm long have been observed in some Ordovician rocks (see Droser and Bottjer 1989). The density and abundance of burrows increased as well; the percentage of burrowed beds is estimated to have increased by an order of magnitude from the Cambrian to Ordovician times (Droser and Bottjer 1989). These changes in bioturbation cannot be fully accounted for by skeletonized metazoans, and thus serve as important indicators of an increase in the biodiversity and abundance of burrowing soft-bodied metazoans. The complexity of deep burrows also increased drastically, from the nearshore Skolithos pipirock ichnofacies of the Cambrian to the multi-levelled networks of the Thalassinoides ichnofacies in deeper shelf settings of the Late Ordovician (Jin et al. 2012).

During the Middle to Late Ordovician, reefs shifted from being mostly microbial to metazoan dominated (thoroughly documented by Webby 2002). The Early Ordovician reefs were confined largely to the continental margins of the tropics, and composed mostly of calcimicrobes (commonly Epiphyton, Renalcis, and Girvanella) sometimes associated with lithisid sponges. These microbes became less dominant in reefs starting in the Darriwilian, as stromatoporoids, calcareous algae, tabulate and rugosan corals, and bryozoans became the dominant framebuilders and began to dominate the intracratonic seas that were beginning to flood the continents. However, microbial components were generally still associated with
Figure 1.3: Evolution of tiering through the Phanerozoic (after Bottjer and Ausich 1986). Note that both the maximum height above the sediment-water interface and depth below increased during the Ordovician. Burrowing depth increased more substantially during the Carboniferous with the evolution of several infaunal bivalve clades.
metazoan reefs (albeit in lower abundances). These more complex metazoan reefs also supported a more complex associated reef dwelling fauna of trilobites, bivalves, gastropods, and brachiopods. This ecological turnover set the stage for reef building through to the Devonian mass extinction.

Another paleoecological innovation was the evolution of many invertebrate groups toward a pelagic lifestyle during the GOBE compared to the preceding Cambrian. Although their fossil record is generally poor and scattered, the first large scale evolution of early fishes occurred during the Ordovician, probably originating from Australia in Gondwana (Elliot et al. 1991) or Laurentia (Smith et al. 2002). Most major vertebrate clades had evolved by the Late Ordovician (Turner et al. 2004). Swimming eurypterids also originated and diversified during the GOBE, with the oldest known from South Africa (e.g. Tetlie 2007). Nautiloids diversifying during the GOBE began to invade open waters starting in the Tremadocian (Kröger et al. 2009), perhaps due to an abundance of diverse food sources evolving in the water column at this time. Nautiloid evolution was most significant in the shallow carbonate seas of the flooded continents in the tropics, reaching peak diversity by the late Katian (Servais et al. 2010), perhaps paralleling the diversification of metazoan reefs (Kröger et al. 2009). Though trilobites are part of Cambrian fauna, pelagic trilobites with enlarged eyes invaded the water column during the Ordovician and diversified, though they disappeared at the end of the period during the Ordovician mass extinction (Adrain et al. 2004).

1.3 Ordovician Brachiopoda

Brachiopods were generally the most abundant components of the shelly benthos during the Ordovician, and thus they can serve excellent indicators of environmental and ecological shifts in the marine environment. In order to understand these changes, it is important to consider how brachiopods were evolving and dispersing during this time. A brief summary of brachiopod evolution and paleogeography is presented here, but the reader is referred to Harper et al. (2004) and Harper et al. (2013) for more detailed information on the evolution and paleobiogeography of this group during the GOBE respectively.
1.3.1 Evolution

Brachiopods became widespread during the Cambrian, with lingulate brachiopods becoming a significant component of the Cambrian evolutionary fauna (Sepkoski 1984), but most of the rhynchonelliform brachiopods that became a dominant constituent of the Paleozoic evolutionary fauna either first originated or diversified extensively during the GOBE. Brachiopod familial diversity more than quadrupled during this interval, from four families at the end of the Cambrian to 19 superfamilies by the end of the Ordovician (Harper et al. 2004). A general overview is presented here, but regional variations in these patterns have also been summarized for Baltica, Avalonia, and Gondwana (see Harper and Hints 2001; Harper and MacNiocaill 2002; Hints and Harper 2003).

Early Ordovician brachiopods are less well-studied than those from later in the period, but a slow but steady diversification is known to have spanned the Tremadocian and Floian (Harper et al. 2013). The brachiopod fauna consisted mostly pentamerides (comprised entirely of Syntophiidina) and orthides (consisting only of Orthidina, as dalmanellidines first emerged during the Tremadocian), with billingselloids widespread through low latitudes (Harper et al. 2004). The first strophomenides, in the form of plectambonitides, emerged during this time, though the main pulse of strophomenide diversification was to follow in the Dapingian–Darriwilian (Harper et al. 2013). Although global diversity remained relatively low, Zhan et al. (2005, 2007) noted an early pulse of biodiversification during the Floian in South China – perhaps a precursor to the global pulses of diversification to come later in the period.

Global brachiopod diversity rose sharply during the Dapingian–Darriwilian. This interval marked the radiation of the strophomenides and dalmanellidines, leading to their widespread distribution by the Late Ordovician (Harper et al. 2013). Notably, the Rhychonellidae that would become common in Laurentia during the Katian (see Chapter 3) first appeared in the late Darriwilian as a low diversity fauna on the continental margins, and the dalmanellidines underwent radiation at the superfamily level (Harper et al. 2004, 2013). The Atrypidae, though more abundant and diverse in Silurian rocks, originated during this interval (Harper et al. 2004).
Maximum biodiversity was reached during the Katian (Late Ordovician), before dropping significantly during the Hirnantian extinction event. The bulk of the diversity was represented by the strophomenoids and plectambonitoids (Harper et al. 2013). The Dalmanellidines, and Strophomenoids underwent radiation, and both became a common components of the brachiopod fauna worldwide along with the rhynphonellides (Harper et al. 2004). Both the earliest spiriferides and athyrides are known from this time in South China (Rong et al. 1994) and Kazakhstan (Nikitin et al. 1996) respectively.

During the Hirnantian at the end of the Ordovician, brachiopods, along with most other components of the shallow marine shelly benthos, plummeted in diversity (Sheehan 2001b), though most of the higher level taxonomic groups survived the event. This is a common trend among most invertebrate groups of this time, and has led to the idea that the extinction had a limited paleoecological impact (Brenchley 2001). The extinction had two phases, but it was the first phase, thought to be linked with the global marine regression associated with the development of ice sheets in Gondwana as it moved over the south pole, that had the largest impact on brachiopods (Sheehan 2001b) due to the draining of the epicontinental seas and reduced ecospace on the continental shelf.

1.3.2 Paleobiogeography

Throughout the Ordovician, the global brachiopod distribution can generally be divided into low-, mid-, and high-latitude provinces. However, brachiopod biogeography changed as a consequence of the shifting positions of the continents during the period. Harper et al. (2013) provided a detailed analysis of these changes based on an extensive database of brachiopod collections including samples from each stage of the Ordovician (Figure 1.4), but a brief synopsis is provided here.

There are distinctly fewer brachiopod fossil localities from the Early Ordovician, but the available data indicates largely cosmopolitan faunas, including a low latitude tropical fauna across Laurentia, the Precordillera terrane (showing faunal affinities to Laurentia in the Early Ordovician), Siberia, South China, and northern Gondwana (Australia), a temperate fauna in
Figure 1.4: Brachiopod biodiversity and paleobiogeography in the Ordovician, with approximate interval in this study highlighted (modified from Harper et al. 2013). Note the rise of many of the Ordovician brachiopod clades that would become dominant through the later Paleozoic began to diversify during the Darriwilian. Diversity peaked during the late Katian before falling significantly during the Hirnantian extinction.
Baltica and the Ural Mountains, and a high latitude fauna in Gondwana and Avalonia (still near the Gondwana at this time). Although there are fewer collections from this interval on most continents, probably due to low sea levels contributing to less shallow marine habitat and poor preservation, a concentration of localities is noted in South China where the continental shelf had remained submerged.

By the Middle Ordovician, the mid latitude province became more endemic. Harper et al. (2013) divided these faunas into a Celtic province and a Baltic province. The Celtic province consists of eastern Gondwana (South America), Avalonia, and a collection of island arc terranes near Gondwana including the Precordillera terrane while Baltic province consists solely of Baltica. Northern China was separated as well, but Harper et al. note that more data is needed to properly determine its faunal affinities. The low latitude and high latitude provinces are largely unchanged from the Early Ordovician, but the faunas on each paleocontinent were becoming more endemic coinciding with the spike in biodiversity associated with this interval (see above).

During the Sandbian, the separate faunas of the mid latitudes unified into a single province, the Anglo-Welsh province, comprised of Avalonia, Baltica, the Urals, North and South China. This shift is due to the movement of Avalonia away from Gondwana toward Baltica, and the southward shift of the South China plate into the mid latitudes. The low-latitude province and high-latitude province remain largely unchanged from the Middle Ordovician. The Precordillera terrane that had shown faunal similarities to Laurentia and Avalonia earlier in the period was now close to Gondwana and exhibited affinities to the high latitude fauna that dominated there. Notably, the deep water *Foliomena* fauna (Rong et al. 1999), best known from the South China paleoplate, achieved a wide distribution, marking the effects of the marine transgression at this time, allowing deep water forms to invade the continental shelf of many paleoplates.

The low-latitude, Anglo-Welsh, and high-latitude provinces persists through the Katian, but the faunas on individual paleoplates are generally much more endemic during the Late
Ordovician compared to other stages. This can be seen in Laurentia, with a separate Scoto-Appalachian fauna consisting of the northern British Isles and the Appalachian basin and a more epicontinental fauna represented by the widespread \textit{Hiscoeccus} fauna (Jin 2001; Sohrabi and Jin 2013b).

Global cooling and the onset of glacial conditions caused a significant shift in faunal provinces during the Hirnantian. The Edgewood province represents a refugia for some of the tropical forms, and is interpreted as a warm water province. This included much of Laurentia, Siberia, and the Kazakh terranes. A more widespread cool water Kosov province, including eastern Laurentia, Avalonia, Baltica, North and South China, and much of Gondwana and high latitude Bani province (isolated to the Mediterranean region) consisted of more cosmopolitan forms, including variations of the widespread \textit{Hirnantia} fauna (Rong and Harper 1988). Biodiversity was significantly reduced worldwide during the Hirnantian due to the extinction and better circulation of the oceans caused by the glaciation in Gondwana that enhanced larval dispersal, reducing endemism.

1.4 The Ordovician world

The GOBE took place in a very different world than that of today. Paleogeography, sea level, atmosphere, and climate were the main factors that are thought to have influenced the evolution of the shelly benthos, including the brachiopod fauna.

1.4.1 Paleogeography

The Late Ordovician brachiopod faunas examined in this thesis lived at a time when Laurentia straddled the paleoequator and was confined entirely in the tropics. These faunas share various degrees of similarity to the faunas from Baltica, Avalonia, Siberia, Kazakhstan terranes, North China, and South China, which were within, or close to the tropics at that time (Figure 1.5; Cocks 2001; Torsvik and Cocks 2013). The northern hemisphere was covered mostly by a single large, continuous ocean known as the Panthalassic Ocean.
Figure 1.5: Global distribution of the continents during the Late Ordovician (460 Ma) (modified from Torsvik and Cocks 2013). Later in the period, terranes continued to rift from the margin of Gondwana, and Avalonia collided with Baltica in the Early Silurian. The wide dispersal of the continents, in conjunction with high eustatic sea level, isolated benthic faunas promoting endemic evolution late in the period.
Baltica was made up of most of what is now northern Europe during the Ordovician (Cocks and Torsvik 2005). Although these landmasses are now in the upper latitudes of the northern hemisphere, during the Early Ordovician Baltica was situated in the temperate southern latitudes near Gondwana as evidenced by the deposition of thin bedded cool water limestones (Cocks and Torsvik 2005, Torsvik and Cocks 2013). By the Middle Ordovician, Baltica began an accelerated shift northward and rotated counter clockwise, not slowing until late in the period (Fortey and Cocks 2003, Cocks and Torsvik 2005). This relative isolation from both Gondwana in the high latitudes and most of the other continental terranes throughout most of the Ordovician led to the development of an endemic, termed the Baltic fauna or the mid-latitude Anglo-Welsh province (see below; Harper et al. 2013).

Remnants of Avalonia can be found today in the extreme northeastern United States and the maritime provinces of Canada, eastern Newfoundland, southeastern Ireland, Wales, England, Belgium, the Netherlands, southern Denmark, and the northwestern part of Germany, but during the Ordovician, these land masses were united in the form of a peri-Gondwanan terrane (Cocks and Fortey 2009). The terrane rifted from the margin of Gondwana and began to move northeast, passing within about 3300 km of Laurentia by the end of the Landeilo (460 Ma) (Torsvik et al. 1993). Eventually, Avalonia collided with Baltica within the Ordovician-Silurian boundary interval and then later collided with Laurentia along with Baltica during the Caledonian orogeny in the Silurian (Cocks and Torsvik 2005). This dispersal across the ocean can be seen in the benthic fauna—the initially Gondwana-like fauna began to show more similarities with Laurentia and Baltica as it drifted across the Iapetus Ocean (Cocks and Fortey 2009).

Siberia was located near the paleoequator in the southern hemisphere at the start of the Ordovician, but drifted across the equator into northern equatorial latitudes in the late Katian and Hirnantian (Torsvik and Cocks 2013). The paleocontinent was rotated about 180 degrees compared to its modern orientation (Cocks and Torsvik 2007). Though Siberia was still relatively isolated from the other continents, the fauna is not as endemic as other continents—
many trilobite and brachiopod genera are shared with other continents (Cocks 2001). Thus some faunal communication between Siberia and other continents must have been occurring.

North China, consisting of the Korean Peninsula and much of northern and northeastern China, moved very little from the Cambrian into Early Ordovician—situated in the high subtropical latitudes of the southern hemisphere. By the Late Ordovician, the plate had begun shifting northward toward the equator, crossing it during the Early Silurian (Cocks and Torsvik 2013). The Ordovician rocks of North China form elongate facies belts and indicate a relative deepening toward the west (Zhou et al. 1989). A substantial unconformity above the Ordovician rocks separates them from the overlying Middle to Upper Carboniferous (Cocks and Torsvik 2013). The \textit{Parastrophina tarimensis} were collected from the Lianlitag Formation in the Tarim Basin (Chapter 5) that was either united, or very close to the North China Block during the Ordovician (see figs. 5 – 8 in Cocks and Torsvik 2013).

The South China plate was not connected to North China during the early Paleozoic. It consisted of much of modern China and northeastern Vietnam (Cocks and Torsvik 2013). South China migrated northward rapidly during the Ordovician, starting the period near Gondwana around 30°S and reaching the equator by the Late Ordovician (Cocks and Torsvik 2013). The Ordovician fauna showed characteristics similar to Sibumasu (Fortey 1997) and the Kazak terranes (Zhan and Cocks 1998). The fauna seems to have been mostly isolated from Laurentia, as few of the common brachiopod genera that comprise the Late Ordovician fauna are found there, and many of the genera that are shared between the continents seem to be very different from the forms of Laurentia, and may not be truly related.

Much of central Asia is composed of many terranes that were separated during the Early Paleozoic. These terranes make up parts of what are now Kazakhstan, west China, and southwestern Mongolia (Cocks and Torsvik 2013). The exact position of these terranes during the Paleozoic is not known with any certainty, but paleomagnetic data indicate a near equatorial paleolatitude during the Ordovician, before rotating and moving northward across the equator starting in the mid-Silurian (Bazhenov et al. 2012). The early Ordovician brachiopod
and trilobite faunas show some similarity to Gondwana (Popov et al. 2009), but become more endemic later in the period. The Late Ordovician brachiopod fauna from Kazakhstan exhibits some similarities with Laurentia, though the forms are sometimes only superficially similar and it is uncertain how closely related the faunas actually are (see Plectorthis in Chapter 6 for example).

Gondwana, largest of the Ordovician continents, spanned the tropical to southern high latitudes throughout the Ordovician (Cocks and Torsvik 2002). Early Ordovician Gondwana consisted of much of South America, Arabia, Antarctica, Australia, India, Avalonia, Amorica, Iberia, Perunica, Alpine and Balkan fragments, Southern China Sibumasu, New Guinea, New Zealand, and Mexico, but during the tectonically active Middle Ordovician, Avalonia, Amorica, Perunica, Iberia, and the Alpine fragments all rifted from the Gondwanan margin (Cocks 2001; Fortey and Cocks 2003). By the latest Ordovician, Gondwana had drifted over the South Pole, possibly disrupting ocean currents and contributing to the development of the Late Ordovician glacial event (Herman et al. 2004). Widespread glacial deposits of Late Ordovician age can be found in North Africa, which would have been situated near the South Pole at that time (see Sheehan 2001b).

1.4.1.1 Laurentia

Laurentia was relatively stationary during the Ordovician and into the Early Silurian, straddling the paleoequator (Figure 1.2; Cocks and Torsvik 2011; Fortey and Cocks 2003; Jin et al. 2013), rotated approximately 80 degrees clockwise from its modern orientation (Cocks and Torsvik 2011), moving only slightly southward during the Ordovician and Silurian (Cocks 2001; Fortey and Cocks 2003).

Most of the continent became flooded by an epicontinental sea during the last half of the Ordovician due to high eustatic sea levels that further isolated Laurentia from other continents, and created conditions for the evolution of a highly endemic benthic fauna in epicontinental seas. An example of this is the Hiscobeccus brachiopod fauna that became dominant throughout the epicontinental seas during the late Katian (Jin and Zhan 2001).
However, there were still heterogeneities in the fauna – the Transcontinental Arch divided the pericratonic basins in the east from the epicontinental seas of the west isolating trilobite faunas from each other (Fortey and Cocks 2003). Though brachiopod lineages are similar, genera show differing patterns of ornamentation in the basins of the continental margins and the intracratonic basins (Sohrabi and Jin 2013a; Sproat and Jin 2013; Sproat et al. 2014). This effect may also be explained as a latitudinal gradient in Laurentia as well, suggesting that these differences have paleoecological implications as well (Jin et al. 2013).

The tectonic regime through the Early Paleozoic was reversed relative to the Mesozoic and Cenozoic eras, with an active margin forming the Taconic orogeny on the current eastern margin creating a foreland basin (Appalachian Basin), and a passive margin forming a vast shallow carbonate platform on western part of the continent (though apparently there was active volcanism offshore on the western margin – see Cocks and Torsvik 2011). Western Laurentia was much smaller in area during the Paleozoic than in modern times as the orogenic events that would lead to the formation of the Rocky Mountains and Coastal Mountains in the west during Mesozoic had not occurred yet. The eastern margin became active as early as the Floian with the closing of the Iapetus Ocean, causing the Taconic orogeny later in the period. This would continue until the Silurian when Laurentia became sutured with Avalonia and Baltica during the Caledonian orogeny (Cocks 2001). The southern margin of North America was passive during the Ordovician, not becoming active until at least the Mississippian (Miall 2008). Further information on the major structures of Laurentia can be found in Chapter 2.

1.4.2 Sea level

Sea level was high during the Ordovician, particularly late in the period when sea levels may have been the highest of the Phanerozoic and large areas of the continents and pericratonic terranes were underwater (Cocks and Torsvik 2005, 2007, 2011, 2013). The wide dispersal of the continents (Torsvik and Cocks 2013) meant large shallow continental shelf settings around the continental peripheries were available for colonization by the shelly benthos.
Globally rising eustatic sea levels during the Ordovician are known from worldwide marine transgressions in the rock record (Figure 1.6; Haq and Schutter 2008), further expanding shallow marine environments. Eustatic sea level rose through the Cambrian and earliest Ordovician, accelerating to peak levels by the Late Ordovician, but ultimately falling at the end of the period with the onset of glaciation in Gondwana.

In Laurentia, a rapid marine transgression is recorded in the rocks of eastern North America at the Turinian – Chatfieldian boundary as well as the late Chatfieldian (early Katian) (e.g. Ettensohn et al. 2004 and Grimwood et al. 1999). However, Zhang (2011) determined that the highest sea levels Laurentia experienced were likely later in the period during the Richmondian (late Katian) in her study of conodonts from the Slave craton, part of the Precambrian Shield in the Northwest Territories (see orange curve, Figure 1.6). This difference in the timing of sea level rise is probably due to the effects of tectonic loading in eastern North America when the Taconic orogeny caused the development of the Appalachian foreland basin. This increased subsidence in the eastern part of the continent would have expanded the shallow pericratonic carbonate platforms inhabited by the Trentonian fauna, setting the stage for diversification of the shelly benthos to take advantage of the empty ecospace.

1.4.3 Atmosphere and climate

Carbon dioxide levels in the Ordovician atmosphere are thought to have been 8–16 times present atmospheric levels, based on modelling (Berner 1994, 2006) and proxies (Tobin and Bergström 2002; Tobin et al. 2005). Carbon dioxide levels rose gradually throughout the period before dropping during the Hirnantian, triggering the glacial event that caused the Ordovician mass extinction. Atmospheric oxygen levels, conversely, were lower than present levels, around 15–18% (Berner 2006, 2009).
Figure 1.6: Global sea level (from Haq and Schutter 2008) and relative sea level on Laurentia (Zhang 2011), δ¹³C (Bergström et al. 2009), δ¹⁸O (Chitinozoan curve from Trotter et al. 2008; brachiopod curve from Shields et al. 2003), events in life history (multiple sources herein; adapted from Droser and Sheehan 1997), paleoecological transitions (multiple sources herein; adapted from Droser and Sheehan 1997), and tectonic events in North America (multiple sources herein) over the Ordovician period.
The relatively constant atmospheric carbon dioxide levels would suggest that temperatures probably remained relatively stable, but Fortey and Cocks (2005) determined that a brief warming event occurred during the Late Ordovician in the period leading up to the Hirnantian glaciation. This was based on the widespread faunal endemism that developed in the Katian due to adaptation to the warmer temperatures in the tropics, unusually thick Ashgillian (late Katian) carbonate deposits in otherwise siliciclastic successions at high latitudes in Gondwana (Villas 2002), and a shift of some formerly tropical taxa into the mid-latitudes (e.g. as in brachiopods documented by Havliček et al. 1994 and Villas 2002). Several δ¹⁸O values obtained from marine carbonate in the Appalachian basin (Tobin and Bergström 2005) and phosphatic chitinozoans from Canada and Australia (Trotter et al. 2008) indicate a relatively constant 22–33°C sea equatorial surface temperature during the Late Ordovician with slight warming through the late Katian before the Hirnantian glacial interval. However, the large temperature range is indicative of uncertainty of ¹⁸O values, as there was likely an enrichment in ¹⁸O due to interactions between sea water and oceanic basalt that may have altered isotope ratios in the ocean remains unknown δ¹⁸O records (Shields et al. 2003; Quintin and MacLeod 2014). This brings the accuracy of geochemical proxies into question when going as far back in the rock record as the Ordovician.

On the contrary, some have suggested that this interval may correspond to cooling, and may have been a long, drawn out period of cooling associated with the Hirnantian glaciation at the end of the period. Brookfield (1988) hypothesized that the Blackriveran and Trenton limestones, equivalent to the Simcoe Group being studied as part of this thesis, were deposited relatively slowly due to slow carbonate production, and featured a bryozoan, brachiopod, and crinoid rich fauna that could be analogous to modern temperate water faunas. The same idea has been suggested to explain pervasive bryozoan mud mound development in Baltica and Avalonia (Cherns and Wheeley 2007), though Avalonia and Baltica should be expected to have been cooler than the more equatorial continents. It should be noted, however, that complex metazoan reefs that inhabited the paleotropics later in the Ordovician had not evolved yet (see Webby 2002), and thus bryozoans had less competition for resources and may have been more
abundant overall. Brookfield also noted the lack of ooids and dominantly bioclastic and carbonate mud-poor deposits as evidence for temperate to cool-water deposition. Saltzman and Young (2005) used elevated $\delta^{13}C$ values from micrite in the Monitor and Antelope ranges in central Nevada to suggest that atmospheric carbon dioxide drawdown may have contributed to a longer glacial period at the end of the Ordovician.

Still others, based on the compilation of $\delta^{18}O$ data from Laurentia (Quintin and MacLeod 2014) suggest that there was neither cooling nor warming, and that the Katian climate was marked by an episode of relative stability.

Two important caveats must be considered here: there is no direct evidence of Ordovician glacial deposits with accurate age dating to older than the Hirnantian (Fortey and Cocks 2005); and the uncertainty associated with $^{18}O$ changes in the seawater that make temperature calibration to $\delta^{18}O$ data in the Ordovician difficult. Thus, the Ordovician climate remains somewhat uncertain, but the majority of geological, geochemical, and paleontological evidence thus far indicates a generally warm Late Ordovician, though perhaps cooler than the Early Ordovician.

1.5 Previous work on the “Trentonian” fauna

The fauna of the Simcoe Group limestones in south-central Ontario has not been well studied. Although fossil content has been incorporated in biostratigraphic studies (e.g. Liberty 1969; see Chapter 2 for detailed discussion), its treatment is generally no more than a checklist for biostratigraphic purposes without any systematic descriptions or photographic plates.

The Trentonian fauna has been studied by several early North American paleontologists. Hall (1847) erected many of the Ordovician brachiopod genera and species still used today based on his study of the Ordovician rocks of New York. These were refined later by Hall and Clarke (1892). Winchell and Schuchert (1893) studied equivalent fossils from Minnesota, but the Canadian material from Ontario received comparatively little detailed study.
Foerste (1924) mentioned the Trentonian fauna of Ontario in his Upper Ordovician Faunas of Ontario and Quebec. Although the taxonomy of Foerste is becoming dated, his systematic descriptions are as precise as they were 92 years ago. Included are discussions on paleobiogeography, including ideas on faunal migration during the Ordovician. Most of the memoir focused on the later Edenian to Richmondian strata, however, with only his discussions of the Trenton and Black River faunas being applicable to this project.

The last worker to provide detailed paleontological descriptions of the Trentonian brachiopod fauna in Canada was Wilson (1946a) following her report on the geology of the Ottawa valley (Wilson 1946b). In addition to systematic descriptions, brachiopod species level diversity was determined and tables denoting the presence or absence of the species in each formation were provided. Unfortunately, the taxonomy is somewhat outdated and the stratigraphic classification scheme in use for the Ottawa Valley has changed since Wilson’s study. Nine photographic plates were provided by Wilson, but unfortunately the photo quality is not always sufficient to observe diagnostic features in the shells, and photos of shell interiors are lacking. Locality descriptions in the report are not detailed, and it may prove difficult for any contemporary worker to accurately locate the localities where the collections were made. Nevertheless, this was a key contribution in systematic paleontology, and still serves as a starting point for systematic studies today. To incorporate these faunal data in the modern paleobiodiversity framework, both the brachiopod taxonomy and stratigraphy of the old literature must be updated and revised using contemporary methods.

1.6 Objectives and significance

There are two main objectives to this thesis.

1. The taxonomy of the Late Ordovician brachiopod fauna must be reviewed and updated using contemporary statistical tools. This will include studying the evolution of several brachiopod lineages to try to determine how the brachiopods were evolving (in terms of morphological change), and why they were evolving.
2. Paleoecological and paleobiogeographical trends in the Trentonian fossil fauna will be investigated to determine what effect rising sea levels may have had on the shelly benthos. To complement the first objective at the scale of individual brachiopod lineages, the second objective aims to examine the evolution of entire faunas at the regional and continental scale to detect broader ecological and environmental factors governed the composition and distribution of the fauna.

1.6.1 Systematic paleontology

Over the 20th century brachiopod taxonomic methods changed substantially, shifting from a single character approach to using cladistics and statistical methods to classify material (for a summary of this shift, see Carlson 2001). Though higher order brachiopod taxonomy has more or less stabilized, work on re-evaluating older systematic work at the genus and especially species level is ongoing.

In many academic journals, systematic studies are being displaced by paleobiodiversity, paleobiogeography, and paleoecology studies that have broader appeal to paleontologists as a whole. In lieu of detailed systematic work, large fossil collection databases are often used in these studies to investigate trends in regional fossil faunas. Unfortunately, fewer and fewer workers are taking the time to look at these fossil collections that these databases are based on, leading to inaccurate data being used as the basis for these studies. Ongoing systematic work is necessary to verify the taxonomic and evolutionary relationships proposed in previous references and update as necessary based on new information. Though the results of systematic work are often not as broadly appealing as these other studies, it is just as important to paleontology today as it has been in the past.

An additional benefit to detailed systematic studies is that we gain a better understanding of the changes that occurred in the evolution of individual lineages, as systematic studies involve the study of species in other regions for comparison as well. This can, for example, provide clues as to why individual lineages survived and diversified while others stagnated and eventually disappeared.
Thus, the initial chapters fill an important, often overlooked gap in current literature by critically re-examining several brachiopod lineages to better determine their taxonomic validity and evolutionary relationships between species before incorporating this data into a broader study of the paleoecology of the fauna as a whole.

1.6.2 Paleoecological and paleobiogeographical analysis

The lithology of Simcoe Group alternates between argillaceous mudstone and crinoidal grainstone, with petroliferous calcareous shale at its top, and it has been hypothesized that these shifts in lithology are controlled by fluctuations in sea level, water circulation, or perhaps both (Melchin 1994; Grimwood et al. 1999). However, it is not well understood how these fluctuations may have affected the benthic fauna living on the shallow carbonate platform in eastern North America. Previous work on modern brachiopods (Peck and Harper 2000) has shown that some brachiopod groups decrease in size with depth. In studies of Permian brachiopods, shell size has been shown to decrease with depth (perhaps due to interspecific competition – see He et al. 2010), or conversely, not change with depth but faunal diversity decreased with depth (Shi et al. 2016). These observations may, however, be unique to the Permian ecosystem.

The Trentonian fauna colonized the shallow seas that were transgressing onto the Laurentian craton during the early Late Ordovician. The carbonate platform was also regularly subjected to storms, contributing to an unstable environment. These fossils provide the opportunity to study what effect this fluctuating environment would have had on the shelly benthos during the early Paleozoic. There have been few paleoecological or paleobiogeographical studies of the Trentonian fauna to understand what effect these environmental changes have on the shelly benthos.

On many modern shorelines, sea levels are expected to rise with global warming, altering the marine habitat on the shallow continental shelf. The effects of this are difficult to study in modern oceans due to the relatively short term record that modern biology provides in terms of geological time. The Trentonian fauna of south-central Ontario serves as an ancient
analogue for the changes we can see in the modern oceans. By looking at ancient examples, we can look for changes in the shelly benthos that occurred over millions of years of sea level changes that are preserved in the fossil record.

1.7 Organization of thesis

To achieve the two main objectives outlined above, this thesis is organized in the following framework.

Chapter 1 serves as a general introduction to the background and broad concepts related to the Ordovician world in which the brachiopod fauna lived. A brief summary of previous work on the “Trentonian” brachiopod fauna in eastern North America follows the background information, noting the lack of studies done in the southern Ontario outcrop belt. Chapter 2 provides a more detailed account of the geological setting and the stratigraphy dealt with in the thesis. The lithology and depositional environment of each member of the Simcoe Group is examined in detail, and a stratigraphic column is included. Other formations noted throughout the thesis are described in brief.

Chapter 3 describes the material and methods used throughout the thesis. Detailed materials and methods are included in each of the subsequent chapters, but a brief overview is provided here.

Chapter 4 is a study on the *Rostricellula-Rhynchotrema-Hiscobecus* lineage of North America, building on the work of Sohrabi and Jin (2013a). PCA and cluster analysis are used to link the evolution of this lineage that would become a common component of the Laurentian Late Ordovician brachiopod fauna. *Rhynchotrema* is common in rocks of the Simcoe Group, usually as *R. increbescens* or *R. wisconsinense*. This is one of the key evolutionary lineages that migrated from pericratonic to intracratonic basins during the Late Ordovician marine transgression, and diversified in the epicontinental seas.
Chapter 5 examines *Parastrophina* from North America and the Tarim basin in northwest China. Although not common at any one locality, as part of the Trentonian brachiopod fauna, *Parastrophina hemiplicata* is a widespread species in eastern North America, including the Simcoe Group limestones. The species was compared to a similar species from the Tarim Basin in northwest China, *Parastrophina tarimensis*. Despite being rare at any one locality, *Parastrophina* has a wide distribution across eastern North America during the Late Ordovician. Unlike the other lineages studied here, only one species is common throughout its range—the type species *P. hemiplicata*.

Chapter 6 investigates *Plectorthis*, focusing on the type species found in eastern North America. Although commonly reported worldwide, the type specimens of *Plectorthis* have not been examined since the early 20th century. This has led to a vague definition of the genus, and assignment of species that may not be directly related. The original type specimens of Hall (1847) are re-described systematically, with discussion of several other species from other continents. *Plectorthis plicatella* and associated subspecies are a relatively common component of the fossil brachiopod fauna in eastern North America, reported from Ontario to Tennessee and Virginia. Other species are locally abundant, particularly in the Cincinnati region.

Chapter 7 focuses on the paleoecological and paleobiogeographical aspect of the Trentonian brachiopod fauna in Ontario. This chapter will use new quantitative faunal data from Ontario to investigate the effect that changing sea levels and storm deposition had on the shelly benthic fauna. This data will be incorporated into a larger dataset of contemporaneous brachiopod faunas in Laurentia to determine if any paleobiogeographical trends can be discerned at a continental scale.

Chapter 8 is a brief summary of the conclusions of the thesis and a brief discussion of the significance of the findings presented herein.
1.8 References


Havlíček, V., Vaněk, V., and Fatka, O. 1994. Perunica microcontinent in the Ordovician (its position within the Mediterranean Province, series division, benthic and pelagic


Torsvik, T.H. and Cocks, L.R.M. 2013. Chapter 2 – New global palaeogeographical reconstructions for the Early Palaeozoic and their generation. In Early Palaeozoic


Chapter 2 — Geological Setting

2.1 North America during the Late Ordovician

A major marine transgression flooded North America during the Late Ordovician, marking the beginning of the Tippecanoe cratonic sequence (Sloss 1963), an interval of submergence that would last through to the Devonian, with only minor interruptions of sea-level lowstands. As Laurentia straddled the equator during the Ordovician (Cocks and Torsvik 2011), the newly flooded continent became a productive carbonate factory and new habitat for a wide variety of marine organisms that were diversifying during the GOBE. The Appalachian, Michigan, and Illinois basins, as well as the carbonate platforms and ramps surrounding the basins like the St. Lawrence platform and the Cincinnati arch became productive carbonate depositional systems (Figure 2.1), and the organisms that lived there provide a record of the Late Ordovician phases of the GOBE and peak marine diversity in Laurentia before the Late Ordovician Mass Extinction. Once seawater reached the continental interior, the broad epicontinental carbonate platform that dominated most of western North America throughout the Early Paleozoic was initiated, and the Williston Basin became a locale for the evolution of a specialized fauna adapted to the relatively stable marine environment this created (e.g. Jin and Zhan 2001).

The tectonic polarity of the margins of North America was reversed during the Ordovician (e.g. Cocks and Torsvik 2011). Much of what is now western North America simply did not exist, as it was built up much later during the Mesozoic. Western North America was a passive margin, composed of a broad continental shelf. In Eastern North America, the Taconic orogeny was initiated when peri-Laurentian terranes docked to form what is now part of the Eastern United States and the Maritime provinces of Canada (Ganis and Wise 2008; Wise and Ganis 2009). After a pause in the Silurian and early Devonian, the mountain building process resumed by the Middle Devonian in eastern North America with the Acadian orogeny, when Baltica and Avalonia collided with Laurentia during the closing of the Iapetus Ocean.
Figure 2.1: Major arches and Basins of eastern North America during the Late Ordovician. Base map modified from Cocks and Torsvik 2011, using information on structural elements from Sloss 1988, Cecile and Norford 1993, and Sanford and Grant 2000. Extent of flooding is only an approximation as much of the Ordovician limestones have been removed by erosion.
2.1.1 Major structures of eastern North America during the Ordovician

Many of the structures of North America are long lasting features that have been given different names corresponding to different periods (e.g. Appalachian Basin/Alleghanian Basin) that may have different geological significance throughout the Phanerozoic. This section concentrates on the Ordovician history of these basins, but summaries of the Phanerozoic history of the sedimentary basins and carbonate platforms of North America can be found in Stott and Aitken (1993) and Sloss (1988).

2.1.1.1 St. Lawrence Platform

The St. Lawrence Platform is located between the Precambrian Shield, Michigan Basin, Anticosti Basin, and Appalachian basins. Though the remnants of this platform are confined to the area around the St. Lawrence Valley today, during the Ordovician it must have been much larger and connected to the Southeast Arctic Platform and intracratonic basins and platform based on the distribution on carbonate inliers on the Precambrian shield (Sanford 1993a) and similar fossil faunas that evolved initially in eastern North America but spread over the entire continent by the late Katian (e.g. Rhynchotrema/Hiscobeccus lineage in Chapter 4). The bulk of this study is focused on the Simcoe Group on the St. Lawrence Platform.

Sanford (1993a) divided the St. Lawrence Platform into three parts based on the underlying structures of the region. The western portion is the main study area of the current thesis, and is separated from the central by the Frontenac Arch, connects the Michigan and Appalachian basins, and lies largely on top of the Findlay and Algonquin arches (Figure 2.1). The central part of the platform is bounded to the west by the Frontenac Arch and to the east by an impingement of the Appalachian orogeny against the Saguenay Arch, and contains the Ottawa Embayment. The geology and brachiopods of this area were studied by Wilson (1946a, b), and are discussed in subsequent chapters of this thesis. The eastern section of the platform runs from the Saguenay Arch out to the Gulf of St. Lawrence where it meets the Anticosti Basin.
The platform contains a nearly complete suite of sediments from the lower Ordovician to the Carboniferous, although Devonian to Carboniferous strata are commonly absent over the center of the arches that underlie the platform (Sanford 1993b). During the Ordovician, the platform supported a widely distributed and relatively diverse fauna that has been used to broadly correlate rocks across the platform (Sanford 1993b): the lowest Ordovician is marked by occurrences of the cephalopod *Diphragmoceras* and the trilobites *Bolbocephalus* and *Goniotela*; the middle Ordovician by the brachiopod *Rostricellula* (see Chapter 4), coral *Eofletcheria*, and cystoid *Bolboporites*; Blackriveran by the cephalopod *Gonioceras* and Trentonian by the trilobite *Cryptolithus*; *Triarthrus* and *Pseudogygites* trilobites in the Edenian; and the Maysvillian and Richmondian by solitary rugose coral *Grewingkia* and stromatoporoid *Beatricea*. Despite these widely distributed lineages, detailed correlations between the basins have not yet been attempted (Armstrong and Carter 2010; see discussion below).

### 2.1.1.2 Michigan Basin

The Michigan Basin was an intracratonic basin that developed on the other side of St. Lawrence Platform from the Appalachian Basin, centered in the lower peninsula of Michigan but also covering parts of the upper peninsula of Michigan, Wisconsin, Indiana, Ohio, and Ontario (Figure 2.1; Fisher et al. 1988). The basin is bounded by the Wisconsin, Kankakee, Findlay, and Algonquin arches, and the Precambrian basement rock north of Lake Huron. The origin of the basin has been linked to a failed continental rifting during the breakup of the supercontinent Rhodinia during the late Precambrian and subsequent thermal subsidence (Klein and Hsu 1987). The basin contains a largely continuous stratigraphic section from the upper Cambrian to the Carboniferous (except for the unconformities that separate cratonic sequences) and Jurassic “red beds” at the center of the basin (see fig. 8 in Fisher et al. 1988). The Ordovician rocks consist of a basal sandstone and sandy shale, with the Mohawkian (upper Sandbian to lower Katian) consisting mostly of limestone that is capped by dolomite at the top, overlain by Cincinnatian (middle to upper Katian) alternating limestone and shale. Tectonic stresses associated with the Taconic orogeny may have increased subsidence in the basin during the Middle Ordovician until the Late Ordovician, increasing accommodation for these
Ordovician carbonates (Howell and van der Pluijm 1990). The Ordovician carbonates on Manitoulin Island are located on the periphery of the Michigan Basin, and are discussed below.

2.1.1.3 Appalachian Basin

Appalachian Basin developed during the Middle to Late Ordovician as a foreland basin in front of the ongoing Taconic orogeny (below). This basin extends from the Great Lakes in the north to the southern Tennessee border in the south and from the Taconic front in the east to the Cincinnati Arch in the west (Figure 2.1; Milici and de Witt 1988). The basin contains sediments from the Proterozoic to the Permian, and the rock record contains the remnants of the Taconic, Caledonian, and Alleghanian orogenic sequences accumulated along the Laurentian margin during the Paleozoic.

A complete summary of the sedimentary succession can be found in Milici and de Witt (1988). The Ordovician sediments can be divided into lower, middle, and upper Ordovician sections. The lower Ordovician consists of various limestones, dolostones, and sandy limestones with interbedded shales and sometimes show nodular bedding or algal laminations. These sediments are separated from the overlying middle and upper Ordovician sediments by a prominent disconformity. The middle and upper Ordovician sediments generally consist of varying proportions of bioclastic limestone and calcareous shale, similar to the Simcoe Group of Ontario (below) but consist of a greater proportion of silt and clay than their platform equivalents due to closer proximity to the Taconic orogeny. Notably, the Trenton Limestone in New York, from which the Trentonian fauna was originally described by Hall (1847), is part of this section. At the top of the Ordovician section in the northern part of the basin, the Queenston Delta contains red shales that represent the infilling of the Appalachian Basin and subsequent subaerial exposure with a reduction in sedimentary accommodation. This is represented in Ontario on the platform by the Queenston Shales that form the base of the Niagara escarpment in many localities.
2.1.1.4 Illinois Basin

The Illinois Basin consists of most of Illinois, but also parts of southwestern Indiana and western Kentucky (Figure 2.1; Collinson et al. 1988) and is bound by the Wisconsin, Kankakee, Cincinnati, and Pascola arches. Like the Michigan Basin above, the Illinois Basin was probably initiated by thermal subsidence following a failed continental rift during the Late Precambrian (Klein and Hsui 1987). This latent thermal subsidence has been used to explain increased subsidence during the Ordovician (Hedilauf et al. 1986), but this subsidence could also be associated with the onset of the Taconic orogeny, as in the Michigan Basin (above; Howell and van der Pluijm 1990). The basin contains sediments from the Cambrian through to the early Permian (though the early Permian is only found in the center of the basin), with Mesozoic and Cenozoic rocks overlapping the succession on the edge of the basin (summarized in Collinson et al. 1988). The Ordovician rocks consist of the lower Ordovician Everton Dolomite and St. Peter Sandstone, Blackriveran and Trenton Platteville and Galena groups, and upper Ordovician Maquoketa Shale.

2.1.1.5 Hudson Bay Basin

The Hudson Bay Basin is now separated from the basins of eastern North America by the Precambrian Shield (Figure 2.1), but during the early Paleozoic these basins were probably connected based on the similarity of their faunas. The basin contains a nearly continuous section from the Cambrian through the Devonian (separated only by the cratonic unconformities found across the continent), with Jurassic and Cretaceous in the neighboring Moose River Basin (Norris 1993a, b). The Ordovician is represented by the Katian succession comprising the Bad Cache Rapids Group, Boas River Shale (restricted in distribution), Churchill River Group, and Red Head Rapids Formation (Norris 1993b; age based on conodonts in Zhang and Barnes 2007). The sequence consists of micritic limestones, black calcareous shale (where the Boas River Shale is present), micritic and dolomitic limestones, and dolomite and calcareous dolomite respectively. Fossils are abundant in parts of the Bad Cache Rapids Formation and much of the Churchill River Group, but relatively rare in the mostly dolomitic Red Head Rapids Formation.
Jin et al. (1997) examined the fossil brachiopod fauna of the Hudson Bay Lowlands, and found two assemblages. The lower assemblage, the _Tetraphalerella churchillensis-Kjaerina hartae_ zone was found in the Bad Cache Rapids Group. The much more diverse _Plaesiomys occidentalis-Hiscobecus capax_ zone is present in the in the Churchill River Group, with some genera persisting through to the Red Head Rapids Formation. This latter assemblage dates the rocks as Maysvillian to Richmondian and shares strong similarities with the Late Ordovician limestones of southern Manitoba, showing that these now separate carbonates were probably connected during the Ordovician.

2.1.2 Taconic orogeny

A number of island arcs and the Dashwood microcontinent collided with eastern North America during the Ordovician. These collisions, collectively referred to as the Taconic orogeny, were diachronous, occurring over different intervals at different locations along the margin of Laurentia (see Table 1 in Ganis and Wise 2008). The main stages of the orogeny lasted 15–20 million years (Ganis and Wise 2008; Wise and Ganis 2009), but the earliest indications of the event date back to the Cambrian and the latest stages continued into the Early Silurian (van Staal et al. 2007; see Figure 1.6).

The three main stages of the orogeny were summarized by van Staal et al. (2007), and elaborated on by Ganis and Wise (2008), van Staal et al. (2009), and van Staal and Hatcher (2010). Only a brief summary is presented here. Ganis and Wise (2008) summarized the chronology of the events, showing that the orogeny occurred diachronously along the Laurentian margin. Taconic I (beginning stage) occurred off of the margin of Laurentia, and consists of the collision of the Lushs Bight arc crust onto the Dashwoods microcontinent around 495–490 million years ago—a narrow ribbon of islands that rifted from the Laurentian margin during the opening of the Humber Seaway in the Cambrian (Waldron and van Staal 2001 updated timing from Ganis and Wise 2008). This combined landmass began moving toward the Laurentian margin, colliding during Taconic II (intermediate stage), 472–450 million years ago (Ganis and Wise 2008). Also during this time, the Notre Dame volcanic arc collided with
Newfoundland and the Ascot arc collided into Quebec. This was the main accretionary interval, with metamorphic grades reaching granulite facies at the core of the orogeny. Taconic III (final stage), consisted of the accretion of several small peri-Gondwanan island arcs onto the Laurentian continent, forming a narrow band of rocks of low metamorphic grade along the edge of the continent, and continued into the Early Silurian.

Although Ontario was not directly affected by the Taconic orogeny, the event had several indirect effects on the carbonate platform in south-central Ontario. First, the increased load on the margin of Laurentia warped the eastern margin downward, causing a relative rise in sea level (Coakley and Gurnis 1995). This down-warping would have contributed to the expansion and aggradation of carbonate shelves during the Ordovician preserved in the rocks of eastern North America as sedimentary accommodation increased. Additionally, the uplift associated with the orogeny would have caused increased erosion rates on the Laurentian margin. Much of the sediments would have been transported into the developing foreland basin landward of the main mountain-building event (Appalachian Basin), and is likely the origin of much of the increased argillaceous content in the rocks of the Simcoe Group.

2.2 Stratigraphy

To facilitate the discussions on paleoenvironment and paleoecology related to the brachiopod faunas examined in this thesis, the following focuses on the lithology and depositional environments of the various formations of the Simcoe Group, as this is the primary study area, but other localities mentioned in this thesis is are described in brief as well.

For further information on the geological formations of Ontario, the reader is referred to Armstrong and Carter (2010). This publication from the Ontario Geological Survey contains practical information on all of the rocks of Ontario from the basal Cambrian sandstones to the upper Devonian carbonates, including lithology, formation tops, and geophysical characteristics.
Figure 2.2: Map of the Paleozoic bedrock of southern Ontario. Lower Upper Ordovician formations are indicated in blue (left) and upper Upper Ordovician formations are indicated in purple (right). Other depositional intervals shown on the map include the Precambrian (red), Silurian (yellow), and Devonian (green). Faults are indicated in bright blue. Note that the Ottawa Valley is extensively faulted. Most of these are normal faults, probably associated with a failed rift event. Image created using the OGS Earth Paleozoic Geology overlay (http://www.mndm.gov.on.ca/en/mines-and-minerals/applications/ogsearth/) in Google Earth.
**Figure 2.3:** Stratigraphic chart of the Upper Ordovician strata from each region that fossils were studied in as part of this thesis. Note the two stratigraphic schemes for the Ottawa Valley: (a) from Williams 1991; (b) from Salad Hersi and Dix 1999. See text for explanation.
2.2.1 The Simcoe Group of Ontario (Blackriveran and Trenton; Ottawa Valley equivalents)

The Simcoe Group consists of lower Katian (Turinian to Maysvillian) carbonates that form an outcrop band between the St. Lawrence River in the east and Lake Huron in the west (see Figure 2.2 and 2.3) and continue in the subsurface across southern Ontario where they are referred to as “the Trenton”. The group is bounded by Precambrian basement rocks and Cambrian sandstones where present below and the Late Ordovician Nottawasaga Group above.

The group forms part of a larger carbonate platform composed of Lower Paleozoic rocks that form the bedrock of southern Ontario. This platform is bounded in the north by the Frontenac Arch and in the west by the Algonquin Arch (Sanford 1993a). The strata dip into the Appalachian Basin, and are approximately laterally equivalent to the Ottawa Group of the Ottawa Valley (Armstrong and Carter 2010). The rocks on Manitoulin Island are interpreted as lateral extensions of the rocks in southern Ontario, but dip toward the Michigan Basin instead. This continuity points to the connection of these two basins during the Ordovician.

Three different stratigraphic schemes need to be considered for these units. In the outcrop belt of south-central Ontario, the rocks are classified as the Simcoe Group. This system of classification was first established by Liberty (1968, 1969) and Liberty and Bolton (1971), and remains largely unmodified except for realignment according to updated geochronological units and the most recent global geochronological system, and a slight modification to the definition of the Lindsay Formation by Russell and Telford (1983).

A second system of classification formalized by Beards (1967), primarily used by subsurface workers, labels these rocks as the Trenton Group, for easier correlation with equivalent sections across the border in New York with the Trenton Limestone there. Fortunately, these units can be approximately correlated with their outcrop belt counterparts (Armstrong and Carter 2010), but precise correlation has yet to be attempted.
Several stratigraphic schemes have been employed in the Ottawa Valley region. Wilson (1946a) attempted to use a primarily biostratigraphic scheme to divide the rocks based on an earlier stratigraphic framework devised by Kay (1937) for the rocks of southern Ontario, but noted that it had little correlation to the lithology, making it difficult to apply at a regional scale. Williams (1991) suggested that the rocks could be approximately correlated between the Ottawa Valley and southern Ontario, and used the same formation names used by Liberty (1969) in for the Simcoe Group in southern Ontario for the rocks of the Ottawa Valley under the name of the Ottawa Formation. However, accurate correlation between the Ottawa Group and Simcoe Group to the west again has yet to be completed (Armstrong and Carter 2010). Salad Hersi and Dix (1999) tried to accommodate both systems, using the schemes of Kay (1937) and Wilson (1946a) for the “Blackriveran” strata (Shadow Lake to lower Bobcaygeon of Liberty’s terminology), while adopting the system of Williams (1991) for the Trentonian rocks (Bobcaygeon and Verulam). It is beyond the scope of this thesis to evaluate the validity of any of these schemes, but it should be noted that the brachiopods described by Wilson (1946b) are documented using her older stratigraphic scheme (Wilson 1946a). Regardless of the stratigraphy, collections made from southern Ontario can be approximately correlated to similar strata in the Ottawa Valley. The most notable difference between the carbonate platform of the Ottawa Valley is structural - the region is more extensively faulted than the Ordovician rocks of southern Ontario (Figure 2.2; Wilson 1946a; Rimando and Benn 2005), perhaps due to a failed rifting event.

As the bulk of fossils examined from for this thesis were collected from the Lake Simcoe area at surface (Figure 2.4), this project will use the outcrop stratigraphic terminology based on Liberty’s (1969) original stratigraphic section. Approximate correlations to equivalent units in the subsurface and the Ottawa Valley can be found in Figure 2.3.

These rocks predominantly consist of limestone and dolostone, but argillaceous and bioclastic content varying throughout the section. Generally, the coarser grained bioclastic-rich units have been interpreted as shoals (Liberty 1969), or storm deposits based on minor scour
Figure 2.4: Localities in the main study area. Note that the bulk of the collection is from the Verulam Formation, but the Highway 6 stop is Lindsay Formation. Image created using the Paleozoic Geology overly from OGS Earth (www.mndm.gov.on.ca/en/mines-and-minerals/applications/ogsearth/) in Google Earth.
surfaces, trough cross laminations, and graded bedding (Brookfield and Brett 1988) while the carbonate mud-rich beds represent distal platform deposits.

Because of the relative continuity of the section (other than local erosional surfaces associated with some of the bioclastic units), formation boundaries are generally gradational and can be difficult to distinguish. This makes establishing a geochronological framework within the group difficult, but also means that the rocks are representative of the entire Turinian to Maysvillian interval with no major erosion or non-deposition. This makes the Simcoe Group important for studying the effects of rising sea level on the craton.

The depositional setting of these rocks has been debated — traditionally they are interpreted as a deepening tropical-style carbonate platform (e.g. Grimwood et al. 1999), but also as a shift to temperate-style carbonate deposition as shown by the unusual predominance of bryozoans and lack of typical tropical-style grains like ooids and peloids (Brookfield 1988). Globally, coral and stromatoporoid reefs did not become abundant until later in the Late Ordovician (Webby 2002), so the bryozoan and crinoidal dominated fauna of these rocks may or may not be indicative of a cooler climate.

The Simcoe Group is composed of five formations. The Shadow Lake and Gull River were deposited during the initial transgression onto the craton, and represented inter- to supra-tidal deposition while the Bobcaygeon and Verulam are indicative of normal marine conditions. The Lindsay becomes increasingly mud-rich upsection into the organic-rich Collingwood Shales at the top of the Group.

2.2.1.1 Shadow Lake Formation

The Shadow Lake Formation forms the base of the Simcoe Group, overlying either Precambrian basement with a sharp and irregular nonconformity or Cambrian strata with a disconformity where present (Armstrong and Carter 2010). Because of this unconformable basal contact, the Shadow Lake Formation varies considerably in both thickness and lithology
over its extent, and is commonly absent over topographic highs in the basement rocks (Melchin 1994). It is not accessible in this study area.

The lithology of the formation varies, but consists of poorly sorted red and green sandy shales, argillaceous and arkosic sandstone with minor sandy argillaceous dolostones (Armstrong and Carter 2010). An alluvial or deltaic depositional setting with at least intermittent subaerial exposure has been interpreted based on burrowing, ripple marks, and desiccation cracks (Grimwood et al. 1999). Although fossils are rare, conodonts (Barnes et al. 1978), brachiopods, ostracods, bivalves (Copper 1978), and fish denticles (Risk and Liberty 1978) have been reported from the Shadow Lake Formation. A gradational contact marked by decreasing siliciclastic contact separates the Shadow Lake from the overlying Gull River Formation (Melchin 1994).

2.2.1.2 Gull River Formation

The Gull River Formation (Figure 2.5) consists mostly of carbonate mudstones unlike the mixed carbonates and siliciclastics of the Shadow Lake below it, and has been divided into of two members. The lower member is lithologically variable, consisting of light to dark grey and brown fine-grained dolostones; light grey to dark brown, very fine grained non- to moderately fossiliferous carbonate mudstones to wackestone and packstones, green argillaceous sandy dolostones; and green to dark brown shale (Armstrong and Carter 2010). An intertidal to supratidal highly restricted marine environment is indicated by evaporites, dissolution casts, and desiccation cracks (Melchin 1994; Grimwood et al. 1999). This unfavourable environment supported a sparse fauna of trilobites and ostracods (Grimwood et al. 1999), although rare brachiopods, gastropods, and cephalopods have been collected (Liberty 1968, 1969; Melchin 1994). A prominent bed of green dolomitic limestone/dolomite forms a distinctive marker bed that separate the lower member from the upper member (Armstrong and Carter 2010).

Above the green marker bed, the upper member consists of grey sparsely fossiliferous carbonate mudstones that commonly show laminations and intraclasts (Armstrong and Carter 2010). The unit becomes increasingly bioclastic and peloidal upsection (Melchin 1994). The lack
Figure 2.5: Gull River Formation on Manitoulin Island. On Manitoulin Island, the rock is pervasively burrowed, as shown above, imparting a very different appearance from the rest of the Simcoe Group. Zoomed view of burrows in transverse section (bottom left) and on a weathered bedding plane (bottom right).
of evaporites and dissolution casts indicates a deeper environment than the lower member in a shallow subtidal setting (Grimwood et al. 1999). Fossils are more common in the upper member, but still low in diversity, including tabulate corals (especially *Tetradium*), bivalves, gastropods, ostracods, trilobites, bryozoans and brachiopods, with calcareous algae sometimes forming stromatolites (Copper 1978; Melchin 1994). The contact between the upper member and overlying Bobcaygeon Formation is shown by the gradational increase in fossil content and grain size (Armstrong and Carter 2010).

Note that Liberty (1969) originally defined three members of the Gull River Formation. His upper member, referred to as the Moore Hill beds, have been found to have more in common with the overlying lower Bobcaygeon and have been transferred there (see Armstrong and Anastas 1992; Armstrong and Rhéaume 1993; Grimwood et al. 1999). Most authors use this two-member classification, but Armstrong and Carter (2010) still retain Liberty’s three-member system.

### 2.2.1.3 Bobcaygeon Formation

The Bobcaygeon formation is divided into a lower, middle, and upper member. In subsurface terminology, the lower member is referred to as the Coboconk Formation, while the middle and upper member are referred to collectively as the Kirkfield Formation (Armstrong and Carter 2010). The Blackriveran-Trentonian contact is generally placed between the lower and middle members of the Formation (i.e. between the Coboconk and Kirkfield formations). The Bobcaygeon has a blockier appearance than the underlying Gull River and contains a much more diverse suite of fossils (Figure 2.6).

The lower member consists of light-grey to tan, medium- to very thick-bedded, fine to medium grained, bioturbated to laminated, bioclastic and peloidal wackestone, packstone, and grainstones (Armstrong and Carter 2010). Algal coatings, oncolites, micritized grains, and intraclasts are common through the lower member (Melchin 1994). Tabulate corals and stromatoporoids, rugose corals, trilobites, brachiopods, bryozoans, bivalves, gastropods, stromatolites, crinoids, and cephalopods are particularly abundant in the upper part of the
**Figure 2.6:** Bobcaygeon Formation. The Bobcaygeon Formation overlies the Gull River Formation, as seen on Manitoulin Island (left). The Bobcaygeon is generally blocky in appearance, especially near its top (right), as in the Carden Quarry near Brechin where it is used for high quality aggregate.
lower member. Crinoidal debris comprises much of the grains in the rock (Armstrong and Carter 2010). Prasoporid and leafy (moose antler-like) bryozoans begin to become large and abundant locally, and brachiopod shell beds rich in *Paucicrura* and strophomenoids (*Strophomena* and *Rafinesquina*) are found in carbonate mud beds on top of bioclastic packstone. The more abundant fossils and common planar and ripple cross-stratification suggest a shallow shelf with offshore shoals — a less restricted environment compared to the underlying Gull River Formation (Melchin 1994; Grimwood et al. 1999).

The middle member, restricted to the area around Lake Simcoe (Liberty 1969), contains thin to medium tabular-bedded, peloidal to bioclastic, very fine- to fine-grained limestone with green shale interbeds (Armstrong and Carter 2010). The unit is distinguished from the lower unit by the shaly interbeds and lower fossil abundance (Melchin 1994). The limestones often feature flat bases with bioclastic lag deposits, have low angle cross laminations, and uneven undulatory tops, and are interpreted as storm beds (Melchin 1994) — probably proximal indications of the storm-dominated nature of the Trenton carbonates above (Brookfield and Brett 1988). The generally darker and relatively more fine-grained peloidal limestones of this unit compared to the lower Bobcaygeon may indicate marine transgression, or perhaps shallowing and restriction (Melchin 1994).

The upper member is composed of dark grey to light brown, thin- to medium-bedded, irregular to tabular bedded bioturbated to horizontally or low angle cross-laminated fossiliferous wackestones, packstones, and grainstones with less shaly partings and interbeds than the middle member (Armstrong and Carter 2010). Crinoids and crinoidal fragments dominate the bioclasts, but brachiopods, bryozoans, trilobites, and gastropods can also be found (Melchin 1994; Armstrong and Carter 2010). The gradational upper contact of this unit with the overlying Verulam Formation is indicated by a gradual increase in shale content to form significant calcareous shale interbeds (Liberty 1969), and thus is largely arbitrary. Precambrian inliers extend into this member in southern Ontario, and probably would have formed islands on the continental shelf with rocky shorelines (Brookfield and Brett 1988).
Figure 2.7: Mounds in the upper Bobcaygeon Formation. A) Surface on which the mounds were found in the Tomlinson Quarry (most of the larger mounds have previously been removed already). B) Multiple elements within the mound structure — note the crinoid stem on top of and below different generations of burrows. C) One of the mounds in which crinoids (as shown by their holdfasts here) and bryozoans have encrusted on top of a burrow network. D) Enlargement of area circled in C showing that the bryozoan colony (red) has encrusted over the edge of the mound (bedding along the edge of the slab indicated in black). E) Long, linear burrow style. F – Segmented bulb burrow style.
Several distinctive mounds have been found by George Kamp in the Tomlinson Quarry near Lake Simcoe outside of Brechin from the upper Bobcaygeon (see Figure 2.7). The mounds contain multiple elements that reveal a complex history (Figure 2.7b). The base of the mounds is always marked by complex, interconnected burrows. On top of these burrows, crinoids and bryozoans are commonly found. There may be multiple generations of burrows, crinoids, and bryozoans interbedded. In one mound there is a bryozoan encrusted on an overhang (Figure 2.7c-d). This layered nature of the mounds indicates that they are probably erosional in nature, rather than true biogenic mounds, as the burrows would have to have been previously lithified and then exposed through erosion to be colonized by other organisms. Multiple cycles of this process must have taken place to produce multiple layers of burrows and encrusting organisms. This is evidence that although large scale erosional surfaces are unknown in the Simcoe Group, small, discontinuous erosional events were still occurring at that time.

On this same surface, there are several different types of burrows preserved parallel to beddings. Some are simple with bifurcating branches (Figure 2.7e) while others have distinct nodules periodically along their length (Figure 2.7f). These nodules could represent living chambers of some kind of burrowing arthropod.

Brachiopods are abundant on this surface as well, but are not different than what has been found in other beds of the formation, and thus are not likely a specialized fauna associated with the mounds.

2.2.1.4 Verulam Formation

The Verulam Formation (Sherman Fall Formation in subsurface terminology) contains two members. The lower member, comprising most of the formation, exhibits the same rhythmic bioclastic and intraclastic limestone and carbonate mudstone alternations as the Bobcaygeon, but in general has much more carbonate mudstone (Figure 2.8, 2.9). The limestone is very fine- to coarse-grained, thin- to thick-bedded, nodular to tabular, light to dark grey fossiliferous and intraclastic wackestones, packstones, and grainstones (Armstrong and Carter 2010). There is a gradation from a mostly mud dominated succession at the base to a
Figure 2.8: Lower Verulam Formation near Lake Simcoe. The Verulam Formation forms an aquitard at the contact with the underlying Bobcaygeon Formation (arrow in top left) in the Carden Quarry near Brechin. The Verulam is typically more mud-rich and has a more nodular and less tabular appearance than the similar Bobcaygeon, as seen in the James Dick Quarry near Brechin (right). Because it recessively weathers, outcrops of the Verulam are rare, but it can sometimes be found at the bottom of recently cleaned drainage ditches like this one on Ramara Concession Road 2 (bottom-left; photo credit Jisuo Jin).
Figure 2.9: Verulam Formation on Highway 48 near Lake Simcoe. This locality illustrates how recessively the Verulam weathers once exposed and why outcrops of the formation are rare. Early in the year, the outcrop is quite visible after being washed with meltwater from snow and while it is relatively free of vegetation (top-left), but by midsummer, it can be difficult to spot as it becomes overgrown by vegetation (right). The bioclastic beds at this outcrop commonly have undulatory bases (bottom left) as seen elsewhere in the Verulam, indicative of scouring and deposition of storm deposits.
more bioclastic/intraclastic dominated succession at the top (Melchin 1994). The clastic beds have been interpreted as distal storm deposits on a continental shelf based on cross-laminations, channels, and graded bedding (see Figure 2.8; Brookfield and Brett 1988).

The upper member is dominantly bioclastic and intraclastic rather than carbonate mud, consisting of thin- to thick-bedded medium- to coarse-grained, cross-stratified, tan to light grey fossiliferous grainstones (Armstrong and Carter 2010). This upper unit is thickest in the western part of the outcrop belt, thinning to the east. Brookfield and Brett (1988) interpreted this upper unit as being composed of multiple discontinuous beds rather than a single cohesive rock package.

Like most of the Bobcaygeon Formation, the Verulam Formation contains an abundant and relatively diverse fossil fauna, including bryozoans, brachiopods, gastropods, bivalves, and crinoids (Figure 2.10). Distinctive “hat-like” prasoporid bryozoans are characteristic of the Verulam and very abundant in the formation. Some fossils are silicified, providing excellent preservation of the morphology of shells (generally at the cost of fine features). The brachiopod lineages studied herein are most common in the lower Verulam: *Rhynchotrema increbescens* are common throughout the formation, *Plectorthis plicatella laurentina* are found occasionally, and *Parastrophina hemiplicata* are rare. Other forms, including *Anazyga recurvirostra*, *Paucicrura rogata*, *Rafinesquina*, and *Strophomena* are common.

The formation has been interpreted as an open, storm-dominated normal marine shelf. Brookfield and Brett (1988) postulated a basinal setting with a water depth of less than 100 m. The upper, distinctly more clastic unit may represent a marine regression on the platform (Melchin 1994).

### 2.2.1.5 Lindsay Formation

Two members make up the Lindsay Formation – a lower limestone unit (Cobourg Formation in subsurface terminology) similar to the Bobcaygeon and Verulam with carbonate
Figure 2.10: Lower Verulam Formation in the James Dick Quarry near Brechin. The Verulam features a diverse shelly fauna, commonly featuring Rhynchochone increbescens (top-left). The bryozoan Prasopora is abundant throughout the unit, forming small hat-shaped mounds (top-right). Occasionally, long, articulated crinoid stem segments are found (bottom-left). Distal storm beds are represented by cross-laminated calcarenite beds that have undulatory bases and feature graded bedding (bottom-left). Top-left, top-right, and bottom left are bed tops.
Figure 2.11: Lindsay Formation at Highway 6 outcrop near Lake Simcoe. The Lindsay looks similar to the Verulam, but is increasingly mud-rich upsection. There appears to be multiple fining upward successions in the outcrop, perhaps recording minor sea level cycles (top). A particularly rich shell bed was found on a lower bench of the outcrop in the top photo (below).
mudstones interbedded with wackestones, packstones, and grainstones, and the dark black shales of Collingwood Member.

The lower member is lithologically similar to the other carbonate units of the Simcoe Group (Figure 2.11), but is generally more nodular in appearance than the underlying Verulam Formation. It consists of very fine- to coarse-grained, nodular to tabular bedded, blue-grey and grey-brown fossiliferous wackestones, packstones, and grainstones with variable mud content (Armstrong and Carter 2010). Like the other carbonate units, shaly partings and thin shale interbeds are common. The tabular beds commonly show low angle cross-laminations, intraclasts, and graded bedding (Melchin 1994) similar to the other units described thus far, probably representing storm deposition. The formation tends to become more mud-rich upsection, while there is a greater proportion of coarser grained beds near its base. The fossil assemblage in the lower Lindsay Formation is similar to that of the Verulam Formation, with gastropods, brachiopods, and crinoids and crinoidal fragments, but the assemblage is notably less diverse than the Verulam. At the Highway 6 locality in the southwest part of the Lake Simcoe study area, for example, small Rhynchotrema increbescens and Sowerbyella are the dominant brachiopods, replacing the larger orthides and strophomenides that are common lower in lower strata. Notably, large Plectorthis plicatella are found here (see Chapter 7), in agreement with a younger Edenian age compared to the Chatfieldian Verulam Formation.

The Collingwood Member consists of much darker highly fissile carbonate shales, and is differentiated from the rest of the Lindsay based on its high organic content (Figure 2.12; Russell and Telford 1983). The unit is comprised of dark grey and black laminated carbonate mudstones interbedded with occasional thin wackestone to packstones. The fossil fauna is still abundant, but indicative of a much more oxygen-restricted marine environment than the underlying open marine carbonates. Graptolites are common on bedding planes, but less common trilobites, thin-shelled inarticulate and articulate brachiopods, ostracods, conularids, and nautiloids have also been reported. This member was classified as the lower Whitby by Liberty (1969) along with the overlying Blue Mountain Formation, but Russell and Telford
Figure 2.12: Collingwood shales on Manitoulin Island. Outcrops of the shale are rare, but along Highway 6 south of Little Current, the shales are exposed in a road cut. Though the shales weather a light grey colour, on fresh surfaces the original dark black can be seen. The rusty weathering is caused by oxidation of pyrite in the shale. The outcrop has many small fragments of graptolites that are only visible on close examination (bottom-left). In transverse view, they impart a speckled appearance on bedding planes.
(1983) placed it in the Lindsay Formation based on its calcareous content vs. the much more siliceous Blue Mountain Formation. The carbon-rich shales of the Collingwood indicate a shallow but restricted environment (Liberty 1969) that would inhibit bacterial degradation of organic matter, or perhaps a rapidly deepening setting (Brookfield and Brett 1988) that restricted marine life due to reduced dissolved oxygen in the water column and increased carbonate solubility that increased energy demands for biomineralization, making it an unfavourable environment for shelly fauna.

### 2.2.1.6 Overlying Late Ordovician units

In the Lake Simcoe area, the Collingwood Member is the uppermost unit. On Manitoulin Island, the Bruce Peninsula, and southward to Toronto, however, it is overlain disconformably by the Nottawasaga Group (Liberty 1968, 1969). This group is not the focus of this project but is briefly noted below.

The Blue Mountain Formation (sometimes referred to as the Sheguiandah Beds on Manitoulin Island after Sanford 1978) is the lowest formation of the Nottawasaga Group, disconformably overlying the Lindsay Formation. These are blue-grey highly fissile shales with minor dolostone interbeds. Like the Collingwood shales below, the unit is only sparsely fossiliferous, containing a low diversity assemblage of graptolites, brachiopods, and trilobites (Liberty 1968). The unit differs from the Collingwood shales in lacking a significant calcareous component – the Blue Mountain is much more silica-rich, probably due to increased siliciclastic input into the Appalachian basin during the later stages of the Taconic orogeny.

The Georgian Bay Formation overlies the Blue Mountain on Manitoulin Island and the area around Georgian Bay. Liberty (1968) divided the formation into two members. The lower member (Wekwemikongsing Beds of Sanford 1978) consists of grey to bluish- or greenish-grey shale that weather buff to yellow with interbedded with minor beds of dolomite, limestone, and sandstone that become thicker upsection. The upper member (Kagawong and Meaford beds of Sanford 1978) is dominantly bioclastic to microcrystalline limestone with shaly partings. The upper member is richly fossiliferous, but very hard, making individual fossil extraction
difficult. A diverse suite of bryozoans, bivalves, crinoids, and brachiopods can be found, including large and globose brachiopods that are reminiscent of the *Hiscobecus* fauna that became widespread across Laurentia during the late Katian (Jin 2001). Corals and stromatoporoids are common, similar to other Richmondian (late Katian) rocks in North America (Armstrong and Carter 2010).

Further south, especially in the Toronto region, the Georgian Bay Formation is overlain by the Queenston Shales. These are red shales with minor green shale, siltstone, sandstone, and limestone. These shales were deposited under mixed marine and subaerial conditions (as shown by the oxidization indicated by the red colour), and may be derived from clastics that originated from the Taconic orogeny (Armstrong and Carter 2010). The unit is conspicuously absent in the northern parts of the outcrop belt and Manitoulin Island, perhaps indicative of isolation between the regions due to the Algonquin Arch that bisects the St. Lawrence Platform in Ontario. The top of the unit is marked by a significant unconformity between it and the overlying Silurian Whirlpool Formation.

### 2.2.2 Stratigraphy of the Cincinnati type area

Many of the specimens used in Chapter 5 were collected from the Cincinnati region. *Plectorthis* is more common and typically larger in size in this region compared to southern Ontario. The type species *P. plicatella*, along with *P. fissicosta*, *P. neglecta*, and *P. equivalvis* are locally common in the area.

The stratigraphy of the carbonates of the eastern United States is more complex than in Ontario. This complexity is largely due to the application of regional stratigraphic schemes by state geological surveys, resulting in different names for stratigraphically equivalent rocks across state lines, or even different stratigraphic schemes altogether (e.g. Holland and Patzkowsky 1996, fig. 1). This problem is exacerbated by rapid facies changes across the region, meaning sediments deposited at similar times can have very different characteristics depending on where they are examined (Holland 1993; Holland and Patzkowsky 1996).
Holland and Patzkowsky (1996) addressed this problem with allostratigraphy. This approach addresses the lack of temporal control by using regionally mappable erosional surfaces (sequence boundaries) to delineate units that, despite being lithologically heterogeneous, represent time-equivalent deposition. Using this scheme, the old lithological units have been interpreted to represent different depositional settings that are tied together into sequences that represent time equivalent deposition.

For example, the Maysvillian contains two sequences: C2 and C3 (see Figure 2.3). Within these two sequences, the old lithostratigraphic units have been interpreted as different facies – the Fairview, Miamitown, and Corryville represent deep subtidal facies, the Calloway Creek, Bellevue, and Mount Auburn shallow subtidal facies, and Garard, Tate, and Terril peritidal facies with the Gilbert representing lagoonal deposition. However, the all of the lithological units that comprise C2 are the same age, and must be older than those of C3, as they are separated by a regional disconformity that is assumed to represent a single time equivalent surface across the region.

This stratigraphic approach enables the comparison of fossils through time and comparison of time-equivalent fossils across different sedimentary facies. However, sequence boundaries are subject to interpretation, and thus the precise position of these surfaces at individual localities, and the amount of time they represent, may be uncertain. Additionally, sequence boundaries are difficult to delineate in more basinal depositional settings, as there is less contrast between mud-rich units at outcrop scale than in shallow settings where the facies change is more apparent.

In general, the geology of the Cincinnati area resembles that of Ontario, with alternating layers of carbonate mudstone and bioclastic/intraclastic grainstones and packstones. As in Ontario, the relative proportions of mud to clastic units are thought to be correlated with water depth (Read 1985 in Holland and Patzkowsky 2007). The formations interpreted as deep subtidal, for example, have only very thin beds of bioclastic grainstones, packstones, and calcisiltites. Deep subtidal deposition is indicated by more bioclastic grainstones and packstones.
in thin to medium beds with Hummocky cross-stratification. Shallow subtidal deposition is marked by the appearance of nodular to wavy-bedded bioclastic limestones with less carbonate mud. Peritidal deposition is interpreted for deposits that of less fossiliferous limestone and dolostone with desiccation cracks.

Notably, the upper Mohawkian and lower Cincinnatian strata (M5-C3 sequences of Holland and Patzkowsky 1996) are composed of the same temperate-style of carbonate deposition as is seen on the St. Lawrence Platform in southern Ontario, dominantly bioclastic in character, lacking ooids and peloids and a fossil fauna dominated by bryozoans and brachiopods. This transitions upwards into tropical-style carbonates in the C4 sequence with a more diverse benthic fauna that includes tabulate and rugosan corals, trilobites, brachiopods, mollusks, and crinoids (Holland and Patzkowsky 1996, 2007; Patzkowsky and Holland 1996) thought to represent a shift to a warmer climate (see Climate in Chapter 1; Fortey and Cocks 2005), or perhaps a change in paleoceanographic conditions (i.e. rising eustatic sea level and terrigenous input from the rising Taconic highlands; see Patzkowsky and Holland 1996).

Fossils are very diverse in the Cincinnati succession. A relatively complete guidebook of the common fossils by Davis (1985) indicates that the brachiopod genera found in the Cincinnati area are generally similar to those of the St. Lawrence Platform. Some examples of common brachiopods from the upper Mohawkian and lower Cincinnatian include *Rafinesquina*, *Strophomena*, *Paucicrura*, *Zygospira* (and the closely related *Anazyga*; see Copper 1977), *Sowerbyella*, and *Hebertella*. Many of these genera continue into the Richmondian, but other larger forms, such as *Plaesiomys*, *Retrorsirostra* and *Hiscobecus* become more common with a return to tropical-style carbonate deposition. *Onniella* and *Cincinnetina* become the most common dalmanellides rather than *Paucicrura* and *Thaerodonta* replaces *Sowerbyella*. Corals like *Tetradium* and *Grewingkia* only become abundant in the Richmondian (late Katian) in the Cincinnati region, mostly replacing the abundant bryozoans found in lower formations that filled a similar niche.
2.2.3 Amadjuack Formation on Baffin Island

Several collections from Upper Ordovician Amadjuack Formation exposed at Silliman’s Fossil Mount on Baffin Island were used in this study. This well-known locality is located approximately 23 km west of Iqaluit between the Foxe, Southampton, and Ungava basins on the Southeast Arctic Platform.

The Amadjuack Formation, composed of three subunits, was initially defined informally by Sanford and Grant (1990) It was re-described and formalized by Sanford and Grant (2000) who chose Silliman’s Fossil Mount as the type locality. Sanford and Grant (2000) recognized three subunits at the locality. The lowest interval consists of medium grey to black shale interbedded with grey to grey-brown shaly limestone in thin, uniform beds. The base of the middle unit is marked by massive beds of resistant grey-brown limestone, abruptly changing upsection into grey, thin and nodular bedded shaly limestones with interbedded grey shales that weather recessively. The top of the unit is more massive grey nodular limestone with minor shale partings and interbeds. The uppermost unit is hard light to medium brown nodular bedded limestone with a distinctive yellowish-orange weathering colour. This formation comprises most of Silliman’s Fossil Mount, and is most accessible there. It forms a sharp and probably disconformable contact with the more crystalline limestone and dolomitic limestones of the Frobisher Formation below. The contact with the overlying Boas River Formation is not exposed anywhere on the island, but shares a gradational contact with the Amadjuack Formation at one locality on Southampton Island at the mouth of Hudson Bay.

Exposed at the formation can also be found near Amadjuack Lake and elsewhere on the Melville Peninsula. The lower part of the formation is always interbedded limestone and shale, but grades into a massive hard limestone at its top, commonly forming escarpments across the landscape. Petroliferous shales have been found in the formation along the Jordan and Nuvungmiat rivers where up to 9-15% total organic carbon has been reported, although it is thermally immature in terms of hydrocarbon production (Macauley et al. 1990).
The Amadjuack Formation contains a rich fossil fauna, with corals and nautiloids being most abundant throughout the formation (Bolton 2000). Tabulate corals are more abundant than rugose, and include Calapoecia coxi, Calapoecia ungava, Manipora sinclairi, Macleodoea martini, Cypriophyllum lambei, Cypriophyllum pattersoni, Catenipora aequabilis, and Catenipora rubra. Grewingkia robusta is the most common rugose form.

Two distinct fossil faunas were recognized by Bolton (2000) in the Amadjuack Formation. The Pseudogygites-Climacograptus fauna is found only in the bituminous beds in the basal part of the formation, consisting mostly of the trilobites Pseudogygites arcticus, Pseudogygites hudsoni, Triarthus (Triarthus) eatoni, and Triarthus (Danacrcus) glaber along with the graptolites Amplexograptus and Climacograptus. These graptolites provide an early Edenian (early Katian) age in the bottom of the formation. Crinoid ossicles are commonly found associated with this assemblage, along with lingulate and sowerbyellid brachiopods, low spired gastropods, Ischyrodonta(?) bivalves, and Geisonoceras nautiloids.

The much more diverse Kochoceras-Denella fauna from the rest of the formation indicates much less restrictive living conditions. The fauna has been dated to the Edenian and early Maysvillian (early-mid Katian) (Bolton 2000). Endoceras, Actinoceras, Kochoceras, Lambeoceras, Narthecoceras, Farroceras, Ephippiorthoceras, and Gorbyoceras are the most common orthocones but other nautiloids including Probillionsites, Beloitoceras, Allumettoceras, Rasmussenoceras, Westonoveras, Neumatoceras, and Charactoceras have also been collected. The trilobites Denella, Ilaenus, Nanillaenus, and Anataphrus are also characteristic of the fauna. Brachiopod fauna is dominated by Paucicrura rogata, similar to the lower Lindsay Formation in Ontario, but is relatively diverse, including Lingula sp., Hesperorthis interplicata, Glyptorthis sp., Plaesiomys subcircularis, Austinella cooperi, Plectorthis inaequiconvexa, Plectorthis sp., Hebertella(?) sp., Platystrophia magnisulcata, Resserella sillmani, R. diminutiva, Sowerbyella sp., Strophomena sp., S. fluctuosa, Rafinesquina(?) pronis, R.(?) declivis subnutans, Rafinesquina sp., Kjaerina sp., Parastrophina minor, Hiscobeccus arctica, H. breve, Idiospira maynei, Cyclospira schucherti, and Cyclospira sp. Parastrophina are rare in the collection, and Plectorthis are uncommon.
2.2.4 Lianglitag Formation of the Tarim Basin in northwest China

This study also incorporated some *Parastrophina* specimens (see Chapter 5) from the Lianglitag Formation in the Tarim Basin, part of the Tarim paleoplate, in northwest China. The Tarim paleoplate was near the equator during the Ordovician close to the northeast margin of Gondwana (Cocks and Torsvik 2003, 2013). Structurally, the plate consists of the southern Tarim Land, western Tarim-Taklamakan Platform, Yining Basin, and southern Tien Shan Basin (see Zhan et al. 2014, fig. 1).

The Lianglitag Formation consists of light grey, thickly bedded calcirudites, calcarenites, and algal limestones up to 60 m thick, with significant carbonate mud mounds in the middle and top of the formation. The type locality of the formation is at Yijanfang-Tangwangcheng, east of Sanchakou, Bachu County, northwestern Tarim, as originally defined by Zhou et al. (1990). An upper Sandbian to middle Katian age has been derived from conodonts in the Lianlitag Formation (Wang et al. 2009). The formation is disconformably underlain by the non-reefal limestones of the Tumuxiuke Formation and overlain conformably by the mostly siliciclastic Sangtam Formation.

Despite its similar age to the other carbonate successions examined in this project, the Lianglitag limestones are very different from those of eastern North America. Carbonate mud mounds were rare in North America until the late Katian. The lower Katian carbonate deposits rich in bryozoans and crinoids did not form any significant reefs or mounds. By the late Katian reefs developed in some parts of Laurentia, but they are generally dominated by coral and stromatoporoids (e.g. see Cincinnati above).
2.3 References


Chapter 3 — Material and Methods

3.1 Material

Detailed information on the collections used in the following chapters can be found therein, including specimen and locality numbers, and only some general discussions are provided here. Fossils collected as part of this study from the Manitoulin Island and Lake Simcoe areas in Ontario, but some material from Baffin Island, the Ottawa Valley, the Cincinnati Arch area are also incorporated as supplements or for comparison (Figure 3.1). In Chapter 5, specimens from the Tarim Basin in northwest China are used because of their taxonomic and paleobiogeographical significance.

3.1.1 University of Western Ontario collection

Most of the material examined in this thesis from the University of Western Ontario collections originated from localities on Manitoulin Island near the northern shoreline of Lake Huron and near Lake Simcoe southeast of Barrie, Ontario. The fossils from Manitoulin Island represent the fauna from the northeastern Michigan Basin and the collections from the Lake Simcoe region belong to the St. Lawrence Platform paleobiogeographically (see Chapter 2). These two collections are very similar and indicate that these areas were similar in terms of living environment during the Late Ordovician (although there are subtle differences; see section 7.5 in Chapter 7).

The author collected some of the material, but others have contributed to the collection over the years, including Jisuo Jin, Akbar Sohrabi, Nikole Bingham-Koslowski, Cale Gushulak at the University of Western Ontario and Dave Rudkin from the Royal Ontario Museum in Toronto.

Among fossils from multiple localities on Manitoulin Island from both Ordovician and Silurian strata in the collection, only material from the Verulam Formation at one locality on Goat Island road was used for the paleontological study in this thesis. The locality features both roadcut and lakeshore exposures along an abandoned stretch of the old Highway 6 north of Little Current (UTM coordinates: 17T 0429039E, 5093089N; WGS 84 datum). At this locality
**Figure 3.1:** Major arches and basins of eastern North America during the Late Ordovician with the main collection localities. Localities: 1) Silliman’s Fossil Mount on Baffin Island, 2) Manitoulin Island near Little Current, 3) east of Lake Simcoe, 4) Ottawa Valley, and 5) Cincinnati type area. Base map modified from Cocks and Torsvik 2011, using information on structural elements from Sloss (1988), Cecile and Norford (1993), and Sanford and Grant (2000). Extent of flooding is only an approximation as much of the Ordovician carbonates have been removed by erosion.
the Verulam Formation is exposed, characterized by greyish interbedded grainstone and mudstone to wackestone interbeds. The beds commonly have uneven and undulatory bases. At the shoreline outcrop, large ripples are well preserved on several bedding surfaces. The outcrop is richly fossiliferous, with prasoporid and trepostome bryozoans, brachiopods, and crinoids (with some articulated stems and holdfasts). Common brachiopods here include small *Rhynchothrema increbescens* and *Parastrophina hemiplicata*, with less common *Strophomena* and *Rafinesquina*.

Collections from five localities near Lake Simcoe were used in this thesis. Locality W-O2 (=Mara ditch 1) is located on Ramara Concession Road 2 west of Highway 12 consisting of approximately 2 m of exposed lower Verulam Formation along a drainage ditch on the south side of the road (UTM: 17T 0644080E, 492911N; WGS 84 datum). The rock is well weathered and covered by soil. The section is similar to the Goat Island Road section described above with grey, interbedded grainstone and packstone with soft micritic mudstone partings. Prasoporid and trepostome bryozoans are abundant and numerous brachiopod shells occur in the soft, mudstone layers and concentrated shell beds (storm deposits). *Rhynchothrema increbescens*, *Rafinesquina*, and *Anazyga recurvirostra* are most common, but the fauna is diverse, also including significant numbers of *Parastrophina hemiplicata*, *Plaesiomys browni*, *Strophomena*, *Paucicrura rogata*, and *Sowerbyella sericea*. “Platystrophia” (probably *Vinlandostrophia*) have been collected here, but are not common. Orthooids have been collected here, including *Glyptorthis*, *Dinorthis*, *Hesperorthis*, and *Dolerorthis*, though they are not as common as other genera. Lingulids are rare.

A second exposure of Verulam Formation in the Lake Simcoe area consists of roadside low bluffs along Highway 48 (UTM: 17T 0649693E, 4928876N; WGS 84 datum). The outcrops are similar greyish alternating packstones/grainstones and mudstones, but the proportion of mudstones is much higher here than at the other localities. Relatively small and delicate prasoporid and trepostome bryozoans are common alongside numerous brachiopods. *Paucicrura rogata* are the most common brachiopod here by far, but *Rhynchothrema increbescens* and *Sowerbyella sericea* can be found in large numbers. “*Platystrophia*” *amoena*
and *Anazyga recurvirostra* are uncommon. Other brachiopods including orthoids and strophomenoids, are rare.

Locality W-O1 (=Centennial Park Road) is north of Highway 48 on Centennial Park Road (part of Highway 33) before crossing the bridge. This locality consists of a series of benches of Verulam Formation that step down toward the lake. Unlike the other localities below, the locality consists of thick (about 30 cm) beds of grainstone and packstone with thin interbeds of carbonate mudstone. The fossil fauna is considerably less abundant and diverse than the other lower Verulam localities, but a collection mostly comprised of *Anazyga recurvirostra* and *Rhynchotrema increbescens* were gathered from the tops of the benches.

The Highway 6 bluff locality (Kirkfield Road) is a roadside cliff section forming two benches of the Lindsay Formation (UTM: 17T 0663332E 4928445N; WGS 84 datum). The stratigraphic section is similar to the Mara ditch locality above, with greyish interbedded grainstones and packstones with carbonate mudstones. A dense shell bed is located on top of the lower bench associated with an intraformational conglomerate. Prasoprid bryozoans are common with crinoid ossicles. The most common brachiopods collected were *Sowerbyella sericea* and *Paucicrura rogata* with *Rhynchotrema increbescens* common. Orthoids and strophomenoids were uncommon. This is the only locality from which *Vellamo* has been collected. Notably, *Plectorthis plicatella plicatella* can be found at this locality alongside smaller *Plectorthis plicatella laurentina*, unlike any other locality in the Lake Simcoe area. Some of the earliest known representatives of *Megamyonia* have also been collected from here (referred to as *Rafinesquina* and *Strophomena* in other publications).

Several slabs and a small collection of loose material were also recovered from the Carden Quarry near Brechin, Ontario from the uppermost Bobcaygeon Formation on the floor of the quarry. A *Paucicrura*-rich fossil fauna was found in a soft shaly parting on the top bench which has since been quarried away. The tiny *Protozyga exigua* can be found by a good eye in the fine material here.
The only specimens used in this study from outside of Ontario from the University of Western Ontario collection are a box of *Rhynchotrema ainsliei* from an uncertain locality near Montreal (see Chapter 3).

### 3.1.2 Geological Survey of Canada (GSC) collections

All material studied from the Ottawa Valley and Baffin Island are from the Geological Survey of Canada in Ottawa (GSC). The Ottawa Valley material was collected mostly by Alice E. Wilson during the first half of the century, described in Wilson (1946). The material from Baffin Island was collected by multiple researchers from the GSC over the last century, but most notably by B.V. Sanford, A.D. McCracken, and R.G. Blackadar. The megafauna was noted and partially described by Bolton (2000), although the brachiopods lack any systematic description.

### 3.1.3 Nanjing Institute of Geology and Palaeontology (NIGP) collections

Several specimens of *Parastrophina* from the Upper Ordovician Lianglitag Formation in the Tarim basin of northwest China featured in Chapter 4 were provided by the Nanjing Institute of Palaeontology and Stratigraphy in Nanjing, China. These specimens were named a new species, *Parastrophina tarimensis* Sproat, Jin, and Zhan (see Chapter 5).

### 3.1.4 Collections from the American Museum of Natural History and Cincinnati Museum Center

Some of the material examined in Chapter 5 was loaned from the American Museum of Natural History in New York (AMNH) and the Cincinnati Museum Center in Cincinnati, Ohio (CMC). The material from AMNH consisted of the original type lot from Hall (1847) for *Plectorthis plicatella* and *Plectorthis fissicosta*. Precise locality information is usually lacking for these early collections, but they originated from Maysvillian (Katian) strata in the Cincinnati type area. The specimens borrowed from CMC was supplementary material used to describe both *P. plicatella* and *P. fissicosta*. Detailed locality information can be found in Chapter 5, but all specimens were from the Maysvillian strata around the Cincinnati arch region.
3.1.5 Field Museum collection

Several specimens from Roy’s classic collection from Silliman’s Fossil Mount, Baffin Island, now stored at the Field Museum were used for Chapter 4, including various species originally labelled as *Rhynchotrema* (now considered *Hiscobecus* – see Sohrabi and Jin 2013).

3.2 Methods

Detailed methodology can be found in each of the following chapters, but some of the general, broadly applicable methods used in this thesis are described in general here.

3.2.1 Fossil collection and preparation

For the purposes of paleontological study, it is important to try to collect as representative of a sample collection as possible. This entails getting close to the outcrop and carefully checking for smaller and less common fossil types. For this thesis, an effort was made to try to collect similar proportions of fossils to what was seen in the outcrop, and several intact slabs that preserved the original abundance and proportion of the specimens were collected to analyze the fossil diversity.

Once the fossils were collected, they were carefully packaged to be returned to the laboratory. Smaller specimens were wrapped in toilet paper or newspaper. Both are relatively soft, preventing abrasion caused by specimens rubbing against each other, and when wrapped loosely, provide protection from impacts. Larger slabs can be isolated from each other by cardboard, cloth bags, or multiple pieces of newspaper to prevent abrasion to fossils on the surface.

Back in the lab, the fossils were unpacked and rinsed to remove dirt and dust from their surface. Larger specimens and slabs were simply rinsed in the sink and left to soak. Smaller slabs and specimens were placed in a plastic tray to allow many specimens to be cleaned at once, and then rinsed and left to soak as well. Care was taken to only wash specimens from a single locality at a time to avoid any mixing. Once the fossils have been left to soak to soften
and loosen any matrix material on their surface (generally for a day or two), they were cleaned with a toothbrush to remove any remaining loose material and then rinsed. This process is repeated two to three times to ensure that the fossils are clean.

For some specimens, especially those being photographed, more detailed cleaning was required to expose delicate surface features. First, these specimens were soaked in an ultrasonic bath for several days to loosen the attached sediment. With the help of a dissecting microscope, a fine needle was used to clean matrix material from the shell surface (Figure 3.2). This was especially helpful for cleaning between ribs on brachiopods and the posterior interarea region to observe small and delicate features like aditicules and the cardinal process.

3.2.2 Photography

Several representative specimens were photographed as part of this thesis. Some preparation after cleaning is required to get good contrast in photos of fossil brachiopods. Generally, a very fine powder coating is applied to the fossil to enhance any surface relief. For this thesis, ammonium chloride was used. A very small bundle of fiberglass strands was first placed in the bottom of a test tube that has a hole in its tip to hold the powdered ammonium chloride in the test tube. Powdered ammonium chloride was placed in a test tube with a small hole in the bottom. Fiberglass fibers were loosely packed into the open end of the test tube to prevent any spillage. The fiberglass must be loosely packed to allow air to flow through the test tube.

The test tube was then heated in a fume hood until a fine white vapour (similar to smoke) began coming out of the end of the test tube. These fumes were pumped out of the small hole in the bottom of the test tube using an aquarium pump attached to the other end of the tube via a small hose and a cork stopper. The vapour was passed briefly over each shell to be photographed, leaving a very fine powder residue on the fossil. Some trial and error was required to determine an adequate coating thickness for photographing. The full apparatus is shown in Figure 3.2.
Figure 3.2: Various tools used as part of this thesis. Top left: dissecting microscope with attached DD-2 digital camera and pick used for cleaning fossils and microscopic photography. Top right: apparatus used to coat the specimens for photography to enhance the contrast of morphological characters. Bottom left: copystand used to photograph specimen. Bottom right: parallel grinder used in the creation of serial sections. Note that the specimen is attached to the circular hole in the middle of the top piece on the left. The silver column in the far right of the photo is used to adjust the height of the specimen.
Once prepared, the specimens were moved to a copy stand where they were illuminated by LED lights (Figure 3.2). Other lights in the room were turned off to avoid interference. The specimens were then photographed using a DSLR camera on aperture priority mode and a macro lens (generally either 60 mm or 85 mm focal length). The aperture was kept at f16-f32 to provide as much depth of field as possible. Often negative exposure compensation was applied to reduce the brightness caused by photographing a near white specimen on a dark background. Usually a dorsal, ventral, anterior, posterior, and lateral photo was taken for each specimen with a scale included in each shot to show the size and shape of the specimen.

After photography, the digital files were processed using Corel Photopaint, versions X5 and X8. None of the details were altered on the specimens, but the backgrounds of the photos were removed and contrast of the specimens enhanced to better illustrate shell morphology. The photos were then converted to grayscale and imported into photographic plates for use in the thesis.

A similar process was undertaken for microscopic photography. The specimens were prepared similarly, but were carefully oriented to provide as flat of a surface as possible for photography due to the extremely shallow depth of field typical of microscope photography. When possible, the aperture was stopped down on the microscope to enhance the depth of field, but this was not always an option – particularly at higher magnifications where more light is needed. The photos were taken using a DS-FI2 digital camera attached to the microscope. The photos were initially processed using NIS Elements 4.20. The software can automatically insert a scale into the image based on the objective used on the microscope. Once captured and saved, the image was transferred to Photopaint for additional processing, similar to the copy-stand photography. Sometimes focus stacking was required for increased depth of field. NIS Elements 4.20 provides mostly automatic tools for aligning and combining several photos with different focal points into a single image to increase focal depth.
3.2.3 Serial sectioning

In chapters 4 and 5, serial sections were used to examine the internal morphology of the shells. These were not standard thin sections, but rather acetate peels that are simple and inexpensive to make. To make the sections, a Croft manual parallel grinder (Figure 3.2) was used. A specimen was attached to a metal puck on the bottom of the top piece of the grinder using beeswax. The specimen was mounted on the puck posterior-up, but the puck is attached upside down so that the posterior of the shell faces the grinding surface.

A fine aluminum oxide powder is used to grind the specimen. Coarser powders polish faster, but finer powders make a smoother finish that create better sections. For this thesis 400 grit powder was used, but coarser compound may be needed depending on the type of material being sectioned and the size of the specimen. The powder is mixed with water to make a soupy paste so that the specimen will slide over it. The consistency should be similar to dish soap when the ratio is right. A water bottle was helpful to add water to the mixture as the polishing compound dries with use.

Once the specimen was mounted, the top of the grinder was set on the ball bearings on the base, and the height adjustment on the grinder was set so that the specimen is just touches the grinding surface. The height setting was then recorded to serve as a baseline. For this thesis, an interval of 0.1 to 0.3 mm was used between sections depending on specimen size and stage of grinding. Larger specimens do not require as small an interval to capture all of the internal structures. It is critical to have a small interval near the posterior where most of the structures are located, but once past most of the critical structures, the size of the interval can be increased. Once the first interval is set, the top of the grinder moved in circles until the specimen is ground down to the set measurement. This can be difficult to determine, but the specimen is likely ready when there is very little resistance and the specimen is not rubbing against the grinding surface.

After grinding, the puck in the bottom of the grinder was removed and the specimen was washed to remove any extraneous polishing compound. A few drops of dilute (~3%)
hydrochloric acid were used to etch the surface for 5-10 seconds. The specimen was then washed again to remove any remaining acid and dried using either a towel or compressed air.

To create the peels, a drop of acetone was placed on the polished surface of the fossil, and a small piece of acetate film was applied to the polished surface. This had to be done quickly but carefully, as the acetone vapourizes quickly but bubbles can form between the film and the surface if done too quickly, ruining the peel. The film was left on the specimen for a minute or two – the time necessary depended on the size of the surface as larger surfaces took a longer time to set. Once ready, the peel should feel rigid around the edge of the specimen and can be peeled off of the specimen. Several peels were taken of each surface before resuming grinding to ensure that a good quality peel showed each internal feature clearly.

To keep the peel flat, it was placed between two glass slides for examination and photography under a transmitted light microscope. A Nikon Coolscan V slide scanner was used for some specimens to simplify this process. Once photographed, the outline and growth lines within the shell material were traced with Photopaint, and several tracings were combined together on a single page to illustrate the internal morphology of the specimen from back to front.

3.2.4 Measurement of specimens

In general, basic measurements of length, width, and thickness were used for this thesis, with other supplemental characters measured depending on the genus studied. Different genera changed in different ways through evolution, and thus it was necessary to evaluate the significance of a measurement for each genus, though most of the measurements were similar. The measurements were taken using a set of digital calipers to ensure accuracy, and found to be accurate within approximately +/- 0.3 mm through multiple measurements. Ratios were used as a proxy to quantify the shape of shells (e.g. globosity and convexity = thickness:length, outline = length:width). Again, the choice of ratios used was dependent on the genus being examined.
3.2.5 Software used for analysis

The basic univariate and bivariate statistics were run and plotted using Microsoft Excel in conjunction with the graphing program CoPlot (v. 6.4 - http://www.cohort.com/coplot.html) and the graphing component of the PAST software package (v. 3 - http://folk.uio.no/ohammer/past/).

The more complex statistical techniques were run using the PAST software package v. 3 (Hammer et al. 2001). The software runs on Windows or OS X and provides a simple graphical user interface to run many statistical analyses commonly used in earth sciences. The program can be freely downloaded, along with a helpful manual in pdf format.

3.2.6 Univariate and bivariate statistics

Univariate and bivariate statistics were used in chapters 4–6 to quickly and simply compare variations between species. Univariate statistics, especially mean measurement values, are a simple metric that can be used to compare differences in characters between species or genera. Standard deviation, minimum, and maximum values were also used as indications of the overall range of values.

Bivariate plots of length vs. width and thickness vs. width are commonly used in paleontology to determine if specimens are conspecific or not. If the data points cluster along a trend line, the specimens are usually considered conspecific, with the trend indicating ontogeny. By using bivariate statistics, ontogenetic effects can be minimized as generally overall shell shape does not significantly change as the shell grows. These plots were used in the detailed systematics of the proceeding chapters.

3.2.7 Principal component analysis

Principal component analysis (PCA) is a statistical method for analyzing complex multivariate datasets. It is used to display a dataset governed by multiple variables (e.g. a set of measurements, as in the following chapters) in a simplified two-dimensional form that still preserves as much variance of the original dataset as possible (Hammer and Harper 2006).
The type of data being analyzed must be considered when working with PCA. If the data is in a single unit of measurement (e.g. mm, number of ribs, etc.), a simple variance-covariance matrix can be used. If the measurements are in different units, the data must first be standardized through the use of a correlation matrix (Hammer and Harper 2006).

Each principal component reflects a given proportion of the variance, and thus it is easy to determine if the resulting scattergram has any real significance. The principal components can be interpreted as reflecting underlying factors influencing a group of variables in the dataset.

In this thesis, PCA has been used to detect possible trends of evolution through time and separate species based on sets of measurements and differentiate faunal provinces. The correlation coefficient was used rather than covariance to separate species, as covariance requires all variables to be in the same units. The measurements were mixed with ratios, and thus analyses based on covariance would produce an inaccurate scattergram. The co-variance coefficient was used in the paleobiogeographic analysis, as the data was without units, and thus standardization was unnecessary.

3.2.8 Cluster analysis

Cluster analysis is also used for multivariate data, but while PCA is used to interpret underlying factors that may be influencing the data, cluster analysis is used to assign data points to groups of similarity (Hammer and Harper 2006). In paleontology, this can be used on a series of biometric measurements to try to differentiate between different species. When based on a presence-absence or abundance matrix in paleoecological studies, the analysis can be used to determine biogeographic provinces or ecological communities. Cluster analysis was used in Chapter 5 on morphometric data from several species of *Parastrophina*, and in Chapter 7 on abundance and presence/absence data to detect faunal provinciality among the collections from Trentonian localities of Ontario, and other regions of Laurentia.
Several methods can be used in cluster analysis to construct the clustergrams. Ward’s method is generally favoured when using morphometric data, while the Paired Linkage method can provide better results with other types of data. A variety of coefficients of similarity and dissimilarity can be applied to the data, each with pros and cons (see Hammer and Harper 2006 for a full list). Here, the Euclidean coefficient was used for numerical or percentage data, and the Jaccard coefficient for binary presence/absence data. The Euclidean coefficient describes the variance in terms of the squared Euclidean distance between data points, while the Jaccard coefficient is used for analyzing binary data (Harper and Hammer 2006). The Dice coefficient, another tool for analyzing presence/absence data that emphasizes matches between localities, was also applied to the data, but produced an identical clustergram that was not included as the Jaccard coefficient is less complex. Euclidean distance can be defined as:

\[ \text{Euclidean distance: } ED = |\mathbf{u} - \mathbf{v}| = \sqrt{\sum (u_i - v_i)^2} \]

where \( \mathbf{u} - \mathbf{v} \) is the vector between two points (as in Harper and Hammer 2006; see also Krebs 1989) and the Jaccard coefficient is defined as:

\[ \text{Jaccard coefficient: } JC = \frac{M}{M+N} \]

where \( M \) is defined as the number of species present in both samples and \( N \) is the total number of remaining species (as in Harper and Hammer 2006; see also Jaccard 1912).

3.2.9 Diversity indices

The biodiversity of a fossil community in conjunction with the abundance of a given set of species can indicate several important characteristics of the shelly benthic community. For example, a low diversity community with high abundance of one or two species may indicate an assemblage that is opportunistic, perhaps colonizing the seafloor following storm deposition. A more diverse and evenly abundant community may represent a more mature benthic assemblage that lives in a relatively stable environment.
In Chapter 7, these ideas were applied to the fossil collection from the Lake Simcoe area and Manitoulin Island. However, more specialized measurements of diversity can be applied to more accurately reflect the true diversity of a fossil assemblage by taking into account both the number of specimens and number of species or genera. Two indices that are generally applicable to a wide range of data types are the Simpson index of diversity and the Shannon-Wiener diversity index.

The Simpson index is a measure of the dominance of taxa in a fossil collection, commonly expressed as Simpson diversity, the inverse of dominance, as shown by the two formulae below (after Hammer and Harper 2006; see also Simpson 1949):

**Simpson dominance index:** $\lambda = \sum(p_i^2)$

**Simpson index of diversity:** $1 - \lambda = \sum(p_i^2)$

where $p_i = \frac{n_i}{n}$ (proportion of species $i$). Unfortunately, there has been some confusion regarding the formula for the Simpson index in published literature, and thus the formula should always be explicitly stated (see Harper and Hammer 2006). The index will be closer to 1 if there is a single dominant species or genus, while a lower value would reflect a more even distribution among the species in an assemblage. Essentially, it indicates the chance (as a decimal) that two randomly chosen specimens are the same species (Harper and Hammer 2006).

Shannon-Wiener index is another measure of diversity that reflects the entropy of a collection. It is calculated as (after Harper and Hammer 2006; see also Shannon and Weaver 1949, Krebs 1989):

**Shannon-Wiener index:** $H' = -\sum p_i \ln p_i$

where $p_i = \frac{n_i}{n}$ (proportion of species $i$). The lowest possible value (0) would indicate that the sample is composed of a single species. A higher value reflects more species. Rather than the raw dominance/diversity expressed by the preceding Simpson index, the Shannon-Wiener is...
based on not only the relative dominance, but also the number of taxa (Harper and Hammer 2006).

In Chapter 7, both indices show a similar trend across localities, as would be expected if they accurately reflected diversity. The number of species, number of taxa, Simpson index values, and Shannon-Weiner index values are each presented to provide a clear snapshot of diversity of each locality for comparison.
3.3 References


Chapter 4 — The early evolution of Middle–Late Ordovician rhynchonellide brachiopods in Laurentia

4.1 Introduction

The brachiopod order Rhynchonellida first appeared during the late Darriwilian (late Middle Ordovician), relatively late compared to many other groups (e.g. Orthida, Strophomenida, and Pentamerida), and is one of the few brachiopod orders that are still living today. The oldest known rhynchonellides are represented by *Rostricellula* Ulrich and Cooper, 1924, from Avalonia and eastern Laurentia (Cooper, 1956; Cocks, 2008). *Rostricellula* later gave rise to *Rhynchotrema* in the late Sandbian, which became widespread worldwide in the Katian and evolved into the *Hiscobeccus* fauna (Jin 2001; Sohrabi and Jin 2013) that was an important component of the epicontinental shelly benthos of Laurentia during the late Katian (Maysvillian to Richmondian).

*Rostricellula* is characterized by the absence of a cardinal process and by having a small, subtriangular, strongly costate shell generally lacks the distinctive growth lamellae found in its descendants such as *Rhynchotrema* and *Hiscobeccus* (Cooper 1956; Rice 1987; Savage et al. 2002). The earliest *Rostricellula* species are of Darriwilian age, including *R. triangularis* Williams, 1949 from Wales (mostly consisting of poorly preserved internal molds; see MacGregor 1961; Cocks 2008) and *R. basalaris* Cooper, 1956, *R. plena* (Hall, 1847) and *R. orientalis* (Billings 1859) from eastern North America (see Cooper 1956). By the end of the Darriwilian, *Rostricellula* achieved a cosmopolitan distribution, occurring in both tropical and temperate zones including Siberia (Rozman 1979), North China (Fu 1982), Gondwana (Havlíček 1961, 1971, 1989; Havlíček and Branisa 1980; Leone et al. 1991, Villas 1992), and Laurentia. The greatest diversity of the genus was achieved in Laurentia (Jin 1996), where it can be found in pericratonic settings, such as Alabama, Tennessee, New York, Vermont, and the Mingan Islands in Quebec. *Rostricellula* survived the End Ordovician extinction event, with species being reported in rocks as young as Llandovery (e.g. *R. serrata* of Telychian age; see Cocks 2008), though the diversity of the genus was substantially reduced.
Rhynchotrema is similar to Rostricellula in its subpentagonal shape and simple costate ornamentation (Savage et al. 2002). Ulrich and Cooper (1942) suggested that Rostricellula is differentiated from Rhynchotrema based on its lack of lamellose ornamentation and lack of a cardinal process, but Rice (1987) recognized that these features were not mutually exclusive, and suggested that presence or lack of a cardinal process would provide a more useful classification scheme. Rice suggested that species of Rostricellula show no evidence of a cardinal process, while Rhynchotrema does possess a cardinal process.

The earliest known Rhynchotrema, *R. wisconsinense*, is from the Platteville Formation in Minnesota of late Sandbian (Turinian) age (see Sohrabi and Jin 2013) and is also found in the younger Decorah Shale (Fenton and Fenton 1923; Weiss 1955; Cooper 1956; Howe 1965; Rice 1987). *R. increbescens* first appeared in the Trentonian Limestone of New York (early Katian, Chatfieldian – Wang 1949; Titus 1986) and quickly spread across Laurentia, also being found in the Decorah Shale (see references above), Bucke Formation of Ontario near Lake Timiskaming (Hume 1925), and Lexington Limestone of Kentucky (Cooper 1956; Howe 1965, 1969, 1979). Rhynchotrema can be found worldwide; including Siberia, Kazakhstan, North China, and Australia (see Jin 1996). The youngest species of Rhynchotrema, *R. parviseptatum* Jin, 1989, is known from Llandoverian rocks on Anticosti Island, Quebec.

Hiscobecus shares many similar features with Rhynchotrema but was separated by Wang (1949) on the basis of the large size, lamellose and rounded shells as part of Lepidocyclus. Amsden (1983a, b) further differentiated Hiscobecus from Lepidocyclus based on deltidial plates – those species possessing deltidial plates were described as Lepidocyclus while those with an open delthyrium were designated as Hiscobecus.

Unlike Rostricellula and Rhynchotrema, Hiscobecus is virtually unknown outside Laurentia, except for a few reports that did not provide any information on internal structures. The earliest known species, *H. mackenziensis*, is found in the early Katian (Chatfieldian) Advance Formation of British Columbia, Canada (Jin and Norford 1996). The characteristic Hiscobecus fauna (Jin 2001) can be found throughout North American rocks of Katian
(Maysvillian to Richmondian) age and includes other rhynchonellides such as *Lepidocyclus* and *Hypsiptycha*. Although common in the late Katian rocks of North America, no species of *Hisacobeccus* are known from the Hirnantian (Gamachian) or younger rocks.

### 4.2 Morphological change in the *Rostricellula*-Rhynchoatrema lineage

In general, both *Rostricellula* and *Rhynchoatrema* have a small, subtriangular to subpentagonal, dorsibiconvex shell with a distinctly uniplicate anterior commissure. Although superficially very similar, there are several differences or morphological transitions between the two genera, especially in the development of shell sculpture, ribbing style, and absence or presence of a cardinal process.

#### 4.2.1 Shell size

The oldest forms of *Rostricellula* of late Darriwilian–early Sandbian age, such as *R. basalaris* and *R. orientalis* (Figure 4.1), are notably smaller compared to later species. By the late Sandbian and early Katian, some species of *Rostricellula* started developing a relatively large shell that exceeds 10 mm in diameter (e.g. *R. rostrata*; Figure 4.1) but they are rarely larger than 20 mm. The oldest *Rhynchoatrema* from the upper Sandbian Platteville Formation of Minnesota, *R. wisconsinense* (see illustrations in Sohrabi and Jin, 2013) are all small in size (~10 mm in length or width) compared to later forms, although they are somewhat larger than the pioneer species of *Rostricellula*. This suggests that *Rhynchoatrema* may have evolved from relatively small-shelled *Rostricellula*.

#### 4.2.2 Shell ribbing

The early forms of *Rostricellula* typically have four ribs in the fold and three in the sulcus, as the archetype of the family Rhynchotreematidae, but these rib numbers become variable in some later Ordovician rhynchotreematid forms. For example,
*Rhynochotrema ainsliei* may have up to 7 ribs in sulcus, 8 in fold, and 8-10 on shell flanks (Figure 4.2 A-E). In ribbing style, however, most *Rhynochotrema* clearly shows the trait of early *Rostricellula* in the consistent development of four simple (non-branching), subangular costae on the fold and three corresponding costae in the sulcus (*R. increbescens*, Figure 4.2 F-J; and *R. wisconsinense*, Figure 4.3). Species of *Rostricellula*, however, are more variable in the pattern of ribs.

4.2.3 Growth lamellae

As suggested by Cooper (1956), *Rostricellula* does not have the strong growth lamellae usually present in *Rhynochotrema*. Sohrabi and Jin (2013) interpreted the increasing lamellosity from *Rhynochotrema* to *Hiscobecus* as an evolutionary trend in the warm water of epicontinental seas (Figures 4.2–4.4). *Rostricellula* originated in the cool-water environment of high-latitude Gondwana (Cocks, 2008) and, in Laurentia, it was most abundant in the subtropical pericratonic setting along the southeastern continental margin (Cooper, 1956) and was absent from the equatorial intracratonic depositional environments (e.g. Hudson Bay and Williston basins). Thus the lack of strong growth lamellae in *Rostricellula* corroborate the interpretation of Sohrabi and Jin (2013) and suggests a *Rostricellula-Rhynochotrema-Hiscobecus* lineage that evolved from cool-water to warm-water environments during the Late Ordovician (Figure 4.5).

4.2.4 Cardinal process

Unlike *Rhynochotrema*, *Rostricellula* lacks a cardinal process, which is a small plate-like partition along the medial line of the septalium to provide additional attachment surface for the diductor muscles (Jin, 1989). A crucial test of the proposed *Rostricellula-Rhynochotrema* evolutionary lineage lies in the discovery of an intermediate species between the two genera to show the origin of the cardinal process. Rice (1987) noted the possible presence of a rudimentary cardinal process in smaller, perhaps immature forms of *Rhynochotrema ainsliei* — a feature that is absent in larger, more mature forms. On this basis, he considered the species
Figure 4.2: Early Katian (Chatfieldian) species of *Rhynchotheca*. *Rhynchotheca ainsliei* (Winchell, 1886). A–E, specimen W-2980 from locality near Montreal, Quebec (original collection locality unknown, but probably early Katian (Chatfieldian) in age); dorsal, ventral, lateral, anterior, and posterior views. *Rhynchotheca increbescens* (Hall, 1847). F–J, specimen from locality on highway east of Clarence, Ontario (across from ferry road). Specimens from the Geological Survey of Canada, but no collection number. Sample labelled as collected by A.E.W. on July 17, 1929. If the sample is truly from the Chazy Limestone, this would be the oldest collection of *R. increbescens* reported. However, it is more likely from the early Katian (Chatfieldian) Ottawa Group. Dorsal, ventral, lateral, anterior, and posterior views.
Figure 4.3: *Rhynchotrema wisconsinense* Fenton and Fenton, 1923. A–J, uncatalogued specimen from the GSC collection from the Ottawa Group at the Ottawa River, Ontario; dorsal, ventral, lateral, anterior, and posterior views. Same species; F–J, specimen W-2977 from locality W-O2 in ditch off of Ramara Concession Road 1 near Lake Simcoe, Ontario; dorsal, ventral, lateral, anterior, and posterior views.
Figure 4.4: *Hisacobecus arcticus* (Roy, 1941) from Silliman's Fossil Mount on Baffin Island, Nunavut. A–F original holotype of *Rhynchotrema capax arcticum* Roy, 1941, PE-P28277; dorsal, ventral, lateral, posterior, and anterior views, magnified view of coarse growth lamellae. G–L original holotype of *Rhynchotrema anticostiense breve* Roy, 1941, PE-P28278, dorsal, ventral, lateral, posterior, and anterior views, magnified view of coarse growth lamellae. M–V two hypotypes, GSC 113533 (M–Q) and GSC 113541 (R–V); dorsal, ventral, lateral, posterior, and anterior views.
Figure 4.5: Proposed evolution of the *Rostricellula-Rynchotrema-Hiscobeccus* lineage. The evolution of *Hiscobeccus* from *Rynchotrema* was discussed in detail in Sohrabi and Jin (2013). Thickness of bars indicates approximate abundance of each genus through time.
more closely affiliated to *Rhynchotrema* than to *Rostricellula*. In any case, this species is the only case known so far to show a possible ontogenetic gradation between *Rostricellula* and *Rhynchotrema*.

4.3 Objective of this paper

To carry out a comprehensive test of the *Rostricellula-Rhynchotrema* lineage, large collections of the key species will be needed for multivariate analyses of biometric characters and cladistic analysis. This is beyond the scope of this study.

Sohrabi and Jin (2013) have provided a detailed study on the evolution of *Hiscobeccus* from *Rhynchotrema* during the early Katian (Chatfieldian to early Maysvillian). This will not be repeated here.

The main goal of this paper is to provide some key morphological information on some of the key species of *Rostricellula* and *Rhynchotrema*, which will form part of the basis for multivariate and cladistic analyses of the proposed *Rostricellula-Rhynchotrema* lineage. An additional species (*'Rhynchotrema' arcticus* Roy, 1941), which shows transitional morphology from *Rhynchotrema* to *Hiscobeccus*, is also examined taxonomically.

4.4 Systematic paleontology

Specimens labelled FM are from the Field Museum in Chicago, Illinois, United States. Specimens labelled GSC are from the Geological Survey of Canada in Ottawa, Ontario, Canada. All others are from the University of Western Ontario Paleontology Collection in London, Ontario, Canada.

Order Rhynchonellida Kuhn, 1949

Superfamily Rhynchotrematoidea Schuchert, 1913

Family Rhynchotrematoidae Schuchert, 1913
Subfamily Rhynchotremadinae Schuchert, 1913

*Rhynchotrema* Hall, 1860

*Type species.* *Atrypa increbescens* Hall, 1847 p.146, pl. 33, figs. 13a–d (non e–y), from the Trenton Limestone of New York, early Katian (Chatfieldian).

*Diagnosis.* See Savage et al. 2002 for most recent diagnosis in the *Treatise of Invertebrate Paleontology*.

*Rhynchotrema ainsliei* (Winchell, 1886) (Figs. 4.2 A–E, 4.6)

1886 *Rhynchonella ainsliei* Winchell, p. 315, pl. 2, figs. 5, 6.

1895 *Rhynchotrema ainsliei* (Winchell); Winchell and Schuchert, p. 459, pl. 34, figs. 1–8.

1955 *Rhynchotrema ainsliei* (Winchell); Weiss, p. 773, pl. 69, fig. 12, pl. 70, fig. 2.

1956 *Rostricellula ainsliei* (Winchell) Cooper, p. 649, pl. 139, B, figs. 12–22.


*Types.* Cooper (1956) named the holotype specimen 36550a (pl. 139, B, figs. 12–16); figured paratype: 36550b (pl. 139, B, figs. 17–22); measured paratypes: 36550c, d from the Swift Current Formation in Ontario, Canada at North-east corner of St. Joseph Island on St. Marys River.

*Studied material.* 7 measured specimens from the early Katian(?) (Chatfieldian?) near Montreal.

*Description.* Shell medium in size, dorsibiconvex, subtriangular to transverse in outline, large for the genus, with average length 14 mm (max 16.64 mm), width 15 mm (max 19 mm), and
Figure 4.6: Serial sections of *Rhynchotrema ainsliei* (Winchell, 1886). Specimen W-2981 from a locality near Montreal, Quebec. Numbers indicate distance from ventral umbon in mm. Note the lack of a cardinal process in this specimen. Sections oriented dorsal valve up.
thickness 10 mm (max 13 mm). Hinge line short with sloping, rounded cardinal extremities. Maximum width at mid-length (Figure 4.2a, b). Costae simple, with 5–7 in sulcus and 6–8 in fold, and 8–10 on shell flanks. Lateral margins rounded; anterior margin broadly uniplicate (Figure 4.2d).

Ventral umbo suberect in younger forms, becoming slightly incurved in gerontic forms (Figure 4.2 C). Delthyrium open. Ventral interarea apsacline. Sulcus beginning 3–4 mm from ventral umbo, widening rapidly to form a wide, but shallow tongue at anterior forming a weakly but broadly uniplicate commissure (Figure 4.2d). Dorsal umbo strongly incurved, interarea obscured in delthyrium. Small, medial furrow at umbo transformed to fold approximately 4–5 mm anterior to dorsal umbo. Fold low and flat-topped, becoming prominent near anterior commissure (Figures 4.2a, d).


Remarks. These specimens show the characteristic ribbing pattern in the fold and sulcus of some *Rostricellula* species, and no cardinal process was observed in sectioning the specimen. However, Rice (1987) noted the presence of a cardinal process in two dorsal valves of *Rhynchotrema ainsliei* from the Decorah Shale in Minnesota, but explained that the specimens represent immature forms and that a third, larger form shows no cardinal process. He suggested that the small cardinal process may have become covered by secondary shell material later in ontogeny. There is no evidence of any cardinal process in the specimen sectioned here (Figure 4.6), but this specimen probably represents a mature form. No smaller immature forms are available from this collection.
**Rhynchotherea wisconsinense** Fenton and Fenton, 1923 (Figures 4.3, 4.7)

1895 *Rhynchotherea inaequivalvis* (Castelnau); Winchell and Schuchert (in part), p. 459, pl. 34, figs. 12–14, 18–23, 24?, 25?

1923 *Rhynchotherea wisconsinense* Fenton and Fenton, p.71, pl. 1, figs. 6–8.

1955 *Rhynchotherea increbescens increbescens* (Hall); Weiss, p. 722, pl. 70, figs. 3–7.

1956 *Rhynchotherea wisconsinense* Fenton and Fenton; Cooper, p. 630; pl. 128, H, figs. 40–48; pl. 138, G, figs. 43–45.

1987 *Rhynchotherea wisconsinense* Fenton and Fenton; Rice, p. 160, pl. 4, fig. 2.

**Types.** Cooper (1956) figured 3 hypotypes: 24843a (pl. 128, H, figs. 40-44), b (figs. 45–48), 117210a (pl. 138, G, figs. 43–45) from the Decorah Formation (Ion member) in Minnesota and Wisconsin.

**Studied material.** 22 measured specimens from the Verulam Formation (early Katian, Chatfieldian) at locality W-O2 in ditch off Ramara Concession Road 1 near Lake Simcoe, Ontario, Canada and 20 measured specimens from the Ottawa Group at the Ottawa River, Ontario.

**Description.** Shell small to medium in size, subtriangular to transverse in outline, dorsibiconvex; with average length 10 mm (maximum 13 mm), width 11 mm (maximum 14 mm), and thickness 6 mm (maximum 9 mm). Hinge line short, with sloping cardinal extremities. Maximum width located at mid-length. Costae simple, with three in sulcus and four in fold, and seven to eight on each flank (Figure 4.3a, b, f, g). Concentric growth lamellae covering most of shell surface, most prominent in anterior one third of shell averaging 6–7 per 5 mm of shell length on well-preserved specimens. Lateral margins rounded; anterior margin strongly uniplicate (Figure 4.3d, i).
Figure 4.7: Serial sections of *Rhynchotrema wisconsinense* Fenton and Fenton, 1923. Uncatelogued specimen from the GSC collection from the Ottawa Group at the Ottawa River, Ontario. Numbers indicate distance from the ventral umbo in mm. Specimen shows typical cardinal process of *Rhynchotrema*. Sections oriented dorsal valve up.
Ventral umbo arched; beak suberect (Figure 4.3c, h). Ventral interarea apsacline. Sulcus beginning 3–4 mm from apex of ventral umbo, widening and deepening to form tongue at the prominently uniplicate anterior commissure (Figure 4.3b, g). Dorsal umbo small with incurved beak obscured in delthyrium (Figure 4.3e, j). Faint medial furrow becoming fold 2–3 mm from apex of dorsal umbo (Figure 4.3a, f). Fold low and flat-topped, but more significant in anterior one third of the dorsal valve.


**Remarks.** *Rhynchotrema wisconsinense* is here documented from the Ottawa Valley for the first time. Wilson (1946) reported several species of *Rhynchotrema* from the region, including a newly defined species – *Rhynchotrema intermedia*. Her description of this is brief and the figures are of a poorly preserved specimen which may be *R. wisconsinense*.

Wilson’s suggestion that *Rhynchotrema intermedia* intergrades with *R. increbescens* in particular suggests close affinities to *R. wisconsinense*, as these two species are similar in their diagnoses. *R. wisconsinense* differs from *R increbescens* in its somewhat more transverse outline (average L/W of 0.94) and the presence of prominent growth lamellae in mature, well preserved specimens near the anterior commissure (Figure 4.3). The prominent growth lamellae may have been missing in Wilson’s original material due to poor preservation.

*Rhynchotrema wisconsinense* shares the prominently uniplicate outline of other *Rhynchotrema* species, and shows the distinctive pattern of four ribs on the fold and three ribs in the sulcus exhibited by most species of the genus.
*Hiscobecus* Amsden, 1983b

*Type species:* *Atrypa capax* Conrad, 1842 (p.264, pl. 14, fig. 21; text-fig. 22) from the Upper Ordovician at Richmond, Indiana.

*Diagnosis.* See Savage et al. 2002 for most recent diagnosis in the *Treatise of Invertebrate Paleontology*.

*Hiscobecus arcticus* (Roy, 1941) (Figures 4.4, 4.8)

1941 *Rhynchotrema capax arcticum* Roy, p.100, fig. 66.

1941 *Rhynchotrema anticostiense brevis* Roy, p.100, fig. 67.

1977 *Rhynchotrema arcticum* Roy; Bolton, p. 68, pl. 15, figs. 8–10.

2000 *Lepidocyclus arctica* (Roy); Bolton, Pl. 20, fig. 9–11, 13-15, 20.

2000 *Lepidocyclus brevis* (Roy); Bolton, Pl, 20, fig. 19, 24.

*Types.* *Rhynchotrema capax arcticum*, FM P28277, holotype (original of Roy, 1941, p. 100, fig. 66) and *Rhynchotrema anticostiense brevis*, FM P28278, holotype, original of Roy (1941, p.101, fig. 67) from Silliman’s Fossil Mount, Frobisher Bay, Baffin Island. Roy (1941) initially assigned a broad “Richmondian” age to the strata exposed at Silliman’s Fossil Mount. In modern stratigraphy, the strata at Silliman’s Fossil Mount belong to the Amadjuak Formation and are of Maysvillian age (Bolton 2000; Sanford and Grant 2000). This represents the type locality and type stratum.

*Studied material.* 7 measured specimens from the Amadjuak Formation (late Katian, Edenian to Maysvillian) at locality GSC 113531 northwest of Silliman’s Fossil Mount, Baffin Island, Nunavut, Canada.

*Diagnosis.* Small, subcircular, strongly biconvex shells of *Hiscobecus*, with strong concentric growth lamellae covering more than three-quarters of shell length.
Figure 4.8: Serial sections of *Hiscobccus arcticus* (Roy, 1941) from GSC loc. 0104507, Amadjuack Formation, Baffin Island, Nunavut. Number indicate distance from ventral umbo. Ventral valve oriented upward in sections.
Description (emended herein). Shell small, subcircular, equi-biconvex to dorsibiconvex; with average length 9.86 mm (maximum 11.89 mm), width 10.47 mm (maximum 13.62 mm), and thickness 7.14 mm (maximum 10.01 mm). Hinge line short, with sloping and rounded cardinal extremities. Maximum width located at mid length. Costae simple, usually three in sulcus, four on fold, and seven to eight on each flank. Concentric growth lamellae strong, frill-like (Figure 4.4f, L, 2.6–2.8 mm from apex), covering more than three-quarters of shell length, average 16 lamellae per 5 mm of shell length. Lateral margins rounded; anterior margin uniplicate, with truncated appearance in globular forms (Figure 4.4e, k, q, v).

Ventral umbo strongly convex and arched; beak suberect in younger forms, incurved into umbonal area of dorsal valve in gerontic forms. Sulcus beginning at 4–5 mm from apex of valve, widening and deepening rapidly towards anterior margin to produce prominent tongue and distinctly uniplicate anterior commissure. Dorsal umbo of moderate to low convexity, with small beak obscured in area of delthyrial cavity. Faint medial furrow in umbonal area transformed to fold at about 5 mm from apex of valve. Fold generally low, flat-topped, but well defined in anterior one-third of shell (Figure 4.4a, g, m, r).

Dental plates low, forming small dental cavities, extending slightly anterior of hinge line (Figure 4.8) Teeth small, weak. Ventral muscle field poorly impressed. Sockets small, shallow. Septalium small, narrow, minute trough-like, anteriorly not extending beyond hinge line (2.5–2.8 mm, Figure 4.8). Septalial plates short, poorly delimited. Hinge plates strong but narrow and short. Median septum relatively high for small shell size. Cardinal process short, blade-like. Crura slender, radulifer. Adductor muscle scars not well impressed.

Remarks. Roy (1941) established two species of Rhynchotrema, R. arcticum, and R. anticostiense breve, based on specimens from the same set of “Richmondian strata, Frobisher Bay Formation in Silliman’s Fossil Mount, Baffin Island”. In this study, examination of Roy’s original types and many topotypes in the collections of the Geological Survey of Canada (Ottawa) indicates that the two species are synonymous. Roy (1941) initially treated R. breve as a subspecies of “R. anticostiensis” (Billings 1862) because of its slender shell, and R. arcticum a
subspecies of “R. capax” because of its globular shell. “Rhynchotrema anticostiensis”, however, has been assigned to *Hypsiptycha* because of the presence of deltidial plates (Jin 1989). The large collection now available from Baffin Island indicates that the holotype of *R. breve* is an immature form of *R. arcticum* because it has a much smaller shell than *Hypsiptycha anticostiensis* and lacks deltidial plates.

Among the species of *Hiscobecus* in North America, *H. arcticus* has some similarity to the pioneer species, *H. mackenziensis*, in its small shell size and relatively fine growth lamellae, but differs in being more strongly biconvex to globular and having a greater portion of shell covered by prominent lamellae (see Figure 4.4, 2.6 and 2.8 mm from apex) in spite of its smaller shell size. All other species of *Hiscobecus* have considerably larger shells, with proportionally denser and stronger lamellae than *H. arcticus*.

Apart from the Silliman’s Fossil Mount collection, the only other known occurrence of *H. arcticus* is from the Cornwall area of Ontario (GSC Loc. 37136).

Subfamily Rostricellulinae Rozman, 1969

*Rostricellula* Ulrich and Cooper, 1942

*Type species: Rostricellula rostrata* Ulrich and Cooper, 1942 (p. 625, OD)

*Diagnosis.* See Savage et al. 2002 for most recent diagnosis in the *Treatise of Invertebrate Paleontology.*

*Remarks.* The pattern of ribbing in *Rostricellula* is inconsistent. Some species show a ribbing pattern similar to the *Rhynchotrema* archetype, with four ribs on the fold and three ribs in the sulcus. As stated above, however, some species have more numerous ribs in the fold and sulcus. This is unlike *Rhynchotrema*, which almost always has four ribs on the fold and three ribs in the sulcus (although there are exceptions like *Rhynchotrema ainsliei* above). However, the
shared pattern of four ribs on the fold and three ribs within the sulcus suggests a close evolutionary relationship between *Rostricellula* and *Rhynchotrema*. Unfortunately, because this feature is variable within the *Rostricellula* genus, it cannot be used as a diagnostic feature for all species but can suggest that the affinities of a specimen likely lie with *Rostricellula* when more than four ribs are found on the fold and three in the sulcus.

*Rostricellula orientalis* (Billings, 1859) (Figures 4.1, 4.9)

1859 *Rhynchosella orientalis* Billings, p. 443, fig. 21.

1863 *Rhynchosella orientalis* Billings; Logan, p. 126, fig. 57.

1911 *Camarotoechia orientalis* (Billings); Raymond, p. 223, pl. 33, figs. 32, 33.

1938 *Camarotoechia orientalis* (Billings); Twenhofel and Whiting, p. 51, pl. 7, figs. 22–24.

1956 *Rostricellula orientalis* (Billings); Cooper, p. 624, pl. 129, G, figs. 26-32; pl. 135, C, figs. 11–15; pl. 137, I, figs. 61-65.

*Types.* Cooper (1956) figured three hypotypes: 111489 (pl. 129, G, figs. 26-32), 111490a (pl. 135, C, 11–15); GSC 2184 (pl. 137, I, 61–64) from the Mingan Formation, Mingan Islands, Quebec.

*Studied material.* 20 measured specimens from the Mingan Formation on Ilde de Havre, Mingan Islands, Quebec, Canada.

*Description.* Shell small, subtriangular, equibiconvex to slightly dorsibiconvex in larger specimens; average length 6.45 mm (maximum 8.31), width 7.10 mm (maximum 8.62), and thickness 5.09 (maximum 7.15). Hinge line short (Figure 4.1k). Anterior commissure
Figure 4.9: Serial sections of *Rostricellula orientalis* (Billings, 1859). Specimen W-2976, Mingan Formation, Ile de Havre, Mingan Islands, Quebec. Numbers indicate distance from ventral umbo in mm. Dorsal valve oriented upward in sections.
strongly uniplicate (Figure 4.1n). Costae simple, with three in sulcus, four in fold, and six to seven on each flank (Figures 4.1k, l).

Ventral umbo small with suberect beak. Ventral interarea apsacline (Figure 4.1m). Sulcus beginning 1.5 to 2 mm from umbo, rapidly deepening to form a prominent tongue and uniplicate anterior commissure (Figure 4.1l). Dorsal umbo small with incurved beak obscured in the delthyrial cavity. Faint medial furrow near the ventral umbo transformed to fold approximately 0.1 to 0.2 mm from umbo (Figure 4.1k). Fold low and flat-topped, becoming well defined in anterior one-third of shell.


Remarks. This species has, thus far, only been identified from the Mingan Formation of the Mingan Islands in the St. Lawrence River as described by Cooper (1956). Here, the internal structure is shown for the first time through serial sections (Figure 4.9). Note the distinct curved dental plates not seen in other species. The serial sections also show the small sockets and teeth and lack of cardinal process characteristic of Rostricellula which differentiates the genus from the closely related Rhynchotrema.
4.5 References


Hall, J. 1860. Contributions to paleontology, 1858 and 1859. 13th Annual report of the Regents of the University of the State of New York, on the condition of the State Cabinet of Natural History, pp. 55–128.


Chapter 5 — Morphological variability and paleoecology of Late Ordovician *Parastrophina* from eastern Canada and the Tarim Basin, northwest China

5.1 Introduction

*Parastrophina* is a widely reported syntrophiidine pentameride brachiopod, characterized by a relatively small, posteriorly smooth and anteriorly plicate shell. It is a common faunal component of Late Ordovician tropical marine settings. This genus was part of the largely cosmopolitan benthic marine shelly fauna that thrived from late Darriwilian to the earliest Katian. The brachiopod fauna of this interval evolved chiefly following the mid-Darriwilian faunal turnover (Harper et al. 2004) during a major eustatic sea-level rise in the Sandbian–early Katian interval (Haq and Schutter 2008). The genus suffered a decline in both species diversity and general abundance from middle Katian to Hirnantian, but survived the Hirnantian mass extinction event. Its occurrences in the late Katian and Silurian tend to be sporadic, and some reports are putative because of the lack of information on internal structures, such as *Parastrophina* sp. from the upper Ashgill Dolhir Formation of North Wales (Hiller 1980), or *Parastrophina rotunda* Menakova, 1991 from the upper Ashgill of the Zeravshan-Gissar Range of Tadzhikistan. Globally, *Parastrophina* largely disappeared by the end of the Ordovician, except in the Urals (eastern margin of the Siberia plate) region where it survived until the Wenlock–early Ludlow (Sapelnikov 1972).

One of the most commonly reported species of *Parastrophina* from Laurentia is *Parastrophina hemiplicata* (Hall, 1847), although it usually occurs as a rare taxon in shelly benthic assemblages of eastern North America, including the type area of northwestern New York state (for example, see Titus, 1986). In the “Trenton limestone” of the Ottawa area, the species is probably the most common among its known localities (Wilson 1914). Elsewhere in Ontario, only a sporadic occurrence of *P. hemiplicata* has been reported by Sinclair et al. (1969) from the Verulam Formation of Lakefield Quarry.
*Parastrophina hemiplicata* has been studied since 1847 and has been treated as the eponymous genus and species for the family Parastrophinidae Ulrich and Cooper, 1938. Despite this, its internal structures have remained incompletely known, particularly with regard to its dorsal interior, as there have been no detailed serial sections available to examine its internal microstructures.

Recently, a diverse shelly fauna with relatively common *P. hemiplicata* has been found in a ditch section in the Lake Simcoe area near Orillia, Ontario (Figure 5.1). These shells are largely identical to the conspecific material from New York State (type locality) and from the Ottawa River Valley in Ontario. Paleogeographically, these three areas were located on the edge of the Appalachian Basin and the St. Lawrence Platform, and shared very similar faunas. The shells of *P. hemiplicata* from the Ottawa area were preserved in dark-grey, micritic mudstone, which provided an ideal opportunity for examining its internal structures through serial sectioning. The moderate-sized species populations also made it possible to assess the range of morphological variability and plasticity of the type species.

The main objectives of this paper, therefore, are 1) to provide a thorough investigation of external and internal characters of *Parastrophina hemiplicata*, and to compare it with some congeneric and broadly coeval species from other tectonic plates, such as those from the Kazakhstan terranes and the Lianglitag Formation of the Tarim paleoplate, and 2) to explore the paleoecological and paleogeographical implications of the various morphotypes of *Parastrophina*.

### 5.2. Known occurrences of *Parastrophina*

*Parastrophina* has a widespread distribution on paleotropically located plates during the Ordovician (see Appendix A for a complete listing of known occurrences), such as Laurentia, Baltica, Siberia and peri-Siberia terranes, Kazakhstan, Australia, North China and its adjacent terranes (Cooper 1956; Williams 1962; Wright 1974; Nikiforova and Andreeva 1961; Severgina 1978; Nikiforova 1989; Popov et al. 2002; Nikitin et al. 1996; Fu 1982; Modzalevskaya 2003; Percival 2009). The oldest occurrences of *Parastrophina* are known from the latest Darriwilian
Figure 5.1: *Parastrophina hemiplicata* was collected from a section in the ditch alongside Mara Concession Road 2. The outcrop was well exposed in 2002 (top-left), but has since become overgrown (top-right). The Verulam Formation overlies the Bobcaygeon Formation (bottom). The contact between these formations in the Dufferin Aggregates quarry near Brechin, Ontario, forms an aquitard (arrows), making it easily distinguishable due to the springs that have developed on the quarried surface.
(Llandeiliian) Stinchar Limestone of the Girvan District, Scotland, and coeval strata of the Pratt Ferry Formation in Alabama, and the Gulang Formation of North China, represented by *P. anceps* Reed, 1944, *P. bilobata* Cooper, 1956, and *P. pugnoidalis* Fu, 1982, respectively.

5.3 Geological and stratigraphical settings

5.3.1 Geology and paleontology of the Simcoe Group and the Verulam Formation of southern Ontario

The Simcoe Group of southern Ontario (approximately equivalent to the Trenton in subsurface terminology, see Armstrong and Carter 2010) is composed predominantly of limestone and dolostone, with varying amounts of argillaceous and bioclastic components (see Chapter 2). The carbonates sit unconformably on the Precambrian basement rocks, and are overlain by the dominantly siliciclastic Nottawasaga Group (Liberty 1969). The Simcoe Group includes (from the oldest to the youngest) the Shadow Lake, Gull River, Bobcaygeon, Verulam, and Lindsay formations, forming a continuous section spanning the uppermost Sandbian-lower Katian interval with no significant unconformities (Liberty 1969; Russell and Telford 1983; Grimwood et al. 1999). These units can be approximately correlated to equivalent units of the same name in the Ottawa Valley as part of the Ottawa Group (Figure 5.2). The Ottawa Group is retained here because its correlation with the Simcoe Group remains to be refined.

The Verulam Formation has been divided into a lower and upper member (Liberty 1969). The lower unit consists of micritic nodular mudstones, bioclastic packstones, and interbedded grainstones forming discontinuous lenticular beds within grey-green calcareous shale (Armstrong 2000), and has been interpreted as a storm-influenced open shelf environment (Brookfield and Brett 1988; Melchin 1994; Grimwood et al. 1999; McFarland et al. 1999). The upper unit is comprised a shoal facies and intershoal shelf facies. The shoal facies is characterized by cross stratified crinoidal grainstones and rudstones (Armstrong 2000), and is restricted to the Lake Simcoe area (Liberty 1969). Laminated mudstones, shales, siltstones, and coarser bioclastic limestones interpreted as storm beds make up the shelf facies (Melchin 1994; Armstrong 2000).
Figure 5.2: Stratigraphy of the Simcoe and Ottawa groups in Ontario (based on Melchin 1994 and Armstrong and Carter 2010) and the Upper Ordovician units of Tarim in northwest China (based on Zhan et al. 2014). Specimens were collected from the Verulam Formation near Lake Simcoe in Ontario for this study. Although names of the groups differ, the strata can be approximately correlated across southern Ontario to the Ottawa Valley. Detailed correlations have never been attempted, however, thus both the Simcoe Group and Ottawa Group names tentatively remain in use. The Tarim specimens were collected from the Lianglitag Formation in the Tarim Basin. No accurate correlation is implied by this figure — only that the units are approximately similar in age.
These rocks are abundantly fossiliferous, hosting a Chatfieldian (early Katian) fauna, with abundant bryozoans, brachiopods, and crinoids, and less common trilobites, bivalves, and gastropods (Melchin 1994; Armstrong 2000). Fossil material is generally abundant and relatively diverse, though lower diversity intervals are recorded in individual beds (Brookfield 1988).

Some fossils in the lower part of the Verulam Formation are silicified, contributing to the good preservation of general morphotypes, but destroying the fine details in the shells. This is advantageous for descriptions of general morphotypes and shell counting, but makes the specimens less useful for description of fine details often necessary for statistical analysis.

Previous work on the fossils from the Simcoe Group and Ottawa Group has focused on biostratigraphy rather than faunal descriptions. The most recent systematic study, by Wilson (1946), was confined to fossils from the Ottawa Valley and much of the taxonomy is in need of revision.

5.2.2 Geology and paleontology of the Lianglitag Formation of the Tarim paleoplate

The Tarim paleoplate was located in low latitudes close to the northeastern margin of the Gondwana supercontinent during the Ordovician period (Cocks and Torsvik 2003, 2013). It comprises, from south to north in present day orientation, the southern Tarim Land, the western Tarim-Taklamakan Platform, the Yining Basin (western Tarim) and the southern Tien Shan Basin (eastern Tarim) (Zhan et al. 2014, text-fig. 1).

The material studied in this paper was collected from the Lianglitag Formation near Bachu on the Tarim-Taklamakan Platform. The Ordovician sequence in this area is almost complete, including, in ascending order, the Upper Qiulitag Group, Tumuxiuke, Lianglitag, Sangtam, and Kepingtag (part) formations.

The Lianglitag Formation was named by Zhou et al. (1990) with its type locality at Yijianfang-Tangwangcheng, east of Sanchakou, Bachu County, northwestern Tarim. It is characterized by some 60 m of light grey, thick-bedded calcirudites, calcarenites, and algal
limestones, with a significant build-up of carbonate mud mounds in the middle and upper parts of the formation. It is conformably overlain by the Sangtam Formation (mainly siliciclastic rocks) and disconformably underlain by the Tumuxiuke Formation (non-reefal limestone). Conodonts from the Lianglitag Formation indicate an upper Sandbian to middle Katian age (Wang et al. 2009).

The parastrophid brachiopods formed part of a shelly fauna dwelling inside some of the cavities within the mound facies, represented in the upper part of the formation of early-middle Katian age. The brachiopods and conodonts, along with some trilobites (e.g. *Dulanaspis* sp.), gastropods (e.g. *Maclurites sinkiangensis*), and bryozoans, constitute a typical shallow water community (Zhou et al. 1990; Zhang et al. 2014).

5.3 Materials and Methods

A total of 112 specimens were measured for this study, including 54 from the Verulam Formation of Ontario (36 from Lake Simcoe and 18 from the Ottawa Valley), 4 from the Amadjuack Formation on Baffin Island in northern Canada, and 54 from the Tarim Basin, southern Xinjiang, northwest China.

From these specimens, 11 biometric characters were measured (Figure 5.3) with 8 indices formulated to quantify the shape of each specimen.

**W** – *Width*, used as a proxy for size that isn’t influenced by elongation of the shell;

**L/W** – *Length/width*, proxy for shell outline – a lower value corresponds to a more subelliptical outline whereas a higher value indicates a more subpentagonal outline;

**T/W** – *Thickness/width*, proxy for overall globosity of the shell – a larger value indicates a more globose profile;

**Td/T** – *Thickness of the dorsal valve/total thickness*, measurement of how much globosity is accounted for in the dorsal valve;
**Rs** – **Ribs in sulcus**, number of ribs within the sulcus at the anterior margin;

**Rs/Rt** – **Ribs in sulcus/total number of ribs**, proportion of the total ribs accounted for in the sulcus of the ventral valve;

**Ws1/Ws2** – **Sulcus width 1/sulcus width 2**, shape of the sulcus – a lower value indicates a more triangular-shaped sulcus at the anterior commissure;

**Ws1/Ds** – **Sulcus width 1/depth of sulcus**, shape of the sulcus – a lower value indicates a longer, narrower sulcus.

See Supplementary Data A for a complete table of measured values.

The PAST Software Package v. 3.01 (see Hammer et al. 2001) was used to perform Principal Component Analysis and Cluster Analysis. Both the primary measurements from the specimens and the formulated indices were used in the analyses. Both analyses are well suited to comparing morphological differences in fossil material (Hammer and Harper 2006).

Principal Component Analysis (PCA) was used to create a scattergram illustrating the relationships between the different collections in terms of the indices above. The correlation matrix was used rather than covariance, as the measurements were not all in the same units (as required when using covariance) and thus should be standardized in the analysis. Biplots for each index were included in the scattergram.

Cluster Analysis (CA), using Ward’s method, was also performed to further supplement the results from PCA. Other methods were attempted but Ward’s produced the most reasonable cluster pattern, and is often recommended for morphometric data (see Hammer and Harper 2006). A distinct group of small (immature) shells from the Tarim Basin was excluded to avoid biasing the cluster analysis too heavily towards difference in size. Before excluding these specimens, the resulting dendrogram segregated these smaller specimens into a separate cluster, but the remaining specimens were scattered unexplainably among the
Figure 5.3: Measurements used in this study. Photo is of Parastrophina hemiplicata from the Lake Simcoe area in Ontario. Most measurements are in mm, but Rs (ribs in sulcus) and Rt (total ribs on ventral valve) were counted. See text for full explanation of abbreviations.
remaining clusters. Only the original measurements were used for the analysis — the formulated indices were excluded.

5.4 Results

5.4.1 Principal component analysis

PCA produced a scattergram showing two main clusters of datapoints. Cluster A in the upper left half of the scattergram is dominated by *Parastrophina tarimensis* n. sp. from the Lianglitag Formation of Tarim. These brachiopods are typically globose and subpentagonal in outline. Within this cluster, two subclusters can be differentiated, with the larger specimens (more than 11 mm long and 12 mm wide) plotting to the upper right of the cluster and the smaller specimens (smaller than 7 mm long and 9 mm wide) plotting to the lower left (Figure 5.4).

Cluster B consists of *Parastrophina hemiplicata* specimens from the Lake Simcoe and Ottawa Valley collections. These specimens are typically less globose and exhibit a more subelliptical outline than *P. tarimensis*. The Ottawa specimens tend to cluster further to the top-right of the scattergram than those of Lake Simcoe, but there is substantial overlap between the two localities within the cluster.

The four specimens of *Parastrophina minor* from Baffin Island plot near the center of the scattergram, forming a third, smaller cluster, intermediate to clusters A and B. These specimens are typically more globose than *P. hemiplicata* but are still more subelliptical in outline vs. the subpentagonal *P. tarimensis*.

The final cluster contains four specimens of *Parastrophina iliana* from Kazakhstan selected from photos in Popov et al. (2002), and plot closer to the *P. hemiplicata* specimens in the scattergram than the *P. tarimensis*. 
Figure 5.4: Principal component analysis scattergram. Numbers represent individual samples. Biplots of each index used in the analysis are labelled. Note that the two main groups studied here plot in two distinct regions of the scattergram — the specimens from northwestern China in the upper left and the Ontario specimens in the lower right. The specimens from Baffin Island and Kazakhstan (measured from Popov et al. 2002) both plot in the middle of the scattergram between the two large clusters.
5.4.2 Cluster analysis

Four main clusters were differentiated on the dendrogram created as a result of cluster analysis: A, B, C, and D (Figure 5.5). These clusters approximately correspond to the grouping produced in the PCA scattergram (Figure 5.4).

Cluster A is composed primarily of *P. hemiplicata* from Lake Simcoe and the Ottawa Valley with a single specimen of *P. minor* from Baffin Island and a single specimen of *P. tarimensis* from Tarim. Specimens in this cluster are typically less globose (smaller mean T/W of 0.57) and more elliptical in outline (smaller mean L/W of 0.84).

*P. minor* from Baffin Island and two specimens selected in Popov et al. (2002) from Kazakhstan are grouped in Cluster B, along with three specimens of *P. hemiplicata* from Lake Simcoe and five from the Ottawa Valley. These specimens are similar to those of Cluster A, but are typically thinner, slightly smaller, and possess a shallower depth of the sulcus than those of Cluster A.

*P. tarimensis* makes up the entirety of Cluster C. These specimens are distinctly larger and typically possess more ribs on both the flanks of the shell and within the sulcus at the anterior, than other specimens from China.

Cluster D contains multiple specimens from all species except *P. minor* from Baffin Island. This is a relatively diverse cluster, as shown by the loose grouping in the dendrogram. This group consists of shells that are moderate to large in size. The Tarim specimens in this cluster have fewer ribs on the shell flanks compared to the other specimens from Tarim in other clusters. Specimens from Ontario in this cluster have more ribs on the shell flanks than the specimens from Ontario in other clusters. The number of ribs on the shell flanks is similar, however, in all specimens in this cluster.
Figure 5.5: Cluster analysis dendrogram. Each number corresponds to an individual measured specimen. The clusters approximately correspond to the clusters in the principal component analysis scattergram (Figure 5.4). See text for explanation of the clusters.
5.4.3 Interpretation

The four species of *Parastrophina* examined in this study can be differentiated by three main morphometric indices: *W*, *L/W*, and *T/W*. Two additional indices, *Td/T* and *Ws1/Ws2*, also indicate differences among the species, but these may be linked to the above three characters (see Table 5.1 for the mean values of each variable for each species).

Table 5.1: Mean values of key indices used in principal component analysis

<table>
<thead>
<tr>
<th>Parastrophina species</th>
<th><em>W</em></th>
<th><em>L/W</em></th>
<th><em>T/W</em></th>
<th><em>Td/T</em></th>
<th><em>Ws1/Ws2</em></th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. hemiplicata</em>, Ontario, Canada</td>
<td>12.61</td>
<td>0.83</td>
<td>0.56</td>
<td>0.69</td>
<td>0.55</td>
</tr>
<tr>
<td><em>P. tarimensis</em>, Xinjiang, China</td>
<td>8.78</td>
<td>0.94</td>
<td>0.67</td>
<td>0.71</td>
<td>0.69</td>
</tr>
<tr>
<td><em>P. minor</em>, Nunavut, Canada</td>
<td>9.99</td>
<td>0.86</td>
<td>0.68</td>
<td>0.61</td>
<td>0.61</td>
</tr>
<tr>
<td><em>P. iliana</em> (Popov et al. 2002), Kazakhstan</td>
<td>9.10</td>
<td>0.892</td>
<td>0.637</td>
<td>N/A</td>
<td>N/A</td>
</tr>
</tbody>
</table>

The measured *P. hemiplicata* specimens plot in the bottom right sector of the PCA scattergram. These specimens, overall, have a larger width than the specimens from China (as shown by *W* in Figure 5.4), but this may have been biased by the large number of smaller specimens in the Tarim collection and should not be considered definitively diagnostic.

The *L/W* and *T/W* ratios are more diagnostic of each species. The specimens of *P. tarimensis*, on average, have a greater *L/W* value compared to *P. hemiplicata* from both Lake Simcoe and Ottawa localities in Ontario. Specimens of *P. minor* from Baffin Island have a similar *L/W* to *P. hemiplicata*. Figure 5.6 illustrates this pattern — *P. hemiplicata* and *P. minor* specimens plot along a similar trend, differing from *P. tarimensis*.

*P. tarimensis* and *P. iliana* have a greater *T/W* value than *P. hemiplicata* from Ontario, indicating a more globose lateral profile in the specimens from Tarim and Kazakhstan (Figure 5.6). Although *P. minor* shares a similar outline with *P. hemiplicata*, it has a *T/W* value much larger than *P. hemiplicata* and similar to *P. tarimensis*. The *Td/T* values of each species reveal that although the *P. tarimensis* and *P. minor* specimens share similar *T/W* values, *P. tarimensis*...
Figure 5.6: Length vs. width (left) and thickness vs. width (right) plots of specimens with average trend lines indicated. Note that *Parastrophina hemiplicata* and *Parastrophina minor* share similar L/W values while *Parastrophina tarimensis* n. sp. and *Parastrophina minor* share similar T/W values.
has a higher Td/T value than *P. minor*. This higher Td/T value indicates that less of the increase in globosity is accounted for in the dorsal valve of *P. minor*, and that the ventral valve is more convex than that of *P. hemiplicata* and *P. tarimensis*.

The Ws1/Ws2 ratios may have some taxonomic utility as well, with *P. tarimensis* exhibiting a larger value than those from Ontario. *P. minor* has an intermediate value of 0.61. This implies that the sulcus tends to be subrectangular shaped in *P. tarimensis* but subtriangular in *P. hemiplicata*. However, this could be linked to the increased convexity of the dorsal valve in the Tarim specimens.

Interestingly, only T/W varies significantly when considering the minimum and maximum values (see Supplementary Data A). This underscores the morphological variability that has been documented thus far in this genus (e.g. see Wilson 1914, Wright 1974, Popov et al. 2002).

Of the remaining indices, the ribbing pattern (in particular) appears to be so variable that, as Wilson (1914) pointed out, it has little utility for differentiating species of *Parastrophina* (Figure 5.7). However, the PCA scattergram indicates that ribbing may serve as an indicator of maturity, with larger specimens within each population showing a greater number of ribs within the sulcus and a somewhat larger proportion of ribs in the sulcus. This suggests that during growth, rib division occurs at a greater frequency near the anterior margin than on the shell flanks and may indicate faster growth at the anterior margin of shells than on the flanks.

5.5. Paleoecological and paleogeographical implications

*Parastrophina hemiplicata* and *Parastrophina tarimensis* n. sp. represent two end members of morphotypes: less globose specimens with a wider, subelliptical outline and more globose specimens with a subpentagonal outline respectively. *Parastrophina minor* and *Parastrophina iliana* can be regarded as intermediate between the two end members. The morphological differences discussed above may be inferred to show phenotypic
Figure 5.7: Frequency polygons showing number of ribs in the sulcus (left) and number of ribs total (right). The number of ribs in specimens of each species is highly variable, as previously noted by other authors.
responses to the environments in which these brachiopods would have inhabited.

The *P. hemiplicata* specimens are from the lower Katian (Chatfieldian) carbonate deposits that accumulated on level-bottom substrates of epeiric seas from southern Ontario to western New York, on the western side of the Appalachian Basin. These regions of eastern Laurentia were paleogeographically located in the subtropical or higher tropical latitudes and thus were probably subjected to frequent intense storm activity (Jin et al. 2013), promoting mixing of the water column. Additionally, cool ocean currents with higher organic/inorganic nutrient content would have been directed onto the carbonate platform in eastern Laurentia with the onset of the Taconic orogeny and creation of the Appalachian Basin and the Sebree Trough (Ettensohn and Brett 2002). These currents would have increased circulation and enhanced productivity, thereby enriching the basal food chain in the water column. This resulted in increased organic carbon content in the deposits, as represented by black shale accumulation in some regions (e.g. the Utica Shale of New York). The influence of these cool-water currents is shown by a significant shift in carbonate deposition away from the typical tropical carbonates to temperate-style deposition (see Ettensohn 2010 for a summary of this event).

The specimens from the Tarim paleoplate, however, were from carbonate mud mound deposits that accumulated close to the Late Ordovician equatorial zone in an epeiric sea. These regions would have been subject to much fewer and less intense storm disturbances than eastern Laurentia during the early Katian, and circulation would have been more sluggish in the epeiric sea relative to a continental margin in higher tropics. The Lianglitag Formation consists of clean carbonate deposits, and like much of the Upper Ordovician carbonates in equatorial epicontinental seas of Laurentia (e.g. the Hudson and Williston Basins), there is a general lack of evidence for cold-upwelling or eutrophication (e.g. increased phosphate content or black shale accumulation).

These contrasting paleoenvironments likely influenced the evolution of the shelly benthos in different ways, and could explain the contrast in morphology of each species
examined in this study. In eastern Laurentia, the selection pressure for a larger lophophore in brachiopods would have been low due to greater marine circulation and possibly higher productivity. If the organism was attaining adequate nutrition and gas exchange was already sufficient, a larger lophophore would not necessarily provide an evolutionary advantage. However, the Tarim specimens were in a more sluggish water column and less nutrient-rich habitat, where primary productivity may have fluctuated between dry and wet seasons depending on inorganic nutrient supply from nearby landmasses. Here, larger lophophores may have been necessary for the organism to meet their metabolic requirements as they grew in size. To attain a larger lophophore size, the shells would have necessarily evolved toward a more globose profile, especially a deeper dorsal valve which housed the lophophore.

This pattern of increasing globosity in brachiopod shells from the Late Ordovician epicontinental seas of the equatorial latitudes relative to species in the higher tropics has also been noted in other groups of brachiopods. Species of the Late Ordovician Plaesiomys from Ontario and Cincinnati near the eastern margin of Laurentia are generally less globose compared to similar sized species from the interior of North America from coeval formations (Sproat and Jin 2013). This same pattern has also been demonstrated in the Rhynchotrema-Hiscobecus lineage as well (Sohrabi and Jin 2013; Sproat et al. 2014). Although these morphometric analyses have focused mainly on brachiopod faunas of North America, this study suggests that morphological disparity in different paleoenvironmental or paleolatitudinal zones may have been a common phenomenon during the Late Ordovician.

Additionally, the contrasting outlines of shells from eastern North America and Tarim may have been due to selection in different living environments as well. The consistently wider shells of eastern North America would better distribute weight on the potentially soft substrate they inhabited. The Tarim specimens would have been less exposed to this problem in a mud mound setting. The carbonates from which these specimens were collected are relatively pure, unlike the argillaceous carbonates of southern Ontario. The shells of P. hemiplicata from the Ottawa Valley, for example, are hosted in black to dark grey, organic-rich, micritic mudstone, which suggests a soft muddy substrate and corresponds to the wider shell morphology.
Differences in ribbing pattern are much more difficult to interpret. As seen in Figure 5.7, there is not a large difference in the ribbing pattern of the Ontario and Tarim specimens. In fact, there is a large variation within collections from each region, indicating intraspecific variability. As noted above, larger shells tend to possess more ribs, so this may be an approximate indicator of maturity.

5.6 Conclusions

Two main patterns of morphology are evident in species of the genus *Parastrophina*.
1. *Parastrophina hemiplicata* and *Parastrophina minor* from the paleosubtropics of Late Ordovician Laurentia are more subelliptical in outline than *Parastrophina tarimensis* n. sp. from coeval deposits from near the paleoequator in the Tarim paleoplate;
2. *Parastrophina tarimensis* n. sp., *Parastrophina minor*, and *Parastrophina iliana* are more globose than *Parastrophina hemiplicata*, although *P. minor* has a relatively more convex ventral valve while *P. tarimensis* n. sp. has a more convex dorsal valve.

Ribbing pattern is highly variable both among species and within species of *Parastrophina*. A greater number of ribs tend to develop in larger specimens, suggesting it may indicate maturity of an individual.

The greater dorsal convexity of *P. tarimensis* n. sp. may reflect a need for a larger lophophore to cope with lower nutrient levels and sluggish circulation at the equator relative to the subtropics. A wider, more subelliptical outline would stabilize *P. hemiplicata* and *P. minor* better on the muddy flat-bottom substrates on the margin of Laurentia but would not be selected for in the evolution of forms in a mud mound environment, such as *P. tarimensis* n. sp.

5.7 Systematic paleontology

Specimens are deposited in the Royal Ontario Museum Invertebrate Palaeontology collection, Toronto, Ontario, Canada (ROM), the Geological Survey of Canada, Ottawa, Ontario (GSC), and Nanjing Institute of Geology and Palaeontology, Nanjing, China (NIGP).
Order Pentamerida Schuchert and Cooper, 1931

Suborder Syntrophiidina Ulrich and Cooper, 1936

Superfamily Porambonitoidea Davidson, 1853

Family Parastrophinidae Ulrich and Cooper, 1938

**Genus Parastrophina Schuchert and LeVene, 1929**

*Type species.* Atrypa hemiplicata Hall, 1847. Trenton Limestone (Caradoc), northwestern New York State.

*Remarks.* Although similar externally, *Parastrophina* and the related genus *Parastrophinella* exhibit slightly different internal features. In *Parastrophina*, the dorsal median septum is notably higher and elevates the septalium clearly above the valve floor along its entire length. The septalium in *Parastrophinella* is largely sessile, especially in the anterior portion of its extent, with a primitive median septum buried mostly in the shell thickening of dorsal valve (Jin and Cooper 1997).

Serial sectioning of *Parastrophina hemiplicata* and *Parastrophina tarimensis* n. sp. in this study, however, shows that the two species have essentially the same type of junction between the dorsal median septum and the inner hinge plates, as the plates converge on each side of the median septum near its ventral edge (Figure 5.8). This type of septalium is structurally different from that in the pentameroids, in which the plates converge towards the floor of the dorsal valve into a single unified structure with no development of a separate median septum (Jin and Cooper 1997).
Figure 5.8: Both *Parastrophina hemiplicata* (left) and *Parastrophina tarimensis* n. sp. (right) possess a cruralium duplex. Both crural plates merge with a central median septum. Dorsal valve oriented upward in figure.
Parastrophina hemiplicata (Hall, 1847)

Figures 5.9, 5.10, and 5.11

1847 Atrypa hemiplicata Hall, p. 144, pl. 33, figs. 10a–f.

1856 Atrypa hemispheric Hall; Billings, p. 208, figs. 20–23.

1892 Camarella bernensis Sardeson, 1892, p. 328, pl. 4, figs. 4–6.

1893 Anastrophia? hemiplicata (Hall); Winchell and Schuchert, p. 382, pl. 30, figs. 29–31.

1893 Anastrophia? hemiplicata var. rotunda Winchell and Schuchert, p. 383, pl. 30, figs. 32–35.


1894 Parastrophia hemiplicata (Hall); Hall and Clarke, 1894, p. 221, pl. 63, fig. 1–3.

1914 Parastrophia hemiplicata (Hall); Wilson, p. 131, pl. 4, figs. 1–34.

1932 Camerella hemiplicata (Hall); Schuchert and Cooper, p. 168, pl. 25, figs. 3, 4, 6, 9–11, 16, 24, 43.

1937 Parastrophina hemiplicata (Hall); Kay, p. 330, pl. 9, figs. (not individually numbered).

1941 Parastrophina hemiplicata (Hall); St. Joseph, 1941, p. 377, text-figs. 3–5.

1946 Camerella hemiplicata (Hall); Wilson, p. 118, pl. 11, fig. 4.

1956 Parastrophina hemiplicata (Hall); Cooper, p. 606, pl. 106, figs. 33-44; pl. 117, figs. 19–27.

1969 Parastrophina hemiplicata (Hall); Sinclair et al., p. 26, photo 8.14.
Figure 5.10: *Parastrophia hemiplicata* from the Verulam Formation in the Ottawa Valley. A–E GSC 1606; conjoined shell in dorsal, ventral, anterior, posterior, and lateral views. F–J GSC 1606a; conjoined shell in dorsal, ventral, lateral, anterior, and posterior views. K–O GSC 1606d; conjoined shell in dorsal, ventral, lateral, anterior, and posterior views.
Figure 5.11: Tracings of *Parastrophina hemiplicata* serial sections. GSC 1606a from the Verulam Formation in the Ottawa Valley. Numbers indicate distance from posterior tip of dorsal umbo. Dorsal valve oriented upward in figure. The raised cruralium on the dorsal septum indicates affinities to *Parastrophina* rather than *Parastrophinella*. The well-defined alate plates rule out affinities with *Camarella*. 
Types: Hall (1847) did not select any type specimens, but the specimens were collected from the Trenton Limestone (early Katian, Chatfieldian) in northwestern New York State at Middleville and other localities.

Material: 33 complete specimens from Mara ditch locality near Lake Simcoe and 18 measured complete specimens from the Ottawa Valley, Ontario, Canada. ROM 63132-63135 photographed in Figure 5.9.

Remarks: The type species of *Parastrophina* is well-known and has been described in detail by previous workers (e.g., Wilson 1914; St. Joseph 1941). The specimens from the Lake Simcoe area tend to have various degrees of silicification and are not ideally suited for serial sectioning. Serial sections of a specimen from the Ottawa area revealed two characteristics, which have not been noted before:

1) A short, ventrally curved, transverse plate in the apical portions of the spondylium (Figure 5.11), probably analogous to a pedicle collar. This structure has not been found in the closely related genus *Parastrophinella*.

2) The configuration of the septalium is similar to that in *Parastrophinella reversa* (Jin and Copper, 1997) in that the base of the septalium is not formed through bifurcation of the dorsal median septum (as is the case in pentameroids) but rather by the inner hinge plates bending medially at their dorsal ends and fusing onto each side of the median septum. Anteriorly, the median septum protrudes through the septalium floor to form a low median ridge (Figure 5.11). Thus, the only difference in the dorsal interior between *Parastrophina* and *Parastrophinella*, as characterized by their type species, is that the median septum is relatively high, raised above the valve floor along its entire length in the former, whereas it is buried in the thickened shell wall posteriorly and barely becomes free anteriorly in the latter.
Parastrophina tarimensis n. sp.

Figures 5.12 and 5.13

Types. Holotype NIGP 161371, conjoined calcareous shell, figured paratypes NIGP 161372–NIGP 161375.

Type locality and stratum. Yijianfang, Bachu County, southwestern Xinjiang, NW China; upper Lianglitag Formation (lower-middle Katian).

Material: A total of 54 complete specimens from the upper Lianglitag Formation, Tarim Basin, southwestern Xinjiang, northwest China.

Diagnosis: Shell small to medium; transversely subpentagonal; dorsal valve highly convex, 2.5–3 times as deep as ventral valve; ventral sulcus rounded at anterior.

Description: Shell small to medium size, moderately dorsibiconvex, transversely subpentagonal; average length 4.80 mm, width 4.87 mm, thickness 2.62 mm; maximum length 14.34 mm, width 14.67 mm, and thickness 12.30 mm, dorsal valve 2.5–3 times depth of ventral valve. Hingeline short, approximately one third shell width. Ventral umbo low, suberect beak extending over hingeline; interarea minute, apsacline; sulcus beginning 5–7 mm from apex of ventral valve, deepening rapidly to form tongue at approximately 45 degrees to commissure. Dorsal umbo more prominent than ventral, arching ventrally beyond hingeline somewhat obscuring interarea; fold low, inconspicuous posteriorly but more prominent in anterior third of shell. Posterior and posterolateral portions of shell smooth; anterior costae simple, subrounded, usually two to four in sulcus (correspondingly three to five on fold), and one to two to on each flank of shell in smaller specimens and four to eight on larger specimens (see Figure 5.12c, n, h, r, and w).
Figure 5.12: *Parastrophina tarimensis* n. sp. from the Lianglitag Formation in the Tarim Basin, southern Xingjiang, China. A–E NIGP 161371; conjoined shell in dorsal, ventral, anterior, posterior, and lateral views. F–J NIGP 161372; conjoined shell in dorsal, ventral, anterior, posterior, and lateral views. K–O NIGP 161373; conjoined shell in dorsal, ventral, lateral, anterior, and posterior views. P–T NIGP161374; conjoined shell in dorsal, ventral, anterior, posterior, and lateral views. U–Y NIGP 161375; conjoined shell in dorsal, ventral, anterior, posterior, and lateral views. NIGP 161371–161373 are examples of the larger morphotype described in the text while specimens NIGP 161374 and NIGP 161375 are examples of the smaller morphotype.
Teeth small, knobby; spondylium narrow, V-shaped; median septum narrow, low, buried in shell floor apically, becoming well-defined anteriorly, extending for about one third of shell length (Figure 5.13). Hinge sockets small and shallow, inner hinge plates thin, high, converging onto median septum to form main portion of narrow, V-shaped septalium; outer hinge plates low, poorly defined; alate plates well developed, broadening and more curved anteriorly; dorsal median septum of consistent height along its entire length, and of similar length as ventral median septum.

Remarks: Superficially, this species is similar to *Parastrophina iliana* Popov et al., 2002 of Kazakhstan, sharing a similar pattern of ribbing near the anterior, and has a significantly more globose form than *P. hemiplicata* from the Lake Simcoe and Ottawa Valley of Ontario. This species from China is slightly more globose than *P. iliana*, though similar in profile. The collection analyzed in this study contains two different morphotypes — a smaller form with less ribbing and a larger, more globose form with significantly more ribbing (Figure 5.12). Rather than separate these two forms into two different species, the two forms probably represent juvenile and mature forms respectively. This is also supported by the principal component analysis as the two forms seem to plot in the same region of the scattergram (Figure 5.4), suggesting a common lineage.

*Parastrophina minor* (Roy, 1941)

Figure 5.14

1900 *Parastrophia hemiplicata* Schuchert (not Hall), p. 158.

1941 Parastrophiella hemiplicata minor Roy, p. 94, fig. 57.

2000 *Parastrophina minor* (Roy); Bolton, pl. 20, figs. 3–6, 8, 18.
Figure 5.13: Tracings of *Parastrophina tarimensis* n. sp. serial sections. NIGP 161376 from the Lianglitage Formation in the Tarim Basin, southern Xinjiang, China. Numbers indicate distance from posterior tip of dorsal umbo. Dorsal valve is upward in figure. Note the raised cruralium and well-defined alate plates characteristic of *Parastrophina*.
Types: The holotype (USNM No. 28156) and four paratypes selected by Roy (1941) are in the U.S. National Museum of Natural History. The types are from the Amadjuack Formation, Silliman’s Fossils Mount, Baffin Island, Canada. Bolton illustrated four additional specimens (hypotypes), GSC 113527, GSC 113528, GSC 113529, and GSC 113530 from the same formation and locality.


Remarks: Roy (1941) only provided a brief description of this species, justifying its designation as a separate sub-species from Parastrophina hemiplicata due to its relatively small size compared to those from the Trenton in New York and a longer, less wide form.

As discussed above, P. minor exhibits intermediate characteristics between the wide but thin P. hemiplicata specimens from Ontario and the more globose but longer and thin Parastrophina tarimensis n. sp. from China. Only four specimens were available for examination for this study, however, and additional specimens may allow a more detailed description.

Occurrence: Amadjuack Formation (early Katian/Edenian to Maysvillian), Silliman’s Fossil Mount, Frobisher Bay, Baffin Island, Nunavut, Canada.
Figure 5.14: Parastrophina minor from the Amadjuack Formation, Baffin Island, Nunavut. A–E GSC 113527; conjoined shell in dorsal, ventral, lateral, anterior, and posterior views. F–J GSC 113528 conjoined shell in dorsal, ventral, anterior, posterior, and lateral views. K–O GSC 113529 conjoined shell in dorsal, ventral, anterior, posterior, and lateral views. P–T GSC 113530 conjoined shell in dorsal, ventral, anterior, posterior, and lateral views.
5.9 References


Billings, E., 1856. On some of the fossil shells of the Niagara and Clinton formations. Canadian Naturalist and Geologist, 1, 131–139.


Chapter 6 — The Middle-Late Ordovician brachiopod *Plectorthis* from North America and its paleobiogeographic significance

6.1 Introduction

*Plectorthis* Hall and Clarke, 1892, commonly reported Late Ordovician orthide brachiopod of the family Plectorthidae, is characterized by a gently ventribiconvex shell, generally subelliptical outline, with an anterior commissure ranging from slightly sulcate to subtly uniplicate, and costate shell surface (Williams and Harper 1997). These characters, however, are highly variable among species described so far in the literature, with shapes from subcircular to rather wide, and the ribbing from simple costate to strongly multicornellate or fascicostellate. In the early Late Ordovician, *Plectorthis* was an important part of the benthic shelly fauna that initially colonized the shallow epeiric seas along the continental margin in response to the sea level rise and marine inundation of the continents (Haq and Schutter 2008). The earliest occurrences of *Plectorthis* are known from the uppermost Darriwilian, but the genus is most diverse in Laurentia during the Sandbian and early Katian (Figure 6.1). One species has been assigned to the genus in the Hirnantian (*Plectorthis magna* Cooper and Kindle, 1936), but its affinity to *Plectorthis* remains doubtful. The youngest known species in Laurentia is *Plectorthis inaequiconvexa* Roy, 1941 from the Amadjuack Formation (Edenian–Maysvillian, mid-Katian) of Baffin Island (Bolton 2000).

In the Late Ordovician faunas of Laurentia, various species of *Plectorthis* usually occur as a common, but non-dominant taxon of brachiopod assemblages, such as in localities of the eastern United States (Hall 1847, 1859; Meek 1872, 1873; Raymond 1905, 1910; Willard 1928; Schuchert and Cooper 1932; Weiss 1955; Cooper 1956; Titus 1982, 1986; Davis 1985) and Canada (Logan et al. 1863, Wilson 1946), Baffin Island (Roy 1941, Bolton 2000), Nevada (Cooper, 1956; Ross 1967, 1970), California (Phleger 1933, Greife and Langenheim 1963), and the peri-Laurentian terranes of Scotland and northern Ireland (Williams 1962; Wright 1964; Mitchell 1977; Candela 2003). Elsewhere, the genus has been reported from the
**Figure 6.1:** Known ranges of *Plectorthis* species. The earliest reported species are from the upper Darriwilian, but these species are not well preserved, rare, or poorly documented. *Plectorthis* was most diverse during the Sandbian with a number of species reported Cooper (1956) from the eastern United States. Some of the most recognizable species, including the type species *P. plicatella plicatella*, are from the early Katian. Only a single doubtful species was reported in the Hirnantian by Cooper and Kindle (1936). Figure includes all species of *Plectorthis* previously assigned that have not been reassigned to other genera prior to this paper excluding only those assigned as *Plectorthis* sp.
Shropshire inlier (Avalonia) in England (Williams 1974), the Farewell terrane of Alaska (Rasmussen et al. 2012), Australia (Laurie 1991; Percival 1991), China (Rong et al. 1999; Zhan and Cocks 1998; Zhan et al. 2002, 2014), Kazakhstan (Nikitin and Popov 1983; Popov et al. 2002; Nikitin et al. 2006; Popov and Cocks 2006, 2014), Norway (Owen and Harper 1982; Harper and Owen 1984; Neuman et al. 1997), and Siberia (Severgina 1967; Kulkov and Severgina 1989; Cocks and Modzalevskaya 1997), although the true identity of some of these remains to be confirmed.

Despite the wide geographic range of the genus, the original types of the type species of Plectorthis, Orthis plicatella Hall, 1847, have not been thoroughly examined for over a century in terms of contemporary taxonomy. Comparisons to these types have largely been limited to broad morphology (i.e. outline, ribbing pattern, etc.). Furthermore, the internal structures of Plectorthis have only been described once (Schuchert and Cooper 1932), and some microstructures (e.g. aditicules) may have been overlooked in previous studies. This has led to some ambiguity about the definition of Plectorthis (sensu stricto), making it a ‘dump bag’ genus in some cases.

This study re-examines the types of Orthis plicatella and Orthis fissicosta used originally by Hall (1847) and subsequent studies from the collections at the American Natural History Museum (AMNH) in New York, supplemented with topotype material from the Cincinnati Museum Center (CMC). The main objective is to clarify the diagnostic characteristics of Plectorthis and to discuss its significance for understanding the evolutionary, paleoecological, and paleobiogeographical significance, as part of Late Ordovician benthic shelly fauna that invaded epicontinental seas during Late Ordovician marine transgressions.

6.2 Previous studies of Plectorthis

Hall and Clarke (1892) established Plectorthis based on Orthis plicatella Hall, 1847, for a group of orthides with strong external ribs that are not invariably simple, a low cardinal area, and subequally convex, with internal structures being essentially the same as their Group I (i.e. the Hesperorthis Group, with a blade-like cardinal process).
Schuchert and Cooper (1932) further refined the genus, noting the cordate, or heart-shaped, ventral muscle field and the nature of cardinalia. In particular, they noted the curved brachiophores that differentiate the Plectorthinae from other orthides that feature straight brachiophores, and the fulcral plates that form the base of the sockets in the dorsal valve that are characteristic of *Plectorthis* only. They considered the cardinal process of *Plectorthis* to be similar to that of *Dinorthis* in that it has a stout compressed shaft bearing a crenulated myophore. However, the cardinal process, especially myophore, of plaesiomyids (e.g. *Dinorthis* and *Plaesiomys*) is usually more bulbous (especially in late Katian forms – see Sproat and Jin 2013).

Subsequent studies commented on the large degree of variability between species, usually only in systematic remarks (e.g. Mitchell 1977, Laurie 1991, Percival 1991, Zhan and Cocks 1998), but detailed comparisons between species are lacking. The heart-shaped (cordate) ventral muscle field, for example, is a relatively reliable diagnostic feature for separating *Plectorthis* from other similar orthides, but is rarely mentioned in systematic discussions. This is probably due to the relatively rare occurrence of disarticulated valves in the genus.

### 6.3 Type specimens and other material

The type species of *Plectorthis, Orthis plicatella* Hall, 1847, was based on four syntypes, now in the American Museum of Natural History in New York (Figure 6.2). The only specimen designated *Orthis fissicosta* in the original lot (Figure 6.3f–j) was also examined in this study for comparison with the *Orthis plicatella* type specimens. AMNH 30259, one of the fascicostellate *Orthis plicatella* syntypes is here assigned to *P. plicatella fissicosta* (Figure 6.3a–e). Detailed descriptions of these types follows in the systematics section.
**Figure 6.2:** Photos of *Orthis plicatella* types of Hall (1847) from the American Museum of Natural History and interior of the dorsal valve of two specimens from the Cincinnati Museum Center collection. A–E AMNH 30256 (paralectotype); dorsal, ventral, anterior, posterior, and lateral views. F–J AMNH 30257 (paralectotype); dorsal, ventral, anterior, posterior, and lateral views. K–O AMNH 30258 (lectotype); dorsal, ventral, lateral, anterior, and posterior views. P–Q two specimens from CMC 16880 showing the interior of the dorsal valve of *P. plicatella plicatella*. No interior of the ventral valve is available.
Figure 6.3: Photos of the *Orthis fissicosta* holotype from the American Museum of Natural History and one of the *Orthis plicatella* types of Hall (1847) here assigned to *P. plicatella fissicosta*. A–E AMNH 30259 (previously assigned by Hall (1847) to *Orthis plicatella* - paratype) dorsal, ventral, anterior, posterior, and lateral views. F–J AMNH 30255 (holotype) dorsal, ventral, anterior, posterior, and lateral views. Note that the specimen is crushed, with compressional damage to the anterior of the ventral valve.
Supplementary *P. plicatella* and *P. fissicosta* were borrowed from the Cincinnati Museum Center (CMC) for comparison with the original types. A selection of 50 well-preserved specimens of *P. plicatella* and *P. fissicosta* were measured for biometric analysis (see Appendix B for specimen numbers and measurements). One particularly well-preserved specimen of *P. plicatella* was photographed to illustrate the main features of the type species, including well-preserved double-rowed aditicules on the shell surface (Figure 6.4).

Additional specimens were examined from the collections of the Geological Survey of Canada (GSC) and the University of Western Ontario (W) as part of this study. Two well-preserved specimens (GSC 113506 and a specimen from GSC locality O-104229) from a moderate collection of 26 specimens from Silliman’s Fossil Mount on Baffin Island were also studied for comparison (see Figure 6.5), and 19 additional specimens were measured (5 specimens were too poorly preserved to make a complete set of measurements). Several *Plectorthis plicatella laurentina* from the Lake Simcoe area of Ontario were also examined (Figure 6.6).

A complete list of specimens from the AMNH, CMC, and GSC collections can be found in Appendix B.

### 6.4 Ribbing style

Ribbing style is the primary feature that distinguishes species of *Plectorthis* and can be divided into three types: specimens with simple ribbing, multiplication of ribs through bifurcation, and multiplication of ribs through implantation.

Simple costae are the most common in *Plectorthis* as in the type species *P. plicatella* (e.g. Figures 6.2 and 6.4). There are few rib multiplications outside the umbonal area, and the ribs are relatively uniform in size.
Figure 6.4: Photos of a well preserved *P. plicatella* topotype from the Cincinnati Museum collection. A–E Specimen from CMC 6395; dorsal, ventral, anterior, posterior, and lateral views. F–G Magnified view of ventral valve showing well preserved double-rowed adyticules on the rib crests.
Figure 6.5: Photos of *P. inaequiconvexa* Roy, 1941. A–E Specimen from GSC locality O-104229 (box labelled *Austinella cooperi*) dorsal, ventral, anterior, posterior, and lateral views. F–J GSC 113506 dorsal, ventral, lateral, anterior, and posterior views.
Figure 6.6: Photos of *Plectorthis plicatella laurentina* collected from the lower Verulam Formation at locality W-O-2 in the Lake Simcoe area of Ontario. A–E W2980 dorsal, ventral, anterior, posterior, and lateral views. F–J W2981 dorsal, ventral, anterior, posterior, and lateral views.
Less commonly, some species like *P. fissicosta* exhibit bifurcating ribs (see Figure 6.3). Close to the umbo, the ribs in these species resemble the ribs of *P. plicatella* in being simple and uniform in size. However, at a certain point, the ribs bifurcate. In some specimens, rib multiplication may form clearly bundled fascicostae, as in *P. fissicosta*. This is also commonly seen in *P. equivalis*, although the ribs typically branch in bifid fascicles, rather than the trifid fascicles of *P. fissicosta*.

*P. neglecta* represents a third ribbing style. In this species, ribs typically multiply through intercalation rather than bifurcation. Rib multiplication in these species is less ordered than those where ribs bifurcate, and often occurs at random distances from the umbo, but generally not near the anterior margin. This is the most variable ribbing style, and least common of the three morphotypes of *Plectorthis*.

In examination of large collections from the Cincinnati type area, some specimens show ribbing styles of both *P. plicatella* and *P. fissicosta* (see Figure 6.7), with simple ribs changing to fascicostae near the anterior margin of the shell, as in *P. fissicosta* (e.g. Figure 6.3a–e). This suggests that these two species have considerable overlap in terms of ribbing style.

To determine whether these species can be differentiated based on additional characteristics, seven characters were measured in 50 specimens of *P. plicatella* with definitive simple ribs and 50 specimens of *P. fissicosta* with definitive fascicostae (see Figure 6.8 for characters measured and Supplementary Data B for measurement values). Principal component analysis, using the PAST program (Hammer et al. 2001), was used to determine if the two species are distinguishable based on multiple characters. The measured values for number of ribs were excluded so as not to bias the results with the obvious difference in number of ribs. A correlation matrix was used rather than co-variance matrix, as not all values were in the same measurement units — two ratios were also used in the input (L/W and T/L).
Figure 6.7: Three styles of ribbing in *Plectorthis* species: left — simple ribbing (e.g. *P. plicatella*), right — complex ribbing (e.g. *P. fissicosta*), and center — intermediate form. The lines represent tracings of the central four ribs of specimens selected from each form.
Figure 6.8: Measurements used for principal component analysis. **L**=length, **W**=width, **T**=thickness, **Td**=thickness of dorsal valve, **Tv**=thickness of the ventral valve, **Rp**=number of ribs within an approximately 5 mm radius of the dorsal umbo, **Ra**=number of ribs at anterior margin.
The resulting scattergram (Figure 6.9) indicates no sharp separation between these species, as *P. plicatella* and *P. fissicosta* specimens are scattered randomly over the entire scattergram. All biplots trend in different directions, indicating no common correlation between measured characters. Essentially, none of the measured characters are useful for differentiating between two species.

As an additional test, length and width of the two species was compared. Length divided by width serves as a suitable proxy for outline – a higher value would indicate a less elliptical and more circular outline. The results are presented in Table 6.1.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean</th>
<th>St. Dev.</th>
<th>Min</th>
<th>Max</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. plicatella</em></td>
<td>0.73</td>
<td>0.04</td>
<td>0.64</td>
<td>0.81</td>
</tr>
<tr>
<td><em>P. fissicosta</em></td>
<td>0.76</td>
<td>0.05</td>
<td>0.45</td>
<td>0.86</td>
</tr>
</tbody>
</table>

The results are very similar, with mean values within 0.03. The low standard deviation indicates a narrow distribution of values. A simple x-y scattergram with a linear regression performed on the values also illustrates this similarity (Figure 6.10).

The results of PCA, univariate statistics, and bivariate plots above all indicate that the only significant difference between *P. plicatella* and *P. fissicosta* is the ribbing style. The use of this feature alone to differentiate these species is problematic, as an immature *P. fissicosta* shell would appear identical to *P. plicatella* as rib multiplication would not yet have occurred.

In light of the above analysis, the *P. fissicosta* is downgraded to a subspecies of *P. plicatella*, since the opposite extreme members of the two species, those with simple costae and those with multi- or fascicostellae, are sufficiently distinct.

### 6.5 Ventral muscle scar field

Schuchert and Cooper (1932) described the ventral muscle scars in *Plectorthis* as being heart-shaped (cordate), occupying between one third and one half length of the shell, with linear adductor scars confined within subcrescentic diductor scars, and a low
Figure 6.9: Scattergram from principal component analysis using PAST software (Hammer et al. 2001). Note that there is no distinct separation of *P. plicatella* and *P. fissicosta* specimens.
Figure 6.10: Scattergram plot of length and width measurements for both *P. plicatella* and *P. fissicosta*. R² values for the linear regression were 0.90 for *P. plicatella* and 0.89 for *P. fissicosta*. Note the very close relationship between both datasets.
ridge extending anterior to the adductor muscle scars in some specimens. They also provided the only illustrations of the interior of the ventral valve of the type species.

Several species assigned to *Plectorthis* possess a different type of muscle scar, similar to *Plectorthis ponderosa* Cooper, 1956 from the basal Martinsburg Formation in Tennessee. This type of muscle field with subtriangular adductor scars, flanked by a pair of diverging diductor scars, differs from the heart-shaped ventral muscle field in a typical *Plectorthis* (Figure 6.11; Cooper 1956, pl. 83, fig. 32; Williams and Harper 1997, fig. 548, 2e–g). The fulcral plates that form the base of sockets in other *Plectorthis* are conspicuously absent, as noted by both Ross (1970) and Laurie (1991). Ross described two species from Nevada that at least in part fit this *P. ponderosa*-like morphotype. *Plectorthis obesa* Cooper, 1956 exhibits the same distinctive subtriangular ventral adductor as *P. ponderosa*, and lacks the fulcral plates of a typical *Plectorthis* (see Ross 1970 pl. 6, fig.19). Ross’s description of *Plectorthis* cf. *perplexus*, also from Nevada, indicated the presence of variable muscle scars — some specimens possessed the bilobed field while others possessed a trilobed muscle field. True *Plectorthis perplexus* (Ross, 1967), however, has a heart-shaped ventral muscle scar.

Although some intrageneric variability is to be expected in the ventral muscle scar field in orthoids (see Howe 1966), these species clearly represent a different morphotype (referred to as *P. ponderosa*-type species in this study). Ross (1970) and Laurie (1991) suggested that these species with a subtriangular ventral muscle field are more closely allied with *Austinella* (Plaesiomyidae). The muscle scars of *Austinella* are generally more subtrapezoidal and closely resemble the pattern shown here. *Austinella* Williams and Harper (1997, fig. 540–3a) has a ventral muscle field that closely resembles that of *P. ponderosa*, with a similar subtriangular adductor scar and linear diductor scars. *P. ponderosa* also seems to have a more bulbous cardinal process than the generally simple, ridge-like cardinal process of most *Plectorthis* — a characteristic found in plaesiomyids. The most significant morphological difference between these lineages is the predominance of a strongly dorsibiconvex shell in most plaesiomyid
Figure 6.11: Simplified diagram showing tracings of various types of muscles scars seen in species previously assigned to *Plectorthis*. A) *P. plicatella* (traced from plate 11, figure 9 in Schuchert and Cooper 1932), B) *P. jamesi* (traced from plate 11, figure 2 in Schuchert and Cooper 1932), C) *P. ponderosa* (traced from plate 83, figure 32 in Cooper 1956), and D) *P. cliefdenensis* (traced from fig. 8.7 in Percival 1991). A and B are similar, and characteristic of *Plectorthis*, while C and D represent unusual forms. Ad=adductor, Di=diductor.
genera except for *Austinella*. The ventribiconvex *Austinella* is unlike other plaesiomyids, and may be an appropriate genus in which to assign these species.

In this study, it is observed that species with a subtriangular ventral muscle field usually have a significantly more convex dorsal valve than the type species *P. plicatella*, although these shells are always ventribiconvex. There are other *Plectorthis* species that fit this morphology which lack internal descriptions that may possess a similar muscle field. For example, Cooper (1956) noted that *Plectorthis compacta* is similar to *P. ponderosa* in form, but smaller in size. In the lack of free valves to study internal structures, an unusually convex dorsal valve may serve as a clue to the muscle field morphology.

Species assigned to *Plectorthis* from other tectonic regions need to be re-examined to determine their muscle field morphology. For example, several species from Kazakhstan seem to exhibit this subtriangular muscle field. *Plectorthis licta* Popov and Cocks, 2006 from the Dulankara Formation clearly has a subtriangular adductor scar (see Popov and Cocks 2006, pl. 6, fig. 10), though the ribbing style differs from *P. ponderosa* in that it is somewhat more branching. *Plectorthis cf. P. licta* Popov and Cocks, 2014 from the Chiniz Terrane may share this feature, though it is difficult to determine from figured material (Popov and Cocks 2014, fig. 21N). *Plectorthis burultasica* Popov, Cocks, and Nikitin, 2002 is also described as possessing a subtriangular ventral muscle scar field, though it is difficult to determine the exact shape of the muscle scars from the figured specimen (Popov et al. 2002, pl. 10, fig. 43).

*Plectorthis cliefdenensis* Percival, 1991 from the Fossil Hill Limestone of Australia is described as having a cordate ventral muscle field with lanceolate to linear adductor scars surrounded by large flabellate crescentic diductor scars. The adductors in the figured specimens appear to be much less linear than a typical *Plectorthis*, and the diductors seem more flabellate than heart-shaped. However, the overall shape of the muscle scars and the presence of fulcral plates indicate that the species is related to *Plectorthis*. As noted by Percival (1991), *Plectorthis cf. scotica* (McCoy, 1852), described by Mitchell (1977) from the Bardahessiagh Formation in
Northern Ireland also shares this type of muscle scars. Both of these forms may represent distant relatives of the typical North American *Plectorthis* species.

*Plectorthis whitteryensis* Williams, 1974 has an oval ventral muscle field, lacking the prominent heart-shape in the type *P. plicatella plicatella*. This species probably belongs in a different orthid genus and is not closely related to *Plectorthis*. In his discussion, Williams (1974) initially suggested that it may be a distant relative to the North American *Plectorthis*, or may be closely related to *Desmorthis*.

6.6 Aditicules

Both aditicules and exopunctae are a form of superficial ornamentation (Williams and Brunton 1997). The use of these two terms has been somewhat confusing, and Jin et al. (2007) proposed to use the term exopunctae for fine circular pits that are shallow and generally perpendicular to the shell surface, and aditicules for oblique tubules that are known to house chitinous setae (see also Jin and Copper 2010). The fine perforations in *Plectorthis* reported in some previous work as exopunctae (e.g. Williams and Harper 1997) are actually aditicules. Aditicules may be difficult to observe because a well-preserved shell needs to be weathered just enough or cleaned perfectly to expose superficial perforations, but not weathered too much or over cleaned so as to damage the shell surface. Recrystallization or mineral replacement in a shell will easily destroy such microstructures.

Double-rowed aditicules were first noted by Cooper (1956) in *Plectorthis punctata*, and subsequently in two other species. Popov et al. 2002 described radial rows of fine rounded exopunctae on both sides of each rib in *Plectorthis burultasica* from the Anderken Formation in Kazakhstan. Rasmussen et al. (2012) described similar structures on the surface of *Plectorthis* sp. 1 from Alaska, but the material is very poorly preserved.

An examination of the syntypes of *Plectorthis* revealed that specimen AMNH 30258 has very little matrix material on the shell surface but under the microscope it is clear that the outer shell layers have been damaged, as indicated by longitudinal scratches on the surface and
exposure of fibrous shell material in the troughs between ribs. Double-rowed aditicules, however, are present, as indicated by sporadic perforations on each side of some ribs (see Fig. 6.12a). The presence of double-rowed aditicules in the type species is confirmed by a well-preserved tootype of *P. plicatella* from the Cincinnati Museum Center collection (Fig. 6.12b).

*Plectorthis* from other regions also exhibit this feature. Two specimens of *Plectorthis inaequiconvexa* Roy, 1941 from Baffin Island, Nunavut, show very prominent double-rowed aditicules on each rib (Fig. 6.12c). Due to the excellent preservation of relatively large shells, it is clear that the aditicules open anteriorly at a low angle to the shell surface. *P. plicatella laurentina* from the Lake Simcoe region of Ontario also displays such aditicules (see Fig. 6.12d), though the specimens from Baffin Island show much clearer evidence of this feature due to their better preservation (note the fine growth lamellae preserved between the ribs of the specimen in Fig. 6.12c).

The presence of double rows of aditicules per rib in the type species and other North American species of *Plectorthis* may serve as one of the diagnostic characters of this widely reported genus.

### 6.7 Paleobiogeography

*Plectorthis* has a relatively short stratigraphic range from the top Darriwilian to mid-Katian, with a broadly synchronous first appearance and last appearance datum worldwide (Figure 6.1). Several observations can be drawn from the known distribution of the genus.

#### 6.7.1 Laurentia

*Plectorthis* was most common in pericratonic settings of Laurentia. The earliest known *Plectorthis* are from rocks of latest Darriwilian (Chazyan) age, including *P. exfoliata* from Tennessee and Virginia and *P. mazourkaensis* and *P. patula* from California. None of these forms are well known, and the shells from California are deformed (*P. mazourkaensis* shows longitudinal stretching (Phleger 1933). Their identity as *Plectorthis* remains to be determined because their internal structures are unknown.
**Figure 6.12:** Aditcules on the surface of *Plectorthis* shells. A) *Plectorthis plicatella plicatella* (lectotype) AMNH 30258. B) *Plectorthis plicatella plicatella* from CMC 6395. C) *Plectorthis inaequiconvexa* from Baffin Island, Nunavut (GSC locality O-104229). D) *Plectorthis plicatella* from the Lake Simcoe area of Ontario (W-O2 locality). Note that the aditcules form prominent radiating double-rows along rib crests. Although much more apparent in well preserved shells (e.g. C) *P. inaequiconvexa* from Baffin Island), the aditcules are still visible in less well preserved specimens (e.g. D) *P. plicatella laurentina* from Ontario).
The Sandbian (late Chazyan and Turinian) marked the highest diversity and widest geographic distribution of *Plectorthis* in Laurentia. Ten species evolved along the eastern margin (Cooper 1956), in Tennessee, Virginia, Pennsylvania (*P. pennsylvanica*), and Oklahoma (*P. punctata*) — a belt that was to develop into the well-defined Appalachian foreland basin by the early Katian. The earliest known species of the *P. ponderosa*-type, *Plectorthis* cf. *perplexus* from the Antelope Limestone of Nevada (approximately Chazyan), appeared during this interval (Ross 1967). It appears that the pericratonic setting for *Plectorthis* persisted to the Sandbian.

Although not as diverse, the most recognizable and abundant *Plectorthis* in Laurentia are from the early–middle Katian (Chatfieldian to Maysvillian). The type species *P. plicatella plicatella* and associated subspecies have been recorded from across eastern Laurentia, including Ontario (Wilson, 1946), Minnesota (Weiss 1955), and the Cincinnati region (Hall 1847, Foerste 1910, Davis 1985). Its occurrence in New York is doubtful (Foerste 1910; Titus 1982, 1986). Other notable species, including *P. equivalvis* and *P. neglecta* became locally common, often associated with *P. plicatella*. *P. ponderosa*, the typical form with a subtriangular ventral muscle field, occurred in pericratonic settings, such as the basal Martinsburg Formation of Virginia. Species from this interval usually had larger shells than those from the Sandbian.

*Plectorthis inaequiconvexa* from the Amadjuack Formation (Edenian–Maysvillian) of Baffin Island is perhaps the youngest species of the genus in Laurentia. This species came from the subequatorial pericratonic setting and developed a notably larger shell than other *Plectorthis* species, with most prominent double-rowed aditculae.

In Laurentia, *Plectorthis* disappeared by the beginning of the Richmondian (late Katian) time. Cooper and Kindle (1936) reported *Plectorthis magna* from the Hirnantian of eastern Quebec, but this form differs from all other *Plectorthis* in having very fine costae, and may be more closely related to *Hebertella* than *Plectorthis*.

Occurrences of *Plectorthis* have been reported from Northern Ireland and Scotland, although *P. scotica* is the only named species of *Plectorthis* from the region, resembling the *P.*
ponderosa-type species with an acutely triangular ventral muscle field but still possessing the
typical simple ridge-like cardinal process of Plectorthis. Other shells are poorly preserved and
can be identified only tentatively as Plectorthis sp., Plectorthis cf. australis, or Plectorthis cf.
scotica (see Williams 1962, Wright 1964, and Mitchell 1977). Several of these shells seem to
bear a ventral muscle field similar to P. ponderosa. Considering the preference of Plectorthis for
pericratonic settings, its presence in peri-Laurentia seems probable.

6.7.2 Avalonia (Shelve Inlier)

There are only two species of Plectorthis described from Avalonia: P. whitteryensis and
Plectorthis sp. Williams, 1974. The distinct, oval muscle field of P. whitteryensis may have
evolved due to its relative isolation from the majority of Plectorthis on Laurentia. More material
is required to confirm the affinity of this species.

6.7.3 Baltica

Occurrences of Plectorthis in Baltica are represented by a few moulds and casts from
the Kalstad Limestone of Norway (Plectorthis sp. Neuman et al. 1997), Norderhov Formation
(Plectorthis sp. Harper, 1982), and Kirkerud Group (Plectorthis sp. Harper, 1984) of Caradoc to
earliest Ashgill age. None of these unnamed species are particularly abundant, and the first two
are known only from moulds and casts. If these species can be confirmed to be true Plectorthis,
their occurrences would be in cool-water subtropical environment similar to the Cincinnatian
Arch area in Laurentia.

6.7.4 Kazakhstan

In Kazakhstan, several Plectorthis have been reported in Nikitin and Popov 1983, Popov
and Cocks (2006, 2014), Nikitin et al. (2006), and Popov et al. (2002). Plectorthis licta Popov and
Cocks, 2006, and Plectorthis cf. licta are of the P. ponderosa-type, with a clearly subtriangular
ventral muscle field. Plectorthis akzhara Nikitin and Popov, 1983 and Plectorthis numerosa
Nikitin and Popov, 1983 may also share this type of ventral muscle field, though definitive
identification is not possible due to the preservation of figured specimens. Both species exhibit
branching ribs, which differ from *P. ponderosa* in Laurentia. *Plectorthis? burultasica* has an extremely strong sulcus unseen in other *Plectorthis* species, and is probably not congeneric. Thus, the occurrence of true *Plectorthis* in the Kazakhstan terranes remains to be determined.

### 6.7.5 South China

Although species have been reported from south China, they are typically poorly preserved (usually as moulds), and it is difficult to examine their shell microstructures. It is uncertain if these species show the characteristic heart-shaped ventral muscle scar or double-rowed aditicles. Further study is needed to determine whether they are true *Plectorthis*.

South China generally lacked the characteristic brachiopods from the Upper Ordovician of Laurentia, such as *Dinorthis, Plaesiomys, ‘Platystrophia’, Rostricellula, and Rhynchotrema*. It is thus doubtful that true *Plectorthis* was present there.

### 6.7.6 Siberia

Several species were reported from Siberia, but the affinities of these species are questionable. Although the photographed specimens in Severgina (1989) from Gorny Altai superficially resemble *Plectorthis*, the apparent deformation of the fossils and lacking details on internal structure only allow for questionable assignment. Cocks and Modzalevskaya (1997) reported a single dorsal valve from the Korotkinskaya Formation but the shell exhibits an extreme convexity unknown in other *Plectorthis* species. They mention additional shells that were reported by Nikiforova (1985), but explain that these are badly exfoliated, and thus identification at the species level would be difficult or impossible.

### 6.7.7 Paleotropical Gondwana

Only a single species (*Plectorthis cliefdenensis*) has been reported from Australia. Percival (1991) suggested affinities with *Plectorthis cf. scotica* (McCoy, 1852) by Mitchell, 1977 based on the lanceolate to linear adductor scars surrounded by large flabellate crescentic diductor scars in the ventral muscle field. This is the only confirmed species of *Plectorthis* from
Gondwana. At present, it is difficult to explain why such two widely separated tectonic regions could share a unique species of *Plectorthis*.

### 6.7.8 Summary and implications

The oldest known *Plectorthis* appeared in the shallow epeiric seas of the continental margin of Laurentia, where it remained the most diverse throughout its evolutionary history. The relatively high diversity and abundance of *Plectorthis* in the basins on the margin of Laurentia suggests that it favoured the cool, nutrient-rich waters derived from upwelling along the continental margin and troughs during the initiation of the Taconic orogeny (Ettensohn 2010). This is thought to explain an abundance of bryozoans (generally considered a cold water group) and an apparent drop in ocean temperature as seen in the carbon isotope record (e.g. Trotter et al. 2008). This enhanced circulation of nutrients may have favoured the spread and diversification of the filter feeding brachiopods.

The apparent disappearance of confirmed *Plectorthis* species at the approximately the same time, particularly across Laurentia where the genus became most diverse, is in sharp contrast to many other taxa that composed the brachiopod fauna of eastern North America in the early Katian. The *Strophomena-Nasutimena* lineage (Jin and Zhan 2001), *Dinorthis-Plaesiomys* lineage (Sproat et al. 2013), and the *Rhynchotrema-Hiscobeccus* lineage (Jin et al. 2013, Sohrabi and Jin 2013, Sproat et al. 2014) first established in pericratonic seas by the early Katian and subsequently expanded and diversified in the vast intracratonic seas of Laurentia. One possible explanation is that *Plectorthis* was unable to adapt to the warm inland seas, especially the paleoequatorially located intracratonic basins of Laurentia.

### 6.8. Systematic Paleontology

**Order Orthida Schuchert and Cooper, 1932**

**Suborder Orthoidea Woodward, 1852**

**Superfamily Plectorthoidea Schuchert and LeVene, 1929**
Family Plectorthidae Schuchert and LeVene, 1929

Genus *Plectorthis* Hall and Clarke, 1892

*Type species* *Orthis plicatella* Hall, 1847. (See below.)

*Diagnosis* (emended herein). Transversely semioval, subequally biconvex with faintly sulcate to uniplicate anterior commissure, costate to coarsely costellate, filate; ventral interarea short, shorter dorsal interarea orthocline to faintly anacline; dental plates divergent, ventral muscle field subcordate with linear adductor track usually not confined by subcrescentic diductor scars anterior separated anteriorly by low median ridge; dorsal adductor scars separated bilaterally by a prominent medial septum; pedicle callist not reported; cardinal process a thick, rounded ridge and crenulated myophore. Double-rowed aditicules on each rib.

*Remarks*. There has been some ambiguity in previous descriptions of the ventral muscle field of *Plectorthis*. The ventral adductor tract is linear, and the diductor scars subcrescentic and usually do not enclose the adductor scars anteriorly. *P. cliefdenensis* from Australia, the only reported species in which the diductor scars completely enclose the adductor scars, is probably only distantly related to the North American *Plectorthis* from the type area. Double-rowed aditicules are characteristic of the type species and should be regarded as diagnostic of the genus.

A full list of species assigned, questionably assigned, and rejected is provided as an appendix (Appendix C).

*Plectorthis plicatella plicatella* (Hall, 1847)

Figures 6.2 and 6.4

1847 *Orthis plicatella* Hall, p. 122, pl. 32, fig. 9a–g; non pl. 32, fig. 9 f–g.

1873 *Orthis plicatella* Hall; Meek, p. 108, pl. 8, fig. 7a–h.
1893 *Plectorthis plicatella* (Hall); Winchell and Schuchert, p. 436, pl. 33, figs. 5–7.

1910 *Plectorthis plicatella* (Hall); Foerste, p. 49, pl. 6, figs. 5a–b.

*Type material.* AMNH 30258 lectotype (Figure 6.2k–o), selected herein; AMNH 30256 (Figure 6.2a–e) and 30257 (Figure 6.2f–j), paralectotypes. AMNH 30259 (Figure 6.3a–e; Hall 1847, fig. 9f–g) reassigned to *P. plicatella fissicosta*. These specimens are the original lot of *Orthis plicatella* Hall, 1847 in the American Museum of Natural History in New York consisting of two small specimens (AMNH 30256 and 30257) and two large specimens (AMNH 30258 and 30259) (Table 6.2). Each of these specimens were illustrated by Hall (1847) on pl. 32: AMNH 30256 and 30257 correspond to fig. 9a and 9b respectively in pl. 32, AMNH 30258 to fig. 9c and 9d, and AMNH 30259 to fig. 9g and 9f.

AMNH 30258 is selected as a the lectotype as it is best preserved of the four syntypes. Between ribs, however, the outer layers of the shell have been scraped away, as indicated by longitudinal scratches. This has mostly removed any fine detail on the shell surface, though fine concentric growth lines found in well-preserved *Plectorthis* are sometimes still visible. Small, secondary ribs are present near the lateral margins of the shell, although these are much less pronounced than in AMNH 30259. The shell has some damage to the posterior on the right flank (with dorsal valve upward and anterior facing downward). Hall depicted a clean interarea in his illustration (pl. 32, fig. 9c), probably an embellishment by the illustration artist, as the interarea of the specimen is mostly covered by matrix.

Paralectotypes AMNH 30256 and AMNH 30257 are notably smaller. AMNH 30256 is partly covered by matrix and AMNH 30257 is significantly damaged. However, both specimens have simple ribbing and the characteristic subelliptical outline of *Plectorthis*. In Hall’s original figures the interarea is shown as exposed, but the interarea of both specimens are covered by matrix. In addition, although fine details are shown in the sketch, matrix obscures much of the surface structures in both specimens. Near the center of AMNH 30257, however, fine concentric growth lines can be seen between the costae.
AMNH 30259 has a slightly more prominent and curved ventral umbo than the others. The ribs are clearly fascicostellate anteriorly, as is typical of *P. plicatella fissicosta*, to which this specimen is assigned in this study.

**Table 6.2: *P. plicatella plicatella* type measurements (mm). Lectotype in bold.**

<table>
<thead>
<tr>
<th>Specimen no.</th>
<th>L</th>
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<tbody>
<tr>
<td>AMNH 30256</td>
<td>8.1</td>
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<tr>
<td>AMNH 30257</td>
<td>6.4</td>
<td>9.3</td>
<td>2.1</td>
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<tr>
<td>AMNH 30258</td>
<td>10.6</td>
<td>16.5</td>
<td>6.3</td>
</tr>
</tbody>
</table>

*Type locality.* Very little information is associated with these specimens, with collection tags only indicating that they originated from the Upper Hudson River Group near Cincinnati. It is likely that they originated from the Maysvillian rocks (mid-Katian) of the Cincinnati region. In his description, Hall (1847) only noted that the species is common in Cincinnati (Ohio), Maysville (Kentucky), and Madison (Indiana).

*Type horizon.* Fairmount Member of the Fairview Formation (Maysvillian).

*Other material.* In addition to the syntypes, 50 specimens from the Cincinnati Museum Center (Ohio) were borrowed. One well-preserved specimen is figured here (Figure 6.4). Locality information can be found in Appendix B.

*Diagnosis.* Transversely subelliptical to subcircular, ventribiconvex; costae generally simple, with week bifurcation near anterior margin in some shell; double-rowed aditicules.

*Description.* Shell medium sized for the genus, transversely subelliptical to subcircular, ventribiconvex, with average length 9.7 mm, width 13.3 mm, and thickness 5.5 mm (Table 6.3). Hingeline long, slightly shorter than maximum shell width attained near mid-length. Costate with simple ribs that sometimes become fascicostellate near the shell anterior (Figure 6.7). Growth lamellae regular, strong. Aditicules double-rowed on each rib (Figure 6.12). Anterior commissure symmetrical; weakly uniplicate to weakly unisulcate, but fold and sulcus always broad occupying about three-fifths of shell length. Dorsal valve smaller and less convex than
ventral, with less prominent umbo than ventral valve. Dorsal interarea short and anacline, with open notothyrium. Ventral interarea larger and apsacline with open delthyrium.

**Table 6.3: Summary statistics for measured *Plectorthis plicatella plicatella* (mm).**

<table>
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<tr>
<th></th>
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<td>1.1</td>
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<tr>
<td>Min</td>
<td>6.4</td>
<td>8.4</td>
<td>2.1</td>
</tr>
<tr>
<td>Max</td>
<td>15.3</td>
<td>20.8</td>
<td>8.4</td>
</tr>
</tbody>
</table>

Ventral interior. Teeth supported by divergent dental plates. Muscle field subcordate, about one third of shell length; long linear adductor scars sometime with elevated ridge at anterior flanked by subcrescentic, heart-shaped diductor scars.


Remarks. This study shows that double-rowed aditicules can always be observed in well-preserved specimens of the type species, especially after careful removal of matrix using an ultrasonic bath (Figure 6.12a, b). It is thus proposed here that other species previously assigned to the genus should be examined to determine the presence or absence of this character.

*Plectorthis plicatella fissicosta* (Hall, 1847)

Figure 6.3

1847 *Orthis fissicosta* Hall, p. 121, pl. 32, fig. 7a, b.

1847 *Orthis plicatella* Hall, (in part) p. 122, pl. 32, fig. 9 f–g

1872 *Plectorthis triplicatella* Meek, p. 281.
1873 *Orthis fissicosta* Hall; Meek, p. 106: pl. 8, figs. 6a–h.

1910 *Plectorthis fissicosta* (Hall); Foerste, p. 48, pl. 6, fig. 4.

1985 *Plectorthis fissicosta* (Hall); Davis 1985: pl. 3, figs. 6, 8–10.

*Type material.* AMNH 30255 (Figure 6.3f–j), holotype by monotypy. This is the original specimen of Hall (1847, pl. 32, fig. 7a, b). The specimen is free from matrix but displays prominent indentation and cracking of the ventral valve, indicating dorso-ventral compression. Although length and width are probably reasonably preserved, thickness of the shell has been altered. The fine secondary ribs bifurcating from prominent primary ribs at the same point (fascicles of Foerste 1910) that are characteristic of *P. fissicosta* are very well-preserved. Other specimens of *P. fissicosta* in the CMC collection show the characteristic ventribiconvex profile of *Plectorthis*. See Table 6.4 for measurements of the type material.

As discussed under *P. plicatella plicatella*, AMNH 30259 (Figure 6.3a–e), one of the *Orthis plicatella* syntypes, is here transferred to *P. plicatella fissicosta*.

**Table 6.4: *P. plicatella fissicosta* type measurements (mm). Holotype in bold.**

<table>
<thead>
<tr>
<th>Specimen no.</th>
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<tr>
<td>AMNH 30255</td>
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<td>19.4</td>
<td>6.1</td>
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<tr>
<td>AMNH 30259</td>
<td>11.6</td>
<td>18.6</td>
<td>6.7</td>
</tr>
</tbody>
</table>

*Type locality.* Precise location unknown. Foerste (1910) remarked that specimens of this type are rare in the upper part of the Fairmount bed at Cincinnati, Ohio. Given that this is the same region from which the types of *Plectorthis plicatella* originated, this is probably also origin of the *Orthis fissicosta* holotype.

*Type horizon.* Fairmount member of the Fairview Formation (Maysvillian).

*Other material.* In addition to the type above, 50 specimens from the CMC were borrowed. Locality information can be found in Appendix B.
**Diagnosis.** Transversely subelliptical to subcircular, ventribiconvex; fascicostellate, with bifurcation occurring in each rib at similar length from the umbo.

**Description.** Shell medium sized for the genus, transversely subelliptical to subcircular, ventribiconvex, with average length 10.1 mm, width 13.4 mm, and thickness 5.4 mm (Table 6.5). Hingeline long, with subrounded cardinal extremities; maximum shell width attained approximately at mid-length. Trifid fascicostellae bifurcation starting at similar distance from umbo in a shell (Figure 6.7). Anterior commissure weakly uniplicate to weakly unisulcate; but fold and sulcus broad occupying about three-fifths of shell length. Dorsal valve less convex than ventral. Dorsal interarea short and anacline, with open notothyrium. Ventral interarea larger and apsacline with open delthyrium.

**Table 6.5: Summary statistics for measured Plectorthis plicatella fssicosta (mm).**

<table>
<thead>
<tr>
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<td>Avg</td>
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<td>SD</td>
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<td>3.0</td>
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<td>Min</td>
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<td>7.6</td>
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<tr>
<td>Max</td>
<td></td>
<td>16.3</td>
<td>19.4</td>
<td>8.5</td>
</tr>
</tbody>
</table>

**Interior.** Not examined in this study.

**Remarks.** As shown above, *P. plicatella* and *P. fissicosta* share similar characters and dimensions in the Cincinnati type area, and thus *P. fissicosta* is here downgraded to a subspecies of *P. plicatella*. The main difference between the subspecies is the trifid fascicostellate ribbing style of *P. plicatella fssicosta* while *P. plicatella* exhibits mostly simple costae. Intermediate forms have simple ribs that become fascicostellate near the anterior commissure only. One of the original types of *Orthis plicatella* (Hall, 1847), AMNH 30259, has strong fascicostellae that closely resemble those of *P. plicatella fssicosta*, and is transferred to the latter subspecies in this study.
Plectorthis plicatella laurentina Wilson, 1946

1946 Plectorthis plicatella laurentina Wilson, p. 28, pl. 2, fig. 4.

Type material. Wilson only mentions that the holotype is from Research Council Laboratories, Sussex Street, Ottawa in the private collection of G.W. Sinclair.

Type locality. Ottawa Valley region in Ontario.

Type horizon. Sherman Fall or Cobourg beds (Verulam or lower Lindsay Formation in Liberty 1969).

Material. W 2980 (Figure 6.6a–e) and W 2981 (Figure 6.6f–j) from Verulam Formation (early Katian, Chatfieldian) at locality W-O2 and three additional specimens collected from an outcrop along Highway 6 in the Lake Simcoe area in Ontario.

Remarks. A number of P. plicatella subspecies have been erected based on slight differences in size or ribbing pattern. These subspecies are confined to the “Trenton” strata (mostly Chatfieldian, early Katian). The diagnostic utility of these differences are debatable, but the subspecies are all subtly different when compared to the P. plicatella from the Cincinnati region and have evolutionary significance. Foerste (1910) suggested that P. plicatella trentonensis likely represented an ancestral stock that evolved into P. plicatella. The subspecies named by Wilson (1946) and Weiss (1955) are also smaller forms.

This subspecies was originally described by Wilson from the Ottawa Valley, but is confirmed here for the first time from the Verulam Formation in the Lake Simcoe area. The subspecies lacks secondary ribs similar to P. plicatella plicatella, but is significantly smaller than specimens of the type species from the Cincinnati region. In all other characters it closely resembles P. plicatella plicatella. Double-rowed aditcules are reported here for the first time in
the species identical to those found in other species (Figure 6.7), though they are not as well-preserved as those seen in the specimens from the Cincinnati region or Baffin Island.

_Plectorthis inaequiconvexa_ Roy, 1941

Fig. 6.5

1941 _Plectorthis inaequiconvexa_ Roy, p. 85, fig. 47.

2000 _Plectorthis inaequiconvexa_ Roy; Bolton (fauna list with figures), p. 50, pl. 9, figs. 4 and 5.

_Type material._ USNM 28151 by original designation.

_Type locality._ Silliman’s Fossil Mount, Baffin Island, Nunavut, Canada.

_Type horizon._ Richmond (probably equivalent to the Edenian to Maysvillian Amadjuack Formation, see Bolton 2000).

_Material._ GSC 113506 from locality O-104198, 15 un-numbered specimens from the GSC collection at locality O-104229 (box labelled _Austinella cooperi_), and three additional unlabelled specimens in the GSC collection from locality O-104187 – all from the Amadjuack Formation at Silliman’s Fossil Mount.

_Remarks._ These specimens are generally larger than most other _Plectorthis_ species, with GSC 113506 in particular noticeably larger (Table 6.6). This gives the appearance of a more orthocline ventral interarea than other species, but this may be due to growth of this generally larger species.
Table 6.6: Summary statistics for measured *P. inaequiconvexa* (mm).

<table>
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<td>6.6</td>
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<tr>
<td>Max</td>
<td>19.8</td>
<td>21.8</td>
<td>11.5</td>
</tr>
</tbody>
</table>

The shells of *Plectorthis inaequiconvexa* are perhaps the best preserved among all materials of the genus examined. The fine growth lamellae and well-preserved double-rowed aditicules are in agreement with the microstructures of the type species (Figures 6.5 and 6.12).
6.9 References


Sedgwick, A. and McCoy, F. 1851-55. A synopsis of the classification of the British Palaeozoic rocks, with a systematic description of the British Palaeozoic fossils in the geological museum of the University of Cambridge, xcviii.


Chapter 7 —Diversity of the Trentonian brachiopod fauna in Ontario and its relationship to other Trentonian faunas of Laurentia

7.1 Introduction

The Trentonian (early Katian) fossil brachiopod fauna of eastern North America (Laurentia) occupies an important juncture in terms of the evolution, paleoecology, and paleobiogeography of the Early Paleozoic shallow marine shelly benthos. During this time, the Great Ordovician Biodiversification Event (GOBE) was fully underway (Webby 2004) — the early Katian corresponds to a plateau in brachiopod diversity after the greatest rise in diversity during the Dapingian-Darriwilian and prior to its peak in the late Katian (Harper et al. 2004). In Laurentia, the shelly benthos was colonizing and expanding into the newly flooded continental interior, marking the onset of carbonate production in the intracratonic basins and formation of carbonate platforms near the continental margin that would extend across the continent in the late Katian. Because of rising sea levels, continental carbonate platforms and basins were becoming increasingly isolated from those of adjacent tectonic plates, and the brachiopod fauna was becoming more endemic as a result, unlike the relatively cosmopolitan Early and Middle Ordovician fauna (Harper et al. 2013).

The Trentonian brachiopod fauna in the area around Lake Simcoe in Ontario, has thus far been poorly studied, and treated only in a biostratigraphic sense by Liberty (1969). Ongoing work has systematically described several of the brachiopod lineages (e.g. see Sohrabi and Jin 2013a; Sproat and Jin 2013, 2016; Sproat et al. 2014, 2015), but no study has yet attempted to quantitatively describe the fauna.

Until recently, little work has been done on the paleoecological and paleobiogeographical aspects of this fauna. Sohrabi and Jin (2013b) noted two distinct Laurentian brachiopod faunas: an early Katian Scoto-Appalachian fauna derived from the early Sanbian (Chazyan) Scoto-Appalachian fauna found in the Appalachians, northeastern Ireland,
and Scotland; and an epicontinental Laurentian fauna that later evolved into the endemic late Katian epicontinental fauna across Laurentia.

This study aims to address these two gaps in our understanding of the Trentonian brachiopod fauna. It addresses the lack of quantitative abundance data from several localities in the Lake Simcoe area and Manitoulin Island in Ontario, and examines how this new data fits into the paleobiogeography of the Trentonian brachiopod fauna of Laurentia.

**7.2 The Trentonian brachiopod fauna of Laurentia**

In terms of brachiopods, the Trentonian fauna is moderately diverse, commonly dominated by several characteristic forms. *Paucicrura, Rhynchotrema, Sowerbyella, Strophomena,* and *Rafinesquina* are common at most localities (Figures 7.1, 7.2), but vary in terms of species, diversity, and dominance. These more dominant forms are usually found alongside some combination of orthides (*e.g.* *Plaesiomys, Hesperorthis, Glyptorthis,* and *Plectorthis*), *Anazyga, Parastrophina,* and *Platystrophia* with other forms being less common and less abundant. Brachiopod shells are commonly associated with crinoids ossicles (with rare holdfasts and calices) and bryozoans (treptostome, prasoporid, and leafy forms). Corals are notably rare in the Trentonian fauna, unlike in the late Katian fossil faunas of North America.

Trentonian-aged fossils have been documented from across eastern North America and parts of the continental interior (Table 7.1). Fossils from Scotland and northeastern Ireland are also considered in this study, as they were peri-Laurentian terranes during the Ordovician (Cocks and Torsvik 2011). A similar, but slightly younger (Edenian-Maysvillian, middle Katian) fauna from Baffin Island is also incorporated in this study to determine its relationship with the older Trentonian faunas.
**Table 7.1: Trentonian fauna of Laurentia references**

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<th>Region</th>
<th>Rock units</th>
<th>Reference</th>
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</thead>
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<td>Lake Simcoe</td>
<td>Upper Bobcaygeon, Verulam, and Lindsay Formations</td>
<td>Sinclair 1969; this study (see Appendix D)</td>
</tr>
<tr>
<td>Ottawa Valley</td>
<td>Rockland, Hull, Sherman Fall, and Cobourg Formations</td>
<td>Wilson 1946</td>
</tr>
<tr>
<td>Manitoulin Island</td>
<td>Cloche Island beds, Verulam Formation</td>
<td>Cooper 1956, Copper and Long 1993; this study</td>
</tr>
<tr>
<td>Newfoundand (Port-au-Prince Peninsula)</td>
<td>Long Point Formation</td>
<td>Cooper 1956; Weerasingehe 1970</td>
</tr>
<tr>
<td>Champlain Valley in New York and Vermont</td>
<td>Isle la Motte Formation</td>
<td>Cooper 1956</td>
</tr>
<tr>
<td>Appalachian Valley from Pennsylvania to Alabama</td>
<td>Ben Hur Formation, Can Creek Formation, Nealmont Formation, Collierstown Formation, Hardy Creek Formation, Mercerburg Formation, Jacksonburg Formation, lower Martinsburg Formation, Moccasin Formation, Oranda Formation, Salona Formation</td>
<td>Cooper 1956</td>
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<tr>
<td>Central Basin of Tennessee</td>
<td>Carters Formation, Kimmswick limestone, Hermitage Formation, Tyrone Formation</td>
<td>Cooper 1956</td>
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<td>Disturbed area—Division 8</td>
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</tr>
<tr>
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<tr>
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<td>Viola Formation</td>
<td>Cooper 1956, Alberstadt 1973</td>
</tr>
<tr>
<td>Black Hills of South Dakota</td>
<td>Whitewood Formation</td>
<td>Cooper 1956</td>
</tr>
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<td>Nevada</td>
<td>Dark Shale with <em>Reushella</em></td>
<td>Cooper 1956</td>
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<td>Northern Rocky Mountains</td>
<td>Advance Formation</td>
<td>Jin and Norford 1996</td>
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</tr>
<tr>
<td>Scotland (Girvan)</td>
<td>Craighead Limestone, Albany Mudstone Formation, Mycoch Formation</td>
<td>Cocks 2008 (and references therein)</td>
</tr>
<tr>
<td>Northeastern Ireland (Tyrone)</td>
<td>Bardahessiagh Formation</td>
<td>Cocks 2008 (and references therein)</td>
</tr>
</tbody>
</table>
Figure 7.1: Common fossils of the Simcoe Group on Manitoulin Island and near Lake Simcoe. A. Upper Bobcaygeon Formation at Carden Quarry; large, flat strophomenide Rafinesquina alternata surrounded by shell debris that includes Sowerbyella sericea and Paucicura rogata. B. Lower Verulam Formation at Goat Island Road; bedding surface showing numerous Strophomena filiforma. C. Lower Verulam Formation at Mara ditch; bedding surface showing numerous large convex Strophomena filiforma. D. Lower Verulam Formation at Mara ditch; numerous Rhynchotrema increbescens alongside trilobite fragments (top left), gastropod shells (bottom right), bryozoan debris and a strophomeoid. E. Lower Lindsay Formation at Highway 6 bluff; bedding surface with multiple Sowerbyella sericea and Paucicura rogata. Each photo is of the top surface of the slabs. Scale bars = 1 cm.
Figure 7.2: Slab from Mara ditch near Lake Simcoe. Note the relatively diverse fauna. This particular slab has a large number of highly convex *Rafinesquina*. Low convexity *Rafinesquina alternata* are more common lower in the Simcoe Group. The debris in the center of the slab dominantly consists of bryozoan fragments, with occasional *Anazyga recurvirostra* and *Rhynchotrema increbescens*. Top surface of bedding plane in photo.
7.3 Trentonian geology of Ontario

The upper part of the Simcoe Group comprises the Trentonian rocks in Ontario. The group consists of varying proportions of alternating bioclastic grainstone and fine grained carbonate mud. In the subcrop, the rocks are formally referred to as the Trenton Group, similar to New York State, but precise correlation between subcrop and outcrop has not yet been attempted (see Armstrong and Carter 2010 for approximate correlations).

The Simcoe Group can be broadly divided into two components — a Blackriveran (Turinian, Sandbian) and Trentonian (Chatfieldian, early Katian) component (see Melchin 1994). The lowest part of the Simcoe group is considered Blackriveran in age. This includes the Shadow Lake Formation, Gull River Formation, and lower member of the Bobcaygeon Formation. The Trentonian portion of this group is limited to the middle and upper Bobcaygeon Formation, Verulam Formation, and Lindsay Formation.

The group has been interpreted as a broadly deepening upward sedimentary succession that contains two lower order shallowing upward cycles in the Bobcaygeon and Verulam formations (see fig. 2.1 in Melchin 1994). The dominantly bioclastic grainstones of the Bobcaygeon and upper Verulam formations represent a shallow shelf or lagoonal setting while the more carbonate mud-rich sections of the Lower Verulam and Lindsay formations are indicative of a deeper shelf environment. In the Lindsay Formation, this culminates in the dark black petroliferous shale at the top in the Collingwood Member forming the top of the Simcoe Group.

The Simcoe Group is significant in terms of paleoecology as well, with Brookfield (1988) suggesting that the dominance of bryozoans, crinoids, and brachiopods, in contrast to the typical warm water coral and brachiopod dominated deposits in the later Katian indicates a temperate-style carbonate deposition. However, complex, large metazoan reefs probably had not evolved by this point, as the first burst of complex coral-dominated reefs occurs much later in the Katian (Webby 2002). Additionally, isotopic evidence, although far from being conclusive,
indicates a slightly cooler but stable Late Ordovician climate (e.g. Trotter et al. 2008), rather the one punctuated by a cooling pulse as proposed by Brookfield.

**7.4 Faunal analysis of Ontario localities**

**7.4.1 Collection of material**

Several fossil brachiopod collections were made from localities in the Lake Simcoe region. Specimens from the Upper Bobcaygeon Formation were collected from the Carden Quarry. Samples from Mara ditch, Centennial Road, and Highway 48 localities are from the Verulam Formation. The Highway 6 bluff locality is composed of Lindsay Formation. An additional locality from a road cut section on Goat Island Road just north of Little Current on Manitoulin Island was also included for comparison (see Chapter 3 for locality information).

Care was taken to collect a representative sample of brachiopods at each locality from the most common to relatively rare species, including small shells of *Anazyga* and *Protozyga*. This approach aims to ensure that the results of the analyses here most accurately reflect the fauna at each locality.

Not all specimens from the collection were included in the analyses. Specimens that could not be identified confidently to at least the genus level or those that could only be questionably assigned due to poor preservation or incomplete shells were excluded to reduce uncertainties. Additionally, any linguliformeans and craniformeans were also excluded due to their lack of in-depth study and taxonomic uncertainty. *Lingula*, for example, has been widely reported from Trentonian localities, but probably includes a number of lineages that are not necessarily related, and including it may make localities seem artificially similar. This left a total of 3,783 specimens from south-central Ontario to be considered in the analysis.

For the samples from Manitoulin Island and Lake Simcoe areas, species identification and specimen counts were carried out in this study to generate a first-hand spreadsheet (see Supplementary Data C), which formed the basis for biodiversity and paleoecological analyses using the PAST software package (v. 3.12, see Hammer et al. 2001).
7.4.2 Diversity metrics and multivariate analyses

7.4.2.1 Methods

Because diversity is not a simple concept to define, four different metrics were calculated for each locality to illustrate the differences in diversity between the localities. The first two, abundance and taxonomic richness, do not directly describe diversity in terms that can be directly comparable between localities, but are useful in considering overall diversity. For example, an apparently poorly diverse locality may reflect truly lower diversity, or may be a consequence of preservation or collection bias, with massive and hard lithology commonly having a negative effect on fossil collection.

The two statistical diversity indices used in this study were Simpson diversity index and the Shannon-Weiner diversity index. Simpson diversity index reflects the chance of picking specimens that are the same taxa. The other index, Shannon-Weiner diversity index, also attempts to describe the diversity of a collection, but rather than describing diversity in terms of dominance, it is a measure of entropy. See Chapter 3 for formula of each index.

7.4.2.2 Results

There are significant differences in terms of diversity between the localities near Lake Simcoe (Figure 7.3). Both the Goat Island Road and Centennial Park Road localities are two to three times less diverse than the next lowest diversity (at four and six species respectively). However, given the size of the collections, the raw diversity may be influenced by the variation in collection size.

Rarefaction analysis was used to determine the effects that sample size may have had on the fossil collections. The results show that the Centennial Park Road locality is likely being affected by a smaller collection size according to rarefaction analysis (Figure 7.4). The Goat Island Road fauna, however, is probably near representative of the true diversity in the collection as the rarefaction curve has already plateaued. The apparently diverse Highway 6
Figure 7.3: Number of species, number of specimens, Simpson diversity index, and Shannon-Weiner diversity index for each of the Ontario localities. The Mara ditch and Highway 6 bluff localities are significantly more diverse than the other localities. Despite high abundances, the Carden Quarry and Highway 48 localities are dominated by only a few species.
**Figure 7.4:** Rarefaction analysis of the Ontario collections. Solid line is the rarefaction curve with 95% confidence intervals (dotted lines). The Mara ditch, Highway 48, and Carden Quarry collections probably represent near true diversity for the locality, as the slope has already reached maximum and is decreasing. The Centennial Park Road and Highway 6 Bluff localities both plot with high slopes, indicating probable sample size biases in the collection. Both of these localities are difficult to collect from: Centennial Park road due to limited exposure of carbonate mud-rich layers amenable to fossil collection, and Highway 6 bluff due to the steep incline of the outcrop.
bluff may be underrepresented in terms of diversity according to rarefaction, suggesting that a larger collection may have a higher diversity. The remaining localities show a relatively low sloping rarefaction curve, indicating that the diversity was relatively unaffected by the collection size.

The Simpson and Shannon-Weiner diversity indices are very similar in terms of the relative variation among the localities (Figure 7.3). Both indices are high for the Mara ditch and Highway 6 Bluff (0.85 and 0.80 Simpson index values and 2.4 and 1.95 Shannon-Weiner index values respectively), and with lower values for the remaining collections (<0.56 Simpson index values and <1.0 Shannon-Weiner index values). The diversity curves show some similarity with the raw species count, but the diversity indices for the Carden Quarry and Highway 48 are relatively low compared to their raw species diversity, as a result of being dominated by a few species, with *Paucicrura rogata* and *Sowerbyella sericea* far more abundant than the other species at each locality. *Rhynchotrema increbescens* is also disproportionately abundant at the Highway 48 locality. Collections from other localities have a more even distribution of species.

### 7.4.3 Multivariate analyses

#### 7.4.3.1 Methods

Principal component analysis (PCA) and cluster analysis were also applied to the dataset to detect any trends in the composition of the fossil fauna of the localities. Because the data used here is simply numerical values, a co-variance matrix was used for PCA. For the cluster analysis, both the paired group method using the Euclidean coefficient and Ward’s method (which also uses the Euclidean coefficient) were used in this study.

#### 7.4.3.2 Results

The PCA scattergram shows three main clusters (Figure 7.5). Cluster A consists entirely of the Mara ditch locality. It is separated from the other localities by large numbers of highly convex *Rafinesquina*, *Parastrophina hemiplicata*, and *Anazyga recurvirostra*. Cluster B contains collections from Centennial Park Road, Highway 6 Bluff, and Goat Island Road. Samples in
Figure 7.5: Principal component analysis scattergram showing similarity between Ontario localities. The localities fall into three main clusters, but most (96.6%) of the variation is accounted for in component 1, and thus clusters A and B are actually relatively closely related compared to Cluster C.
Cluster C are from Highway 48 and the Carden Quarry, separated from the other localities by the dominance of *Paucicrura rogata* and *Sowerbyella sericea*. Note that the difference between clusters A and B is an order of magnitude lower than that between either cluster A or B and cluster C because component 2 (Y axis in Figure 7.5) only accounts for 1.59% of the total variance, whereas component 1 (X axis in Figure 7.5) accounts for 96.6% of the variance. Clusters A and B can be considered as a single cluster given their close similarity.

The cluster analysis dendrograms show groupings similar to the PCA scattergram (Figure 7.6). The paired group method yields two main clusters, comparable to the A-B and C clusters in the PCA scattergram. Ward’s method produced a similar dendrogram, except the Highway 6 bluff locality clustered with the Carden Quarry localities rather than the Mara ditch, Goat Island Road, and Centennial Park Road localities. This difference may be indicative of greater dominance of *Paucicrura rogata* at the Highway 6 Bluff, as in the Carden Quarry and Highway 48 collections, in comparison to the Goat Island Road, Mara ditch, and Centennial Park Road localities. The Highway 6 bluff also has a more even diversity similar to the Mara ditch locality and a similar spectrum of species to the Goat Island Road and Centennial Park Road localities. Despite this, the dendrogram indicates a large degree of difference between the Highway 6 bluff and the Carden Quarry-Highway 48 cluster, perhaps reflecting the higher overall diversity at the Highway 6 bluff (see Figure 7.3).

### 7.4.4 Faunal characteristics of the Ontario localities

Through the quantitative analyses discussed above, some detailed differences in diversity and faunal similarities among the Ontario localities can be detected. Collections from the Carden Quarry and Highway 48 represent a numerically rich and relatively diverse fossil fauna, but dominated by only a few species (*Paucicrura rogata*, *Sowerbyella sericea*, and *Anazyga recurvirostra*). The geology at these localities is different — the Bobcaygeon Formation is dominated by grainstone and packstone while the Highway 48 locality has a higher proportion of carbonate mud and calcareous shale. The majority of both collections, however,
Figure 7.6: Dendrograms of fossil localities in Ontario using the paired group method with Euclidean coefficient (left) and Ward’s method (right). Using both methods, the localities form two broad clusters, similar to the cluster in the PCA scattergram (Figure 7.5). The Highway 6 bluff locality plots in opposite clusters in each method, perhaps reflective of the large number of *Paucicrura rogata* found there, similar to the Carden Quarry and Highway 48 localities, but has a more even diversity like the Mara ditch locality and has a similar spectrum of species to the Goat Island Road and Centennial Park Road localities.
were from the relatively easily weathered carbonate mudstone, as the grainstone is well-cemented and does not easily yield complete brachiopod specimens for study.

Brookfield and Brett (1988) hypothesized that the coarser grainstone and packstone beds represent distal storm deposits. Many of the grainstone and packstone beds show cross-stratification and have scoured bases indicative of erosion of the underlying strata during storm events (Figure 7.7). Large ripples are also visible on bedding surfaces at the Goat Island locality on Manitoulin Island, indicating episodes of high energy deposition. If these are storm deposits, the benthic fauna would have been episodically buried by sediments.

High dominance faunas usually represent the success of opportunistic species in a stressed environment. In the Ontario localities, high dominance faunas may have represented a pioneering community of generalist or opportunistic species, which was able to quickly colonize a storm dominated substrate, whereas the communities with more evenly distributed species represented a more mature benthic assemblage. This would imply that the large strophomenoids and orthides were less adaptable to rapid changes in the environment compared to Paucicrura, Sowerbyella, and Anazyga. Rhynchotrema was found in both assemblages, but was more dominant in the more diverse assemblage.

The sample from the Highway 6 bluff is unusually diverse considering the relatively small size of the collection. Additionally, the Highway 6 bluff locality has been reported to be Lindsay Formation (see chapters 2 and 3), which was deposited during a sea level rise under sluggish ocean circulation based on the decreasing proportion of grainstones and packstones to carbonate mudstone. The strata at this locality is near the base of the formation, indicating that the environment had not yet deteriorated to the point that increasing water depth and hypoxic
Figure 7.7: Evidence of high energy events in the Simcoe Group. Above: large ripples at the Goat Island locality on Manitoulin Island (Verulam Formation). Below: uneven, scoured base of grainstone bed overlying carbonate mudstone at the Highway 48 locality near Lake Simcoe (Verulam Formation).
—anoxic conditions severely affected the biodiversity of the marine shelly benthos, as in the black Collingwood shales at the top of the Lindsay Formation.

7.5 Analysis of the Trentonian fauna across Laurentia

7.5.1 Method

To analyze the Trentonian fauna at a continental scale, all of the abundance data from Ontario and the species lists from literature were converted to binary presence/absence data at the genus level (see Supplementary Data D). This will avoid any potential biases due to differing interpretation of species by different workers, especially those that have not been critically re-examined using contemporary statistical methods.

Cluster analysis was applied to this larger dataset, but Jaccard’s coefficient was used with the paired group method as it is well-suited for the binary dataset. The Dice coefficient, another coefficient designed to make use of binary data, was also tested, but produced a nearly identical dendrogram, differing only in absolute similarity values of clusters, and thus was not included as Jaccard’s coefficient is conceptually simpler (see Chapter 3).

7.5.2 Results

The faunas form two main clusters in the dendrogram (Figure 7.8): cluster A consists of the Appalachian Valley, north eastern Ireland, Nevada, and Scotland. Cluster B comprises the Hudson Valley, Tennessee, Manitoulin Island, Mississippi Valley, Baffin Island, Ottawa Valley, western New York, Lake Simcoe, Indiana, Oklahoma, South Dakota, northern Rocky Mountains, Champlain Valley, and Newfoundland faunas. The faunas in cluster A are notably more diverse than the those of cluster B — northeastern Ireland is most diverse (65 genera), with those of Scotland (33 genera) and the Appalachian Valley (48 genera) also unusually diverse compared to the mean diversity of the regions in Cluster B (15 genera).
Figure 7.8: Dendrogram comparing Trentonian localities of Laurentia. The two main clusters (A and B) correspond to the Appalachian fauna and epicontinental fauna of Sohrabi and Jin (2013b). With cluster B, four subclusters can be recognized that approximately correspond to different geographic regions of Laurentia.
Cluster B contains the faunas from localities west of the Appalachians, and can be divided into four subclusters:

- Cluster 1 consists mostly of intracratonic faunas from the Hudson Valley, Tennessee, Manitoulin Island, the Mississippi Valley, Baffin Island, Ottawa Valley, western New York, and Lake Simcoe.
- Cluster 2 consists of faunas from Indiana, Oklahoma and South Dakota.
- Cluster 3 consists only of the northern Rocky Mountains.
- Cluster 4 is comprised of the Champlain Valley and Newfoundland, between the Appalachian belt and the more intracratonic faunas.

These results are similar to those in the global review of the Trentonian fauna by Sohrabi and Jin (2013b), showing two main clusters that show far more variation between them than the subordinate clusters. The subclusters that make up Cluster B, however, are different. Additionally, the Advance Formation in the northern Rocky Mountains is a subcluster in Cluster B here, rather than clustering with the localities in Cluster A as in Sohrabi and Jin (2013b). These differences can probably be attributed to using different methods—Sohrabi and Jin (2013b) used the Raup-Crick coefficient for their analysis. This coefficient was not desirable here as it created unstable dendrograms, perhaps because of significantly less variation between the localities included in this study. Additionally, the updated faunal lists for the Ontario localities, as used in the present analysis, may have altered the groupings to some extent.

7.5.3 Interpretation

7.5.3.1 Appalachian fauna

Cluster A is comprised of northeastern Ireland and Scotland, which were peri-Laurentian terranes during the Middle and Late Ordovician. This explains the evolution of a fauna different from the epicontinental fauna there, but the Appalachian terranes were connected to the continent by this point. However, the Appalachian fauna consists of a number of localities from the southeastern United States that may have originated from peri-Laurentian terranes that later docked with Laurentia during the Taconic orogeny.
This pattern was noted in earlier Sandbian fossil faunas by Jaanusson and Bergström (1980), who recognized a distinctly different fauna in the Blount confacies belt of the Appalachians that exhibited a higher diversity than the faunas of Laurentia, and consisted of 26 endemic forms that were not found in Laurentia. The Blount belt biofacies also showed a higher degree of paleobiogeographic similarity to contemporary faunas in Scotland, northeastern Ireland, and the Estonian confacies belt of Baltica. Sohrabi and Jin (2013b) recognized the continuation of this differentiated fauna in the Appalachians in the early Katian.

This Appalachian fauna is notably more diverse than the epicontinental fauna (above), and contains several genera that are absent in the epicontinental fauna but present in the Scotland and northeastern Ireland faunas. These include the genera *Bilobia, Bimuria, Campylorthis, Christiana, Colaptomena, Eoplectodonta, Cristiferina, Cyphomena, Dactylogonia, Glyptambonites, Laticrura, Leptellina, Nicolella, Oxoplecia, Palaeostrophomena, Ptychopleurella, and Reushella*. The higher diversity may have been the result of niche partitioning—the peri-Laurentian terranes would have evolved in a much more variable environment due to their geographical location and a wider range of habitable depths. Jin et al. (2013) showed that the paleoequatorial region was subjected to less storm activity, meaning that the subtropical Appalachian fauna would have had to deal with storm sedimentation while the equatorial epicontinental fauna inhabited relatively low energy inland seas. Additionally, the Appalachian fauna would have been able to adapt to a full range of water depths from intertidal down to abyssal depths off the continental shelf. Despite the presence of intracratonic basins, the epicontinental fauna inhabited a relatively flat seafloor with a much smaller gradient of water depth. Both of these factors would have driven speciation at a higher rate in the Appalachian fauna compared to the relatively stable environment of the epicontinental fauna.

There must have been some faunal dispersal barrier between the Appalachian faunas and the rest of Laurentia, as even the nearby faunas in Newfoundland and the Champlain Valley show a closer affinity to the epicontinental fauna than to the Appalachian fauna. Jaanuson and Bergström (1980) suggested that water depth, temperature, and/or substrate type may have
driven the provincialism, and these factors may have continued to divide these two faunas into the early Katian.

The clustering of Nevada with the Appalachian fauna is difficult to interpret. Ross (1970) explained that much of the Antelope Valley fauna is probably pre-Trentonian, and is more indicative of a Chazyan (Sandbian) fauna. It is difficult to determine exactly how the section that Cooper (1956) described fits into the stratigraphy, as the unit is described as being below the Eureka Quartzite which forms an unconformity, but this may explain the discrepancy. Nevada does share a number of genera with the Appalachian fauna, including *Reushella*, *Pauorthis*, *Bilobia*, *Bimuria*, *Eoplectodonta*, *Leptellina*, and *Oxoplecia*, which were holdover taxa in the Trentonian and were more common in Sandbian time (see also Jin and Norford 1996).

7.5.3.2 Epicontinental fauna

Cluster B consists of localities from across cratonic Laurentia and corresponds to the epicontinental fauna described by Sohrabi and Jin (2013b), but it shows some difference in internal relationships among the faunas within this cluster.

The subclusters of cluster B exhibit a grouping pattern according to geographic regions. The bulk of the localities fall into cluster B1. Two main groups in B1 correspond to eastern and western geographic regions. The fauna from the Lake Simcoe area has a closer affinity to those of the Ottawa Valley and western New York, while the Manitoulin Island fauna shows closer affinities to the Mississippi Valley and Tennessee. Despite their close geographic proximity, the Lake Simcoe and Manitoulin Island faunas fall into two different paleogeographic realms. The Lake Simcoe locality was part of the St. Lawrence Platform while Manitoulin Island is located on the northeastern edge of the Michigan Basin. This may reflect patterns of faunal dispersal along intracratonic basins and depressions as sea levels were rising. Alternatively, this could reflect periodic geographic isolation between the fauna, perhaps corresponding to periods of relatively low sea level, contributing to faunal differentiation. Both of these groups are very similar to each other, however, so faunal isolation would have only been periodic.
The Baffin Island collection falls into cluster B1, showing closest similarity to the Ontario and western New York collections. Although the Ordovician rocks of Baffin Island and the St. Lawrence Platform seem isolated from each other by the Precambrian Shield, this probably was not the case in the Ordovician. Inliers of Late Ordovician carbonates in the middle of the Precambrian Shield are known (e.g. the Timiskiming Inlier in Dix et al. 2007), indicating that a shallow epicontinental seaway probably once covered at least part of the Precambrian Shield. The faunal similarity shown here reaffirms that assertion. This similarity also indicates that the Edenian-Maysvillian fauna on Baffin Island shows a close similarity to the earlier Trentonian fauna, and may in fact be closer to the lower range of this age, rather than the Maysvillian during which the *Hiscobeccus* fauna began to dominate Laurentia (Jin 2001). The paleoequatorial location of the Baffin Island fauna may have contributed to the survival of Trentonian (early Katian) fauna into the Edenian and Maysvillian (mid-Katian) because of its more stable environment.

The Hudson Valley collection has the lowest degree of similarity to any others in cluster B1. The reason for this is unclear, as the only genera present at this locality that aren’t present at localities elsewhere in eastern North America are *Bilobia* and *Christiana*, which the Hudson Valley shares with the Appalachian fauna.

The faunas from Indiana, Oklahoma, and South Dakota form Cluster B2. These faunas seem to represent a distinct southern fauna from Oklahoma and Indiana that may have migrated into the interior of the continent to reach South Dakota. It should be noted, however, that the faunas from Indiana and South Dakota only contain a few genera, so this grouping may have some fossil preservation or a collection bias.

The northern Rocky Mountain fauna from the Advance Formation forms its own cluster, B3. This fauna shows some similarity to the Trentonian fauna in eastern North America, and may have been derived from it rather than the peri-Laurentian fauna in Cluster A. This is in contrast to the results of Sohrabi and Jin (2013b) where the northern Rocky Mountain fauna clustered with the Appalachian fauna. *Eoplectodonta*, *Leangella*, and *Scaphorphthis* are present in
both the northern Rocky Mountains fauna and the Appalachian fauna and lacking in the epicontinental fauna. However, the northern Rocky Mountain fauna is considerably less diverse than the Appalachian fauna. The northern Rocky Mountain fauna does contain some Sandbian or older taxa, such as *Bimuria* and *Christiania*, that are characteristic taxa of the classic Scoto-Appalachian fauna of Caradoc age (Jin and Norford 1996).

The Champlain Valley and Newfoundland faunas are apparently dissimilar to the other Trentonian localities in eastern North America. This may reflect some influence from the peri-Laurentian faunas, or their lack of in-depth taxonomic study. With only eight genera from Newfoundland, and five from the Champlain Valley, it is likely that a more thorough collection may lead to a more diverse fauna and more meaningful results in an analysis such as this. It seems unusual for the Champlain Valley fauna to cluster with the distant Newfoundland fauna rather than with the more proximal Ottawa Valley fauna.

### 7.6 Conclusions

The Trentonian faunas from the Lake Simcoe area and Manitoulin Island are taxonomically similar to other Trentonian faunas in eastern North America. A fauna dominated by *Paucicrura rogata* and *Sowerbyella sericea* can be distinguished from a more evenly diverse fauna that also contains numerous *Rhynchotrema increbescens*, *Anazyga recurvirostra*, *Parastrophina hemiplicata*, and large orthoids and strophomenoids. The *Paucicrura*- and *Sowerbyella*-dominated fauna is interpreted to be the result of successful colonization by generalist or opportunistic taxa in stressed substrate conditions, such as frequent storm disturbances and episodic hypoxia during sea level rise, whereas the fauna with more evenly distributed species represented a more mature community that developed during periods of stability.

Two major faunal groups can be recognized among the Trentonian faunas of Laurentia. One group corresponds to a more diverse Scoto-Appalachian fauna from northeastern Ireland, Scotland, and the Appalachians. The other is the epicontinental fauna that is less diverse but
widespread across the epeiric seas of Laurentia. The epicontinental fauna has a relatively high degree of homogeneity in species composition, although there are subtle differences among the individual faunas from eastern Laurentia, southern Laurentia, northern Rocky Mountains, and Champlain Valley and Newfoundland.

Despite the close geographic proximity of the Lake Simcoe and Manitoulin Island localities, their faunas show affinities to two slightly differentiated fossil faunas. The Lake Simcoe localities show greater similarity to the Ottawa Valley, New York, and Baffin Island while the Manitoulin Island fauna is more similar to fossil faunas from the Mississippi Valley. This implies a significant paleobiogeographic separation between pericratonic and intracratonic faunal provinces in Laurentia during the early stage of a major sea level rise and marine transgression in the early Katian.
7.7 References


Chapter 8 — Conclusions

8.1 Summary

This thesis addressed two main aspects of the Late Ordovician brachiopod fauna of Laurentia: a detailed investigation of the evolution of three brachiopod lineages, and a quantitative paleoecological and paleobiogeographical analysis of the Laurentian brachiopod faunas.

Rhynchonellide brachiopods originated in the Middle Ordovician as a new order and became a major component of Late Ordovician epicontinental faunas. The *Rostricella*- *Rhynochotrema-Hiscobecus* lineage examined in this thesis traced the origin of the cardinal process for improved diductor muscle attachment between *Rostricella* and *Rhynochotrema* during the Sandbian, and increased shell size, globosity, and imbricated growth lamellae from *Rhynochotrema* to *Hiscobecus* from early to late Katian.

These trends of morphological change are not unique to this lineage. The increasing size and prominence of the cardinal process in late Katian forms has been noted in other lineages as well (e.g. *Plaesiomys*; see Sproat and Jin 2013). This evolution towards “extravagant” shell structures may be related to paleoecological shifts that occurred in the Late Ordovician driving the evolution of the epicontinental fauna in the tropical epeiric seas of Laurentia.

*Parastrophina* is a widely reported early Katian pentameride brachiopod from North America and other tectonic plates. Detailed examination of the type species, *P. hemiplicata* in this study clarified the complex internal structures and the intraspecific variation of external morphology (such as the development of ribbing, fold, and sulcus). This led to an improved definition of species in North America and the recognition of a new species (*Parastrophina tarimensis*) from the Tarim microplate, northwest China. Such detailed taxonomic work helped the establishment of more reliable biodiversity inventories for various regions, a foundation for further paleobiogeographic analysis.
The global distribution of *Parastrophina*, for example, shows the paleobiogeographic connection between the widely separated Laurentia and Tarim plates, but at the same time revealed different morphological adaptations to the storm-dominated, level-bottom substrate in eastern Laurentia, compared to the subequatorial, protected carbonate mud mound environment in Tarim during the Late Ordovician (Sproat et al. 2015).

Revision of the Trentonian brachiopod fauna also required the study of the common genus *Plectorthis* from Laurentia, based on the type material of *Orthis plicatella* Hall, 1847 from the Cincinnati Arch region. The discovery of double-rowed aditicules, a type of shell microstructure, in the type species and new materials from Ontario and Baffin Island, as well as the range of intra-species variations in shell ribbing and musculature, provided a more reliable set of criteria for identification of species in Laurentia and other tecotnic plates (Sproat and Jin 2016).

Several species reported previously from other continents will need taxonomic reassessment in light of the new diagnosis, which will further improve our understanding of brachiopod evolution and paleobiogeography during the Late Ordovician, a critical interval of biotic radiation and mass extinction.

At a large scale of faunal evolution in Laurentia, this thesis focused on the biodiversity and paleobiogeography of the early Katian (Trentonian) brachiopod faunas, incorporating new quantitative faunal data from the Lake Simcoe area and Manitoulin Island, in comparison with many other related faunas across North America. Multivariate and other numerical analyses of the faunal data revealed that, despite the general similarities in the Trentonian fauna across Ontario, there are subtle variations between collection localities, which is interpreted as the result of fluctuating paleoenvironmental conditions that favoured an opportunistic fauna dominated by a few species when conditions were less stable, perhaps due to the effects of storm deposition (Brookfield and Brett 1988), or a more mature, evenly diverse assemblage during episodes of environmental stability.
Subtle differences can also be discerned in the fauna at a continental scale. A more diverse Appalachian Trentonian fauna along the southeastern Laurentian margin can be distinguished from a less diverse epicontinental Laurentian fauna. This epicontinental fauna can be subdivided into several slightly differing faunas that reflect four different geographic regions: eastern North America, south-central North America, the northern Rocky Mountains, and the Champlain Valley and Newfoundland. Within the eastern North America subcluster, faunal differentiations can be recognized between the Mississippi Valley and Michigan Basin, and the faunas of Ontario and New York. Such faunal differences may have been controlled by differences in water masses, proximity to the incipient Taconic orogenic belt, and paleolatitudes. These faunas are all fairly similar, however, with common taxa like *Plectorthis*, *Paucicrura*, *Parastrophina*, *Rhynchotrema*, *Rafinesquina*, *Strophomena*, and *Anazyga* in most faunas.

The slightly younger (Edenian–Maysvillian) Baffin Island brachiopod fauna showed closest affinity to the Trentonian brachiopods faunas of Ontario and New York. The Baffin Island fauna is significant in its relatively high diversity with early Katian faunal characteristics. Its paleoequatorial location suggests that the Trentonian brachiopod fauna persisted more successfully in low-latitude tropics after its decline in mid- and high-latitude tropics, such as Ontario, New York, and the Cincinnati Arch region.

### 8.2 Future Work

More systematic paleontology is needed to better clarify the evolution of the Late Ordovician brachiopod fauna of Laurentia. In particular, the strophomenoids are in urgent need of revision because of their abundance and diversity in the Late Ordovician. Unfortunately, many of the strophomenoid genera have become “dump bag” taxa, and reviewing each lineage will be no easy task. Wilson (1946) tried to devise a scheme to classify the large Ordovician strophomenoids that are a common component of the fauna, based largely on arbitrary divisions in the degree of convexity of the shell and variations in shell outline and profile. However, these characteristics may simply reflect ontogenetic development rather than
different species, as there seems to be a continual gradation between many of the species she named. In Chapter 7, a simplified version of her taxonomic scheme was used for the strophomenoids of Lake Simcoe and Manitoulin Island, but this was not ideal. A detailed study of external characters in conjunction with internal characters is crucial to properly devise a taxonomic framework that accurately accounts for the evolution of these lineages.

Little work has been done on the connection of the Trentonian fauna with the late Katian (Cincinnatian) forms. The Cincinnati Arch area, in which the Trentonian Lexington Limestone is overlain by the complex “layer-cake” stratigraphy of the Cincinnatian Series with abundant and diverse brachiopods, will be an ideal place to start. Unfortunately, little has been published on the fossil fauna of the Lexington Limestone, making incorporating the Trentonian fauna from the Cincinnati region in studies like those in Chapter 7 impossible. A comprehensive inventory of this fauna will enable better understanding of the paleoecology and paleobiogeography of the Trentonian fauna of Laurentia and their relationship to the drastic sea level rise and expansion of epicontinental seas at that time.
8.3 References


Appendices and Supplementary Data

Appendix A — *Parastrophina* occurrences worldwide.

Appendix B — List of *Plectorthis* specimens

Appendix C — *Plectorthis* species assigned, species questionably assigned, species rejected

Appendix D — List of brachiopod species from Trentonian localities

Supplementary data in Western’s electronic thesis and dissertation repository located at: [http://ir.lib.uwo.ca/etd/](http://ir.lib.uwo.ca/etd/)

Supplementary Data A — *Parastrophina* species measurements used for analysis

Supplementary Data B — *Plectorthis* species measurements used for analysis

Supplementary Data C — Abundance data from Ontario localities

Supplementary Data D — Presence/absence matrix of Laurentian Trentonian faunas
Appendix A — *Parastrophina* occurrences worldwide.
Table compiled from references in text of Chapter 5.

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<th>Formation/Age</th>
<th>Locality</th>
<th>Species</th>
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<td>Minnesota, Alabama, Virginia, Peterborough, Lake Simcoe, Ottawa, New York state, Percé, Québec</td>
<td><em>P. bernensis</em> Sardeson, 1892; <em>P. rotundiformis</em> Willard 1928 <em>P. bilobata</em> Cooper, 1956 <em>P. hemiplicata</em> (Hall, 1847); Cooper 1956 <em>P. hemiplicata</em> (Hall, 1847); Sinclair et al. 1969, Titus 1986, Wilson 1914, 1946 <em>P. hemiplicata</em> Hall (1847); Weiss 1955 <em>Parastrophina</em> sp. Sheehan and Lespérance, 1979</td>
</tr>
<tr>
<td>Peri-Laurentia</td>
<td>-Craighead Limestone, upper Caradoc; -Stinchar Limestone, Llandeilo</td>
<td>Girvan, Scotland</td>
<td><em>P. balcletchiensis</em> Davidson, 1883; Williams 1962, Cocks 2008 <em>P. anceps</em> Reed, 1944; Williams 1962, Cocks 2008</td>
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<tr>
<td>Baltica</td>
<td>Boda Limestone</td>
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<td></td>
<td><em>Booksina conjugula – Brooksinastiata</em> zones, Wenlock to lower Ludlow</td>
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<tr>
<td></td>
<td>Silurian</td>
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<td><em>Parastrophina</em> sp. Sapelnikov, Mizens, and Rybkina 1987</td>
</tr>
<tr>
<td>Location</td>
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<td>River Basin, Central Taimyr</td>
<td>Parastrophina lindstroemi pentagonalis Nikiforova 1989; see also Cocks and Modzalevskaya 1997; Modzalevskaya 2003</td>
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<td>Taimyr, Arctic Siberia</td>
<td>Korotkinskaya Formation, Bed 4, uppermost Katian</td>
<td>Lower Taimyr River Basin, Central Taimyr</td>
<td>Parastrophina lindstroemi pentagonalis Nikiforova 1989; see also Cocks and Modzalevskaya 1997; Modzalevskaya 2003</td>
</tr>
<tr>
<td></td>
<td>Tolmachevskaya Formation, Caradoc</td>
<td>Central and East Taymyr</td>
<td>Parastrophina pentagonalis Nikiforova, 1989; see Modzalevskaya 2003. The only serial sections in Nikiforova 1989 did not show alate plates</td>
</tr>
<tr>
<td>North China</td>
<td>Jinghe Formation, Caradoc</td>
<td>Shaanxi, China</td>
<td>Parastrophina uniplicata Fu, 1982 (= P. plena; see Popov et al., 2002); Parastrophina hemiplicata (Hall, 1847); Fu 1982 (=P. iliana; see Popov et al. 2002); Parastrophina hemisphaerica Fu, 1982</td>
</tr>
<tr>
<td></td>
<td>Gulang Formation, Llanvirn?</td>
<td>Gansu, China</td>
<td>Parastrophina pugnoidalis Fu, 1982</td>
</tr>
<tr>
<td>Kazakhstan</td>
<td>Dulankara Stage, upper Caradoc to lower Ashgill</td>
<td>central Kazakhstan</td>
<td>Parastrophina angulosa nucula, Parastrophina tersa., Nikitin and Popov 1996 (in Nikitin et al. 1996)</td>
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<td></td>
<td>Anderken Formation (lower to middle Caradoc)</td>
<td>Kazakhstan</td>
<td>P. iliana Popov et al., 2002 (=P. haemiplicata of Sapelnikov and Rukavishnikova, 1975a,b; Kolobova and Popov 1986 ; P. plena Sapelnikov and Rukavishnikova, 1975 Popov et al., 2002</td>
</tr>
<tr>
<td></td>
<td>Angrenstor Formation, late Caradoc to early Ashgill</td>
<td>central Kazakhstan</td>
<td>P. asymmetrica Nikitin, Popov, and Bassett, 2006 (top Caradoc–basal Ashgill); P. tersa Nikitin and Popov 1996 (in Nikitin et al. 1996) (top Caradoc–basal Ashgill); P. tersa uniplicata Nikitin Popov, and Bassett, 2006 (basal Ashgill); Parastrophina? quinquecostata Nikitin, Popov,</td>
</tr>
<tr>
<td>Location</td>
<td>Site Description</td>
<td>Region</td>
<td>Species</td>
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<tr>
<td>Australia</td>
<td>Vanden Limestone, Regans Creek Limestone, Quondong Limestone (early Katian)</td>
<td>eastern Australia</td>
<td><em>Parastrophina</em> sp. Percival, 2009</td>
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<td></td>
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<td><em>Parastrophina</em> sp. Nikitin, Popov, and Bassett, 2006</td>
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</tbody>
</table>
Appendix B — List of Plectorthis specimens

This appendix lists all specimens used in this study. Note that the syntypes for Plectorthis plicatella plicatella and Plectorthis plicatella fissicosta are from the American Museum of Natural History collection. Also, CMC numbers are locality numbers, rather than individual specimen numbers. See Chapter 3 for W locality information.

Hall (1847) syntypes from the American Museum of Natural History (AMNH):

- 30255 Orthis fissicosta (P. plicatella fissicosta holotype), Hudson River Group (Upper Ordovician), Cincinnati, Ohio
- 30256 Orthis plicatella (P. plicatella plicatella paralectotype), Hudson River Group (Upper Ordovician), Cincinnati, Ohio
- 30257 Orthis plicatella (P. plicatella plicatella paralectotype), Hudson River Group (Upper Ordovician), Cincinnati, Ohio
- 30258 Orthis plicatella (P. plicatella plicatella lectotype), Hudson River Group (Upper Ordovician), Cincinnati, Ohio
- 30259 Orthis plicatella (P. plicatella fissicosta syntype), Hudson River Group (Upper Ordovician), Cincinnati, Ohio

From the Cincinnati Museum Center (CMC):

- IP16861 Plectorthis fissicosta, Late Ordovician; Hamilton county, Cincinnati, Ohio
- IP16862 Plectorthis fissicosta, Late Ordovician; Hamilton county, Cincinnati, Ohio
- IP16863 Plectorthis fissicosta, Late Ordovician; Fairview Formation (Fairmount Member), Schlosser’s Quarry (Location 3.2A), Covington, Kenton county, Kentucky
- IP16875a Plectorthis plicatella
- IP16876a Plectorthis plicatella, Late Ordovician; Hamilton county, Cincinnati area, Ohio
- IP16878a Plectorthis plicatella, Late Ordovician; Fairview Formation (Fairmount Member), Schlosser’s Quarry (Location 3.2A), Covington, Kenton county, Kentucky
- IP16880a Plectorthis plicatella, Late Ordovician; Fairview Formation (Fairmount Member), quarry near West Fork Creek, Hamilton county, Cincinnati, Ohio
- IP18018 Plectorthis fissicosta, Late Ordovician; Hamilton county, Cincinnati, Ohio
- IP19470 Plectorthis fissicosta, Foster, Warren county, Ohio
- IP19864 Plectorthis plicatella, McMillan Formation (Corryville Member), McMillan Street just east of Ravine Street, Cincinnati, Ohio
- IP2133 Plectorthis fissicosta
- IP22522 Plectorthis fissicosta, Late Ordovician; Cincinnati, Hamilton county, Ohio
- IP23796 Plectorthis plicatella, Late Ordovician; Fairview Formation (Fairmount Member)
• IP23873 *Plectorthis plicatella*, Late Ordovician; Fairview Formation (Fairmount Member), Schlosser’s Quarry (Location 3.2A), Covington, Kenton county, Kentucky
• IP24121a *Plectorthis fissicosta*, Late Ordovician; Fairview Formation (Fairmount Member), near Incline, Cincinnati, Hamilton county, Ohio
• IP27996 *Plectorthis plicatella*, Late Ordovician; Fairview Formation (Mt. Hope Member), Bald Knob, Cincinnati, Hamilton county, Ohio
• IP28777 *Plectorthis plicatella*, Late Ordovician; McMillan Formation (Corryville Member), McMillan Street, Cincinnati, Hamilton county, Ohio
• IP33370 *Plectorthis fissicosta*, Late Ordovician; Cincinnati, Hamilton county, Ohio
• IP33400 *Plectorthis plicatella*, Late Ordovician; Cincinnati, Hamilton county, Ohio
• IP33406 *Plectorthis plicatella*, Late Ordovician; Cincinnati, Hamilton county, Ohio
• IP33450 *Plectorthis plicatella*, Late Ordovician; Lorraine Group, Cincinnati, Ohio and Covington, Kentucky
• IP33475 *Plectorthis plicatella*, Late Ordovician; Lorraine Group, Cincinnati, Hamilton county, Ohio
• IP33566 *Plectorthis plicatella*, Late Ordovician; Lorraine Group, Cincinnati, Hamilton county, Ohio
• IP36034 *Plectorthis plicatella*, Late Ordovician; Cincinnati, Hamilton county, Ohio
• IP38567 *Plectorthis plicatella*, Late Ordovician; Cincinnati, Hamilton county, Ohio
• IP38700 *Plectorthis fissicosta*, Late Ordovician; Cincinnati, Hamilton county, Ohio
• IP63576 *Plectorthis fissicosta*, Late Ordovician; Fairview Formation, Covington, Kenton county, Kentucky
• IP63577 *Plectorthis plicatella*, Late Ordovician; Fairview Formation (Fairmount Member), Cincinnati, Hamilton county, Ohio
• IP6395 *Plectorthis plicatella*
• IP65957 *Plectorthis fissicosta*, Maysville, Mason county, Kentucky
• IP65959 *Plectorthis plicatella*, Ordovician; Fairview Formation (Fairmount Member), Mt. Healthy, Hamilton county, Ohio
• IP65967 *Plectorthis fissicosta*
• IP65971 *Plectorthis plicatella*; Greenhills, Hamilton county, Ohio
• IP65975 *Plectorthis plicatella*, Late Ordovician; Fairview Formation (Fairmount Member), Schlosser’s Quarry, Covington, Kenton county, Kentucky
• IP65980 *Plectorthis fissicosta*
• IP66683 *Plectorthis fissicosta*, Late Ordovician; Cryer Avenue, Cincinnati, Hamilton county, Ohio
• IP69475 *Plectorthis fissicosta*, Late Ordovician; Fairview Formation, KY Route 1019 at AA Highway, Bracken county, Kentucky

Geological Survey of Canada (GSC), see Bolton 2000 for further information:
• GSC 113506 *Plectorthis inaequiconvexa*; Amadjuack Formation, locality O-104198, Amadjuack Formation, Baffin Island, Nunavut
• 3 specimens, *Plectorthis inaequiconvexa*, locality O-104187, Silliman’s Fossil Mount, Amadjuack Formation, Baffin Island, Nunavut
• 15 specimens, *Plectorthis inaequiconvexa*, locality O-104229, Silliman’s Fossil Mount, Amadjuack Formation, Baffin Island, Nunavut (box labelled *Austinella cooperi*)

University of Western Ontario (W):
• W2980 *Plectorthis laurentina*, lower Verulam Formation, locality W-O-2, Lake Simcoe region, Ontario
• W2981 *Plectorthis laurentina*, lower Verulam Formation, locality W-O-2, Lake Simcoe region, Ontario
Appendix C — *Plectorthis* species assigned, species questionably assigned, species rejected

Note: Most species assigned by Cooper (1956) use an old regional geochronological scheme. These names can be converted to the British series through the use of charts in Bergstrom (1988), and the British series can then be converted to the global series (Bergstrom 2009).

**Species assigned:**

*Orthis plicatella* Hall, 1847  
Fairmount bed near Cincinnati (Fairview Formation); Maysvillian (see Foerste 1910).

*Plectorthis plicatella laurentina* Wilson, 1946  
Sherman Fall and Cobourg beds, in Ottawa Valley, Ontario; Chatfieldian (early Katian).

*Plectorthis plicatella minnesotensis* Weiss, 1955  
Upper Macgregor Member of Platteville Formation, Basal Decorah Formation; Chatfieldian (early Katian).

*Plectorthis plicatella trentonensis* Foerste, 1910  
Trenton of Minnesota; Chatfieldian (early Katian): Based on specimens originally described by Winchell and Schuchert (1893).

*Orthis fissicosta* Hall, 1847  
Upper part of Fairmount bed near Cincinnati (Fairview Formation); Maysvillian (see Foerste 1910).

*Plectorthis inaequiconvexa* Roy, 1941  
Silliman’s Fossil Mount, Baffin Island (Adomjuack Formation – see Bolton 2000); Edenian to Maysvillian (early Katian).

*Plectorthis jamesi* Hall, 1859  
Corryville bed near Cincinnati; Maysvillian (see Foerste 1910).

*Plectorthis neglecta* James, 1879  
Mount Hope beds at Cincinnati; Maysvillian (see Foreste 1910).

*Orthambonites perplexus* Ross, 1967  
Swan Peak Formation, Utah; Porterfield (Sandbian).

*Plectorthis punctata* Cooper, 1956  
Tulip Creek Formation, Oklahoma; Ashby (late Sandbian).

**Species questionably assigned:**

*Plectorthis altaica* Severgina, 1967  
Khankhara Formation, Gorny Altai, Russia; early Caradoc (early Katian). Strongly folded dorsal valve seems unusual for *Plectorthis*. Distorted preservation makes it difficult to see muscle scars in its small muscle field.

*Plectorthis aperta* Severgina, 1989 (in Kulkov and Severgina, 1989)  
Khankhara Formation, Gorny Altai, Russia; early Caradoc (early Katian). Ventral muscle scar appears heart-shaped, as in *P. plicatella* but poor preservation makes it difficult to determine.

*Plectorthis australis* Cooper, 1956
Arline Formation in Tennessee, Little Oak Formation in Arkansas; Porterfield (Sandbian): Resembles *Plectorthis* in shape but interior unknown. Ribbing shows bifurcation, but not as fascicles like *P. plicatella fissicosta*.

*Plectorthis cf. australis* Cooper, 1956 by Williams, 1962  
Stinchar Limestone of Brockloch, Girvan, Strathclyde, Scotland; Llandeilian (latest Darriwilian). Difficult to determine affinities based on poorly preserved specimens, but shape and ribbing style resemble *Plectorthis*. Muscle scar is fractured, but seems to resemble *Plectorthis*.

*Plectorthis compacta* Cooper, 1956  
Arline in Tennessee; Porterfield (Sandbian): No interior known, but strongly resembles *P. ponderosa*. Shows more blade-like cardinal process of *Plectorthis* but similar shell shape and ribbing style to the *P. ponderosa*-type species.

*Orthis equivalvis* Hall, 1847  
Fairmount beds near Cincinnati, (Fairview Formation); Maysvillian (see Foerste 1910): Pattern of ribbing closely resembles *Plectorthis fissicosta*, but much longer than a typical *Plectorthis*, giving it a very subcircular outline. Hall’s description of “nearly equal valves” seems unusual for *Plectorthis* which is usually notably ventribiconvex.

*Hebertella exfoliata* Raymond, 1905  
Lower Chazy at New York (Darriwilian?): Species not well documented and poorly figured. No ventral interior known, but tentatively assigned to *Plectorthis*.

*Plectorthis Lebanonensis* Cooper, 1956  
Lebanon Formation, Tennessee; Wilderness (latest Sandbian): Unusually thin costae for *Plectorthis* and interior unknown. Resembles *Plectorthis* in shape and ribbing style.

*Plectorthis Mazourkaensis* Phleger, 1933  
Mazourka Formation, Mazourka Canyon in California; Ashby (latest Darriwilian?): Strange, anterior-posteriorly stretched form. Not well figured, difficult to determine true affinities.

*Plectorthis ottawaense* Wilson, 1946  
Cobourg beds in Ottawa, Ontario; Chatfieldian (early Katian): No interior show, but externally resembles *Plectorthis*. Unique ribbing style – multiplication through implantation in ventral valve but bifurcation in dorsal valve.

*Plectorthis patula* Phleger, 1933  
Mazourka Formation, Mazourka Canyon in California; Ashby (latest Darriwilian?): Seems laterally elongate for *Plectorthis*. Shows branching costae. Interior unknown.

*Plectorthis pennsylvanica* Cooper, 1956  
Rodman Member of the Nealmont Formation, east side of quarry at Spar, Huntingdon (15’) Quadrangle, Pennsylvania; Wilderness (latest Sandbian): Resembles *P. plicatella* with simple costae, but interior unknown.

*Plectorthis pulchella* Wilson, 1946  
Type locality unknown, but occurs in the Leray-Rockland and Cobourg beds, Ontario; Chatfieldian (early Katian): No interior structure known, closely resembles *Plectorthis fissicosta* and may just be a variety. Differs in having stronger secondary ribs.

*Orthisina scotica* McCoy, 1852 – lectotype selected by Cocks 1978
Craighead Limestone, Craighead Quarry, Girvan, Strathclyde, Scotland; Burellian-Cheneyan, Caradoc (late Sandbian-early Katian). Has similar muscle scar to *P. ponderosa*, though the cardinal process is still blade-like, which would suggest affinities to *Plectorthis* rather than *Austinella*. Questionably assigned here, but detailed study may confirm or disprove affinities to *Plectorthis*. Original figured specimens in Sedgwick and McCoy 1852 (see Cocks 1978, 2008).

*Plectorthis* cf. *scotica* McCoy, 1852 in Mitchell, 1977
Bardahessiagh Formation, Pomeroy, Co. Tyrone, Northern Ireland; Burellian, Caradoc (late Sandbian). Unusual ventral muscle scar shared only with *P. cliefdenensis* from Australia. Differs from both *P. plicatella* and *P. ponderosa*. Tentatively assigned to *Plectorthis*.

*Plectorthis symmetrica* Cooper, 1956
Poolville Member – *Oxoplecia gouldi* zone of Bromide formation, Carter county, Oklahoma; Wilderness (late Sandbian): Mostly simple costae similar to *P. plicatella*. Interior unknown, but resembles *Plectorthis* in shape and costae.

*Plectorthis tenuis* Cooper, 1956
Benbolt Formation, Virginia; Porterfield (early Sandbian): Superficially resembles *Plectorthis*, but ribbing unusual. Possesses bifurcating ribs but ribs are of different sizes and branch randomly rather that at similar distances from umbo. Ventral muscle scar looks suspiciously similar to *P. ponderosa* style – fairly wide adductor track. Tentatively assigned but uncertain.

*Plectorthis transversa* Cooper, 1956
Arline formation in Virginia; Porterfield (early Sandbian): Appears to be *Plectorthis* with ribbing style similar to *P. plicatella*, but interior structure is unknown, and thus cannot be confidently assigned.

*Plectorthis whitteryensis* Williams, 1974
Whittery Shale, bank of River Camlad, Shelve Inlier, Shropshire; Burellian, Caradoc (late Sandbian): Ventral muscle scars form an oval field, rather than the cordate field of North American species. Probably a distant relative of the North American *Plectorthis*, or perhaps belongs to a different genus.

*Plectorthis* sp. 1 Cooper, 1956
Shippenburg Formation (Pinesburg member-*Nidulites* zone), Pennsylvania; Porterfield-Wilderness (Sandbian): The three specimens are not figured but said to be similar to *P. lebanonensis*. Could be *Plectorthis*, but hard to say without figures.

*Plectorthis* sp. 2 Cooper, 1956
Murfreesboro formation in Tennessee; Porterfield (early Sandbian): Cardinalia of figured dorsal valve looks similar to *Plectorthis* with its simple ridge cardinal process. Specimens strongly silicified. Not enough detail to confidently assign species to *Plectorthis*.

*Plectorthis* sp. Candela, 2003
Member III of the Bardahessiagh Formation; Cheneyan, Caradoc (early Katian): Ventral muscle field is vaguely cordate but difficult to determine from figures. The figured material seems to resemble *Plectorthis* externally.

Medal A locality, Norderhov Formation, Ringerike, Norway; Caradoc. No ventral muscle scar shown so assignment to Plectorthis is tentative, but resembles the genus. Ribbing style somewhat unusual for the genus.


*Plectorthis* sp. Severgina, 1989 (in Kulkov and Severgina 1989)
Khankhara Formation, Gorny Altai, Russia; lower Caradoc (lower Sandbian). Poorly preserved and highly distorted. Difficult to assign to a genus but superficially resembles *Plectorthis*.

*Plectorthis* sp. Neuman, Brunton, and Projeta, 1997
Kalstad Limestone, upper Hovin Group; Tronheim region, Norway; early Ashgill (Katian), though whole unit ranges from Caradoc to Ashgill. Difficult to determine from figures, but muscle scars probably cordate. Specimens not well-preserved.

*Plectorthis* sp. Nikitin, Popov, and Bassett, 2006
Angrenser Formation, North-central Kazakhstan (Late Caradoc-Early Ashgill). The very strongly apsacline (approaching catacline) ventral interarea and poorly preserved ventral muscle field make the assignment of this species to *Plectorthis* uncertain.

*Plectorthis* sp. 1 Rasmussen, Harper, and Blodgett, 2012
Unnamed formation in the White Mountain area, West-central Alaska; Darriwilian-Sandbian. Limited and silicified material makes assignment at species level impossible, but resembles *Plectorthis* and has fulcral plates forming the base of the sockets. More well-preserved material needed.

*Plectorthis* sp. 2 Rasmussen, Harper, and Blodgett, 2012
Unnamed formation in the White Mountain area, West-central Alaska; Darriwilian-Sandbian. Like, sp. 1, species assignment impossible due to limited material that is poorly preserved. Has blade-like cardinal process characteristic of Plectorthis. More well-preserved material needed.

*Plectorthis* sp. Williams, 1962
Balclatchie Conglomerate, Penwhapple Glen, Girvan, Strathclyde; Burrellian, Caradoc (late Sandbian): Similar to *P. scotica*, though has a bulbous cardinal process rather than the blade-like cardinal process of most *Plectorthis*. Assigned to *Plectorthis* on basis of similarity with *P. scotica* but well-preserved specimens may prove otherwise.

*Plectorthis* sp. Williams, 1974
Aldress Shales, Shelve Inlier, Shropshire; Burrellian, Caradoc (late Sandbian): Muscle field not clear in moulds. More circular outline than North American *Plectorthis*. Tentatively assigned but better preserved material is needed to confirm placement.

*Plectorthis*? tanshiensis (Liang, in Liu et al., 1983) – see Zhan and Cocks 1998
Changwu Formation, Mulinlong (locality 7), in South China; mid Ashgill. Muscle field similar to *Plectorthis*, but adductor on more prominently raised on platform not typical of the genus. Ribbing style resembles fascicostellate *P. fissicosta*. Unusually convex for the genus. Tentatively accepted, but unusual form for the genus.
Species rejected:

Plectorthis akzhariica Nikitin and Popov, 1983

Northern Priishimiya and the Azkhar River in Central Kazakhstan (Darriwilian). The unusually high, triangular, and apsacline ventral interarea and correspondingly large, strongly anacrine dorsal interarea of this species notably differ from typical Plectorthis. The anterior commissure (pl. 1, fig. 11b) is weakly parasulcated, unlike the weakly unisulcated to uniplicate commissure typical of other Plectorthis. The ventral muscle scars are difficult to see in the figured material, but the overall shell shape would make this an unusual Plectorthis if the typical heart-shaped ventral muscle field was confirmed in this species.

Plectorthis cliefdenensis Percival, 1991

Dunhill Bluff Limestone Member, Fossil Hill Limestone, Cliefden Caves Limestone Group, east of Fossil Hill, near Cliefden Caves; Late Gisborian to Mid Eastonian, (=early to middle Caradoc): Ventral adductor generally scar linear, but more rounded than typical Plectorthis.

Orthis dichotoma Hall, 1847

Probably a synonym of Plectorthis equivalvis, as explained by Foerste (1910). Hall’s original type has been lost.

Plectorthis triplicatella Meek, 1872

Probably from Fairview Formation, Cincinnati Ohio; Maysvillian (early Katian). As explained by Foerste (1910) Meek’s description matches P. fissicosta in the distinctive fascicostellate ribbing style. Synonym of P. plicatella fissicosta.

Plectorthis holdeni Willard, 1928

Base of Holston Limestone, Virginia. Assigned to Dinorthis on basis of dorsibiconvexity and nearly square ventral muscle scar (see Schuchert and Cooper 1932, Cooper 1956).

Plectorthis licta Popov and Cocks, 2006

Degeres Member, Dulankara Formation, Chu-Ili Range, Kazakhstan; late Caradoc. Subtriangular ventral muscle field similar to P. ponderosa. Probably more closely related to Austinella.

Plectorthis cf. licta Popov and Cocks 2006 – Popov and Cocks 2014

Akdomback Formation, Chingiz Terrane, Kazakhstan; mid Katian. Difficult to determine from figures, but like P. licta, probably has subtriangular ventral muscle field similar to P. ponderosa. Probably more closely related to Austinella.

Plectorthis magna Cooper and Kindle, 1936

Superficially resembles Plectorthis but possesses much finer ribbing than any known species of Plectorthis and is significantly larger than other species. Ventral muscle scars suggest close relation to Plectorthis. Systematic description was based on two poorly preserved specimens, and as such, assignment to any genus is difficult.

Plectorthis numerosa Nikitin and Popov, 1983

Northern Priishimiya and the Azkhar River in Central Kazakhstan (Darriwilian). Its rather large adductor scars are unlike those of typical Plectorthis. Figured specimen (pl. 1, fig. 8) seems to possess weak capilae superimposed on simple cotae – a feature unknown in Plectorthis from the type area.
**Plectorthis obesa** Cooper, 1956
Upper Copenhagen Formation below Eureka Quartzite, Antelope Mountains, Nevada; Wilderness to early Trenton (=late Sandbian). Probably more closely related to the plaesiomyids (especially *Austinella*) than *Plectorthis* based on subtriangular ventral muscle scar field. No discrete fulcral plates unlike other *Plectorthis*.

**Plectorthis? perditosulcata** Wright, 1964
Portrane Limestone, Portrane, Co. Dublin; Cautleyan (Katian). Small convex plate in delthyrium characteristic of *Desmorthis* and unknown in any other *Plectorthis*. No clear ventral muscle scars field.

**Plectorthis cf. perplexus** Ross, 1967 in Ross 1970
Antelope Limestone beneath Eureka Quartzite, Nevada; Marmor (Darriwilian? Sandbian?). Similar form and style of ribbing as *P. ponderosa*, and thus are probably more closely related to plaesiomyids (especially *Austinella*) than *Plectorthis*. The ventral muscle scars seem to resemble *P. ponderosa*, but Ross commented that there is some variability from specimen to specimen, and some specimens may in fact be plectorthids.

**Plectorthis ponderosa** Cooper, 1956
Basal Martinsburg Formation, County Highway 617=910, 0.15 miles north of Green Mount Church, Broadway, Virginia; Chatfieldian (early Katian). Excluded on the basis of the ventral muscle scars as seen in Cooper 1956, Pl. 83, Fig. 32. Diductor scar is subtriangular, rather than linear, and adductor scars are linear to almost subquadrat, similar to that of the Plaesiomyidae.

**Orthis whitfieldi** Winchell, 1881
Authors describe it to be similar to *Orthis kankakensis* McCchesney—now assigned to *Austinella*. Was transferred to *Austinella* by Foerste in creating the genus (see discussion in Schuchert and Cooper 1932).

**Plectorthis sp.** Cocks and Modzalevskaya, 1997
Korotkinskaya Formation, Taimyr, northern Siberia; Ashgill. No ventral muscle field, but unusually convex dorsal suggests affinities to plaesiomyids alongside *P. ponderosa*.

**Plectorthis? burultasica** Popov, Cocks, and Nikitin, 2002
Anderken Formation, Chu-Ili range, Kazakhstan; Caradoc. Unusual strong sulcus for *Plectorthis*, and seems to have subtriangular ventral muscle field.

**Plectorthis? sp.** Ross 1970
Lehman Formation below the Eureka Quartzite, Nevada; Ashby? to Porterfield (early Sandbian). Ribbing style significantly coarser than other *Plectorthis*. Muscle scar only partially preserved, but seems to resemble *P. ponderosa*. Probably related more closely to *Austinella*.
Appendix D — List of brachiopod species from Trentonian localities

**Ottawa Valley (Wilson 1946): Rockland, Hull, Sherman Fall, and Cobourg formations**

Note: The fauna described by Wilson (1946) appears to be more diverse than other localities, but this is probably artificial, as shown by the number of new species named by Wilson. The taxonomy needs to be revised. Suggestions are offered below by the author when known, but many lineages (particularly the strophomenoids) are still unusually diverse, and need to be reviewed systematically.

**Rockland Formation**

*Camerella hemiplicata* (Hall) = *Parastrophina hemiplicata* (Hall)

*Crania trentonensis* Hall

*Dalmanella pacquettensis* (Sinclair) = *Onniella pacquettensis* Sinclair

*D. rogata* (Sardeson) = *Paucicrura rogata* (Sardeson)

*Didymelasma abruptum* Cooper

*Didymolasus canadensis* Billings

*D. erectus* n. sp.

*D. magnificus* Billings

*Dinobolus canadensis* Billings


*Didymelasma gibbosus* (Billings)

*Eichwaldia subtrigonalis* Billings

*Glyptorthis bellarugosa* (Conrad)

*Hesperorthis tricenaria* (Conrad)

*Microtrypa altilis* Wilson = *Strophomena altilis*

*Microtrypa? nasuta* Wilson = *Strophomena nasuta*

*Oepikina ampla* Wilson

*O. gloucesterensis* Wilson

*O. hemisperica* Wilson

*O. inquassa* (Sardeson)

*O. ovalis* Wilson

*O. platys* Wilson

*O. rugosa* Wilson

*O rugosa avita* Wilson

*O septata borealis* Wilson

*O. sinclari* Wilson
O. subtriangularis Wilson
O. transitionalis (Okulitch)
O. tumida Wilson
Platystrophia amoena McEwan
Platystrophia amoena longicardinalis McEwan
Platystrophia trentonensis McEwan
Plectorthis ottawaensis Wilson
P. pulchella Wilson
Rafinesquina alternata (Conrad)
R. alternata alata Wilson = R. alternata (Conrad)
R. alternata intermedia Wilson = R. alternata (Conrad)
R. alternata plana Wilson = R. alternata (Conrad)
R. alternata semiquadrata Wilson = R. alternata (Conrad)
R. alternata transversa = R. alternata (Conrad)
R. hullensis Wilson = R. alternata (Conrad)
R. lennoxensis (Salmon) = Megamyonia lennoxensis (Salmon)
R. opeongoensis Wilson
R. orleansensis Wilson
R. patula Wilson
R. robusta Wilson
R. subcamerata Wilson
R. ottawaensis Wilson
R. salmon Wilson
R. sinuata Wilson
Rhynchotrema increbescens (Hall)
Rhynchotrema ottawaense (Billings) = Drepanorhyncha ottawaensis (Billings)
Schizocrania filosa Hall
Skenidioides billingsi (Schuchert and Cooper)
Skenidioides? merope (Billings)
Sowerbyella punctostriata (Mather)
S. sericea (Sowerby)
Strophomena billingsi (Winchell and Schuchert)
S. filtexta (Hall)
S. filtexta obesa Wilson
S. magna Wilson
Strophomena? millionensis affinis Wilson
Strophomena rotunda Wilson
Strophomena venustula Wilson
Trematis terminalis (Emmons)
Trigrammaria trigonalis prima Wilson
Triplecia cupidata (Hall) = Triplesia cupidata
Triplesia extans (Emmons) = Triplesia extans
Vellamo trentonensis (Raymond)

Zygospira deflecta (Hall) = Anazyga deflecta (Hall)

Zygospira recurvirostris (Hall) = Anazyga recurvirostra (Hall)

Hull Formation

Camerella hemipllicata (Hall) = Parastrophia hemipllicata (Hall)

Dalmanella rogata (Sardeson) = Paucicrura rogata (Sardeson)

Dinorthis browni n. sp. = Plaesiomys browni (Wilson)

Dinorthis iphigenia (Billings) = Plaesiomys iphigenia

Dinorthis iphigenia minor n. var. = Plaesiomys iphigenia minor

Dinorthis pectinella cf. sweeneyi (Winchell)

Dinorthis regularis Wilson = Plaesiomys regularis (Wilson)

Dinorthis subquadrata (Hall) = Plaesiomys subquadrata (Hall)

Dinorthis subquadrata alternata n.var. = Plaesiomys subquadrata

Lingula curla Conrad

L. elongata Hall

L. hullensis n. sp.

L. obtusa Hall

L. philomela Billings

L. rectilateralis Emmons

L. riciniformis Hall

Oepikina sinclari Wilson

Pholidops trentonensis Hall = Cranios\n
‘Platystrophia’ amoena McEwan

‘P.’ amoena longicardinalis McEwan

Rafinesquina alternata (Conrad)

R. alternata intermedia Wilson = R. alternata (Conrad)

R. alternata plana Wilson = R. alternata (Conrad)

R. alternata transversa Wilson = R. alternata (Conrad)

R. orleansensis Wilson

R. semicircularis Wilson

R. semicircularis minor Wilson

Rhynchothrema increbescens (Hall)

Schizocrania filosa (Hall)

Sowerbyella sericea (Sowerby)

S. subovalis Wilson
Strophomena filtexta (Hall)

Trematis ottawaensis Billings

T. terminals (Emmons)

Zygospira recurvirostris (Hall) = Anazyga recurvirostra (Hall)

Sherman Fall Formation

Camarella hemiplicata (Hall) = Parastrophina hemiplicata (Hall)

Clitambonites ottawaensis Wilson = Vellamo ottawaensis (Wilson)

Dalmanella millipunctata Wilson = Paucicrura millipunctata (Wilson)

Dalmanella rogata (Sardeson) = Paucicrura rogata (Sardeson)

Dalmanella whittakeri Raymond = Paucicrura whittakeri (Raymond)

Dinorthis browni n. sp. = Plaesiomys browni (Wilson)

Dinorthis calderi n. sp. = Plaesiomys calderi (Wilson)

Dinorthis dubia n. sp. = Plaesiomys dubia (Wilson)

Dinorthis iphigenia (Billings) = Plaesiomys iphigenia

Dinorthis iphigenia media n. var.

Dinorthis iphigenia minor n. var. = Plaesiomys iphigenia minor

Dinorthis meedsi germana (Winchell and Schuchert) = Plaesiomys meedsi germana (Winchell and Schuchert)

Dinorthis meedsi plana n. var. = Plaesiomys meedsi plana (Wilson)

Dinorthis pectinella (Emmons)

Dinorthis pectinella cf. sweeneyi (Winchell)

Dinorthis regularis Wilson = Plaesiomys regularis (Wilson)

Dinorthis subquadrata (Hall) = Plaesiomys subquadrata (Hall)

Dinorthis subquadrata alternata n. var. = Plaesiomys subquadrata Platystrophia amoena McEwan

Lingula brissus Billings

L. cobourgensis Billings

L. curla Conrad

L. elongata Hall

L. obtusa Hall

L. philomela Billings

L. sinclaii n. sp.

L. trentonensis Conrad

Microtrypa? plana Wilson = Strophomena

Microtrypa? tersa Wilson = Strophomena
Oepikina tumida Wilson

Pholidops trentonensis Hall = Craniops

‘Platystrophia’ elegantula McEwan

‘P.’ extensa McEwan

Plectorthis neglecta (James)

Plectorthis ottawaensis n. sp.

Plectorthis plicatella laurentina n. var.

Rafinesquina alternata (Conrad)

R. alternata intermedia Wilson = R. alternata (Conrad)

R. alternata plana Wilson = R. alternata (Conrad)

R. alternata pota Wilson = R. alternata (Conrad)

R. alternata quadrata Wilson = R. alternata (Conrad)

R. carlottina Wilson

R. calderi Wilson

R. declivis (James) = Megamyonia declivis (James)

R. deltoidea (Conrad)

R. gibbosa (Wilson)

R. orleansensis Wilson

R. miodeltoidea Wilson

R. normalis Wilson

R. normaloides Wilson

R. patula Wilson

R. prestonensis Salmon

R. robusta Wilson

R. sardesi Salmon

R. semicircularis minor Wilson

R. sinuata Wilson

R. subtrigonalis Wilson

Rhynchothrema increbescens (Hall)

Rhynchothrema intermedium Wilson = R. increbescens (Hall)

Schizocrania filosa Hall

Sowerbyella sericea (Sowerby)

S. subovalis Wilson

Strophomena billingsi Winchell and Schuchert

S. filtexta Hall

S. filtexta obesa Wilson

Trematis ottawaensis Billings

Triplexia extans (Emmons) = Triplesia extans (Emmons)

Vellamo sinclairi Wilson

Vellamo trentonensis (Raymond)

Zygospira recurvirostris (Hall) = Anazyga recurvirostra (Hall)
Cobourg Formation

*Camarella hemiplicata* = *Parastrophina hemiplicata*

*Clitambonites ottawaensis* Wilson = *Vellamo ottawaensis* (Wilson)

*Cornwallia minuta* Wilson

*Cyclospira bisulcata* (Emmons)

*Dalmanella millipunctata* Wilson = *Paucicrura millipunctata* (Wilson)

*Dalmanella rogata* (Sardeson) = *Paucicrura rogata* (Sardeson)

*Dalmanella whittakeri* Raymond = *Paucicrura whittakeri* (Raymond)

*Dinorthis browni* n. sp. = *Plaesiomys browni* (Wilson)

*Dinorthis iphigenia* (Billings) = *Plaesiomys iphigenia*

*Dinorthis iphigenia media* n. var.

*Dinorthis iphigenia minor* n. var. = *Plaesiomys iphigenia minor*

*Dinorthis meedsi germana* (Winchell and Schuchert) = *Plaesiomys meedsi germana* (Winchell and Schuchert)

*Dinorthis meedsi plana* n. var. = *Plaesiomys meedsi plana* (Wilson)

*Dinorthis ottawaensis* n. sp. = *Plaesiomys ottawaensis* (Wilson)

*Dinorthis sub quadrata* (Hall) = *Plaesiomys sub quadrata* (Hall)

*Dinorthis sub quadrata alternata* n. var. = *Plaesiomys sub quadrata*

*Doleroides gibbosus* (Billings)

*Glyptorthis insculpta* (Hall)

*Hesperorthis tricenaria* (Conrad)

*Leptaena affinis* n. sp.

*L.? diminuta* n. sp.

*L. trentonensis* Wilson

*Lingula brissus* Billings

*L. cobourgensis* Billings

*L. cura* Conrad

*L. elongate* Hall

*L. obtusa* Hall

*L. riciniformis* Hall

*Lingulasma eva* Billings

*Microtrypa? modesta* Wilson = *Strophomena*

*M.? nitida* Wilson = *Strophomena*

*M.? plana* Wilson = *Strophomena*

*M.? tersa* Wilson = *Strophomena*

*Oepikina auriculata* Wilson
O. sinclari Wilson
O. piginella affinis Wilson
O. salmon Wilson
Orbiculioidea lamellosa d’Orbigny
Pholidops trentonensis Hall = Craniops
‘Platystrophia’ amoena McEwan
‘P.’ amoena longicardinalis McEwan
‘P.’ elegantula McEwan
‘P.’ extensa McEwan
‘P.’ hermitagensis McEwan
‘P.’ precedens McEwan
‘P.’ preponderosa McEwan
‘P.’ trentonensis McEwan
‘P.’ uniplicata McEwan
‘Platystrophia’ sp. Wilson
Plectorthis neglecta (James)
Plectorthis ottawaensis n. sp.
P. plicatella laurentina n. var.
P. plicatella trentonensis Foerste
P. pulchella n. sp.
Rafinesquina alternata (Conrad)
R. alternata plana Wilson = R. alternata (Conrad)
R. alternata platys Wilson = R. alternata (Conrad)
R. alternata pota Wilson = R. alternata (Conrad)
R. apicalis Wilson
R. calderi Wilson
R. camerata Conrad
R. carlottina Wilson
R. deltaidea Conrad
R. equipunctata Wilson
R. esmondensis borealis Wilson
R. gibbosa Wilson
R. hullensis Wilson
R. laurentina Wilson
R. miodeltoidea Wilson
R. normalilis Wilson
R. normaloides Wilson
R. okulitchi Wilson
R. orleansensis Wilson
R. patula Wilson
R. praedeltoidea Wilson
R. prestonensis Salmon
R. robusta Wilson
R. rotunda Wilson
R. sardesoni Salmon?
R. semicircularis Wilson
New York (Titus and Cameron 1976; Titus 1984; Titus 1986)

Note: taxa organized by community, rather than formations. See appendix in Titus 1986.

**Triplesia community**

**Inarticulates:**

*Dinorthis iphigenia* = *Plaesiomys iphigenia*

**Schizocrania rudis**

**Orthides:**

*D. pectinella*

**Doleroides pervetus**

*Hesperorthis tricenaria*
**Paucicrura rogata**

**Triplesia cuspidata**

**Strophomenides:**

**Oepikina inquassa**

**Rafinesquina lennoxensis = Megamyonia lennoxensis**

**R. presontensis**

**Liospira community**

**Inarticulates:**

**Pseudolingula rectilaterialis major**

**Trematis ottawaensis**

**Orthides:**

**Doleroides pervetus** (L)

**Dinorthis iphigenia = Plaesiomys iphigenia**

**Dinorthis pectinella** (L)

**Hesperorthis tricenaria** (L)

**Paucicrura rogata**

**P. whittakeri** (M)

‘*Platystrophia*’ amoena longicardinalis** (M, U)

**Plectorthis plicatella** (probably *P. plicatella laurentina*)

**Strophomenides:**

**Oepikina inquassa** (L)

**O. transitionalis** (L)

**R. trentonensis = R. alternata**

**Sowerbyella sericea**

**Rhynchonellides:**

**Rhynchorrema increbescens**

**Atrypides:**

**Protozyga exigua**

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**Rafinesquina camerata** (U)

**R. deerensis** (U)

**R. deltoidea** (U)

**R. minuta** (U)

**R. prestonensis** (L)

**R. trentonensis = R. alternata**

**Sowerbyella sericea**

**S. subovalis** (M, U)

**Strophomena conradi** (U)

**S. dignata** (L)

**S. filtexta crenulata** (L)

**S. trilobita** (U)

**Pentamerides:**

**Parastrophina hemiplicata** (L, U)
Rhynchoconellides:  
Rhynchotrema increbescens  

Atrypides:  

Encrinus community  

Inarticulates:  
Acanthocrania setigera (L)  
A. trentonensis (L, M)  
“Lingula” cobourgensis (U)  
Palaeoglossa trentonensis (L)  
Pseudolingula rectilaterialis major  
Schizocrania rudis (L)  

Orthides:  
Dinorthis iphigenia (M, U) = Plaesiomys iphigenia  
Dinorthis pectinella (L, M)  
Paucicrura rogata  
P. whittakeri (M)  
‘Platystrophia’ amoena  
‘P.’ ameona longicardinalis  
‘P.’ robusta (M, U)  
Plectorthis plicatella (probably P. plicatella laurentina)  

Strophomenides:  
Rafinesquina camerata (M, U)  
R. deerensis (U)  

Anazyga deflecta (U)  
Cyclospira bisulcata (U)  
R. deltoidea (M, U)  
R. minuta (U)  
R. praecursor  
R. prestonensis (M)  
R. robusta (U)  
R. trentonensis = R. alternata  
Sowerbyella minnesotensis? (L)  
S. minuta  
S. sericea  
S. subovalis  
Sowerbyella sp. (U)  
Strophomena conradi (L, M)  
S. filtexta crenulata (L, M)  
S. foveata (L)  
S. trilobita (U)  
Trigrammaria trigonalis  
Pentamerides:  
Parastrophiha hemiplicata (M)  
Rhynchoconellides:  
Rhynchotrema increbescens
Atrypides:  
Anazyga recurvirostris = A. recurvirostra (L, M, U?)

*Protozyga exigua* (U)

Cyclospira bisulcata (U)

*Trematis community*

Inarticulates:  
Palaeoglossa trentonensis (L)

R. deltoidea (U)

Pseudolingula rectilateralis major

R. normalis? (U)

Schizocrania rudis (L)

R. ottawaensis (U)

Trematis terminalis

R. praecursor (L, M)

Orthides:

Dinorthis iphigenia = Plaesiomys iphigenia (M)

R. trentonensis = R. alternata (L, M)

Paucicrura rogata

Sowerbyella minuta (U)

‘Platystroria’ amoena

S. sericea (L)

‘P.’ amoena longicardinalis (M, U)

S. subovalis (M, U)

Paucicrura rogata

*Sowerbyella* sp. (probably Sowerbyella)

Rafinesquina camerata (U)

Atrypides:

Anazyga recurvirostris = Anazyga recurvirostra (L)

Cyclospira bisulcata (U)

Protozyga exigua (U)

*Geisonoceras Community*

Inarticulates:

“Lingula” reciniformensis

Orthides:

Paucicrura rogata

Trematis terminalis

Strophomenides:
Rafinesquina trentonensis = R. alternata Sowerbyella subovalis

**Triarthus Community**

Inarticulates: “Lingula” reciniformis
Leptobolus insignis Orthides:
“Lingula” curta Paucicrura rogata

**Manitoulin Island (Cooper 1956; Long and Copper 1993)**

Cloche Island Beds (=Bobcaygeon)

Anazyga recurvirostra Idiospira panderi
Dalmanella rogata = Paucicrura rogata Parastrophina hemiplicata
Dinorthis sweeneyi Rafinesquina alternata
Doleroirdes pervetus Rostricellula rotundata
Glyptorthis bellarugosa Sowerbyella punctostriata
Hallina sp. Strophomena sp.
Hesperorthis tricenaria

Verulam Formation, Goat Island

Anazyga Rafinesquina
Idiospira Rhynchoroma

**Newfoundland (Cooper 1956; Weerasinghe 1970)**

Long Point Formation

Camerella aff. C. volborthi Billings (possibly Parastrophina?) Dinorthis aff. D. iphigenia (Billings)
Dalmanella rogata Sardeson = Paucicrura rogata (Sardeson) Glyptorthis bellarugosa (Conrad)
G. cf. G. crispata (McCoy)
Hesperorthis aff. H. tricenaria  
Plaesiomys sp.  
Rafinesquina alternata (Conrad)  
R. aff. R. deltoidea  
R. aff. R. minnesotensis = Oepikina minnesotensis

Sowerbyella sericea? Sowerby  
S. aff. S. undulata (Salter)  
Triplesia extans (Emmons)  
Valcourea sp.

Champlain Valley, New York and Vermont (Cooper 1956)

Isle la Motte Formation

Dalmanella testudinaria (Dalman) = Plectorthis plicatella (Hall) (probably P. plicatella laurentina)  
Paucicrura rogata  
Dinorthis pectinella (Emmons)  
Strophomena incurvata (Shepard)  
Triplesia extans (Emmons) = Triplesia extans

Hudson Valley (Cooper 1956)

Rysedorf Formation

Christiana trentonensis (Rudemann)  
Dalmanella testudinaria (Dalman) = Plectambonites pisum Rudemann = Bilobia pisum  
Paucicrura rogata  
Dinorthis pectinella (Emmons)  
Protozyga exigua Hall  
Leptaena rhomboidalis Wilckens = L. ordovicica Cooper  
Rafinesquina alternata (Emmons) = Macrocoelia ruedemanni (Salmon)  
Orthis tricenaria Hall = Hesperorthis tricenaria  
R. deltoidea (Conrad)  
Parastrophia hemiplicata Hall = Siphonotreta minnesotensis Hall and Clarke  
Parastrophina hemiplicata  
Triplecia nucleus Hall = Triplesia nucleus  
Platystrophia biforata (Schlotheim)  
Platystrophia biforata (Schlotheim)

Sowerbyella sericea? Sowerby  
S. aff. S. undulata (Salter)  
Triplesia extans (Emmons)  
Valcourea sp.
Zygospira recurvirostris Hall = Anazyga recurvirostra

Appalachian Valley—Pennsylvania to Alabama (Cooper 1956)

Ben Hur Formation, Tennessee

Pinodema miniscula (Willard)  Strophomena sp.

Cane Creek Formation, Tennessee

Chaulistomella lebanonensis Cooper  Pinodema sulcata Cooper

Doleroides tennesseensis Cooper  Strophomena sp.

Oepikina sp.  Zygospira sp. = Anazyga (?)

Nealmont Formation, Tennessee

Ancistrorhyncha australis (Foerste)  O. wagneri (Okulitch)

Ancistrorhyncha sp.  Parastrophina hemiplicata (Hall)

Doleroides perveta (Conrad)  Pinodema sulcata Cooper

Camarotoechia sp. = Rostricellula sp.  Rhynchotrema sp.

Glassia sp.  Sowerbyella punctostriata (Sowerby)

Glyptorthis cf. G. bellarugosa (Conrad)  Strophomena cf. S. filtexta (Hall)

Hesperorthis tricenaria (Conrad)  Strophomena sp.

Leptaena? cf. L. charlottae Winchell and Schuchert = Bellimurina charlottae  Valcourea cf. V. loricula (Hall)

Leptaena cf. L. charlottae Winchell and Schuchert = Limbimurina  Zygospira elongate Cooper = Anazyga elongate

Oepikina inquassa (Sardeson)  Zygospira recurvirostris (Hall) = Anazyga recurvirostra

O. minnesotensis (Winchell and Schuchert)

Collierstown Formation, Virginia

Cyclospira sp.  Doleroides sp.
Rafinesquina trentonensis (Conrad)  
Eggleston Formation, Virginia

Dalmanella rogata (Sardeson) = Paucicrura rogata  
Rafinesquina alternata (Conrad)  
R. minnesotensis (Winchell) = Opikina minnesotensis

Hardy Creek Formation, Virginia and Tennessee

Campylorthis sp.  
Oepikina sp.  
Pinodema minuscula Willard

Housum Member, Mercerburg Formation, SW Pennsylvania

Leptaena cf. L. charlottae Winchell and Schuchert  
Oepikina aff. O. ruedemanni Salmon

Kauffman Member, Mercerburg Formation, SW Pennsylvania

Dinorthis cf. D. pectinella  
Doleroides cf. D. pervetus  
Glyptorthis cf. G. bellarugosa  
Leptaena cf. L. charlottae Winchell and Schuchert = Limburina

Jacksonburg Formation (lower part), NW New Jersey and Pennsylvania

Camarella inornata Weller = Idiospira inornata  
Dalmanella subaequata (Conrad) = Pinodema subaequata

Zygospira sp. = Anazyga (?)  
Strophomena incurvata (Shepard)  
Zygospira recurvirostris (Hall) = Anazyga recurvirostra

Sowerbyella cf. S. punctostriata  
Sowerbyella cf. S. punctostriata (Mather)  
Zygospira recurvirostris (Hall) = Anazyga recurvirostra

Lingula sp. = Skenidioides sp.  
Rafinesquina alternata (Conrad)  
Scenidium antonensis Sardeson = Skenidioides sp.
Strophomena conradi Hall and Clarke  

Jacksonburg Formation (upper part), NW New Jersey and Pennsylvania

Dalmanella subaequata (Conrad) = Pinodema subaequata (Conrad)
D. testudinaria (Dalman) = Paucicrura sp. 2
Dinorthis pectinella (Emmons)

Orthis tricenaria Conrad = Hesperorthis tricenaria
Parastrophina hemiplicata (Hall)
Platystrophia biforata (Schlotheim) = Oxoplecia?
Plectambonites sericeus (Sowerby) = Sowerbyella sericea
Plectorthis plicatella (Hall)

Lower Martinsburg Formation, Virginia

Colaptomena leptostrophaidea Cooper
Cyclospira quadrata Cooper
Cyphomena grandis Cooper
Dalmanella sculpta Cooper
Eoplectodonta alternata (Butts)
Laticrura magna Cooper
Leptaena ordovicica Cooper
Orthambonites bielsteini Cooper
Oxoplecia globularis Cooper

Lower Martinsburg Formation, Southwestern Virginia and Tennessee

Strophomena incurvata (Shepard)
Zygospira nicolletti (Winchell and Schuchert) = Protozyga nicolletti
Zygospira recurvostris (Hall) = Anazyga recurvostris

Strophomena conradi Hall and Clarke
Strophomena sp.
Dalmanella rara Cooper

Dinorthis pectinella (Emmons)

Hesperorthis tricenaria (Conrad)

Onniella fertilis (Ulrich)

**Base of Martinsburg Formation, Pennsylvania**

Christiana lamellose Bassler = Bimuria lamellose

Dalmanella edsoni Bassler = Reuschella americana Cooper

D. testudinaria var. = D. sculpa Cooper

**Moccasin Formation, SW Virginia and NE Tennessee**

Zygospira lebanonensis Cooper = Anazyga lebanonensis

**Oranda Formation, Virginia**

Bilobia hemispherica Cooper

Bimuria lamellosa (Bassler)

Chaulistomella sp. 2

Christiania auriculata Cooper

Cristiferina cristifera Cooper

Cyphomena homostiata (Butts)

Dalmanella costellata Cooper

Eoplectodonta alternata (Butts)

E.? triradiata (Butts)

Furcitella plicata Cooper

Glyptambonites musculosus Cooper

Rafinesquina alternata (Conrad)

Rhynchotrema sp.

Sowerbyella curdsvillensis (Foerste)

Zygospira sp. (probably Anazyga sp.)

Leptaena tenuistriata Sowerby var. = L. ordovicica Cooper

Strophomena? sculpturata Bassler

Triplecia (Cliftonia) simulatrix Bassler = Oxoplecia simulatrix (Bassler)

Laticrura magna Cooper

Leptaena ordovicica Cooper

Leptellina abbreviata Cooper

Nicolella strasburgensis (Butts)

Orthambonites bielsteini Cooper

O. multicostellatus Cooper

Oxoplecia simulatrix (Bassler)

Parastrophina sp. 2

Ptychopleurella sulcata Cooper

Rafinesquina planulata Cooper
Reushella americana Cooper
Skenidioioides rectangulatus Cooper
Sowerbyella cava Cooper

Salona Formation, Pennsylvania to northern Virginia

Colaptomena leptostrophoidea Cooper
Dalmanella sp.
Leptaena sp. aff. L. rhomboidalis (Wilckens) = L. ordovicica Cooper
Leptelloidea pisum (Ruedemann) = Bilobia hemispherica Cooper
Oxoplecia cf. O. simulatrix (Bassler) = O. pennsylvanica Cooper
Parastrophina hemiplicata (Hall)

Central Basin of Tennessee, Wells Creek Basin, and High Bridge, Kentucky (Cooper 1956)

Carters Formation, Tennessee

Camerella bella Fenton
Chaulistomella lebanonensis Cooper
Chaulistomella sp. 1
Doleroides tennesseensis Cooper
Fascifera sulcata Cooper
Hesperorthis tricenaria (Conrad)
Oepikina varia Cooper

Kimmswick limestone, Tennessee

Rafinesquina cf. R. minnesotensis

Rhynchotrema minnesotensis
Strophomena cf. S. scofieldi = Furcitella scofieldi (Winchell and Schuchert)

**Hermitage Formation, Tennessee**

Dalmanella crassicostellata Cooper  
*D. sulcata* Cooper  
*Dalmanella crassicostellata* (Emmons)  
Rafinesquina heritagensis Bassler = *R. tretonensis* = *R. alternata*

Hesperorthis tricenaria  
Onniella? americana  
O.? planoconvexa  
Sowerbyella curdsvillensis

*Pinodema tennesseensis* Cooper  
*“Platystrophia” extensa* McEwan

**Tyrone Formation, High Bridge, Kentucky**

Idiospira panderi (Billings)  
S. cf. S. plattinensis Fenton  
Strophomena auburnensis nasuta Cooper  
Zygospira sp. (probably *Anazyga*)

Strophomena cf. S. dignata Fenton

**Indiana (Cooper 1956)**

**Disturbed area—Division 8**

Crania setigera = Acanthocrania setigera (Hall)  
*R. minnesotensis* = Öpikina minnesotensis (Winchell and Schuchert)

Glyptorthis bellarugosa (Conrad)  
Rhynchotrema minnesotensis (Sardeson)

Hesperorthis tricenaria (Conrad)  
Strophomena tretonensis Winchell and Schuchert

Leptaena charlottae = Bellimurina charlottae (Winchell and Schuchert)  
Zygospira recurvirostris = *Anazyga recurvirostra* (Hall)

Rafinesquina cf. R. heritagensis = *R. alternata* (Conrad)
Disturbed area—Division 9

Hesperorthis tricenaria (Conrad)

Strophomena trentonensis Winchell and Schuchert

Mississippi Valley (Cooper 1956; St. Paul Minnesota—Rice 1987)

Decorah Formation, St. Paul, Minnesota (Rice 1987)

Bellimurina charlottae  
Dalmanella sculpta?  
Dinorthis pectinella  
Doleroides pervetus  
Glyptorthis bellarugosa  
Hesperorthis tricenaria  
Oepikina inquassa  
O. minnesotensis  
Pinodema subaequata  
Plaesiomys meedsii  
‘Platystrophia’ amoena  
Protozyga nicolleti  
Rafinesquina sp.  
R. trentonensis = R. alternata

Spechts Member, Decorah Formation

Dalmanella perveta (Conrad) = Doleroides pervetus (Conrad)

D. subaequata = Pinodema subaequata (Conrad)

Doleroides gibbosus (Billings)
D. meedius (Winchell) = D. winchelli Cooper

Orthis tricenaria (Conrad) = Hesperorthis tricenaria

Pinodema uniplicata Cooper

Plectambonites sericea (Sowerby) = Sowerbyella sericea (Sowerby)

Rostricellula ainsliei (N.H. Winchell) = Rhynchotrema ainsliei

R. minnesotensis (Sardeson)

Strophomena incurvata (Shepard) = S. auburnensis Fenton

Trematis huronensis? Billings

Trematis minnesotensis Sardeson

Zygospira recurvostris = Anazyga recurvostra (Hall)

Guttenberg Member, Decorah Formation

Crania setigera Hall

Craniella? ulrichi Hall = Petrocrania ulrichi (Hall)

Dalmanella hamburgensis Winchell and Schuchert = D. winchelli Cooper

Idiospira panderi (Billings)

Leptaena charlottae Winchell and Schuchert = Bellimurina charlottae (Winchell and Schuchert)

Orthis tricenaria Conrad = Hesperorthis tricenaria (Conrad)

O. (Dalmanella) subaequata perveta Conrad = Doleroides pervetus (Conrad)

O. (Hebertella) bellarugosa Conrad = Glyptorthis bellarugosa (Conrad)

Pinodema subaequata (Conrad)

P. uniplicata Cooper

Plectambonites sericea Sowerby = Sowerbyella punctostriata (Mather)

Rafinesquina minnesotensis inquassa Sardeson = Ōepikina inquassa (Sardeson)

R. prestonensis Salmon

R. sinclairi Salmon

R. trentonensis (Conrad) = R. alternata Conrad

Rhynchotrema ainsliei N.H. Winchell

Rhynchotrema minnesotensis Sardeson = Rostricellula minnesotensis (Sardeson)

Strophomena delicatula Fenton

S. dignata Fenton

S. incurvata (Shepard) = S. auburnensis Fenton

Zygospira recurvostris (Hall) = Anazyga recurvostra (Hall)

Ion Member, Decorah Formation
Dinorthis sweeneyi (Winchell)

Glyptorthis subcircularis Cooper

Orthis tricenaria Conrad = Hesperorthis colei Cooper

O. (Dalmanella) hamburgensis? Walcott = D. winchelli Cooper

O. (D.) tesudinaria Dalman = Paucicrura rogata (Sardeson)

O. (D.) subaequata circularis (N.H. Winchell) = Pinodema circularis (N.H. Winchell)

O. (Hebertella) bellarugosa Conrad = Glyptorthis bellarugosa (Conrad)

Pinodema minnesotensis Cooper

P. uniplicata Cooper

Plectambonis sericea Sowerby = Sowerbyella monilifera Cooper

Prosser Formation

Parastrophina bernensis (Sardeson)

P. rotundiformis Willard

Rostricellula acutiplicata Cooper

Rostricellula sp. 3

Hook Member, Macy Formation

Campylorthis deflecta (Conrad)

Oepikina sp.

Hesperorthis tricenaria (Conrad)

Zell Member, Macy Formation

Ancistrorhyncha sp.

Campylorthis deflecta (Conrad) = C. subplana Cooper

Camarella bella Fenton

Doleroides gibbosus (Billings)

C. gregeri Cooper
D. cf. D. pervetus (Conrad) = D. missouriensis Cooper

Glyptorthis bellarugosa (Conrad)

Hesperorthis tricenaria (Conrad)

Oepikina septata? Salmon

O. transitionalis (Okulitch)

Oepikina sp.

Pinodema subaequata (Conrad)

Protozyga rotunda Cooper

Rhynchotrema sp.

Rostricellula cuneiformis (Fenton and Fenton)

R. cf. R. missouriensis (Fenton and Fenton)

R. plattinensis Fenton

Rostricellula sp.

Sowerbyella punctostriata (Mather)

Strophomena auburnensis Fenton

S. delicatula Fenton

S. dignata Fenton

S. exigua Fenton

S. insconsueta Fenton

S. muscosula Fenton

S. plattinensis Fenton

S. winchelli Hall and Clarke

Strophomena sp.

Zygospira recurvirostris (Hall) = Anazyga recurvirostra (Hall)

Z. variabilis Fenton (probably Anazyga)

Barnhart Formation, Missouri

Campylorthis subplana Cooper

Hesperorthis tricenaria (Conrad)

Pinodema subaequata (Conrad)

Protozyga rotunda Cooper

P. superba Cooper

Rafinesquina sinclairi Salmon

Rostricellula cuneiformis (Fenton and Fenton)

Auburn Chert, Missouri

R. missouriensis (Fenton and Fenton)

Sowerbyella sp.

Strophomena delicatula Fenton

S. dignata Fenton

Trematis foerstei Cooper

Zygospira sp. (probably Anazyga)

Zygospira lebanonensis Cooper = Anazyga lebanonensis (Cooper)
Dalmanella subaequata (Conrad) = Paucicrura rogata (Sardeson)
Pinodema subaequata (Conrad)

D. testudinaria (Dalman) = Paucicrura rogata (Sardeson)

Hallina globularis Cooper

Idiospira panderi (Billings)

Lingula sp.

Orthis tricenaria Conrad = Hesperorthis tricenaria (Conrad)

Plattin Formation, northern Arkansas

Ancistrorhyncha costata Ulrich and Cooper

Camerella aff. C. panderi Billings = Idiospira aff. I. panderi (Billings)

Rafinesquina aff. R. alternata (Emmons)

Strophomena cf. S. incurvata (Shepard)

Zygospira aff. Z. recurvirostris (Hall) = Anazyga aff. A. recurvirostra

Oklahoma—Viola Formation (Cooper 1956; Unit 1C and 2 of Alberstadt 1973)

Cooper 1956

Dalmanella hamburgensis

Dinorthis pectinella

‘Platystrophia’ sp.

Plectambonites sericeus = Sowerbyella sericea

Rafinesquina deltoidea

Rhynchotrema increbescens

Strophomena filitexta

Zygospira recurvirostris = Anazyga recurvirostra

Unit 1c in Alberstadt 1973

Doleroides vescus n. sp.

Onniella sp.
Unit 2 in Alberstadt 1973

‘Platystrophia’ prima n. sp. \hspace{1cm} Leptellina sp.
Paucicrura cf. P. rogata (Sardeson) \hspace{1cm} Rhynchotrema increbescens Hall
Sowerbyella sp. \hspace{1cm} Dinorthis cf. D. transversa Willard

Black Hills, South Dakota—Whitewood Formation (Cooper 1956)

Crania? \hspace{1cm} Rhynchotrema cf. R. minnesotense (Sardeson)
Dalmanella? cf. D. hamburgensis (Winchell, not Walcott) = Dalmanella winchelli Cooper \hspace{1cm} Sowerbyella sp.
Lingula sp. \hspace{1cm} Strophomena sp.
Rafinesquina sp. \hspace{1cm} Zygospira (probably Anazyga)

Nevada—Antelope Valley and Toquima Range (Cooper 1956)

Dark shale with Reushella

Bilobia hemispherica Cooper \hspace{1cm} Pauorthis gigantea Cooper
Bimuria sp. 1 \hspace{1cm} “Plectorthis” obesa Cooper (probably Austinella)
Cristiferina cristera Cooper \hspace{1cm} Reuschella vespertina Cooper
Eoplectodonta alternata (Butts) \hspace{1cm} Rostricellula angulata Cooper
Glyptorthis sp. 1 \hspace{1cm} Sowerbyella merriami Cooper
Hesperorthis antelopensis Cooper \hspace{1cm} Sowerbyella sp. 1 and 2
Leptaena ordovicica Cooper \hspace{1cm} Strophomena sp. 1
Leptellina incompta Cooper
Oxoplecia nevadensis Cooper
Northern Rocky Mountains, British Columbia (Jin and Norford 1996)

Advance Formation

Anazyga bellicosta n. sp.  Oxoplecia globularis
Bimuria cf. B. supreba  Parastrophina sp.
Christiania subquadrata  ‘Platystrophia’ colbiensis
Eoplectodonta (Eoplectodonta) alternata  Pauorthis ponderosa
Dinorthis cf. D. holdeni  Paucicrura rogata
Glyptambonites musculosus  Plaesiomys meedsii
Glyptorthis assimilis  Rafinesquina praecursor
Hisocbeccus mackenziensis  Scaphorthis perplexa
Leangella (Leangella) biseptata n. sp.  Strophomena cf. S. planumbona
Murinella cf. M. biconvexa  Thaerodonta restonensis
Oepikina sp.

Baffin Island (Roy 1941; Bolton 2000)

Amadjuack Formation

Hesperorthis interplicata = Dolerorthis interplicata  Rafinesquina declivis subnutans = Megamyonia declivis subnutans
Glyptorthis bellarugosa  Rafinesquina productivformis
Plaesiomys subcircularis  Rafinesquina (?) pronis
Strophomena fluctuosa  Rafinesquina sp.
Strophomena sp.  Austinella cooperi
Strophomena sp. 1 of Roy  Plectorthis inaequiconvexa
Paucicrura rogata  Plectorthis sp.
Resserella diminutiva
Resserella silmani
‘Platystrophia’ mangisulcata
Sowerbyella sp.
Sowerbyella sp. cf. S. thraivensis
Kjaerina sp.
Parastrophina minor
Lepidocyclus (?) arctica = Hiscobecus arcticus
Lepidocyclus (?) breve = Hiscobecus arcticus
Idiosira maynei
Cyclospira schucherti

Scotland (see Cocks 2008 and references therein)

Stratclyde, Girvan: Kiln Mudstone Member of the Craighead Limestone; Albany Mudstone Formation; Myoch Gormation

Palaeoglossa? maccullochi (Reed, 1917)
Glyptoglossella ardmillanensis (Reed, 1917)
Multispinula scotica (Davidson, 1877)
Multispinula sp.
Longvillia deficiens (Reed, 1917)
Longvillia lata (Williams, 1962)
Bellimurina tenuicorrugata (Reed, 1917)
Dactylogonia homostriata homostriata (Butts, 1942)
Dactylogonia homostriata indicissa (Williams, 1962)
Dactylogonia? multicorrugata (Reed, 1917)
Dactylogonia? semiglobosina (Davidson, 1883)
Trigrammaria cassata (Williams, 1962)
Rafinesquina insidiosa Williams, 1962
Rafinesquina cf. planulata Cooper, 1956
Leptaena (Leptaena) diademata Williams, 1962
Leptaena (Leptaena) infrunita Williams, 1962
Leptaena (Leptaena) cf. ordovicica Cooper, 1956
Leptaena (Leptaena) cf. strandi Spjeldnaes, 1957
Leptaena (Leptaena) sp.
Glyptomenoides girvanensis (Salmon, 1942)
Mjoesina rugata rugata Williams, 1962
Mjoesina rugata plana Williams, 1962
Foliomena exigua Harper, 1989
Christiania bilobata Reed, 1917
Christiania perrugata perrugata (Reed, 1945)

Isophragma pseudoretroflexum (Reed, 1917)

Bimuria youngiana youngiana (Davidson, 1871)

Craspedelia gabata Williams, 1962

Leptellina (Leptellina) llandeiloensis (Davidson, 1883)

Leptellina (Leptellina) sp.

Glyptambonites sp.

Palaeostrophomena subarachnoidea (Reed, 1917)

Palaeostrophomena subfilosa (Reed, 1917)

Titanambonites incertus Williams, 1962

Bilobia etheridgei acuta Williams, 1962

Leangella (Leangella) cf. anatoli (Speldnaes, 1957)

Leangella (Leangella) cf. hamari Speldnaes, 1957

Leangella (Leangella) cf. anatoli (Speldnaes, 1957)

Leangella (Leangella) cf. hamari Speldnaes, 1957

Leangella (Leptestiina) magna Harper, 1989

Xenambonites revelatus Williams, 1962

Chonetoidea restricta (Hadding, 1913)

Chonetoidea sp.

Anoptambonites grayae (Davidson, 1883)

Anisopleurella balclatchiensis (Reed, 1917)

Eoplectodonta (Eoplectodonta)

conspicua (Reed, 1917)

Eoplectodonta (Eoplectodonta)

Semirugata semirugata (Reed, 1917)

Sowerbyella (Sowerbyella) elusa Williams, 1962

Sowerbyella (Sowerbyella) fallax Jones, 1928

Ptychoglyptus irregularis Reed, 1941

Neocramatia diffidentia Harper, 1989

Fardenia scalena Williams, 1962

Craigella grayiae (Davidson, 1869)

Oxoplecia andersoni (Reed, 1917)

Oxoplecia subborealis (Davidson, 1883)

Triplesia? nucleoides (Reed, 1917)

Skenidioides costatus Cooper, 1956

Skenidioides craigensis (Reed, 1917)

Skenidioides sp.
Northern Ireland (see Cocks 2008 and references therein)

Tyrone, Bardahessiagh Formation

Hisingerella sp.

Multispinula sp.

Drummuckina sp.

Gunnarella sp.

Strophomena (Strophomena) cf. medialis Butts, 1942

Dactylogonia homostriata homostriata (Butts, 1942)

Dactylogonia sp.

Oepikina cf. speciosa Cooper, 1956

Oepikina sp.

Colaptomena concentrica (Portlock, 1843)

Leptaena (Leptaena) rugosa Dalman, 1828

Glyptomena sp.

Mjoesina sp.

Foliomena harperi Candela, 2003

Christiania perrugata elongata Mitchell, 1977

Christiania sp.

Bimuria youngiana recta Williams, 1962

Sowerbyites hibernicus Mitchell, 1977

Apatomorpha sp.

Glyptambonites minor Candela, 2003

Palaeostrophomena angulata Cooper, 1956

Palaeostrophomena sp.

Titanambonites incertus Williams, 1962

Toquimia sp.

Leangella (Leptestiina) oepiki ampla (Parkes, 1994)

Aegiria sp.

Cathrynia puteus Candela, 1999

Anoptambonites sp.

Anisopleurella sp.

Eochonetes cf. aspera (Wang, 1949)

Eochonetes celticus Mitchell, 1977

Eopectodonta (Eopectodonta) cf. alternata (Butts, 1942)

Eopectodonta (Eopectodonta) sp.

Sowerbyella (Sowerbyella) cf. monilifera Cooper, 1956

Bicusspina subquadrata Williams, 1974
Caeroplecia tenuis Candela, 2003

Oxoplecia sp.

Triplesia sp.

Atelelasma sp.

Skenidioides elongatus eireanni Candela, 2003

Sulevorthis playfairi (Reed, 1917)

Eridorthis sp.

Glyptorthis cf. concinnula Cooper, 1956

Dolerorthis duftonensis prolixa Williams, 1963

Ptychopleurella cf. mediocostata Cooper, 1956

Campylorthis discreta (Reed, 1952)

Dinorthis sp.

Plaesiomys sp.

Nicolella asteroidea Reed, 1917

Doleroides aff. winchelli Cooper, 1956

Mimella rotunda Mitchell, 1977

Plectorthis scotica (M'Coy, 1851)

Plectorthis sp.

Cremnorthis sp.

Scaphorthis sp.

Dalmanella sculpta Cooper, 1956

Eremotrema paucicostellatum Mitchell, 1977

Paucicrura cristifera (Cooper, 1956)

Reuschella sp.

Paurorthis catawbensis Cooper, 1956

Fascifera sp.

Pionodema cf. subaequata (Conrad, 1843)

Oanduporella cf. reticulata Hints, 1975

Salopina ordovicica Mitchell, 1977

Laticrura cf. heteropleura Cooper, 1956

Camerella sp

Liostrophia sp.

Parastrophina sp.

Drepanorhyncha sp.

Rostricellula simulata (Reed, 1952)

Idiospica plicata (Mitchell, 1977)

“Protozyga” sp.

Cyclospira sp.
Curriculum Vitae

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Brandon University
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