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## The Trentonian (Late Ordovician) brachiopod fauna of Ontario: Evolution through a global warming event

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Graduate Program in Geology  
A thesis submitted in partial fulfillment of the requirements for the degree in Doctor of  
Philosophy  
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**The Trentonian (Late Ordovician) brachiopod fauna of Ontario:  
Evolution through a global warming event**

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by

Akbar Sohrabi

Graduate Program in Geology

A thesis submitted in partial fulfillment  
of the requirements for the degree of  
Doctor of Philosophy

The School of Graduate and Postdoctoral Studies  
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London, Ontario, Canada

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## Abstract

This thesis, which examines the evolution of the Late Ordovician (early Katian) brachiopod fauna of Ontario, consists of two main parts: 1) a case study of the Late Ordovician *Rhynchotrema*–*Hiscobeccus* lineage of North America to investigate the morphological variations and evolutionary trends of brachiopod fauna in time and space, 2) the paleobiogeography of early Katian brachiopod fauna to explore their distribution patterns at a global scale and controlling factors.

During the Katian, the North American craton experienced a first-order marine transgression. The early stage of this event in the early Katian (Trentonian, Chatfieldian) was marked by the development of extensive new habitats for the origin and radiation of brachiopods and other shelly benthos in epicontinental seas.

Multivariate analysis, based on nine biometric characters of 171 Late Ordovician rhynchonellide specimens from nine localities in North America, demonstrated quantitatively that *Hiscobeccus mackenziensis*, as the earliest form of *Hiscobeccus*, evolved transitional characteristics between *Rhynchotrema* and the typical *Hiscobeccus*.

During the late Katian (Maysvillian and Richmondian), *Hiscobeccus* diversified into larger, more globular, and more strongly lamellose shells, especially in the paleoequatorially located inland marine basins. The diversification and morphological trends in the *Hiscobeccus* lineage are interpreted as the result of adaptation to an environment with relatively shallow, muddy substrates, and low oxygen with unsteady nutrient supply in generally overheated epicontinental seas.

Cluster and principal component analyses based on 33 brachiopod faunas of early Katian age, including 252 rhynchonelliform genera, revealed four global distinct faunal provinces, including Kazakhstan, Avalonia, epicontinental Laurentia, and Scoto-Appalachia. The late Darriwilian–early Katian brachiopod faunas of Laurentia show close similarities to those faunas of Siberia, Baltica, and other adjacent tectonic plates and terranes which indicate their semi-cosmopolitan distribution.

During the early Katian, the Scoto-Appalachian brachiopod fauna, had a closer affinity to the brachiopod faunas along the western margins of Laurentia, whereas the early Katian brachiopod fauna of the intracratonic region in Laurentia had a closer affinity to the brachiopod fauna from the platform facies of Baltica than to those in pericratonic Laurentia.

The brachiopod faunas exhibit strong provincialism during the late Katian, as the brachiopod fauna of Laurentia differentiated from those of Siberia, Kazakhstan, and South China. The faunal endemism within Laurentia was controlled by paleoecological factors related to tectonic events such as the Taconic Orogeny, as well as other factors such as paleolatitudinal faunal gradient, and varying substrate types.

**Key Words:** Brachiopoda, Late Ordovician, early Katian, Trentonian, evolution, paleobiogeography.

## Co-Authorship Statement

A shortened version of chapter 3, entitled **Evolution of the *Rhynchotrema-Hiscobeccus* lineage: implications for the diversification of the Late Ordovician epicontinental brachiopod fauna of Laurentia**, has been published in *Lethaia* (2013). The authors are Sohrabi, A., and Jin, J. J. Jin provided assistance with interpretation of data and editing of the manuscript.

A shortened version of chapter 4, entitled **Global palaeobiogeography of brachiopod faunas during the early Katian (Late Ordovician) greenhouse episode**, has been published online in *Palaeogeography, Palaeoclimatology, Palaeoecology* (2013). The authors of this paper are Sohrabi, A., and Jin, J. J. Jin provided assistance with interpretation of data and editing of the manuscript.

## **Dedication**

This dissertation is dedicated to:

my mother, my sisters, my father and my brother, who supported me in various ways to  
achieve my goal to complete this dissertation.

## Acknowledgments

First, I would like to thank my supervisor, Dr. Jisuo Jin, for sharing with me his insights and vast knowledge, and for his contagious enthusiasm and generous support. The plethora of knowledge that he has passed on to me has greatly influenced my perspective of paleontology. He was always available to talk and answer questions whether it was paleontology related or not, with his “open door” policy. I am honoured and pleased to have been given the opportunity to work with him and learn from him.

I would also like to thank Jean Dougherty of the Geological Survey of Canada and Dr. Paul Mayer of the Field Museum (Chicago) for their kindly arrangements of specimen loans for this study. Thanks also to Dr. Paul Copper who collected the *Rhynchotrema* specimens from Minnesota.

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## **Chapter 1 – Introduction**

### **1.1 Introduction**

Two of the greatest evolutionary events in the history of life on Earth occurred during early Paleozoic time. The first occurred in the Cambrian Period with the explosion of skeletonized marine animals which Wilson (1992) called the “big bang of animal evolution” and the second occurred during the Ordovician Period. Following the Cambrian explosion that involved the origin of skeletonization, the Ordovician diversification generated few new higher taxa (e.g. at the level of phylum), but an increase in biodiversity at the order, family, genus and species levels took place (Harper 2006).

There were noticeable differences in the relative intensities between the Cambrian explosion and the Ordovician diversification event. In comparison with the Cambrian diversity, the Ordovician diversity was much larger and the total number of marine orders doubled, and families tripled (Droser and Finnegan 2003). According to Miller and Mao (1995) (who, in turn, cite family-level data from Sepkoski 1993), during the Ordovician Period, the global diversity of marine families increased from about 160 to 530, and the diversity of genera increased from 470 to 1580.

#### **1.1.1 The Great Ordovician Biodiversification Event (GOBE)**

The Ordovician diversification of animal life or Ordovician Radiation is one of the most important diversification events in Earth history. In order to evaluate this great diversification event, in 1997, IGCP project 410, as one of the most successful projects in UNESCO-IUGS research programme, was established. Following the final report of

IGCP project 410 between 1997 and 2002, Webby et al. (2004a) proposed the term “the Great Ordovician Biodiversification Event” (GOBE) which has been widely adopted.

The GOBE occurred during the Early to Middle Ordovician through an interval of 25 Myr. It began during the Dapingian (late Arenig) and continued into the late Katian (Ashgill; see Sepkoski 1995; Webby et al. 2004a).

Sepkoski (1981, 1984) recognized three evolutionary faunas (EF), and illustrated the biodiversity curves of Phanerozoic families. The Cambrian EF (characterized by trilobites, lingulate brachiopods, and eocrinoids) expanded during Early Cambrian radiation; the Paleozoic EF (e.g. articulated brachiopods, echinoderms, cephalopods, corals, bryozoans, graptolites, and conodonts) dominated from the Ordovician to Permian; and the Modern EF (gastropods, bivalves, sponges, reptiles and mammals) rose during the late Paleozoic and became predominant during the Mesozoic and Cenozoic. The biodiversity curves were based on first and last appearances of taxa. According to these curves there was a steep radiation of marine genera during the Ordovician. This major rise in biodiversity in the Ordovician has been confirmed in the recent study by Alroy et al. (2008), who provided new diversity curves based on improved data and confirmed some key features of older curves such as the Cambrian and Ordovician radiation (Figure 1.1).



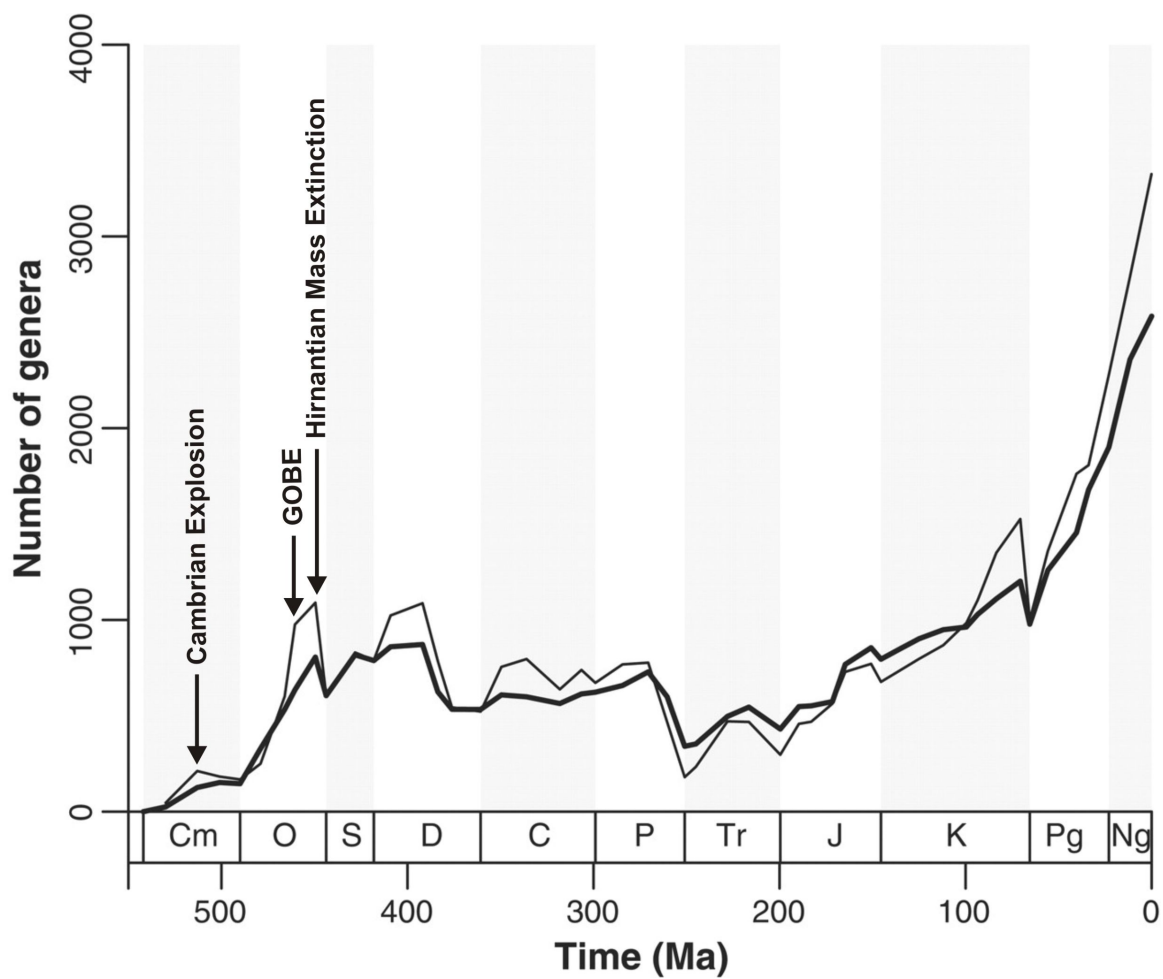


Figure 1.1 Genus-level diversity curves for marine genera. The thin line is based on Sepkoski's (2002) data, and the thick line on Alroy et al. (2008).

Sponges had low diversity during the Early Ordovician and were mostly dominated by demosponges, but Middle and Late Ordovician sponges had a considerable increase in diversity (Carrera and Rigby 1999). Diversification of sponges during the Ordovician shows three major peaks. First peak includes suborder Orchocladina in the Middle Ordovician. The second and third peaks occurred in the Sandbian (mid Caradoc) and mid Katian (early Ashgill), mostly with diversification of Sphinctozoans, Tricranocladina and Sphaerocladina (Rigby and Webby 1988; Carrera and Rigby 1999; Carrera and Rigby 2004).

Two major groups of corals, the Tabulata and Rugosa, diversified during the Ordovician. The tabulate corals had low diversity through the Early and early Middle Ordovician, and went through a radiation across the Middle-Late Ordovician boundary (late Darriwilian–Sandbian; see Scrutton 1998; Webby et al. 2004).

Gastropods and bivalves originated during the Cambrian, but their first radiation took place during the Ordovician. Most gastropods diversified in low latitudes and shallow water, whereas bivalves diversified in higher latitudes and deeper water (Novack-Gottshall and Miller 2003). There were two diversity peaks for Ordovician gastropods (earliest Darriwilian and Katian, Frýda and Rohr 2004).

Brachiopods were certainly one of the most diverse groups of benthic marine invertebrates during the Ordovician. Rhynchonelliformean brachiopods diversified in a number of phases during the Middle Ordovician (Harper and Rong 2001; Harper et al. 2004).

Trilobites also constituted one of the dominant invertebrate phyla of the Ordovician in shallow to deep water worldwide except for the tropics of Gondwana.

Three faunas of trilobites, the "Ibex Fauna I", "Ibex Fauna II" and "Whiterock Fauna" diversified in succession during the Ordovician (Adrain et al. 1998; Adrain et al. 2004).

Nautiloids flourished during the Early and Middle Ordovician, more likely due to the new ecological niches which facilitated their radiation. The increase in the stability of the Ordovician trophic structure, ecosystem complexity, and ecosystem flexibility led to the expansion of cephalopod habitats (Kröger 2009).

Graptolites were the most prominent planktonic-neritic invertebrates during the Ordovician. Chen et al. (2006) suggested that the earliest Ordovician was the beginning of the Ordovician graptolite radiation. Study of graptolites in three regions of Avalonia, Baltica and Australia shows a rapid diversity in the early Dapingian and late Sandbian (Cooper et al. 2004).

Fossil data of marine invertebrates revealed three global diversity maxima during the GOBE (Webby et al. 2004), the first in the earliest Darriwilian (latest Arenig), the second in the late Sandbian (mid-late Caradoc), and the third in the late Katian (mid Ashgill).

#### **1.1.1.1 Causes of the GOBE**

The GOBE was a complex macroevolutionary process, which comprised several global as well as regional pulses of diversity maxima, with some of the pulses showing diachroneity (e.g. Zhan and Harper 2006). Some researchers postulated that there were several possible causes contributing to the GOBE (Liu 2009). The causes for diversification range from extrinsic factors to intrinsic forces. External factors include increased tectonism, major global warming and major sea-level rise.

Miller and Mao (1995) suggested that the Ordovician Radiation coincided with increased tectonic activity, and that the intensive volcanism and orogeny were responsible for the GOBE. They presented new data relating increased levels of orogenic activity and Ordovician Radiation. Data were from several Ordovician paleocontinents, including Laurentia, Baltoscandia, East Avalonia, Bohemia and Australia. According to this hypothesis, the majority of the Ordovician biodiversification took place in foreland basins, which were adjacent to active orogenic belts during the Middle and Late Ordovician. Possible effects of orogenic activity on biodiversification include increased nutrient input from uplifted areas, and increased fragmentation of the sea floor habitats to facilitate allopatric speciation. The nutrient hypothesis has gained support from other recent studies of Ordovician microbiota. The work of Servais et al. (e.g. 2008, 2009) suggests that the rapid diversification of planktonic organisms in the Ordovician was one of the driving forces for the radiation of marine invertebrate by making the trophic structure more complex.

Vermeij (1995) suggested that massive submarine volcanism was the most likely extrinsic cause of biodiversification. Submarine volcanism would have triggered biodiversification because associated sea level rise and marine transgression would have increased global temperatures due to rising levels of atmospheric CO<sub>2</sub>, and increases in organic productivity. Following hydrothermal activity, carbon dioxide was released from the ocean to the atmosphere by upwelling, and injected nutrients into the ocean.

Sepkoski (1979) emphasized that the intrinsic macroevolutionary dynamics might have been a major cause of GOBE. He proposed a two-phase kinetic model of taxonomic diversity. According to this model the initial phase was characterized by the

biodiversification of homogeneous faunas which became widespread and diversified rapidly during GOBE. The second phase was represented by the diversification of heterogeneous faunas in separate geographic regions during the Ordovician.

Diversification of a single or homogeneous fauna is well illustrated by the North American epicontinental benthic marine fauna that evolved during the Ordovician.

Brachiopods as a benthic marine animal group rapidly diversified, bryozoans appeared for the first time, stromatoporids and corals became the most dominant reef builders for the first time in life history, and nautiloids flourished during this period as the top predators of food web.

Another example of an intrinsic factor for the GOBE is diversification of heterogeneous faunas. Marine faunas organized into three evolutionary faunas, and each fauna was influenced by other faunas (Sepkoski 1979; Sepkoski and Sheehan 1983). Major components of the Cambrian evolutionary fauna (EF), such as trilobites and echinoderms, remained abundant and diverse in the Ordovician. The rapid evolution of the Paleozoic EF, typified by rhynchonelliformean brachiopods, stromatoporoids, tabulate and rugose corals, bryozoans, nautiloids and graptolites, was responsible for the bulk of the biodiversity radiation during the GOBE. Elements of the Modern EF (e.g. bivalves, gastropods, and fish) were relatively minor contributors of the GOBE. Thus, the great Ordovician biodiversification can be viewed as a sum of both homogeneous and heterogeneous faunal evolution.

Replacement of Cambrian EF such as trilobites and inarticulated brachiopods with Paleozoic EF can be interpreted in terms of increasing niche and habitat partitions (Droser and Finnegan 2003). During the Early Ordovician, the shallow continental sea that largely

covered Laurentia (North America) provided an expanded habitat area for Paleozoic EF. Eventually the Paleozoic EF (e.g. rhynchonelliformean brachiopods) radiated to fill vacant niches.

More recently, Alroy (2010) proposed that diversity booms and collapses in the Phanerozoic may have been linked to such intrinsic factors as the evolution of high-latitude biota and reef ecosystems. Most of the database for the GOBE, however, came from tropical to subtropical, level-bottom (non-reefal) ecosystems. Thus the two large factors proposed by Alroy (2010) may not have been major causes of the Ordovician biodiversification.

### **1.1.2 Brachiopod diversification in the GOBE**

Brachiopods were undoubtedly one of the most abundant and diverse groups during Ordovician time. The Phylum Brachiopoda used to be divided into two classes: the Inarticulata and Articulata (Williams and Rowell 1965). In the newly revised brachiopod volumes of the Treatise on Invertebrate Paleontology, however, the phylum is now divided into the following major groups (Williams et al. 2000): Subphylum Linguliformea, Subphylum Craniiformea, Subphylum Rhynchonelliformea. In this thesis only rhynchonelliform brachiopods are used in various analyses because the linguliform and craniiform brachiopods (=Inarticulata) are insignificant during this period (Harper et al. 2004).

According to Webby (2000), during the Ordovician radiation there were three global diversity maxima based on major fossil groups such as brachiopods. Brachiopods from different paleocontinents had different diversity trajectories during the Ordovician. Harper (2006) mentioned that brachiopod diversity trajectories from marginal Gondwana

were different from Baltica. He also indicated that within rhynchonelliform brachiopods, orthids were widespread along the margins of Gondwana whereas the margin of Laurentia with carbonate environments was ideal for strophomenides and pentamerides.

The brachiopod diversity curve for the Baltic Province during the Ordovician shows four diversity maxima in mid Darriwilian (early Llanvirn), late Darriwilian (late Llanvirn), late Sandbian (mid Caradoc) and late Katian (mid Ashgill) times, which is quite different than brachiopod diversity curves of Avalonia and Gondwana. In Avalonia the curve shows three peaks in the mid Darriwilian (early Llanvirn), late Sandbian (mid Caradoc), and late Katian (mid Ashgill). The brachiopod diversity curve of Gondwana during the Ordovician shows one diversity peak in the late Sandbian (mid Caradoc), which indicates a delay in diversity (Hints and Harper 2001; Harper and Mac Nicaill 2002; Harper 2006).

### **1.1.3 Ordovician brachiopods in South China**

Stratigraphic and paleontological studies indicate that China (particularly South China) is one of the key areas for study of Ordovician biodiversification probably because of the richly fossiliferous and well-developed Ordovician succession.

The study of the Ordovician brachiopod in South China indicates that brachiopod radiation occurred earlier than in other places in the world (Zhan and Harper 2006). The study of the biodiversification event also shows three diversity maxima in South China; first in early Floian (early Arenig), second in late Darriwilian (Llanvirn), and third in late Katian (mid Ashgill; Zhan et al. 2007).

On the basis of taxonomic diversity or  $\alpha$ -diversity of South China, the orthides radiated from three genera to 22 genera during the lower Tremadocian to upper Floian

(Zhan et al. 2008b). The first diversity peak for the dalmanelloids occurred during the early Floian (Zhan et al. 2008b). In South China the first appearance of rhynchonellides and atrypides occurred during the Sandbian, which was later than in other paleoplates. The mid-Ashgill was the time of first appearance of the spriferides in South China that was earlier than other terranes in the world (Zhan et al. 2008b).

The first peak of brachiopod  $\beta$ -diversity (paleoecological diversity or community diversity) radiation in South China appeared in the Yangtze Platform with diversification of *Sinorthis* Fauna in the early Floian (early Arenig). The second acme was characterized by the development of the *Saucrorthis* Fauna in the middle Darriwinian (Llanvirn), and the third peak was represented by the *Altaethyrella* Fauna in the mid Ashgill (Zhan et al. 2007; Zhan and Jin 2008a; Zhan and Jin 2008b; Zhan et al. 2008b).

#### **1.1.4 Global brachiopods diversity during the Ordovician**

Rhynchonelliform brachiopod diversified during the Dapingian (later Arenig) and Darriwinian (Llanvirn) (Harper and Rong 2001). Within the rhynchonelliforms three diversity maxima have been identified for the Orthida: the early Darriwilian (late Arenig–early Llanvirn), late Sandbian (mid-Caradoc) and late Katian (mid-Ashgill) (Harper 2006). Atrypide brachiopods first originated during the late Darriwillian (Llanvirn) and radiated in the Sandbian and early Katian (late Caradoc), and reached a major peak in the late Katian (early Ashgill; see Cocks and Rong 2000).

The orthides were dominant brachiopods from near-shore to offshore environments during the Ordovician. The first and major peak for the orthides occurred during the early Darriwilian and the second and third peaks in early and late Katian times, respectively. The suborder Dalmanellidina first appeared during the late Tremadocian and



had three peaks of diversity, in the early Darriwilian, early Katian, and late Katian (Harper 2006).

Two superfamilies of the order Strophomenida, the Strophomenoidea and Plectambonitoidea, first appeared in South China during the Early Dapingian (mid Arenig), and reached their highest diversity peaks in the Sandbian (early Caradoc) and late Katian (mid-Ashgill). Plectambonitoids first appeared in mid-shelf (BA3) communities in the early Tremadocian, then expanded rapidly and became abundant in shallower-water, near-shore depositional settings (BA2) by late Darriwilian time (Cocks and Rong 2000). Strophomenoids radiated later than plectambonitoids and attained their first diversity peak in mid-shelf (BA3-BA4) communities during the Sandbian.

The earliest rhynchonellides first occurred in late Darriwilian (Llanvirn) time, and became widespread in Laurentia, Siberia, Kazakhstan and other paleotropical plates in shallow marine environments (Jin 1996). In Laurentia earliest rhynchonellides emerged in the Chazyan (late Darriwilian), whereas in Baltica and Avalonia, one of the earliest rhynchonellids, *Rostricellula*, appeared in the late Darriwilian (Llanvirn; see Cocks 2008). In Siberia and other paleocontinents, the earliest rhynchonellids appeared somewhat later (Jin 1996).

During the Sandbian and early Katian (late Caradoc), there was a rapid increase in the total number of rhynchonellide genera from five to fifteen. One of the best examples of rhynchonellides was *Rhynchotrema*, which first appeared in the Sandbian-Katian boundary interval in eastern Laurentia, New York and Minnesota (Jin 1996; Sohrabi and Jin 2013a). During the late Katian (Ashgill), rhynchonellides became widespread in the North American epicontinental seas, characterized by a widespread *Hiscobeccus* fauna,

which will be one of the subjects of this thesis. This fauna was largely endemic to Laurentia.

## **1.2 Paleogeography of North America during the Ordovician**

### **1.2.1 Background of Ordovician geography**

In the earliest Ordovician there were four major separate continents, Gondwana, Laurentia, Baltica, and Siberia. Kazakhstan is now considered a cluster of small terranes between Siberia and Gondwana, instead of being a single continent. Many other smaller terranes (e.g. Avalonia, Armorica, North China, South China, Perunica) are treated as peri-Gondwana microplates (Cocks 2001; Fortey and Cocks 2003; Cocks and Torsvik 2004; Cocks and Fortey 2009; Candela 2006; Percival et al. 2011).

Throughout the Ordovician, Laurentia straddled the paleoequator, and comprised North America, Greenland, Spitsbergen, northwest Ireland, a small slice of western Norway, and Scotland (Figure 1.2; Cocks and Fortey 1982; Cocks 2001; Cocks and Torsvik 2004). During the Ordovician, Laurentia was rotated about 80° degrees clockwise compared to its present orientation (Cocks and Torsvik 2011). Throughout the Ordovician, Laurentia had a relatively stable position and its paleomagnetic and faunal evidence suggest only minor movement (Cocks 2000; Cocks and Torsvik 2004; Jin et al. 2013).

The Iapetus Ocean was at its maximum extent in the Early Ordovician, bounded by Laurentia to the northwest, Baltica to the east and Avalonia to the south (Figure 1.2), with gradual narrowing through the Middle and Late Ordovician (Van der Voo 1993; MacNiocaill et al. 1997).

The Gondwana supercontinent stretched from south polar regions to the equator,

including most of South America, Africa, Madagascar and Arabia on the west side, and Antarctica, Australia and India on the east (Figure 1.2; Cocks 2001; Fortey and Cocks 2003; Percival et al. 2011).

During the early Ordovician, Baltica (Russian Platform, Novaya Zemlya, East Baltic, and most of Scandinavia) was located in temperate latitudes of the southern hemisphere, but moved into the tropics by the Late Ordovician (Cocks and Fortey 1982; Cocks and Fortey 1998; Cocks 2001; Cocks and Torsvik 2005).

As one of the large continents adjacent to Laurentia, Siberia was in the tropical zone and included south and central Taimyr (Siberia) during this period (Figure 1.2; Cocks 2001; Cocks and Modzalevskaya 1997). The Siberian brachiopods have some similarity with those of Laurentia during the Middle Ordovician, but became isolated from each other during the Late Ordovician. Avalonia was part of Gondwana during Cambrian and earliest Ordovician time and included eastern Newfoundland (Avalon Peninsula), some of northern Germany, southeastern Ireland, Wales, England, Belgium, and Holland (Cocks et al. 1997; Cocks and Torsvik 2004, 2005). By the early Darriwilian Avalonia became separated from Gondwana and the Rheic Ocean widened between them, and it drifted northward towards Laurentia (Cocks et al. 1997; Van Staal et al. 1998; Murphy et al. 2006). This is reflected by increased, albeit episodic invasions of Avalonian brachiopods in Laurentia during the Middle and Late Ordovician.



Figure 1.2 Global paleogeographic reconstruction during Ordovician time (modified from Hints and Eriksson 2007; Cocks and Torsvik 2011).

## **1.3 Paleoenvironmental settings of Laurentia**

### **1.3.1 Taconic Orogeny**

The tectonic effects on Laurentia are obvious in the eastern part of North America. The North American craton witnessed changes from stable, passive tectonic margin during the Early Ordovician to an active foreland basin setting in the Middle and Late Ordovician.

As the plates of Avalonia, Baltica and Laurentia started to converge during the Early Ordovician, the southeast of the Iapetus Ocean became narrower, while in the northeast it began closing during the Middle Ordovician (Williams 1997; Van Staal et al. 1998; Ganis and Wise 2008).

The Taconic Orogeny (first phase of Appalachian Orogeny) was caused by the collision of island arcs along the eastern margin of Laurentia in the Late Ordovician (Sandbian–Hirnantian), between 458–443 Ma (Chapple 1973; Rowley and Kidd 1981; Van der Voo 1993; MacNiocaill et al. 1997; Ganis and Wise 2008). Docking of the volcanic island arcs onto the eastern margin of North America created the Taconic (Appalachian) Foreland Basin and peripheral bulge between 458–450 Ma (Sandbian to earliest Katian). Thrust faulting and the formation of overturned nappes resulted in the destruction of the foreland basin and the accumulation of the large Queenston Clastic Wedge in New York and Pennsylvania between 450–443 Ma (Ganis and Wise 2008). The formation of the Michigan and Illinois basins and the activation of the cratonic arches (e.g. Findaly, Algonquin, Frontenace, and Saguenay arches) also coincided with the Taconic Orogeny during the Late Ordovician (Sanford 1993a).

### 1.3.2 Sea-level changes

During the Late Ordovician, the Laurentian craton was flooded by shallow epeiric seas. The vast central regions of North America contain well-preserved Upper Ordovician rock successions (Sloss 1963; Long 1977; Barnes et al. 1981; Finnegan et al. 2012).

Sloss (1963) defined six sequences in the Phanerozoic strata of North America based on major interregional unconformities and attributed these sequences to subsidence and uplift of the North American Craton. He named these sequences the Sauk, Tippecanoe, Kaskaskia, Absaroka, Zuni, and Tejas. Two major transgressions in North America occurred during the Cambrian and Ordovician. During the Late Cambrian, North America became flooded by the Sauk Sea. During the late Early Ordovician there was a regression of the epeiric sea, with most of the North American craton becoming emergent. Following the Sauk regression, the North American craton was flooded again by the Tippecanoe Sea starting from the late Middle Ordovician (Sloss 1963; Levin 1996; Finnegan et al. 2012).

According to Haq and Schutter (2008), the sea-level curve shows a gradual rise from the Late Cambrian to Early Ordovician, a marked drop during the Middle Ordovician, and the highest peak during the Late Ordovician (early Katian).

During the early Katian (Chatfieldian or “Trentonian”), the sea covered large areas of the North America interior, which was accompanied with increase in Taconian orogenic activity. In the late Trentonian the sea encroached further and the northeastern part of the Hudson and St. Lawrence platforms became inundated. The highest peak of sea level occurred during the Late Ordovician and most of the Canadian Shield was flooded by this major marine transgression (Sanford 1987, 1993a).

Sea-level change is a complex phenomenon and the causes range from global to regional factors. Fairbridge (1961) summarized three global factors, glacio-eustasy, tectono-eustasy, and sedimento-eustasy for sea level changes.

The growth and degradation of continental ice sheets could be an important factor responsible for global sea-level fluctuations (eustasy) during the Ordovician, but there is a lack of evidence for major glaciations (i.e. extensive continental ice cap) in the Early–Middle Ordovician (Artyushkov et al. 2007; Miller et al. 2005).

Tectonic deformation of the ocean basins is a major factor which controls sea level change. Tectono-eustasy refers to changes in ocean basin volume due to variations in mid-ocean ridge volume, which in turn results in the displacement of sea water between oceans and continents (Fairbridge 1961; Fjeldskaar 1989; Rona 1995; Miller et al. 2005). Therefore, plausible causes of sea-level fluctuations during the Early and Middle Ordovician in North America can be attributed to tectono-eustasy on a global scale. Regionally, the Taconic Orogeny was not likely a major factor for sea level changes until the Late Ordovician because the onset of this tectonic event was in the Sandbian (Ganis and Wise 2008).

### **1.3.3 Paleogeographic elements of Laurentia**

During the Ordovician, the western part of Laurentia was a passive continental margin, comprising a continental-margin platform (e.g. the MacDonald Carbonate Platform) and the Williston Basin (McCrossan et al. 1964; Norford et al. 1994).

The eastern and central part of the Laurentian craton comprised the Canadian Shield, three platforms (Arctic, Hudson, and St-Lawrence), and four intracratonic basins (Hudson Bay, Williston, Michigan and Illinois; Figure 1.3). The Canadian Shield is a vast

area of stable Precambrian basement and occupies a large part of eastern and central Canada, with the Hudson Bay Basin in the middle (Long 1977; Wade et al. 1977; Sanford 1987, 1993). Much of the shield was flooded during the middle–late Katian maximum marine transgression that left a rich and diverse record of megafossils in the inland seas (Finnegan et al. 2012).

### **Williston Basin**

During the Late Ordovician, the Williston Basin was one of the largest intracratonic basins of North America and covered the southern part of Saskatchewan, southwestern Manitoba, eastern Montana, northeastern Wyoming and western North and South Dakota (Figure 1.3; Norford et al. 1994; Jin and Zhan 2001). Deposition in the Williston area began with the Deadwood Formation (mainly siliciclastic sandstones, siltstones and shales) during the Middle-Late Cambrian (Hendricks et al. 1998). Following a substantial hiatus, subsidence of the Williston Basin resumed in the early part of the Late Ordovician with deposition of the Winnipeg Formation, which consists of a sequence of sandstone and shale (Foster 1972; Norford et al. 1994). The centre of the Williston Basin was located in northwestern North Dakota during the Late Ordovician. The Ordovician rocks in the North Dakota, Southern Manitoba, and Saskatchewan are divided into four formations: the Winnipeg Formation (lower Katian), Red River Formation (middle to upper Katian, Edenian to Richmondian), Stony Mountain Formation (upper Katian, upper Richmondian), and Stonewall Formation (uppermost Ordovician to basal Silurian; see also Sweet 1979, 1982; Bannatyne 1988; Elias 1991; Norford et al. 1994; Jin and Zhan 2001; Young et al. 2007).



**Illinois Basin**

The Illinois Basin is bounded to the north, northeast, southeast, and south, by the Wisconsin Arch, Kankakee Arch, Cincinnati Arch, and Pascola Arch, respectively (Figure 1.3). From the Late Cambrian to Middle Ordovician, carbonate sediment of the Knox Dolomite Megagroup, Lower Ottawa Limestone Megagroup and St. Peter Sandstone were deposited in the Illinois Basin. During Late Ordovician time, the Upper Ottawa Limestone Megagroup and Maquoketa Shale were deposited (Swann and Willman 1961; Heidlauf et al. 1986).

**Michigan Basin**

The Michigan Basin covered what is now most of the state of Michigan, southwestern Ontario, Lake Michigan, and Georgian Bay, and is bounded by the Wisconsin, Kankakee, Findlay and Algonquin arches (Figure 1.3). A major phase of subsidence of the basin began in the earliest Late Ordovician and it became separated from the Illinois Basin, coinciding with the initiation of the Taconic Orogeny (Howell and van der Pluijm 1990, 1999; Ganis and Wise 2008). Limestone and dolomite are the dominant strata in the Michigan Basin. The Middle–Upper Ordovician stratigraphic succession consists of a thick layer of sandstone (St. Peter Sandstone, Middle Ordovician), limestone (Black River and Trenton, lower Upper Ordovician, lower Katian), and calcareous mudstone and shale (Utica Shale, upper Katian; see Howell and van der Pluijm 1990, 1999).

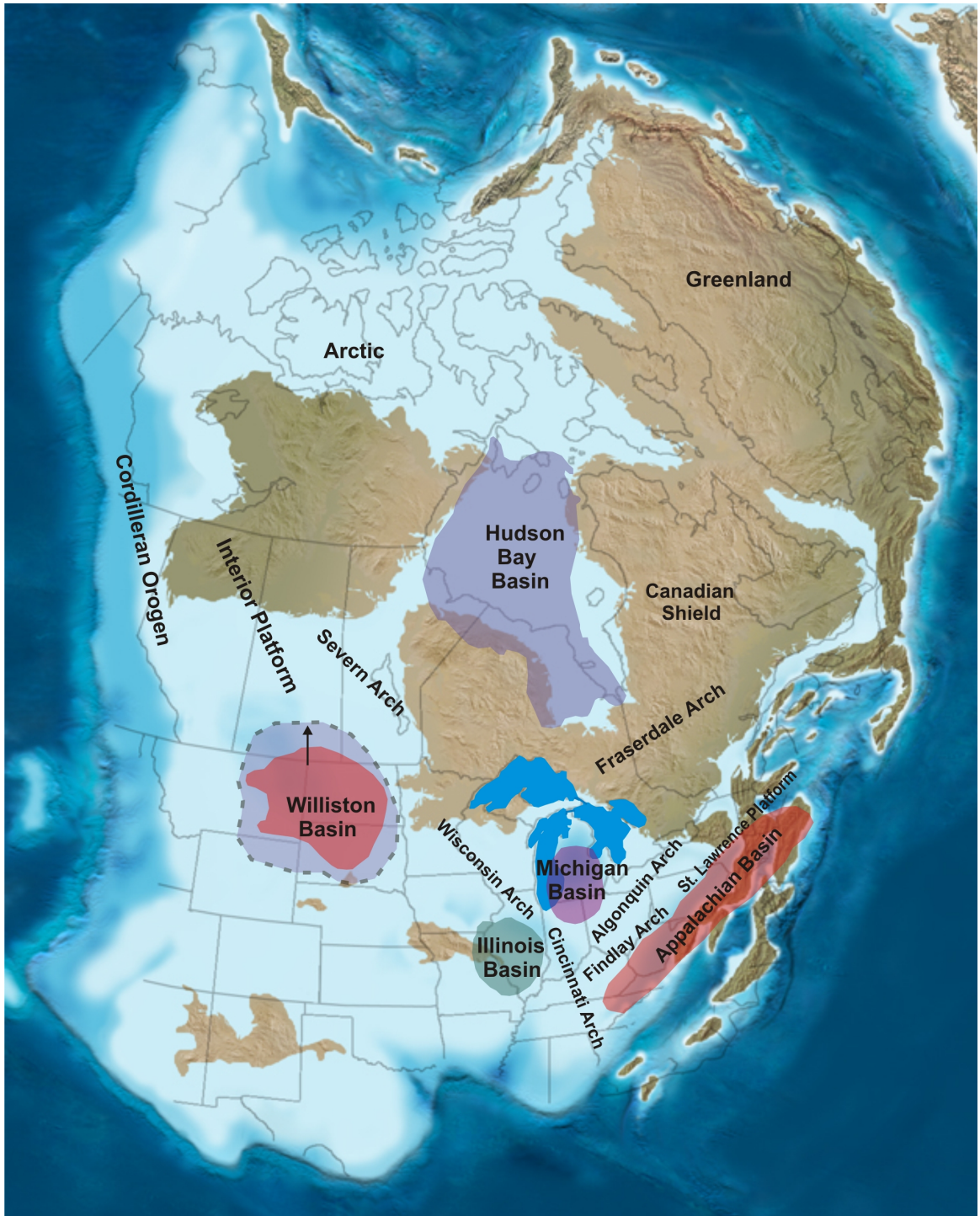


Figure 1.3 Tectonic framework and elements of North American continent during Ordovician time (modified from Levin 1996; Cocks and Torsvik 2011; and Jin et al. 2013).

The Upper Ordovician succession on Manitoulin Island was deposited paleogeographically on the northeast margin of the Michigan Basin, consisting predominantly of limestone and having a general thickness of 250 m (Copper 1978). Benthic shelly fauna including brachiopods are abundant in the lower Katian (Trentonian) Verulam Formation on Manitoulin Island and the brachiopods are included in this study.

### **Hudson Bay Basin (Hudson Platform)**

The Hudson Bay Basin lies in the central part of the Canadian Shield (Figure 1.3) and contains mainly carbonate and evaporite rocks with minor amounts of shale, siltstone and sandstone (Sanford 1993a). The rocks range in age from Cambro-Ordovician to Early Silurian in the northeastern part of the basin and from Late Ordovician to Late Devonian in its central and southern parts. During the Darriwilian (Whiterockian), a 100 m thick sequence of sediments, consisting of orthoquartzitic sandstone, brecciated and stromatolitic dolostone, was deposited in the central and northern parts of the Foxe Basin. These sediments indicate a transgression during the Whiterockian. By the late Whiterockian (Chazyan), the sea regressed from much of the Hudson Bay Basin. The second marine transgression onto the northeastern part of the Hudson Platform took place during the late early Katian (Trentonian), culminating in the accumulation of a richly fossiliferous limestone succession in the middle and late Katian (Maysvillian and Richmondian; see MacLean et al. 1986; Sanford 1987; Jin et al. 1997). The Late Ordovician biofacies of the Hudson Bay Basin, together with similar facies in the Williston Basin and North Greenland indicate a paleoequatorial setting, in agreement with the general paleogeographic reconstructions (Cocks and Torsvik 2011; Jin et al. 2013).

### **St. Lawrence Platform**

The St. Lawrence Platform is bounded by the Appalachian orogen to the southeast and by the Canadian Shield to the north and northwest (Figure 1.3; Sanford 1993a). The St. Lawrence Platform is divided into three parts, the western St. Lawrence Platform, the central St. Lawrence platform, and the eastern St. Lawrence platform (Sanford 1993a). The western and central St. Lawrence platforms are separated by the Frontenac Arch. Within the western St. Lawrence platform, the Allegheny Foreland Basin and the Michigan Basin are separated by the Findlay and Algonquin arches.

The central St. Lawrence platform was bounded on the north by the Laurentian Arch and on the east by the Saguenay Arch, coinciding with the Ottawa-Quebec Lowland (the Ottawa Embayment and the Quebec Basin). The eastern St. Lawrence Platform was bounded on the west by the Sagueny Arch, on the north by Laurentian Arch, and much of the eastern part comprised the Anticosti Basin (Poole et al. 1970; Sanford 1993a).

The deposits of the St. Lawrence Platform consist of carbonates, evaporites, shales and sandstone ranging from the Upper Cambrian to Carboniferous. During the Middle–Late Ordovician, the St. Lawrence Platform had different sedimentary facies in the southern Ontario, New York, Anticosti Basin, Quebec Basin and Ottawa Embayment (Sanford 1993a). There is a complete succession of Ordovician rocks in the Anticosti Basin whereas in the Quebec Basin and Ottawa embayment, the lower Middle Ordovician and part of the Upper Ordovician rocks are missing (Sanford 1993a).

The Ottawa Embayment was an intracratonic extension of the central St. Lawrence Platform, bounded on the west by the Frontenac Arch (Sanford 1993a). During the early Katian (Trentonian), there was an open seaway (Frontenac seaway) between the

Ottawa Embayment and Appalachian Basin. The Trentonian deposits in the Ottawa Embayment are fossiliferous (Wilson 1946; Salad Hersi and Dix 1999).

The regional correlation in the Ottawa area, south-central Ontario (Orillia) and Manitoulin Island suggests a general continuity of formations among the lower Katian (Trentonian) deposits. In the Ottawa area, Lake Simcoe area and Manitoulin Island, the Trentonian carbonate rocks are widely distributed with rich and diverse fauna. Brachiopods are abundant, together with trilobites, bryozoans, gastropods, and echinoderms, indicating normal marine depositional environments during the Trentonian (Liberty 1969; Melchin et al. 1994; Sohrabi and Jin 2013b).

The brachiopods in the Trentonian carbonate rocks in the Ottawa area, Lake Simcoe area, and Manitoulin Island form important parts of this thesis. Detailed geological settings of these localities will be discussed in the following sections.

## **1.4 Geological and stratigraphic settings of the study areas**

### **1.4.1 Ottawa area**

Paleozoic sedimentary successions in the Ottawa area include Sloss's (1963) Sauk and Tippecanoe sequences. The Sauk sequence comprises the Middle Ordovician Potsdam and Beekmantown groups. The Tippecanoe sequence (Upper Ordovician) includes the Rockcliffe Formation, Ottawa Group, Billings Formation, Carlsbad Formation, and Queenston Formation (Wilson 1946; Salad Hersi and Dix 1997; Salad Hersi and Lavoie 2001b).

In the Ottawa area, the Cambrian and Ordovician sedimentary rocks (i.e. the Potsdam and Beekmantown groups) rest unconformably on the Precambrian basement (Williams and Telford 1986). Much of the Ottawa area is underlain by the Upper

Ordovician rocks of the Ottawa Group (Williams and Telford 1986), which is divided into five formations: the Shadow Lake, Gull River, Bobcaygeon, Verulam, Lindsay, and Billings formations (Figure 1.4). The Ottawa Group is overlain by the upper Ordovician siltstone and shale of the Carlsbad Formation, and the Ordovician succession is capped by the Queenston Formation of predominantly fine-grained siliciclastic sediments.

#### **1.4.1.1 Potsdam Group**

The Potsdam Group overlies the Precambrian basement (Figure 1.4) and consists of Upper Cambrian–Lower Ordovician sandstone and conglomerate (Emmons 1938, Williams and Telford 1986). It is divided into the Covey Hill Formation and the overlying Nepean Formation (Wilson 1937; Williams and Wolf 1982; Williams and Telford 1986).

The Covey Hill Formation is composed mainly of sandstone and interbedded feldspathic conglomerate. The formation represents the transgressive phase of the Sauk Sequence into the Ottawa area. This formation is unfossiliferous and ranges in thickness from less than one to 8.8 m (Williams and Wolf 1982; Williams and Telford 1986).

The Nepean Formation contains sandstones and conglomerate, with thicknesses of 60–159 m in the Ottawa area. The upper part of the Nepean Formation consists of dolomitic beds which indicate a rise in sea level in the area. Cross-bedded sandstone with vertical burrows indicates deposition in a lower intertidal to subtidal environment. The conodont fauna in the upper part of the formation indicates a broad Late Cambrian–Early Ordovician age (Wilson 1937; Williams and Telford 1986).

GLOBAL			NORTH AMERICA		OTTAWA AREA		
SYSTEM	SERIES	STAGE	SERIES	STAGE	GROUP	FORMATION	
ORDOVICIAN	UPPER ORDOVICIAN	HIRNANTIAN	CINCINNATIAN	GAMACHIAN		QUEENSTON	
		KATIAN		RICHMONDIAN			
				MAYSVILLIAN			CARLSBAD
				EDENIAN			BILLINGS
	MIDDLE ORDOVICIAN	SANDBIAN	MOHAWKIAN	SHERMANIAN	CHATFIELDIAN (TRENTONIAN)	OTTAWA	LINDSAY
				KIRKFIELDIAN			VERULAM
	DARRIWILIAN	WHITEROCKIAN	TURINIAN (BLACKRIVERIAN)		BOBCAYGEON		
	DAPINGIAN		CHAZYAN		GULL RIVER		
	NOT distinguished		RANGERIAN		SHADOW LAKE		
	ROCKCLIFFE		BLACK HILLSIAN		OXFORD		
	LOWER ORDOVICIAN	FLOIAN	IBEXIAN (CANADIAN)	TULEAN			BEEKMANTOWN
		TREMADOCIAN		STAIRSIAN		POTSDAM	NEPEAN
				SKULLROCKIAN			COVEYHILL
	CAMBRIAN						

Figure 1.4 Cambrian–Ordovician stratigraphic units of the Ottawa area (modified from Wilson 1946; Barnes et al. 1981; Williams and Telford 1986).

### **1.4.1.2 Beekmantown Group**

Lower Ordovician strata of the Ottawa area are represented by the Beekmantown Group which consists mainly of dolostone (Clarke and Schuchert 1899; Williams and Telford 1986). It is subdivided into two formations: the March Formation and the Oxford Formation (Figure 1.4).

The March Formation consists of sandstone and dolostone. Cross-bedding, ripple marks, and burrows are common, suggesting a supratidal to shallow subtidal depositional environment (Bond and Greggs 1973; Williams and Telford 1986). An Early Ordovician age is confirmed by conodont faunas in the March Formation (Greggs and Bond 1971; Bond and Greggs 1973).

The Oxford Formation consists of dolostone with shaly and sandy interbeds (Wilson 1937; Williams and Telford 1986). Calcite-filled vugs and algal lamination indicate a supratidal to intertidal, hypersaline depositional environment (Williams and Telford 1986). Conodonts and trilobites indicate an Early Ordovician age (Bond and Greggs 1976; Ludvigsen 1978).

### **1.4.1.3 Rockcliffe Formation**

In the Ottawa area, the upper Middle Ordovician Rockcliffe Formation consists of interbedded quartz sandstone and shale, assigned to the classic Chazyan in old literature (Wilson 1937; Barnes et al. 1981; Williams and Telford 1986). The presence of desiccation cracks, cross-bedding, and ripple marks indicates a shallow peritidal depositional environment, probably during a sea-level lowstand. The rocks grade from sandstone to shale and limestone up section, pointing to a broad trend of increase in water depth (Williams and Telford 1986).



#### **1.4.1.4 Ottawa Group**

The Ottawa Group, as defined by Wilson (1946a), is a sequence of Upper Ordovician limestone, dolostone, shale, and quartz sandstone (Williams and Telford 1986). It is equivalent to the Simcoe Group in south-central Ontario (Orillia and Manitoulin Island) and the Black River Group and Trenton Group in north-central New York. Williams and Telford (1986) subdivided the Ottawa Group into five formations, including, in ascending order, the Shadow Lake, Gull River, Bobcaygeon, Verulam, and the Lindsay formations (Figure 1.4).

##### **1.4.1.4.1 Shadow Lake Formation**

The Shadow Lake Formation is composed of unfossiliferous sandstone which grades upward to shale and limestone with interbeds of silty dolostone (Williams and Telford 1986). The deposits accumulated in a supratidal to intertidal intracratonic shelf environment (Williams and Telford 1986).

##### **1.4.1.4.2 Gull River Formation**

The Gull River Formation in the Ottawa valley was originally proposed by Liberty (1967) and consists of interbedded limestone, silty dolostone and quartz sandstone of Sandbian (Blackriverian, Turinian) age (Barnes et al. 1981; Williams and Telford 1986). Ripple marks, birdseye structures, stromatolitic structures, and burrows are common, indicating supratidal to intertidal depositional settings (Williams and Telford 1986).

##### **1.4.1.4.3 Bobcaygeon Formation**

The Bobcaygeon is composed of fossiliferous limestone with thin shale partings, with a conodont fauna suggesting a Sandbian to early Katian (Turinian–Chatfieldian, Blackriverian–Trentonian) age (Schope 1966; Barnes 1967; Uyeno 1974; Williams and

Telford 1986). Burrows, cross-bedding and intraclast occurs in the formation, which led Williams and Telford (1986) to propose a shallow subtidal environment above storm wave base.

#### **1.4.1.4.4 Verulam Formation**

The Verulam Formation (Liberty 1967) contains limestone with interbedded shale. The formation ranges in thickness from 32 to 40 m in the Ottawa area. Micritic mudstone and wackestone are dominant, with some shelly packstone interbeds. Burrows, intraclasts and ripple marks are common (Williams and Telford 1986). Common megafossils include brachiopods, trilobites, gastropods, bryozoans, and crinoids. Brachiopods are particularly abundant and diverse, and will be one of the main components of this study. The Verulam Formation is interpreted as deposits in a shallow shelf environment above the storm wave base, and of early Katian age (Barnes et al. 1981).

#### **1.4.1.4.5 Lindsay Formation**

The Lindsay Formation in the Ottawa area overlies on top of the Verulam Formation and contains limestone with shale interbeds (Liberty 1967; Williams and Telford 1986). The formation is Edenian in age (Barnes et al. 1981). Burrows, nodular structure and intraclasts are common, which indicate deposition in an intracontinental shelf environment above storm wave base.

#### **1.4.1.5 Billings Formation**

Wilson (1937) proposed the Billings Formation for the shale-dominated upper Ordovician deposits. The formation is of Edenian age and contains brachiopods, trilobites, and graptolites (Tuffnell and Ludvigsen 1984; Williams and Telford 1986).

#### **1.4.1.6 Carlsbad Formation**

This formation was proposed by Wilson (1937) for the shale, calcareous siltstone and silty limestone deposits in the Ottawa area. Cross-bedding, flute casts and ripple marks are common. The formation is Maysvillian to Richmondian in age.

#### **1.4.1.7 Queenston Formation**

The Queenston Formation is composed mainly of siltstone and shale. This formation is the uppermost Ordovician (Richmondian) rock unit in the Ottawa area (Barnes et al. 1981; Williams and Telford 1986). Brachiopods, bryozoans and crinoids are common in this formation.

#### **1.4.2 Lake Simcoe area**

In the Lake Simcoe area, from Orillia to Peterborough in south-central Ontario, the Late Ordovician rocks overlie the Precambrian basement (Figure 1.5). In this area the regional unconformity indicates regional uplift and erosion of the Sauk sequence during the Cambrian and Early Ordovician. During the Late Ordovician the Tippecanoe transgression inundated the Lake Simcoe area and resulted in the deposition of the Simcoe Group.

The Simcoe Group (Sandbian to middle Katian, Blackriverian to early Maysvillian) is equivalent to the Ottawa Group in the Ottawa area and Black River Group and Trenton Group in New York State. In the Lake Simcoe area the Shadow Lake Formation marks the lowermost unit of the Ordovician sequence (Melchin et al. 1994; Armstrong 1997; Grimwood et al. 1999). The Simcoe Group comprises the Shadow Lake, Gull River, Bobcaygeon, Verulam, and Lindsay (Cobourg) formations (Figure 1.5; Liberty 1969; Melchin et al. 1994; Brett and Rudkin 1997).

#### **1.4.2.1 Shadow Lake Formation**

The Shadow Lake Formation comprises the basal strata in the Lake Simcoe area, consisting of lower arkosic conglomerates and coarse sandstones, grading upward into interbedded silty, calcareous or dolomitic sandstones and terrigenous mudstones (Liberty 1969; Melchin et al. 1994). Sedimentary structures include planar and cross-laminations, ripple marks, mudcracks and *Skolithos*-like burrows. Fossils are very rare in this unit due to the paleo-beach or near-shore depositional settings (Melchin et al. 1994; Brett and Rudkin 1997). Conodont fossils reported from this formation indicate a Sandbian (Blackriveran) age.

GLOBAL	NORTH AMERICA		LAKE SIMCOE AREA	
STAGE	SERIES	STAGE	GROUP	FORMATION
KATIAN	CINCINNATIAN	MAYSVILLIAN	COLLINGWOOD	
		EDENIAN	LINDSAY	
	MOHAWKIAN	CHATFIELDIAN (TRENTONIAN)	SIMCOE GROUP	VERULAM
SANDBIAN		TURINIAN (BLACKRIVERIAN)		BOBCAYGEON
	GULL RIVER			
	SHADOW LAKE			
PRECAMBRIAN				

Figure 1.5 Ordovician stratigraphic units of the Lake Simcoe area (modified from Barnes et al. 1981; Coniglio et al. 1990; Melchin et al. 1994).

#### **1.4.2.2 Gull River Formation**

The Gull River Formation is divided into three members (lower, middle, and upper) by Liberty (1969) in the Lake Simcoe area. It is composed of dolomitic lime mudstone, dolostone, and silty and shaly carbonates towards the base of the formation. More thickly bedded fossiliferous lime mudstone and wackestones are common higher in the formation (Melchin et al. 1994; Brett and Rudkin 1997). Evaporite mineral moulds, sulphate nodules, and mudcracks are common. *Skolithos* and *Diplocraterion* trace fossils are pervasive and well preserved in some thick beds. In the lower member fossils are rare and include fragmentary ostracods and trilobites. Higher in the formation, fossils are more common with brachiopods, trilobites, bivalves, gastropods, bryozoans, and tabulate corals. The lower part of the formation is interpreted as hypersaline supratidal to intertidal flats, grading into a restricted lagoon. Increased fossil content and degree of bioturbation in the upper part of the formation indicate more open marine and subtidal lagoonal conditions (Melchin et al. 1994).

#### **1.4.2.3 Bobcaygeon Formation**

The Sandbian-Katian (Blackriverian-Trentonian) boundary lies within the Bobcaygeon Formation in the Lake Simcoe area. The formation has been divided into lower, middle, and upper members (Liberty 1969; Melchin 1982; Melchin et al. 1994; Brett and Rudkin 1997).

The lower member is equivalent to the Coboconk Formation used by some authors and consists of mainly bioclastic and peloidal grainstones, packstones and wackestones (Melchin et al. 1994). Algal-coated grains (oncolites) and intraclasts are common. Ichnofossils include burrows such as *Planolites* and *Chondrites* (Figure 1.6; E, F).

Sedimentary structures such as planar, ripple and trough cross-bedding are common. Fossils are abundant throughout this formation, including brachiopods, bryozoans, gastropods, bivalves, nautiloids, tabulate and rugose corals, and stromatoporids (Figure 1.6; B, C). Conodonts and chitinozoans indicate a Sandbian-Katian boundary near the top of the lower member (Winder et al. 1975; Melchin et al. 1994), whereas the brachiopods (e.g. common *Paucicrura*) suggest the boundary near the base of the member (see also Liberty 1969). This unit represents a complex of offshore carbonate sand shoals on a shallow shelf (Melchin et al. 1994).

The middle-upper member is approximately correlative to the Kirkfield Formation in earlier usage and consists of limestone beds with thin shaly interbeds near the base which grades upward into bioclastic packstones and grainstones. Trace fossils, hardgrounds, ripples and cross-lamination are common (Figure 1.6; D, F). The member is richly fossiliferous, with abundant bryozoans, brachiopods and echinoderms, suggesting an open marine, shallow subtidal environment.

#### **1.4.2.4 Verulam Formation**

The Verulam Formation consists mainly of interbedded limestone and shale. Liberty (1969) divided this formation into two members in the Lake Simcoe area. The lower shaly member constitutes the bulk of the Verulam Formation. The upper member is well developed only in the Lake Simcoe area, characterized by bioclastic wackestone and packstone (Melchin et al. 1994). The lower member is heterogeneous and composed of varying amounts of interbedded fossiliferous lime mudstones, wackestones, bioclastic packstones, grainstones, and calcareous shales. Above this interval, in the upper member, lime mud-dominated beds decrease while bioclastic beds increase in number and

thickness (Melchin et al. 1994). In the Orillia area the Bobcaygeon Formation separated from the Verulam Formation by an ash bed (Fig. 1.6; A).

Sedimentary structures include nodular bedding and common bioturbation in the lime mudstones and wackestones, planar and trough cross-lamination, and graded bedding (Melchin et al. 1994). Ichnofossil diversity is high, such as *Planolites*, *Chondrites*, *Phycodes*, and *Trypanites* (Brett and Rudkin 1997). The Verulam Formation contains the highest faunal diversity of the Simcoe group. Trilobites, bryozoans, echinoderms, gastropods, cephalopods, and corals are abundant (Melchin et al. 1994; Brett and Rudkin 1997). Brachiopods are a dominant group in this formation and will be the main object of this study.

Based on chitinozoan and conodonts, the Verulam Formation is early Katian in age. In North American stratigraphy, its base coincides with the base of the Shermanian stage and the uppermost part is Edenian (Melchin et al. 1994). Its brachiopods are typical of North American Trentonian fauna (e.g. *Paucicrura*, *Rhynchotrema*, and *Parastrophina*) that can be traced from New York to Minnesota. The recurrent storm-generated shell beds and the presence of a rich and diverse benthic shelly fauna in the Verulam Formation suggest an open marine depositional setting near the normal storm wave base.



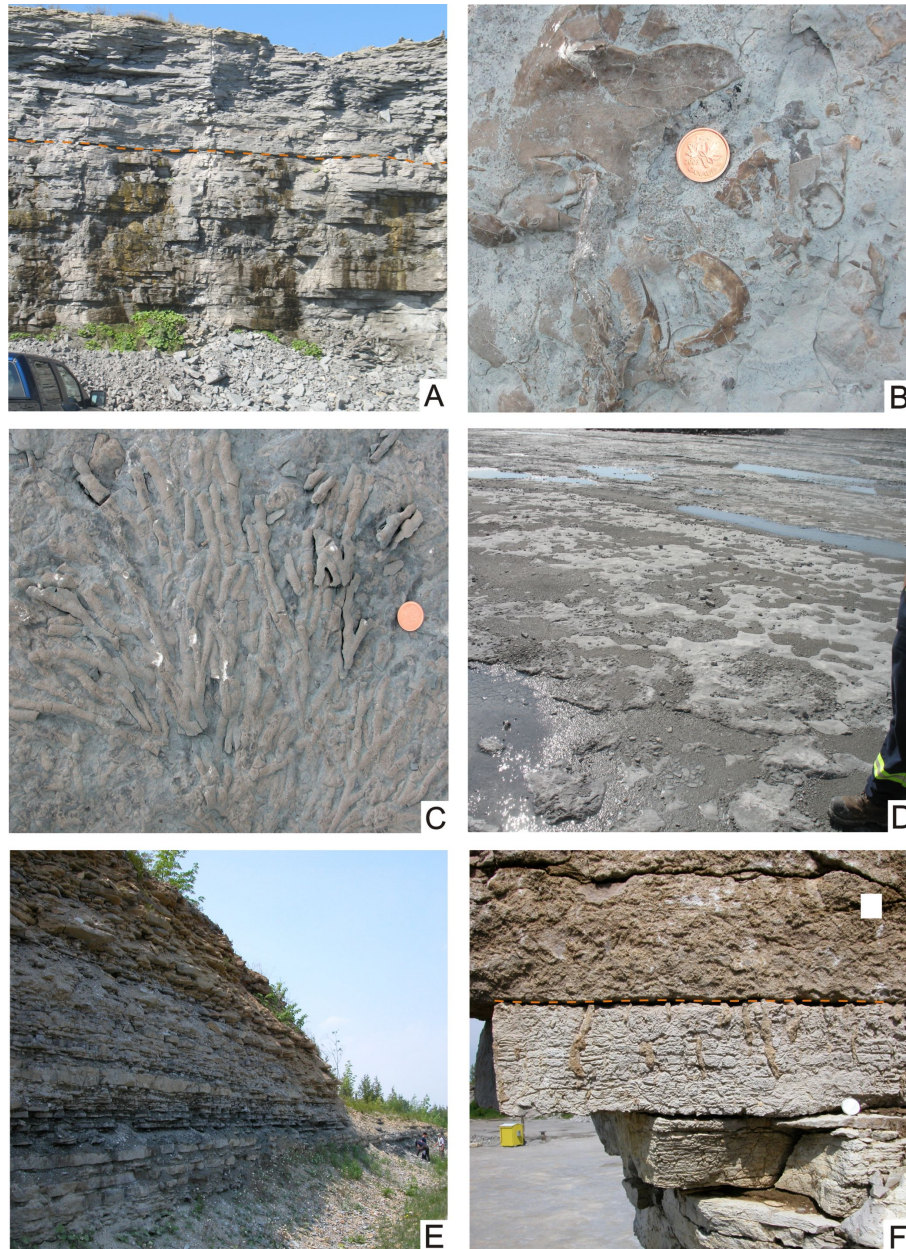


Figure 1.6 Formations and sedimentary structures in the Lake Simcoe area. A) Bobcaygeon and Verulam formations, the dotted line indicates the bentonite bed, which marks the contact between the Bobcaygeon and Verulam formations; B) Bioclastic grainstone with brachiopod shells; C) Ichnofossil *Chondrites* in the Bobcaygeon Formation; D) Hardground in the Bobcaygeon Formation; E) Lindsay Formation; F) Ichnofossil *Skolithos* in the Gull River Formation.

#### **1.4.2.5 Lindsay Formation**

The Upper Ordovician Lindsay Formation is approximately equivalent to the Cobourg Formation of earlier workers (Raymond 1921; Liberty 1969; Winder et al. 1975; Ludvigsen 1978). The formation is divided into a lower and an upper member (Kay 1937; Melchin et al. 1994; Brett and Rudkin 1997). The lower member consists mainly of interbedded bioclastic calcarenites, microcrystalline limestones, and calcareous shales. Intraclasts and hardgrounds are common in the lower member. One of the best natural exposures is a roadside bluff along local Highway 6 southeast of Orillia (Figure. 1.6 E).

The upper member includes the Collingwood Member and consists predominantly of laminated, organic-rich lime mudstones, interbedded with thin wackestone layers (Melchin et al. 1994).

The fauna includes trilobites (e.g. *Ceraurinus*, *Isotelus*, *Ceraurus*), gastropods (e.g. *Hormotoma*, *Fusispira*), echinoderms, and cephalopods. Brachiopods of the lower Lindsay Formation are similar to those of the Verulam Formation, such as *Glyptorthis*, *Paucicrura*, *Vellamo*, *Thaerodonta*, and *Rafinesquina*. The trilobite fauna in the Lindsay Formation, however, indicate an Edenian to early Maysvillian age.

Winder (1960) and Liberty (1969) proposed that the Lindsay Formation represents a deep shelf setting. A shallow shelf to shoal environment has been suggested for the lower member, which grades into deeper shelf conditions for the upper Collingwood Member (Melchin 1982).

#### **1.4.3 Manitoulin Island**

Paleogeographically, Manitoulin Island was located on the northeast margin of the Michigan Basin, where the Ordovician succession overlies the Precambrian basement,

with the Shadow Lake Formation being the oldest Paleozoic strata in the Manitoulin Island area. The Simcoe Group (sensu Liberty 1969) is divided, in ascending order, into the Gull River, Bobcaygeon, Verulam, and Lindsay formations (Figure 1.7). Brachiopods from the upper part of the Shadow Lake Formation, however, are similar to those in the Gull River Formation, and thus it may be convenient to treat the Shadow Lake Formation as the basal part of Simcoe Group in the Manitoulin area (Copper and Long 1993). The Simcoe Lake Group is overlain by the Nottawasaga Group, which comprises the Collingwood, Sheguiandah, and Georgian Bay formations in the Manitoulin area (Liberty 1969; Copper and Long 1993).

#### **1.4.3.1 Shadow Lake Formation**

Foerste (1912) described this formation as the basal bed in the Manitoulin Island area and correlated it with the Lowville from New York. The Shadow Lake Formation was first proposed by Foerste (1912) and consists of reddish and greenish calcareous shales, siltstones and muddy sandstones, and silty dolostone. The upper reddish beds are bioturbated by horizontal burrows about 1 cm in diameter (Copper and Long 1993). On Birch Island the upper part of the formation contains brachiopods (strophomenides and rhynchonellides) and bryozoans (Foerste 1912; Copper and Long 1993).

GLOBAL	NORTH AMERICA		MANITOULIN ISLAND	
STAGE	SERIES	STAGE	GROUP	FORMATION
KATIAN	CINCINNATIAN	RICHMONDIAN	NOTTAWASAGA GROUP	GEORGIAN BAY
		MAYSVILLIAN		SHEGUIANDAH
		EDENIAN		COLLINGWOOD
	MOHAWKIAN	CHATFIELDIAN (TRENTONIAN)	SIMCOE GROUP	LINDSAY
		TURINIAN (BLACKRIVERIAN)		VERULAM
				BOBCAYGEON
SANDBIAN			GULL RIVER	
			SHADOW LAKE	
PRECAMBRIAN				

Figure 1.7 Ordovician stratigraphic units of Manitoulin Island and its vicinity (modified from Copper and Long 1993).

### 1.4.3.2 Gull River Formation

The Gull River Formation was introduced by Okulitch (1939) for the strata overlying the Shadow Lake Formation. The formation is composed of sandy dolostones and red or green shale. The Gull River Formation in the Manitoulin area is relatively thin compared to the Gull River in the type area and probably represents only the upper Gull River in this region (Copper and Long 1993). Burrow traces typical of the *Skolithos* ichnofacies are prominently developed, similar to those in the same formation of the Lake Simcoe area (Figure 1.8; A). This formation is locally fossiliferous, with common nautiloids, corals (e.g. *Tetradium*) and stromatoporids, and relatively rare brachiopods (Copper and Long 1993). A peritidal depositional environment was proposed by Copper (1978).

### 1.4.3.3 Bobcaygeon Formation

The Bobcaygeon Formation named by Liberty (1969) corresponds approximately to the Cloche Island Beds of Foerste (1912) and consists of dark grey calcareous shales at the base and brownish weathering limestones at the top (Copper and Long 1993).

Based on the megafauna, Foerste (1912) proposed the lower part of the formation to be Blackriverian (Sandbian) in age and the limestones at the top Trentonian (early Katian). The upper part of the formation contains abundant brachiopods (*Rafinesquina*, *Anazyga*, *Idiospira* and *Rostricellula*), nautiloids, corals, and stromatoporoids (Foerste 1912; Copper and Long 1993). The formation was interpreted as a shallowing-upward succession, with increased storm influence upsection (Copper and Long 1993).

#### **1.4.3.4 Verulam Formation**

On Goat Island (a small island between Great Cloche and Manitoulin islands), the Verulam Formation is 13–15 m thick and consists of micritic mudstone, brachiopod and bryozoan, wackestone and packstone, and some thin shaly partings. Ripple marks with wavelengths of 30–50 cm are well preserved at some shoreline outcrops, associated with brachiopod shell beds. Megaripples ripple with wavelengths of 1.5 to 3.4 m occur in the upper beds (see figure 1.8, B; Liberty 1969; Copper and Long 1993). These strata are correlative with the upper Trentonian (Shermanian) in New York (Fortey et al. 1991).

In the Manitoulin area (Goat Island) the Verulam Formation is very fossiliferous and various communities replace each other laterally and also from base to top. Trilobites, branching bryozoans, and corals are common (Figure 1.8; S, D, E, F). Brachiopods are dominant and include large *Rafinesquina*, *Rhynchotrema*, *Anazyga*, and *Idiospira*. The rich brachiopod fauna is included in this thesis project. The depositional environment is interpreted to be a shallow, shifting calcareous shoal sequence with water depth above normal wave base (Copper and Long 1993).

#### **1.4.3.5 Lindsay Formation**

The Lindsay Formation is exposed around the town of Little Current (northeastern Manitoulin Island). The formation consists of dark grey, thinly interbedded, calcareous shales, micrites, and dolomicrite. It is correlated with the Edenian of New York (Copper and Long 1993). The fossil preservation in the Lindsay Formation of this area is relatively poor because of dolomitization and no fossil material from this area was deemed suitable for this study.

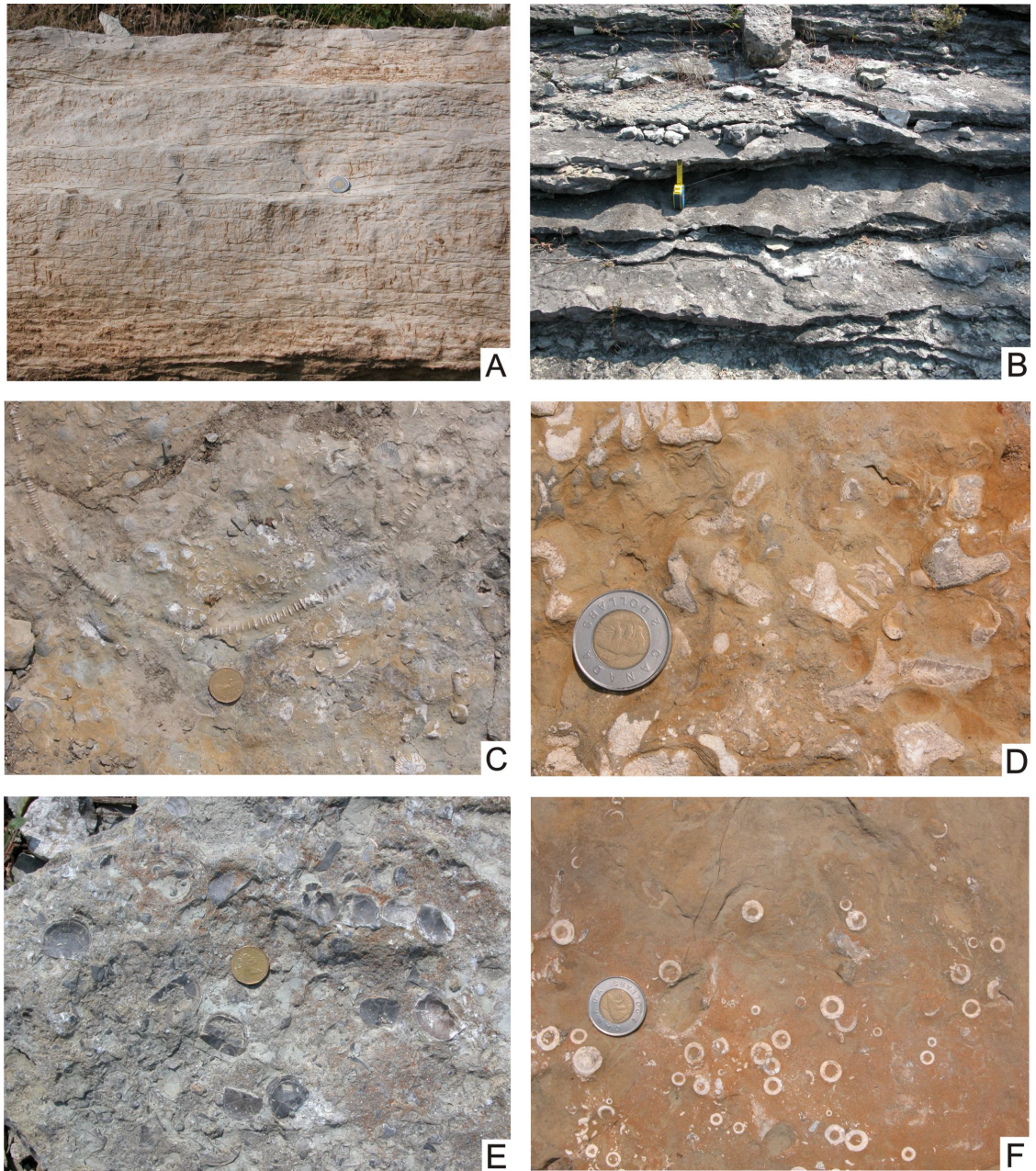


Figure 1.8 Formations and sedimentary structures on Manitoulin Island. A) Gull River Formation; note the ichnofossils *Skolithos* within the formation; B) Ripple mark structure in the Verulam Formation; C) Fossils of crinoids and brachiopods in the Verulam Formation; D) Fossils of bryozoans and brachiopods in the Verulam Formation; E) Fossiliferous slab of the Verulam Formation with fossils of brachiopod shells; F) Crinoidal wackestone of the Verulam Formation.

#### **1.4.3.6 Collingwood Formation**

Raymond (1912) proposed the Collingwood Formation for fine grained limestone with soft brown shale. In the Manitoulin Island area, this unit is treated as a separate formation from the Lindsay Formation. The contact between the Collingwood Formation with the underlying Lindsay Formation is marked by a sharp erosional surface (Russell and Telford 1983). The Formation contains an impoverished fauna of brachiopods (mostly lingulates), trilobites, crushed nautiloids, and graptolites. The depositional environment was predominantly anoxic, with short episodes of oxygenation by severe storms (Copper and Long 1993).

#### **1.4.3.7 Sheguiandah Formation**

The Sheguiandah Formation is exposed in road outcrops between Sheguiandah and Little Current (Foerste 1912). The formation is composed of greenish grey shale and thin limestone beds in the upper unit. The formation contains numerous thin shell beds, with abundant bryozoans and dalmanellid brachiopods that are similar to those of the Kope Formation in the Cincinnati type area, probably of Edenian (middle Katian) age.

#### **1.4.3.8 Georgian Bay Formation**

The Georgian Bay Formation was introduced by Liberty (1964) for carbonates and shales between the Shequiandah (Whitby) and red Queenstone shales which is absent in the Manitoulin area. The formation is divided into a Lower Member and an Upper Member, and the Upper Member is divided further into the Meaford and Kagawong submembers (Liberty 1964, 1969; see also Stott and Jin 2007 for a summary). The Lower Member is claystone-rich, with carbonate interbeds. The Meaford Submember comprises up to 15 m of argillaceous dolostones and dolomitic limestones interbedded with bluish



green claystone interbeds. The overlying Kagawong Submember consists of up to 30 m of fine to medium crystalline, sparsely to moderately fossiliferous dolostone, with minor claystone interbeds. Basal biostromal carbonates with a relatively diverse, open marine shelly fauna dominated by corals and brachiopods change upward to finer grained, sparsely to moderately fossiliferous micrites with a relatively diverse bivalve fauna (Pojeta and Stott 2007).

### **1.5 Objectives and organization of the thesis**

The current study is concerned mainly with the Verulam Formation (lower Katian, Trentonian) in the study areas. The brachiopod-rich limestone (Verulam Formation) provides an important geological setting and faunal samples for the paleoenvironmental and paleobiogeographical reconstruction and interpretation during the Trentonian.

The early Katian, historically known as “Trentonian” in North America and currently formalized as the Chatfieldian, is a significant geological time interval. The Trentonian marine transgression was part of the most widespread global “Caradoc Transgression” (Fortey 1984). The origin of epicontinental fauna coincided with the onset of the Trentonian transgression. The brachiopods constitute the most important and diverse groups of epicontinental fauna which evolved during the Trentonian. Brachiopod fauna from many Ontario localities of the Verulam Formation and equivalent strata (e.g. Ottawa valley, Lake Simcoe area, and Manitoulin Island) are among the classic Trentonian faunas (e.g. Wilson 1946; Foerste 1924), although they are in need of taxonomic revisions. Wilson (1914, 1946) provided a qualitative study on the Trentonian brachiopod faunal characters in the Ottawa area. So far, there has been a lack of quantitative study of Trentonian brachiopod faunas of Ontario or elsewhere in North

America. Thus the true diversity of Trentonian brachiopods is poorly known for the study areas.

The research presented in this thesis employs quantitative approaches, including multivariate analyses of biometric measurements of shell morphology and faunal compositions, with the aim to improve our understanding of Trentonian brachiopod faunas of Ontario, and their relationships to related faunas elsewhere. The organization and objectives of this thesis project are explained below.

Chapter 1. General background on brachiopod evolution, paleoenvironment, and paleogeography during the Great Ordovician Biodiversification Event (GOBE). Discussion on the significance and problems regarding the early Katian (Trentonian) brachiopod faunas of Ontario and elsewhere in North America.

Chapter 2. General discussions on the brachiopod fossil material and methods to be used for numerical analyses to detect trends of morphological changes in time and space, as well as paleobiogeographical patterns.

Chapter 3. An in-depth case study on the Late Ordovician (Katian) *Rhynchotrema-Hiscobeccus* evolutionary lineage, which has an exceptionally well-preserved fossil record in North America. The study also includes the taxonomic revision of a key, but hitherto poorly understood, species in this lineage. This evolutionary lineage originated from the Trentonian brachiopod fauna and subsequently became an important component of the brachiopod fauna that thrived in the epicontinental seas of Laurentia (North America and Greenland). This study aims to explore the evolutionary processes and patterns of the marine shelly benthos evolution during a major sea level rise during the Late Ordovician.

Chapter 4. Paleobiogeography of the Trentonian faunas in North America and comparisons with coeval faunas in other paleocontinents, such as Baltica (northern Europe), Avalonia (England and Wales), Kazakhstan, South China, and Australia. The main objective of this chapter is to use the faunal similarity levels among various regions to interpret the paleoclimatic and paleogeographic control on the evolution of a major group of shelly benthos on the global scale.

Chapter 5. Conclusions. The main findings of the thesis project will be summarized regarding the significance of early Katian Trentonian brachiopod faunas.

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## Chapter 2 – Material and Methods

### 2.1 Early Katian (Trentonian) brachiopod collections

Specimens of brachiopods of early Katian (Chatfieldian, Trentonian) age that are featured in this study were obtained from three main areas in Ontario: the Ottawa area, Lake Simcoe area, and Manitoulin Island. Brachiopods of similar age or related brachiopod faunas of younger Ordovician strata from Baffin Island (northern Canada), Minnesota (USA), and New York (USA) were used for comparative purposes to determine broader trends of evolution, paleoenvironmental gradients, and paleobiogeographical patterns.

#### 2.1.1 The Ottawa area

Most of the Trentonian brachiopods were collected by earlier workers (notably Wilson 1913, 1946) from the Ottawa area and are currently stored at the Geological Survey of Canada. Some of these (samples of *Parastrophina* and *Rhynchotrema* in particular) are on loan for this study. For paleobiogeographic analysis (Chapter 4), Wilson's monographic compilation of brachiopods from the Ottawa area will be used.

#### 2.1.2 Lake Simcoe area (Orillia and vicinity)

Several samples of Trentonian brachiopods were collected from the Orillia area, mostly from quarries and roadside outcrops east of Lake Simcoe. These include samples from the Bobcaygeon and Verulam formations exposed at the Carden Quarry, Mara roadside ditch, Centennial Road section, and the Lakefield Quarry near Peterborough, and the Lindsay Formation at the Highway 6 roadside outcrop (Figure 2.1).

Ramara ditch section (Figures 2.1, 2.2); Sample Mara-1 (0-2), 22 specimens, Verulam Formation (Chatfieldian, lower Katian), Ramara Concession No. 1 west of

Highway 12, roadside ditch section, UTM 170644080E, 492911N, Lake Simcoe area, Ontario. This seasonal drainage ditch exposes about 1.5 to 2 m of the lower Verulam Formation. The strata consist of micritic mudstone, wackestone, with interbeds of skeletal packstone and calcareous shale. The packstone beds have abundant brachiopods, trilobites, bryozoans, and mollusks.

Brachiopods from this locality include the following taxa:

*Anazyga recurvirostra* (21 specimens),

*Lingulid* (1 specimen),

*Parastrophina hemiplicata* (31 specimens),

*Plaesiomys subcircularis* (8 specimens),

*Plectorthis* (2 specimens),

*Strophomena sp.* (7 specimens),

*Rhynchotrema* (3 specimens),

*Thaerodonta* (6 specimens),

Two large slabs of shell beds with abundant brachiopods and other megafossils (Figure 2.2) were collected for use as census assemblages. These are used for assessing the total faunal diversity, especially for the paleobiogeographic analysis in Chapter 4. Well-preserved shells of *Rhynchotrema* are incorporated in the biometric analysis in chapter 3.

The brachiopod fauna recovered from the Ramara ditch section are similar to those reported by Sinclair et al. (1969) from the Lakefield Quarry (Canada Cement Company) near Peterborough, Ontario.

Carden Quarry; Sample CQ-1, Bobcaygeon Formation, and Sample CQ-3, Verulam Formation, exposed in the uppermost 2–3 m of the quarry (Brett and Rudkin 1997). The following brachiopod samples collected during this study are incorporated into the paleobiogeographic analysis in Chapter 4:

CQ-1

*Hesperorthis* sp. (> 10 loose and embedded specimens),

*Idiospira* sp. (2 specimens),

*Sowerbyella* sp. (> 20 loose and embedded specimens),

*Paucicrura* sp. (> 300 loose specimens).

CQ-3

*Paucicrura* sp. (4 specimens),

*Rhynchotrema increbescens* (7 specimens).

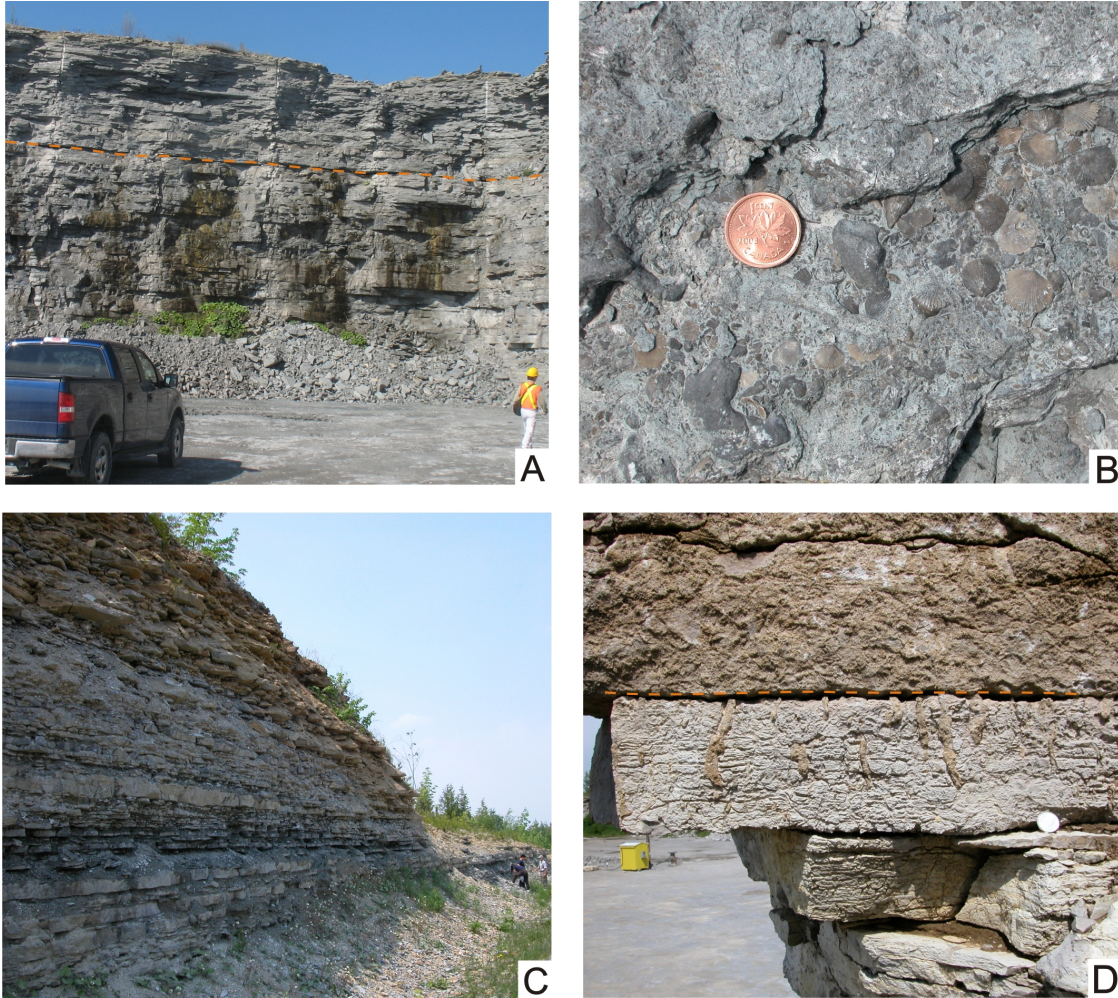


Figure 2.1 Late Ordovician formations in the Lake Simcoe area A) Bobcaygeon and Verulam formations exposed at the Carden Quarry, Lake Simcoe area; the dotted line indicates the bentonite bed between the Bobcaygeon and Verulam formations; B) Carden Quarry floor, shell rich bed with brachiopod shells; C) Lindsay Formation at the Highway 6 roadside outcrop; D) Gull River and Bobcaygeon formations; the dotted line indicates the contact between formations; note the Ichnofossil *Skolithos*.

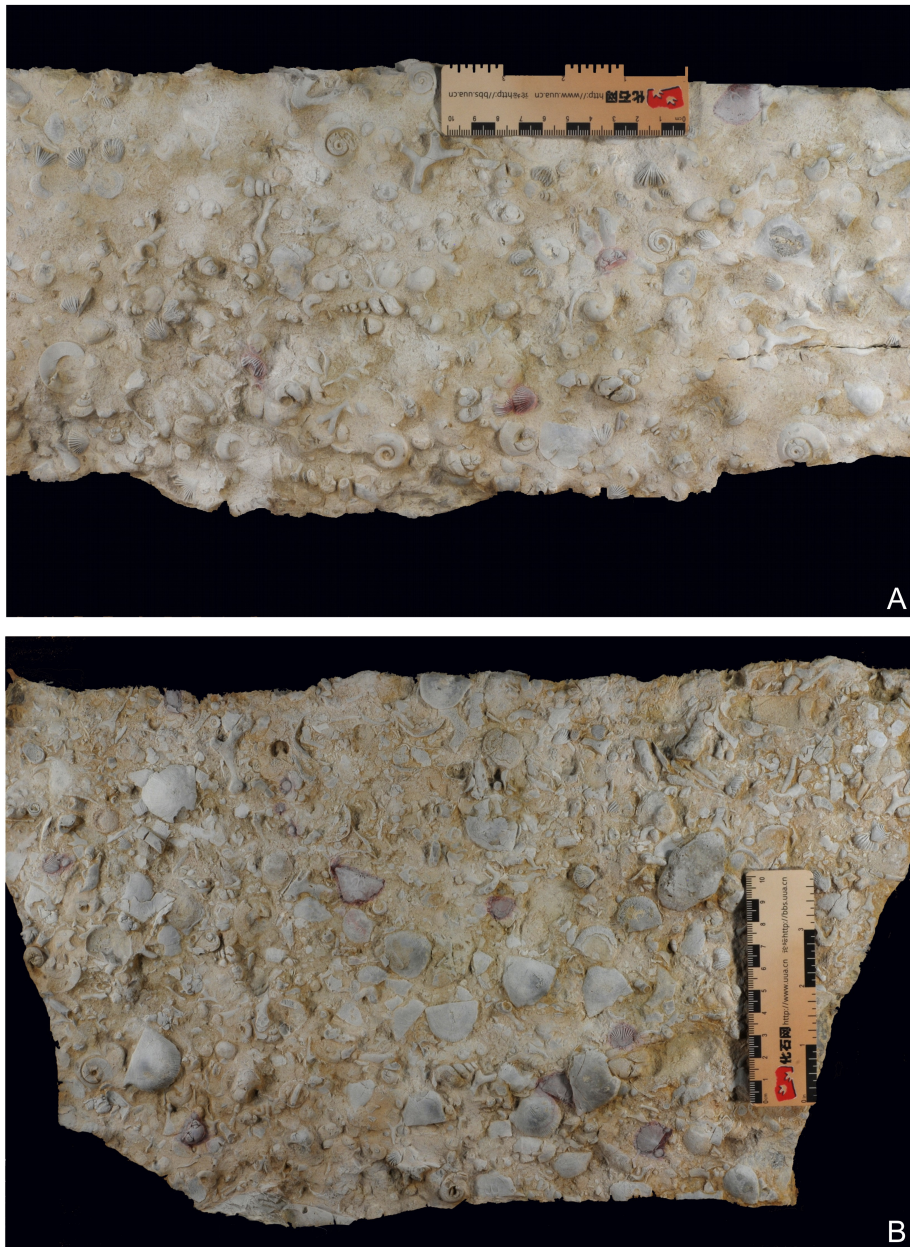


Figure 2.2 Two slabs of shell rich beds (A and B) from Ramara ditch, Lake Simcoe area; note the abundant fossils including brachiopods, gastropods, and bryozoans.

### 2.1.3 Manitoulin Island and vicinity

Goat Island section, Verulam Formation (lower Katian, Chatfieldian), lakeshore section by abandoned Hwy 6 bend, north of Little Current, UTM 17, 429039E, 5093089N.

Brachiopods include:

*Plaesiomys browni* (Wilson, 1946), 27 shells from a thin calcareous mudstone parting between storm-generated, strophomenide-dominated brachiopod shell-beds, with scoured bases and prominent wave ripples of decimeter-scale wave length;

*Rafinequina* sp. (abundant as shell-beds);

*Rhynchotrema increbescens* (> 10 specimens loose and embedded).

Water Street roadcut section by Boyle Marina. Verulam Formation, stratigraphically right above the Goat Island section, 45.982053°N, 81.927463°W. Micritic mudstone and *Prasopora*-dominated bryozoan biostrome beds, with brachiopods in soft calcareous shale partings.

*Rhynchotrema increbescens* (> 30 specimens); these shells are used in biometric analysis in chapter 3.

### 2.1.4 Baffin Island

The Ordovician sedimentary rocks of southern Baffin Island include the Frobisher Bay Formation, Amadjuak Formation, Akpatok Formation, and the Foster Bay Formation (Figure 2.3). The Frobisher Bay Formation (Middle Ordovician) unconformably overlies Precambrian rocks and is very well exposed at southern Baffin Island. The formation consists of uniformly bedded, greyish brown limestone and dolomitic limestone (Sanford and Grant 2000, Bolton 2000).



Brachiopods used in this study are from the Upper Ordovician (middle Katian) Amadjuak Formation, Silliman's Fossil Mount. Here, the formation consists of thinly to thickly bedded limestones and shales. This formation is divided into three informal units: a lower Unit 1 is composed of uniform to nodular grey limestone and interbedded shale; a middle Unit 2 which contains nodular, flaggy to ruby weathering, thin bedded limestone with interbedded shale; and an upper Unit 3 with massive, nodular bedded limestone and dolomitic limestone (Sanford and Grant 2000, Bolton 2000). In the upper part of the Amadjuak Formation (Edenian–lower Maysvillian), brachiopods are abundant, diverse, and well-preserved (Bolton 2000). A small-shelled form of the rhynchonellide brachiopod *Hiscobeccus*, previously reported as two subspecies of *Rhynchotrema* by Roy (1941), forms an important part of the biometric analysis in Chapter 3.

GLOBAL			NORTH AMERICA		BAFFIN ISLAND			
SYSTEM	SERIES	STAGE	SERIES	STAGE	GROUP	FORMATION		
ORDOVICIAN	UPPER ORDOVICIAN	H	CINCINNATIAN	GAMACHIAN		FOSTER BAY		
		KATIAN		RICHMONDIAN				
				MAYSVILLIAN				
				EDENIAN				
		SANDBIAN	MOHAWKIAN	SHERMANIAN	CHATFIELDIAN (TRENTONIAN)	FROBISHER BAY		
				KIRKFIELDIAN				
				ROCKLANDIAN				
		TURINIAN (BLACKRIVERIAN)						
		PRECAMBRIAN						

Figure 2.3 Ordovician stratigraphic units of Baffin Island (modified from Sanford and Grant 2000; Bolton 2000)

### 2.1.5 Minnesota

In Minnesota, the Tippecanoe sequence begins with the St. Peter Sandstone, followed by shale and carbonate rocks of the Glenwood and Platteville formations, and carbonate rocks of the Galena Group (Figure 2.4). The Tippecanoe sequence ended with deposition of the Dubuque and Maquoketa formations (Lively et al. 1997).

The St. Peter Formation consists of fine to medium grained, texturally mature quartz sandstone. The fossils from this formation include mainly gastropods, bivalves, nautiloids, bryozoans, and conodonts (Witzke 1980). Similar sandstone deposits were widespread and diachronous across North America at the base of the Tippecanoe transgressive sequence, as sand accumulations in near-shore shallow marine environments were related to back-stepping shorelines during the transgression (Sardeson 1932; Stauffer 1934; Austin 1969; Ojakangas and Matsch 1982). Similar mature quartz arenite of the Winnipeg Formation in the Williston Basin, for example, also contains brachiopods and other shelly fossils.

In southeastern Minnesota, the Glenwood Formation is underlain by the St. Peter Formation and overlain by the Platteville Formation (Parham and Austin 1967; Mossler and Bloomgren 1992). The Glenwood Formation contains a grey-green shaly unit with a sandy base (Austin 1969). Witzke (1980) interpreted this formation as an off-shore facies of the youngest St. Peter Formation which deposited along the Transcontinental Arch.

The Platteville Formation is a carbonate sequence between the Glenwood and Decorah formations and contains three members in southeastern Minnesota (Weiss 1957; Austin 1969; Mossler 1985; Ludvigson et al. 2004). The lower Pecatonica Member is composed of yellowish-brown, medium to fine grained dolomitic limestone. The middle

McGregor Member consists of grey, fine grained dolomitic limestone with interbedded brown shale. The McGregor Member is divided further into a lower Mifflin Submember and an upper Grand Detour submember (Ludvigson et al. 2004). The Mifflin Submember contains a rich and diverse megafauna dominated by brachiopod and bryozoans. Well preserved shells of *Rhynchotrema* from this unit are among the oldest representatives of the genus and are used in the biometric analysis in Chapter 3. The brachiopod fauna of the McGregor Member straddles the Sandbian–Katian (Turinian–Chatfieldian, Blackriverian–Trentonian) boundary, and is incorporated into the dataset for paleobiogeographic analysis in Chapter 4.

The upper or Carimona Member is composed of fine grained, light olive grey limestone with interbedded shale, and the Deicke K-bentonite at the top (Leslie and Bergström 2005). The Platteville Formation is the most fossiliferous limestone in Minnesota and represents a shallow-marine environment (Weiss 1957; Austin 1969; Ojakangas and Matsch 1982; Mossler and Bloomgren 1992).

The overlying Galena Group contains a thick succession of carbonate and shale strata which covers much of central and eastern Iowa, southeastern Minnesota, Wisconsin and northern Illinois (Ludvigson et al. 2004; Witzke and Ludvigson 2005). The Decorah Formation at the base of the group is the most widespread and thick shale of the Paleozoic deposits in Minnesota (Ludvigson et al. 2004), and is divided into the Spechts Ferry, Guttenberg, and Ion members (Ludvigson et al. 1996, 2004; Emerson et al. 2004).

The Decorah Formation contains diverse and abundant brachiopods, bryozoans, corals, trilobites and conodonts (Witzke 1980). According to Byers et al. (2001) the Decorah Formation was deposited in a tectonic downwarp (Hollandale Embayment)

which was bounded by the Wisconsin Arch and Transcontinental Arch on the east and northwest respectively, with the lower shale facies deposited in dysoxic subtidal settings, and the upper carbonate facies under more oxic conditions (Ludvigson et al.1996).

Above the Decorah Formation, the Galena Group comprises the Cummingsville, Prosser, and Stewartville formations (Austin 1969; Mossler 1985, 1987; see also Figure 2.4 herein), but these units are less fossiliferous than the Decorah Formation.

Brachiopods from the Decorah Formation are characteristic of the early Katian (early Chatfieldian) “Trentonian fauna” of North America (Rice 1987; Jin 2012), and form an important component of the dataset used in the multivariate analyses of this thesis (Chapter 4). Typical taxa include:

*Cincinnetina minnesotensis*

*Doleroides pervetus*

*Hesperorthis tricenaria*

*Manespira nicolleti*

*Paucicrura rogata*

*Pionodema subaeguata*

*Plaesiomys meedsi*

*Rhynchotrema wisconsinense* (5 shells used in Chapter 3)

*Rostricellula minnesotensis*

*Sowerbyella minnesotensis*

*Tetraphalerella planodorsata*

*Zygospira recurvirostris*

GLOBAL		NORTH AMERICA		MINNESOTA			
SERIES	STAGE	SERIES	STAGE	GROUP	FORMATION	MEMBER	
UPPER ORDOVICIAN	HIRNANTIAN	CINCINNATIAN	GAMACHIAN	MAQUOKETA		CLERMONT	
			RICHMONDIAN			ELGIN	
			MAYSVILLIAN			DUBUQUE	
	EDENIAN						
	MOHAWKIAN		GALENA	STEWARTVILLE			
				PROSSER			
				CUMMINGSVILLE			
	SANDBIAN		CHATFIELDIAN (TRENTONIAN)	DECORAH	ION GUTTENBERG SPECHTS FERRY		
			TURINIAN (BLACKRIVERIAN)		CARIMONA MCGREGOR PECATONICA		
	MIDDLE ORDOVICIAN		DARRIWILIAN	WHITEROCKIAN	CHAZYAN	GLENWOOD	
NOT distinguished							
RANGERIAN		ST. PETER					
LOWER ORDOVICIAN	FLOJIAN	IBEXIAN (CANADIAN)	BLACK HILLSIAN	PRAIRIE DU CHIEN		SHAKOPEE	
			TULEAN			ONEOTA	
	TREMADOCIAN		STAIRSIAN				
	SKULLROCKIAN						
	CAMBRIAN					JORDAN	
				ST. LAWRENCE			

Figure 2.4 Ordovician stratigraphic units of Minnesota (modified from Ross et al. 1982; Bergström and Mitchell 1992; Swain 1996; Lively et al. 1997; Kolata et al. 2001; Emerson et al. 2004; Ludvigson et al. 2004).

### 2.1.6 New York

The classic “Trenton Group” in New York was deposited on a carbonate platform west of the Taconic Orogeny (Chapple 1973, Cisne et al. 1982). The lower Trentonian strata, commonly known as the “Trenton Limestone” represent a major phase of marine transgression during the early Katian (Titus and Cameron 1976).

In New York State, the Trenton Group is divided, in ascending order, into the Napanee, Kings Falls, Sugar River, Denley, Steuben, and Hillier formations (Figure 2.5). The basal formation of the Trenton Group is most likely late Sandbian (late Turinian) in age.

The lower Trenton formations (Napanee, Kings Falls, and Sugar River) formed a transgressive (deepening) sequence, from peritidal to relatively deep shelf facies (Titus 1986). This is indicated by the presence of mudcracks, birdseye structures, intraclasts, and channel structures in the lower Napanee Formation (Walker and Laporte 1970; Titus and Cameron 1976). The overlying Kings Falls Formation and Sugar River Formation are characterized by fossiliferous limestone, nodular limestone, interbedded with organic-rich shales, and bearing common horizontal burrows, suggesting a relatively deep and quiet water depositional setting (Kay 1968; Titus and Cameron 1976).

The middle Trenton comprises the Denley Formation, which consists mainly of nodular limestones and laterally changes into the Utica black shale facies of the Appalachian Basin (Kay 1968). The Denley Limestone was probably deposited in an open marine, mid-shelf depositional environment on the west side of the Utica black shale basin (Titus 1986).

The upper Trenton strata (the Steuben and Hillier formations) were accumulated during a general deepening event, punctuated by several shallowing episodes, and truncated by an erosional surface at the top (Titus 1986).

Titus (1986) recorded several high-diversity shelly communities, dominated by brachiopods and trilobites, which shifted with transgressive and regressive cycles. The rich and diverse brachiopod fauna from the Trenton Group of New York is used for paleobiogeographic analysis in Chapter 4.



GLOBAL		NORTH AMERICA		NEW YORK	
SERIES	STAGE	SERIES	STAGE	GROUP	FORMATION
UPPER ORDOVICIAN	KATIAN	CINCINNATIAN	EDENIAN	TRENTON	HILLER
			CHATFIELDIAN (TRENTONIAN)		STEUBEN
					DENLEY
					SUGAR RIVER
					KINGS FALLS
	SANDBIAN	MOHAWKIAN	TURINIAN (BLACKRIVERIAN)	BLACK RIVER	NAPANEE
					SELBY
					WATERTOWN
					LOWVILLE
					PAMELIA
MIDDLE ORDOVICIAN	DARRI WILIAN	WHITEROCKIAN	CHAZYAN	CHAZY	ST. MARTIN
			NOT distinguished		ROCKLIFFE
	DAPINGIAN		RANGERIAN		
LOWER ORDOVICIAN	FLOIAN	IBEXIAN (CANADIAN)	BLACK HILLSIAN	BEEKMANTOWN	OGDENSBURGE
			TULEAN		THERSA
	TREMADOCIAN		STAIRSIAN	POTSDAM	KEESEVILLE
			SKULLROCKIAN		AUSABLE
CAMBRIAN					

Figure 2.5 Ordovician stratigraphic units of New York (modified from Ross et al. 1982; Williams and Telford 1986).

## **2.2 Methods of numerical analyses**

In this study, sample preparation and morphological examinations of brachiopod shells followed standard lab techniques of specimen preparation, such as cleaning using ultrasonic bath, sublimated ammonium chloride coating of shells for photography, and serial sectioning of conjoined shells to study internal structures. These procedures, when necessary, will be explained in greater detail in chapter 3 and 4. Below is a brief summary of the numerical methods used in shell biometric analysis and biogeographic analysis to detect patterns and trends in morphological change or faunal affinities among various biogeographic regions.

### **2.2.1 Multivariate analysis**

In this thesis project, both cluster analysis (CA) and principal component analysis (PCA) are used to study brachiopod morphological variations or changes in space and time, as well as faunal similarities and provincialism on regional and global scales. The PAST software package (Hammer et al. 2001; Hammer and Harper 2006), available free online, has been developed particularly for analyzing paleontological data and was used for this study.

In order to measure shell morphology and morphological change, biometric measurements (see details in Chapter 3) were compiled into a dataset of continuous (non-binary) values. Cluster analysis is based on either the Euclidean coefficient or Ward's methods because of the nature of the dataset. The clusters recognized in the CA dendrogram serve as a guide to delineate approximately corresponding groups in the PCA scattergram.

$$\textit{Squared Euclidean distance} = \textit{sum} (X_i - X_j)^2$$

where  $X_i$  and  $X_j$  are the percentage values of species  $X$  in samples  $i$  and  $j$  respectively.

The greater the sum of squares between samples  $i$  and  $j$ , the greater the dissimilarity between them in either (or both) the species composition or (and) the percentage values of the same species.

For paleobiogeographic analysis, the faunal data from each of the many regions were compiled into a binary dataset (0 = absent; 1 = present), treating faunas as the cases, and the taxa of each fauna as variables. In such a cluster analysis of faunal affinities based on a binary dataset, the Raup-Crick similarity coefficient was used to emphasize the groupings and to generate a more visually intuitive CA dendrogram. Similarly, the same dataset forms the basis of PCA analysis to better explore the spatio-temporal patterns of brachiopod faunal provincialism. More specific details on dataset compilation and multivariate analysis will be given in Chapters 3 and 4.

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## Chapter 3<sup>1</sup> – Evolution of the *Rhynchotrema*–*Hiscobeccus* lineage: implications for the diversification of the Late Ordovician epicontinental brachiopod fauna of Laurentia

### 3.1 Introduction

The brachiopod order Rhynchonellida Kuhn, 1949 is characterized in external morphology by a small to medium-sized biconvex shell, a pointed and rostrate posterior, and strong ribs (Savage et al. 2002). In fossils, the valves are commonly preserved conjoined by virtue of their strong interlocked teeth and sockets, which render the valves less vulnerable to disarticulation resulting from physical agitation. The rhynchonellides originated during the Middle Ordovician (Darriwilian) and are one of a few orders of brachiopods that are still living today.

The genus *Rhynchotrema* Hall, 1860 is a well-known rhynchonellide brachiopod, characterized by a small to medium-sized (rarely large), simple costae shell with a subtriangular to subpentagonal outline, an equibiconvex profile, and generally steep lateral and anterior margins. It first appeared during the Late Ordovician (Sandbian), and became very abundant and diverse throughout the Late Ordovician, especially in North America (Figure 3.1). It survived the latest Ordovician (Hirnantian) mass extinction event but became relatively rare during the Early Silurian, with sporadic occurrences during the Llandovery and becoming extinct by Wenlock time. Various species of *Rhynchotrema* have been reported from many tectonic plates and terranes, such as North America (Hall 1847; Fenton and Fenton 1923; Weiss 1955; Cooper 1956; Wang 1949; Titus 1986; Howe 1965; Rice 1987; Jin 1989; Jin and Lenz 1992), northern Europe (Hints 1975, 1990;

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<sup>1</sup> A shortened version of this chapter has been published online (see Sohrabi and Jin 2012).

Hints and Rõõmusoks 1997; Hints and Harper 2003), northern Africa (Havlíček and Massa 1973; Havlíček 1989), the Urals (Nasedkina 1973), Siberia (Nikiforova and Andreeva 1961; Yadrenkina 1974, 1984, 1989), Kazakhstan (Nikitin et al. 2003, 2006), Kirgizia (Misius 1986; Popov et al. 2002), and Australia (Webby and Percival 1983; Laurie 1991; Percival 1991; Webby 1992; Percival and Webby 1996; Savage et al. 2002).

The earliest rhynchonellide brachiopods, such as *Rostricellula* Ulrich and Cooper, 1942; *Dorytreta* Cooper, 1956; *Sphenotreta* Cooper, 1956; and *Ancistrorhyncha* Ulrich and Cooper, 1942, are characterized by small shells (rarely exceeding 10 mm in length) that lack a cardinal process in the dorsal valve. These rhynchonellide genera first appeared in the Middle Ordovician (Darriwilian, Llanvirn) and they were widespread in shallow tropical marine environments in Laurentia, Siberia, and Kazakhstan. By early Katian (latest Caradoc) time, the total number of rhynchonellide genera increased from five to fifteen (Jin 1996). *Rhynchotrema* most likely evolved from one of these early forms during Sandbian time by developing a blade-like cardinal process in the septalium of the dorsal valve to strengthen the attachment of diductor muscles, but hitherto there is a lack of intermediate forms to show the origin of the cardinal process.

In Laurentia, the oldest known form of *Rhynchotrema*, *R. wisconsinense* Fenton and Fenton, 1923, first appeared in the Platteville Formation (McGregor Member, late Sandbian) of the Chatfield area, Minnesota. Subsequently, the genus radiated in North America during the early Katian (Chatfieldian, traditionally known as the Trentonian) (Figure 3.1), represented by such species as *R. increbescens* (Hall 1847) from the Trenton Limestone of New York (Wang 1949; Titus 1986); *R. wisconsinense* and *R. ainsliei* (Winchell 1886) from the Decorah Shale of Minnesota (Fenton and Fenton 1923; Weiss

1955; Cooper 1956; Howe 1965; Rice 1987; Jin and Lenz 1992) ; *R. increbescens* (Hall 1847) from the Bucke Formation of Lake Timiskaming area, Ontario (Hume 1925); and from the Lexington Limestone, Kentucky (Cooper 1956; Howe 1965, 1969, 1979).

In many aspects, the genus *Hiscobeccus* Amsden, 1983 is similar to *Rhynchotrema* in its subpentagonal, biconvex shell, open delthyrium without deltidial plates, and the presence of a septiform cardinal process. This similarity is reflected by the fact that, in early studies (e.g. Hall and Clarke, 1892-1894; Foerste, 1909, 1917, 1920), various species of *Hiscobeccus* were described under *Rhynchotrema*. Similarly, the genus *Lepidocyclus* was also part of *Rhynchotrema* until Wang (1949) separated *Lepidocyclus* from *Rhynchotrema*. Initially, Wang (1949) lumped in *Lepidocyclus* all the large, rounded, and lamellose shells previously reported under the name of *Rhynchotrema*, either with or without deltidial plates. Amsden (1983) established the genus *Hiscobeccus* for the species without deltidial plates, and confined *Lepidocyclus* for species having deltidial plates.

In general, *Hiscobeccus* is differentiated from *Rhynchotrema* by its notably large, globular and strongly lamellose shell, usually with thickened shell walls. In North America, the *Hiscobeccus* rhynchonellide fauna occurs widely in Upper Ordovician (Maysvillian–Richmondian) carbonate rocks, from continental-margin shelves and platforms to inland epicontinental seas, including various species of *Hiscobeccus*, *Hypsiptycha* and *Lepidocyclus* (Jin and Lenz 1992; Jin 1996, 2001; see Figure 3.1).

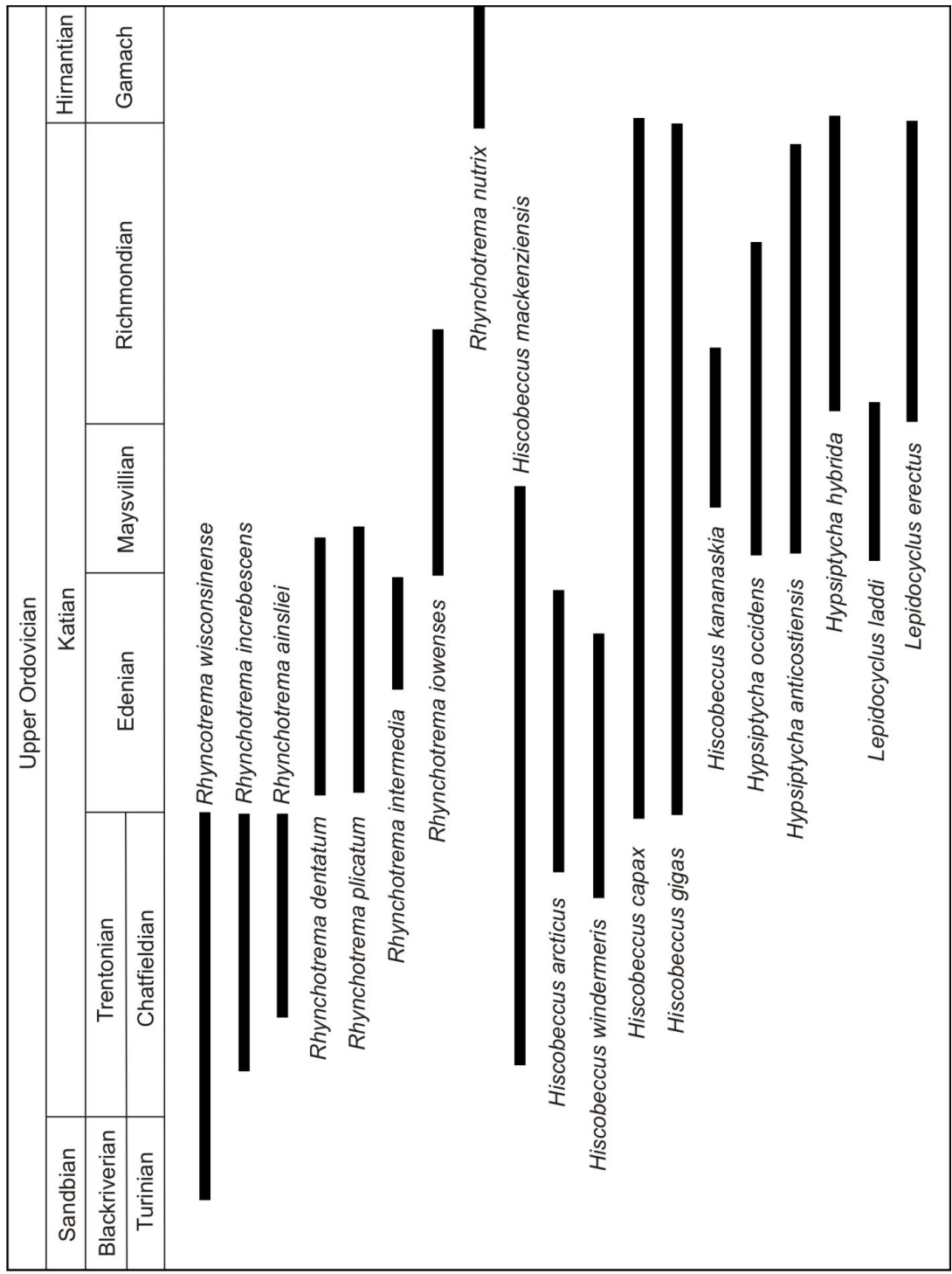


Figure 3.1 Stratigraphical ranges of the rhynchonellide genera *Rhynchotrema*, *Hiscobeccus*, *Hypsiptycha* and *Lepidocyclus* in the Upper Ordovician of North America.

*Atrypa capax* Conrad, 1842 was designated as the type species from Maysvillian strata of Indiana for *Hiscobeccus*, to which have been assigned many other species. The earliest *Hiscobeccus* known, *Hiscobeccus mackenziensis* was reported by Jin and Norford (1996) from the Advance Formation (mid-Trentonian), northern Rocky Mountains, British Columbia. The *Hiscobeccus* fauna in Laurentia contains various species including: *H. arctica* from the Amadjuak Formation (Edenian–Maysvillian) of Baffin Island; *H. kananaskia*, *H. windermeris* from the Beaverfoot Formation (Richmondian), southern Canadian Rocky Mountains (Jin et al. 1989); *H. kananaskia*, *H. mackenziensis* from Edenian–lower Maysvillian, Mackenzie Mountains (Jin and Lenz 1992); *H. capax* from Richmondian strata of the Cincinnati type area (tri-state region of Ohio, Kentucky, and Indiana) (Amsden 1983); *H. gigas* (Wang 1949) from the Gunn Member, Stony Mountain Formation (Richmondian), Southern Manitoba (Jin and Zhan 2001).

The genus *Hypsiptycha* Wang, 1949 is separated from *Hiscobeccus* by well-developed deltidial plates and differs from *Lepidocyclus* by having an elongate oval shell. *Hypsiptycha* first appeared in upper Ashgillian (Richmondian) strata in North America (Figure 3.1). The other species include: the type species *Hypsiptycha hybrida* Wang, 1949 from the Maquoketa Formation (Richmondian), Iowa and Illinois (Howe and Reso 1967); *Hypsiptycha occidens* (Wilson, 1926) from the Beaverfoot Formation (Ashgillian), Rocky Mountains, British Columbia, the Bighorn Dolomite of Wyoming (Macomber 1970), and the Gunn Member (Richmondian) of the Stony Mountain Formation, southern Manitoba (Okulitch 1943; Jin et al. 1989; Jin and Zhan 2001); *Hypsiptycha anticostiensis* from the Vaureal Formation (Richmondian), Anticosti Island and Selkirk Member (Maysvillian), Red River Formation, southern Manitoba (Howe and Reso 1967; Jin et al. 1997; Jin and

Zhan 2001). *Hypsiptycha* is also widespread in the Stony Mountain Formation of eastern Montana (Ross 1957), the Ely Springs Dolomite of southwestern Nevada (Howe and Reso 1967), and the Bighorn Dolomite of Wyoming, (Macomber 1970).

The genus *Lepidocyclus* Wang, 1949 is characterized by a medium to large size with slightly rounded sides, well developed costae and growth lamellae and a strongly biconvex profile (Savage et al. 2002). It is very similar to *Hiscobeccus*, and differs from *Hiscobeccus* only by having a delthyrium closed by deltidial plates. *Lepidocyclus* first appears in the Upper Ordovician (Maysvillian) carbonate rocks of North America (Figure 3.1) and Kazakhstan (Jin and Lenz 1992). In North America, the genus includes: *L. laddi* from the Elgin Member, Maquoketa Formation (Maysvillian), and *L. erectus* from the Brainard Member, Maquoketa Formation (Richmondian) of Iowa (Wang 1949; Jin and Lenz 1992).

It has been suggested that *Hiscobeccus* evolved from *Rhynchotrema* (Amsden 1983; Jin 2001), probably during late Chatfieldian time (Figure 3.2), but the previous studies have been mostly qualitative. Howe (1967, 1969, 1979) initially considered *Hiscobeccus* (lumped with *Lepidocyclus* back then) to be largely Richmondian in age. Later, some species from the Viola Formation of the Arbuckle Mountains of Oklahoma, such as *Hiscobeccus perlamellosus* (Whitfield 1878) and *H. oblongus* (Howe 1966), have been shown to be early to middle Maysvillian in age (Alberstadt 1973; Amsden 1983), although the type species, *H. capax*, is a common and widespread species in Richmondian strata in North America. Jin and Norford (1996) described the oldest *Hiscobeccus* known, *Hiscobeccus mackenziensis* from the Advance Formation (mid Trentonian, late Caradoc), northern Rocky Mountains.

*Hiscobeccus* became widespread and common in North America during Maysvillian–Richmondian time (Alberstadt 1973; Jin 2001, Figures. 3.1, 3.2). By the early Maysvillian, gigantism became evident in many species of these rhynchonellides, which developed increasingly larger, more globular shells with more pronounced, imbricated growth lamellae covering nearly the entire shell surface. The trend of gigantism seems to have been more pronounced in the paleoequatorially located Williston and Hudson Bay basins than in the higher-latitude of the paleotropics (Macomber 1970; Alberstadt 1973; Amsden 1983; Jin et al. 1997; Jin 1996, 2001; Jin and Zhan 2001).

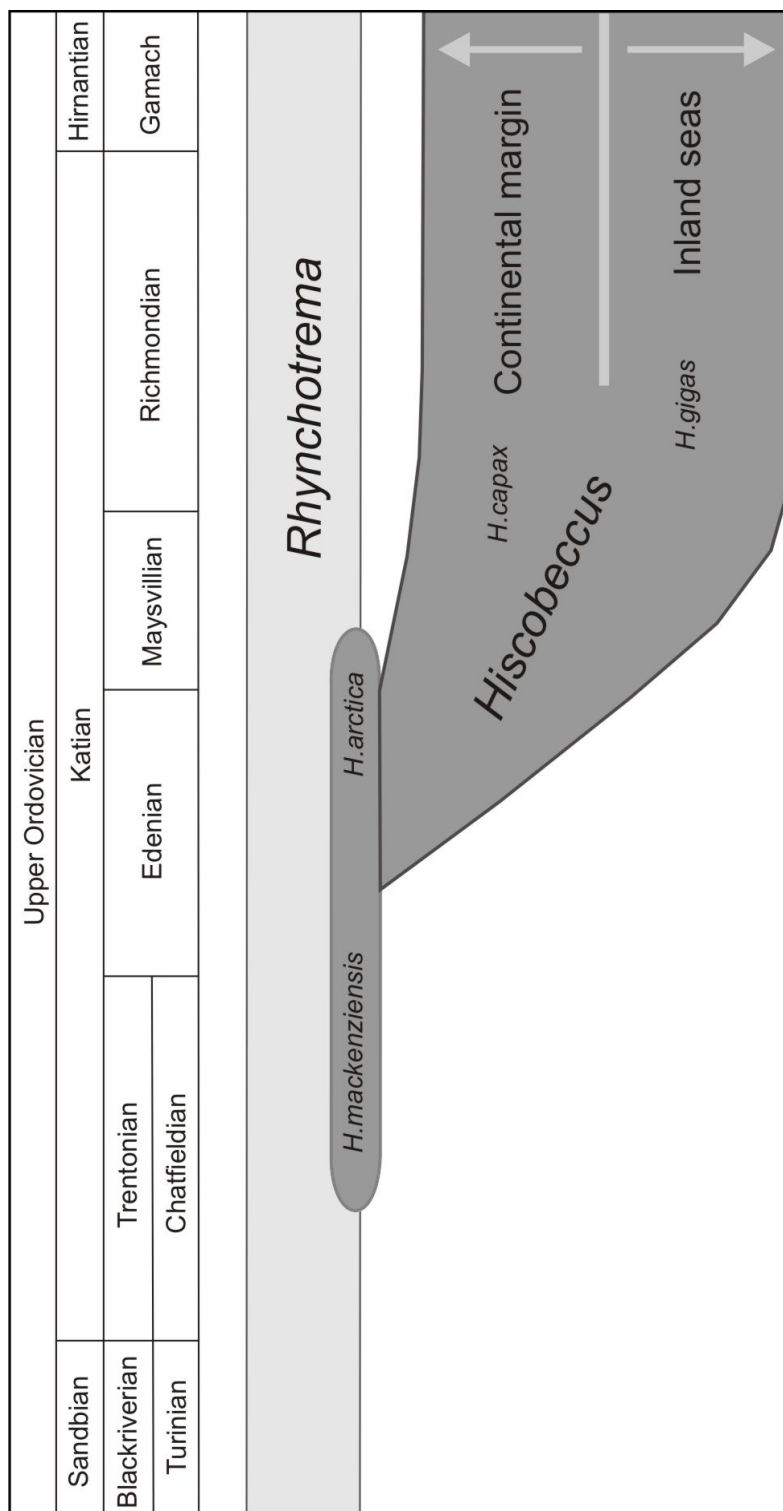


Figure 3.2 Morphological differentiation of *Hiscobeccus* from *Rhynchotrema* during the Late Ordovician based on multivariate analysis in this study.



Despite these early studies, several questions remain to be resolved about the proposed *Rhynchotrema*–*Hiscobeccus* evolutionary lineage:

1. What was the rate of morphological transformation from *Rhynchotrema* to *Hiscobeccus*? Did the changes (e.g. increase in shell size, globosity, and lamellosity) occur gradually or in pulses?
2. In the large tectonic plate of North America, did the morphological changes take place similarly in different areas with different paleoenvironments? Or,
3. Was there a pattern of paleoecological niche partitioning with different species of the *Rhynchotrema*–*Hiscobeccus* lineage occupying different paleoenvironmental settings?
4. What was the effect of sea-level changes on the evolution of the *Rhynchotrema*–*Hiscobeccus* lineage?
5. Why did gigantism become pronounced in some rhynchonellid fauna during the Maysvillian and Richmondian but was not conspicuous in Trentonian time?

To test and investigate the hypothesis of the *Rhynchotrema*–*Hiscobeccus* lineage, a quantitative approach is used in this study, with the following objectives:

- 1) To compile a morphometric dataset of well-preserved *Rhynchotrema* and *Hiscobeccus* in North America, including Minnesota, the Lake Simcoe area, the Ottawa area, the Cincinnati type area, Bay of Quinte, the Rocky Mountains of British Columbia, Baffin Island, and southern Manitoba;
- 2) To conduct a multivariate analysis to detect morphological trends of *Rhynchotrema* and *Hiscobeccus* species in time and space within North America;

3) To explore the evolutionary, paleoecological, and paleobiogeographical implications of such morphological trends, particularly within the paleocontinent of Laurentia.

### **3.2 Material and methods**

The 171 brachiopods used in the present study came from nine localities, ranging in age from the Trentonian to Richmondian (late Sandbian–late Katian). Below is a list of the repository of the examined specimens:

GSC – Geological Survey of Canada; “GSC Loc.” = a lot of specimens from a field locality; “GSC Loc. C -” = collection in the Calgary branch; “GSC Loc. O -” = collection in the Ottawa headquarters.

Mn – Paul Copper collection from Minnesota, stored at Department of Earth Sciences, University of Western Ontario, London, Ontario, Canada.

W (and C, NAPC) – Department of Earth Sciences, University of Western Ontario, London, Ontario, Canada.

*Rhynchotrema* material:

Sample Mn-10, 40 specimens, Plattville Formation, McGregor Member (upper Sandbian), roadcut section about 4 km due east of Chatfield along Highway 74, Minnesota.

Sample W (NAPC-9, stop 1B), nine specimens, Bromley Member (lower Katian, upper Trentonian), Lexington Limestone, Lower Monterey East road cut section, US Highway 127, UTM 16S 0686229E, 4255117N, Kentucky.

Sample Mara-1 (0-2), 22 specimens, Verulam Formation (Chatfieldian, lower Katian), Ramara Concession No. 1 roadside ditch section, UTM 170644080E, 492911N, Lake Simcoe area, Ontario.

Sample Ottawa 1, 20 specimens, Verulam Formation, (Chatfieldian, lower Katian), Ottawa area.

Sample GSC Loc. 1603, nine specimens, Verulam Formation, (Chatfieldian, lower Katian), Bay of Quinte, southern Ontario.

*Hiscobeccus* material:

Sample GSC Loc. 205924, 27 specimens, Advance Formation (Trentonian), northern Rocky Mountains, British Columbia.

Samples GSC Loc. 113531, 24 specimens, Amadjuak Formation (Edenian–Maysvilian), northwest of Silliman’s Fossil Mount, Baffin Island.

Samples GSC Loc. C-205929, 10 specimens, Gunn Member, Stony Mountain Formation (Richmondian), southern Manitoba.

Samples W (C-7a-77), 10 specimens, uppermost Waynesville to Liberty Formation (Richmondian) Caesars Creek Dam Project, upper cut above dam at spillway, north of Oregonia, Ohio.

In order to study the morphological variations and evolutionary trends of the *Rhynchotrema* and *Hiscobeccus* species among these different localities, nine morphological characters (Figure 3.3, Appendix 3.1) were measured for 171 specimens:

1. Shell length (L): linear measurement of maximum length from the shell apex to the anterior margin;

2. Shell width (W): linear measurement of maximum width from the right to the left side of the shell;
3. Shell thickness (T): distance between the highest points of the two valves measured perpendicularly to commissural plane;
4. Sulcus depth (T1): linear measurement of the distance between the crest of the fold and the crest of the costa bounding the sulcus, measured at anterior margin of the shell;
5. Sulcus maximum width (W1): linear measurement of distance between the crests of the two costae bounding the sulcus;
6. Sulcus floor width (W2): linear measurement of the distance between the interspace grooves that correspond to the crests of the two costae bounding the fold;
7. Apical angle (AA): measurement of the angle of the ventral beak in ventral view;
8. Lamella-covered length of the shell (L1): linear length of the lamella-covered part of the shell measured from the anterior margin to the first lamella from the shell apex;
9. Lamella number (Ln): total number of lamellae on the external shell surface.

All linear measurements were taken with a digital caliper in millimetres.

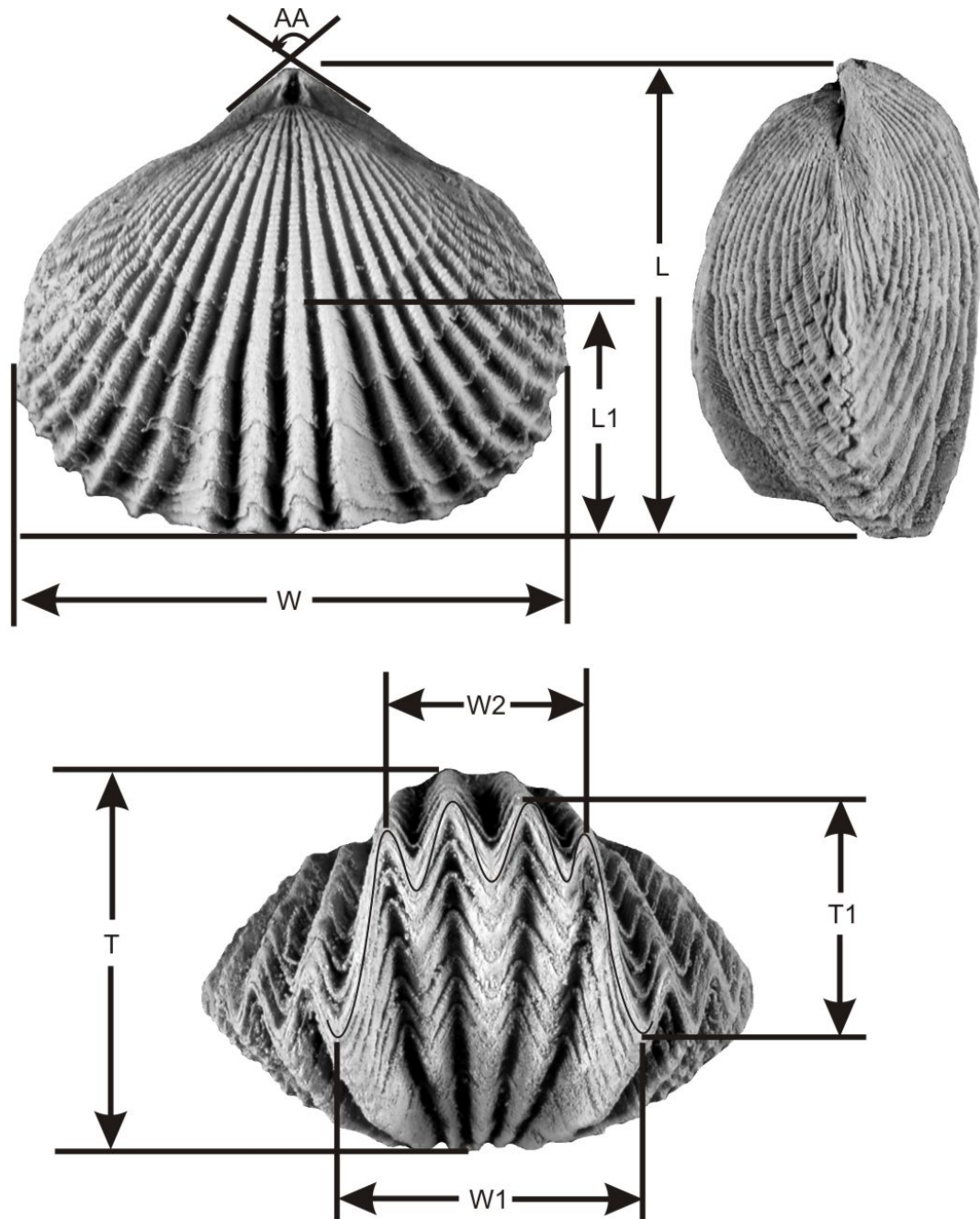


Figure 3.3 Biometric measurements of shell morphology for multivariate analysis.

In order to measure the number of lamellae and the lamellae-covered portion of shell length, the specimens were coated with sublimated ammonium chloride to highlight the features and measured under a Nikon SMZ1500 stereo microscope. For photography, sublimated ammonium chloride also was used to coat the specimens and photographs were taken with a Nikon D80 digital camera. In order to determine the relationships among the various measurements of nine characters, a principal component analysis (PCA) using PAST software (Hammer et al. 2001) was conducted in this study.

### **3.3. Geological setting**

In this study, the 171 brachiopod specimens come from the nine geographic areas in North America (Figure 3.4). The Minnesota specimens are from the McGregor Member of the Platteville Formation, which is one of the most fossiliferous shallow-marine carbonate successions in southeastern Minnesota (Weiss 1957; Austin 1969; Ojakangas and Matsch 1982; Mossler and Bloomgren 1992). The Platteville Formation is divided into the Pecatonica Member, the McGregor Member, and the Carimona Member (Weiss 1957; Austin 1969; Mossler 1985; Ludvigson et al. 2004). The middle McGregor Member is a grey dolomitic limestone with interbedded brown shale (Ludvigson et al. 2004).

The Lexington Formation is well exposed in the Cincinnati Arch region (north-central Kentucky and southern Ohio) with well-preserved fossil shell material, especially brachiopods (Brett et al. 2004; Vogel and Brett 2009). This formation is equivalent to the Trenton Group (Figure 3.5) in New York (Rocklandian, Kirkfieldian, Shermanian; Bergström 1971; Mitchell and Bergström 1991; Brett et al. 2004). The shells of *Rhynchotrema* used in this study are from the Bromley Shale Member, characterized by

stormed-generated shelly packstones and shaly partings, with common hummocky cross stratification (upper Chatfieldian; Cressman 1973; Brett et al. 2004; Vogel and Brett 2009).

In the Lake Simcoe area, *Rhynchotrema* shells are common and best preserved in the Verulam Formation (Chatfieldian). The formation is very fossiliferous and comprises shales and storm-generated shelly wackestones and packstones, with the storm beds (usually 10-20 cm thick) having common scoured bases. The Verulam carbonate strata contain abundant brachiopods and other shelly fossils, and have the highest faunal diversity of the Simcoe Group in Ontario (Figure 3.5).

Among numerous specimens from the Ottawa area (Wilson 1946), 20 well-preserved shells of *Rhynchotrema* from the Ottawa Group, Verulam Formation, were used in this study for measurement. The Ottawa Group, which is equivalent to the Simcoe Group in the Lake Simcoe area, comprises a sequence of Middle and Upper Ordovician strata in the Ottawa area and was subdivided by Williams and Telford (1986), in ascending order, into the Shadow Lake, the Gull River, the Babcaygeon, the Verulam, and the Lindsay formations (Figure 3.5). The Verulam Formation (Liberty 1967) is Trentonian (Shermanian, late Chatfieldian) in age and consists of limestone with interbedded shale (Barnes et al. 1981), with abundant brachiopods. Burrows, intraclasts and ripple marks are common and indicate a generally shallow-water, storm influenced, intracontinental shelf depositional environment (Williams and Telford 1986).

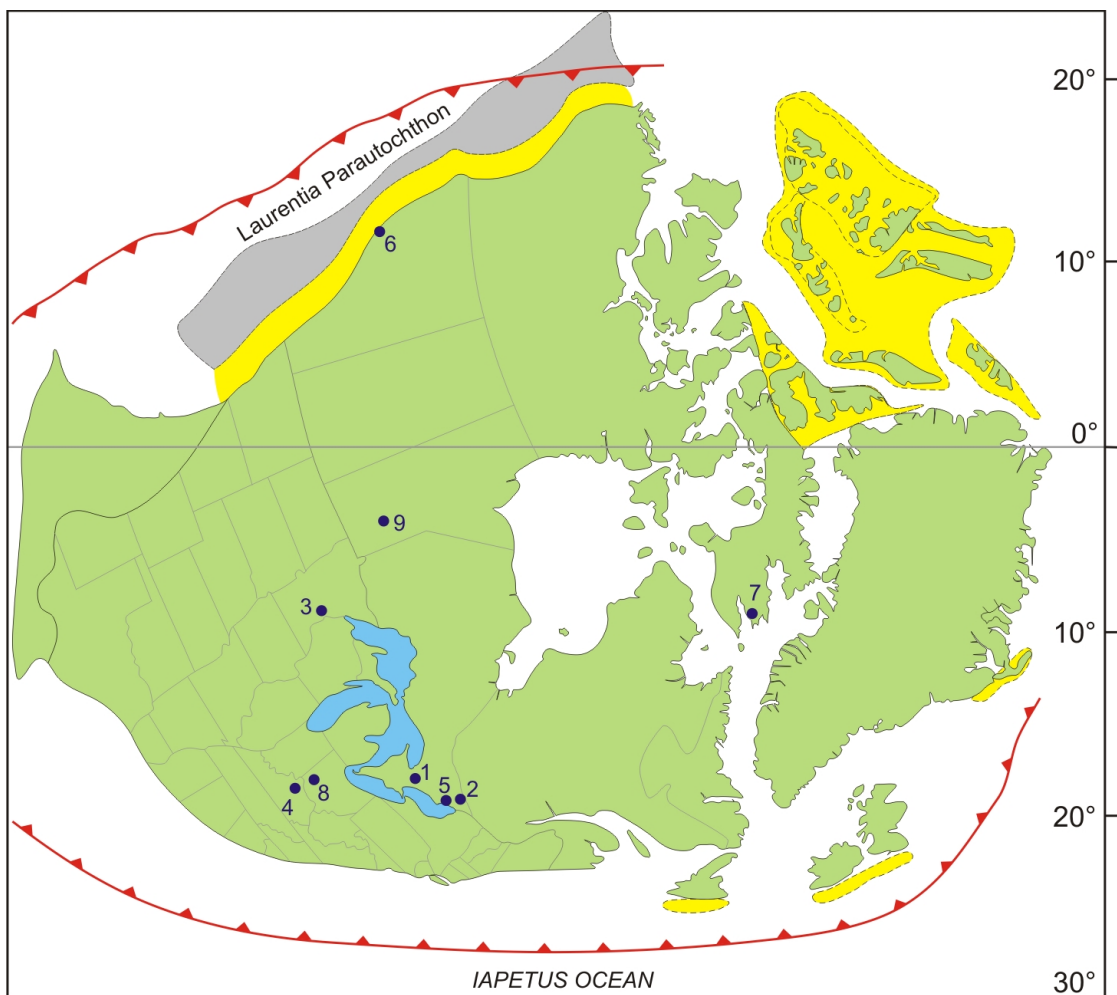


Figure 3.4 Paleogeographical reconstruction of Laurentia during the Late Ordovician (modified after Cocks and Torsvik 2011), and localities of brachiopod collections used for this study. 1) Lake Simcoe area, Ontario; 2) Ottawa area, Ontario; 3) near Chatfield, Minnesota; 4) Lower Monterey East road cut, US Highway 127, Kentucky; 5) Bay of Quinte, Ontario; 6) Advance Mountain, northern Canadian Rocky Mountains, British Columbia; 7) Silliman's Fossil Mount, Baffin Island; 8) Caesars Creek Dam, north of Oregonia, Ohio; 9) Stony Mountain area, southern Manitoba.



The Bay of Quinte material was an early collection made by the pioneer Canadian geologist William Logan, with nine well-preserved shells of *Rhynchotrema* from the Verulam Formation. In the Bay of Quinte, southeastern Ontario, the Ordovician strata rest nonconformably upon the Precambrian basement (Kay 1942; Liberty 1961; Williams and Trotter 1984). The Verulam Formation is composed of interbedded limestone and shale in the Bay of Quinte, and underlies the Lindsay Formation (Liberty 1961, 1967; Carson 1980; 1982; Williams and Trotter 1984; McFall and Allam 1990, 1991).

The brachiopod samples of the Advance Formation (Trentonian), northern Rocky Mountains, British Columbia, contain the oldest known *Hiscobeccus*, *H. Mackenziensis* (Jin and Norford 1996). The formation is composed of thinly bedded, nodular limestone and shales of Trentonian (Kirkfieldian to Shermanian) age (Norford 1996). Paleogeographically, the formation accumulated on the McDonald Platform along the northwestern continental margin of Laurentia.

The Amadjuak Formation was established based on the type section at Silliman's Fossil Mount (Sanford and Grant 2000) where the specimens of *Hiscobeccus* used in this study were collected. The formation is upper Ordovician (Edenian–Maysvilian) in age (Figure 3.5) and consists of thinly to thickly bedded limestones and shales (Sanford and Grant 2000; Bolton 2000). During the Late Ordovician, Baffin Island was located near the southeastern margin of the Laurentian paleocontinent.

NORTH AMERICA		LAKE SIMCOE AREA BAY OF QUINTE		OTTAWA AREA		MINNESOTA		CINCINNATI REGION		N. ROCKIES BC	BAFFIN ISLAND	SOUTHERN MANITOBA					
SERIES	STAGE	GROUP	FORMATION	GROUP	FORMATION	GROUP	FORMATION	GROUP	FORMATION	FORMATION	FORMATION	FM.	MBR.				
CINCINNATIAN	GAMACHIAN	COLLINGWOOD	LINDSAY	OTTAWA	QUEENSTONE	MAQUOKETA	UPPER WHITE WATER	QUARTZITE AND DOLOMITE UNIT	FOSTER BAY	STONY MOUNTAIN	STONEWALL						
	RICHMONDIAN				CARLSBAD		WHITE WATER				WILLIAMS						
	MAYSVILLIAN				BILLINGS		LIBERTY				GUNTON						
	EDENIAN				LINDSAY		WAYNESVILLE				PENITENIARY						
MOHAWKIAN	SHERMANIAN	SIMCOE GROUP	VERULAM	OTTAWA	LINDSAY	STEWARTVILLE	OREGONIA	ADVANCE	FROBISHER BAY	WINNIPEG	RED RIVER						
	KIRKFIELDIAN				VERULAM	GALENA	PROSSER				SUNSET						
	ROCKLANDIAN				BOBCAYGEON	VERULAM	CUMMINGSVILLE				Mt. Auburn	Coryville					
	TURINIAN (BLACKRIVERIAN)				GULL RIVER	BOBCAYGEON	DECORAH				Bellevue	Miamitown					
WHITEROCKIAN	CHAYZYAN	SHADOW LAKE	SHADOW LAKE	SHADOW LAKE	PLATTEVILLE	CARIMONA	KOPE	SKOKI	AKPATOK	AMADJUAJ	RED RIVER						
					SHADOW LAKE	SHADOW LAKE	PECATONICA				TYRONE	LEXINGTON LIMESTONE	POINT PLEASANT	BROMLEY SHALE	DEVILS HOLLOW	GREENDALE	STRODES CREEK

Figure 3.5 Stratigraphic framework of nine geographical areas where rhynchonellide specimens were collected for this study (modified after Barnes et al. 1981; Williams and Telford 1986; Bolton 2000; Sanford and Grant 2000; Ludvigson et al. 2004; Holland and Patzkowsky 2007; Young et al. 2008).

In the Cincinnati Arch region, *Hiscobeccus capax* is the most common representative of the genus, especially in the Richmondian strata (e.g. Waynesville and Liberty formations, Figure 3.5) in Ohio, Indiana and Kentucky tri-state borderlands. The type Cincinnati strata were deposited on a gently sloping, storm-dominated carbonate ramp which was covered by a shallow epicontinental sea (Holland 1993, 2008). Four primary depositional environments: offshore, deep subtidal, shallow subtidal and peritidal settings have been suggested for this ramp (Holland 1993, 2001).

In the Cincinnati region, the Cincinnati strata (middle and upper Katian) were divided into six depositional sequences (C1 through C6; Holland 1993; Holland and Patzkowsky 1996). The lower Cincinnati deposits (C1 to C3) more likely represent cool-water carbonates, which include phosphate deposition with revealed supplies of siliciclastic mud (Patzkowsky and Holland 1993; Holland and Patzkowsky 1996, 1997). The upper Cincinnati (Richmondian) is delimited by C4 to C6 sequences, and displays more warm-water conditions. These conditions are indicated by changes in the carbonate deposits to warm water characters, such as increases in lime mud, peloids, calcareous algae and corals (Holland and Patzkowsky 2007). The Late Ordovician carbonate rocks of the C4 sequence comprise the Sunset, Rowland, Reba, and partly the Arnheim formations (Holland 1993, Brett and Algeo 1999). It has been suggested that there was a major biotic invasion in the Cincinnati region during Richmondian time (Patzkowsky and Holland 1996). This hypothesis of “Richmondian Invasion” suggests an immigration of brachiopods, bryozoans, mollusks, corals and echinoderms from low-latitude paleotropics (e.g. the Williston, Hudson Bay, and Michigan basins in Canada and the western United States) to the higher paleotropical Cincinnati Arch region (Foerste 1912; Holland and

Patzkowsky 2007). However, evidence of the invasion of paleoequatorial brachiopods into the Cincinnati region has not been convincingly demonstrated (for example, see Jin 2012).

In central Kentucky the carbonate rocks of Richmondian time (C5) are represented by the Saluda Member (Holland and Patzkowsky 1996), characterized by partly calcitic and muddy dolomite (Weir et al. 1984; Holland 1993). In the Cincinnati region, Ohio, the Waynesville Formation represents offshore facies of the C5 sequence and overlies the Oregonia Member and underlies the Liberty Formation (Holland 1993; Holland and Patzkowsky 1996). The Waynesville Formation of southwestern Ohio is composed of fossiliferous limestone and shell beds (Nickles 1903; Tobin 1986). The sedimentary structures such as hummocky cross-stratification, graded-bedding, tool marks, flute marks, shale intraclasts in limestone beds, and imbricated brachiopod valves indicate storm-generated deposition (Tobin 1986; Schumacher and Shrake 1997). The Liberty Formation contains planar-bedded limestones and shell-rich beds in Ohio and Indiana (Tobin 1986).

The Upper Ordovician (Edenian to Gamachian) carbonate succession of southern Manitoba (northeastern Williston Basin) records two major environmental cycles (Kendall 1976; Elias 1991; Elias and Young 2004). The first, called the Red River Cycle, began with a transgressive phase and resulted in the deposition of the Red River Formation. The second cycle is represented by the Stony Mountain Formation which is somewhat similar to the Red River Formation, except for a higher siliciclastic or dolomite content. The Stony Mountain Formation of southern Manitoba is divided (Figure 3.5) in ascending order, into the Gunn, the Penitentiary, the Gunton, and the Williams members

(Okulitch 1943; Baillie 1952; Sinclair and Leith 1958; Sinclair 1959; Elias 1983; Jin and Zhan 2001; Young et al. 2008).

Based on conodont data, the Stony Mountain Formation is considered Richmondian in age (Sweet 1979), which is consistent with other macrofossil data (Elias 1991; Jin and Zhan 2001; Elias and Young 2004). The Gunn Member is the lowest unit of the formation (Figure 3.5) and is composed of red to locally greenish gray interbedded, fossiliferous, silty lime mudstones to wackestones, bioclastic grainstones, and packstones (Jin and Zhan 2001; Young et al. 2008).

The Gunn Member and the overlying Penitentiary Member were deposited during a transgressive phase (Elias 1983; Young and Elias 1999). Both members are strongly bioturbated and have similar biotas, which represent deposition under similar environmental conditions. Siliciclastic silts and iron-rich minerals in the Gunn and Penitentiary members indicate that the epicontinental sea may have changed from clear to turbid conditions (Jin and Zhan 2001). Some of the grainstone to packstone beds contain broken and abraded shelly fossils, with ripple marks. These taphonomic and sedimentary features in the formation indicate a shallow-water, non-restricted marine environment, and the grainstone to packstone horizons most likely represent storm deposits in the formation (Young and Elias 1999). The Gunn Member contains abundant and diverse fossils, including brachiopods, solitary rugose corals, bryozoans, cephalopods, and trilobites (Young et al. 2008). Jin and Zhan (2001) assigned the brachiopods to the *Diceromyonia storeya* Community. These brachiopods are diverse, but numerically they are dominated by a few species, including *Hiscobeccus gigas* (Wang, 1949), *Dinorthis*

*occidentalis* (Okulitch, 1943), and *Diceromyonia storeya* (Okulitch, 1943). *Rhynchotrema* is rare in the Red River and Stony Mountain formations.

In comparison with the brachiopods from the Selkirk Member (Red River Formation), the Gunn Member brachiopods are smaller in size. It has been suggested that the numerical dominance and small shell size of the Gunn Member brachiopods were related to higher environmental stress during deposition of the Stony Mountain Formation, probably related to the greater clastic sedimentation (Jin and Zhan 2001). The dominant fossil assemblages such as brachiopods and solitary rugose corals in the Gunn and Penitentiary members indicate a range of tropical marine conditions with sluggish water circulation (Young et al. 2008).

### **3.4. Multivariate analyses**

The multivariate analyses (mainly cluster and principal component analyses) are based on nine characters of 171 brachiopod specimens of *Rhynchotrema* and *Hiscobeccus* from nine localities in North America noted above, ranging from the upper Sandbian to the uppermost Katian (Richmondian) (Appendix 3.1). In order to investigate the relationships among the various forms of *Rhynchotrema* and *Hiscobeccus* and their phylogenetic, paleoecological, and paleogeographic implications, a dataset based on measurements of these specimens was subjected to principal component analysis (PCA). Because the measurements in the dataset are in different units (e.g. millimetres, angle degrees, or number of lamellae), the correlation (instead of variance-covariance) algorithm of the PAST PCA software is used, which normalizes the variables to make them more evenly weighted. The result was plotted as principal components 1 (X-axis) and 2 (Y-axis), corresponding to eigenvalues 1 and 2 respectively.

Among the specimens of nine localities shown in Figure 3.6, those of *Rhynchotrema* and the early forms of *Hiscobeccus* (samples A to G: Minnesota, Lake Simcoe, Ottawa, Kentucky, Bay of Quinte, Rocky Mountains and Baffin Island) are clearly separated from the later forms of *Hiscobeccus* (samples H and I: Stony Mountain and Cincinnati type area) of Richmondian age. In Figure 3.7, the specimens of *Rhynchotrema* and *Hiscobeccus* from seven localities (samples A to G) show an increase in variable I (lamella number), from the early forms of *Rhynchotrema* (samples A, B, and C) to the early forms of *Hiscobeccus* (samples F and G: Rocky Mountains and Baffin Island).

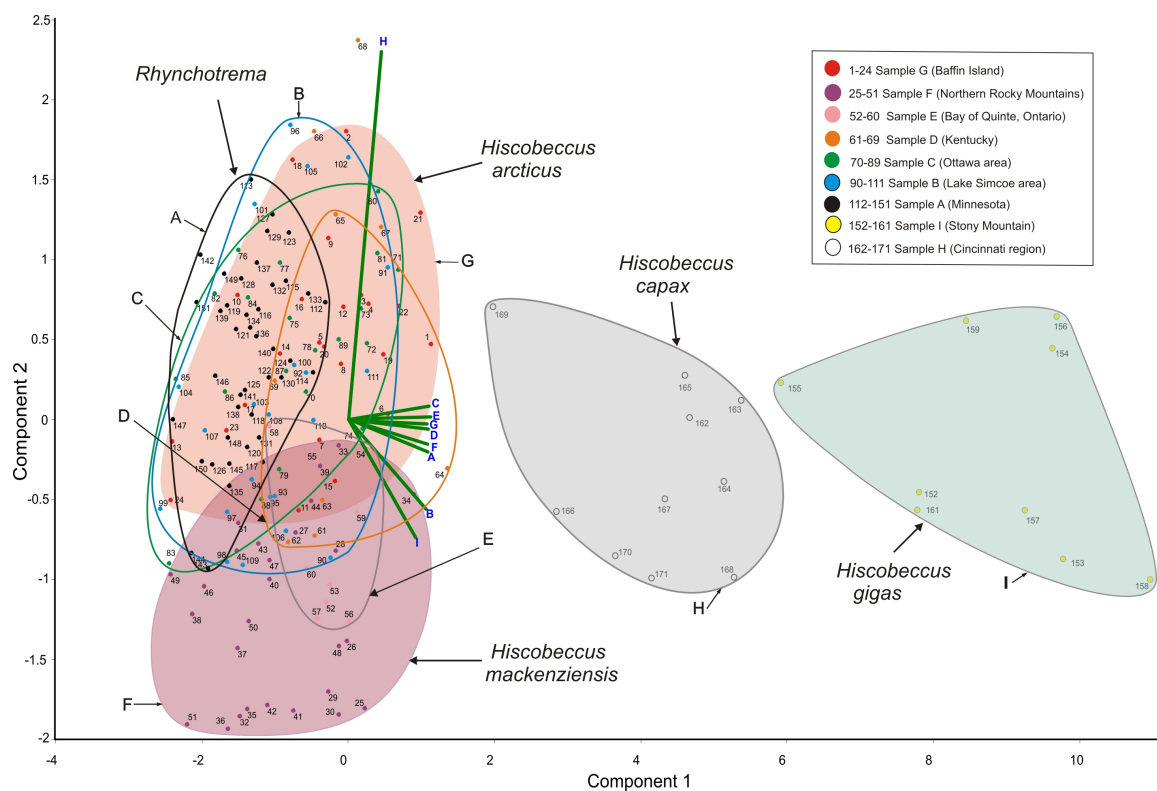


Figure 3.6 Principal component analysis based on nine biometric measurements (A–I) derived from 171 specimens of *Rhynchotrema* and *Hiscobeccus* from nine localities (samples A–I). Note complete separation of *Hiscobeccus capax* and *Hiscobeccus gigas* from older *Rhynchotrema* and *Hiscobeccus*.



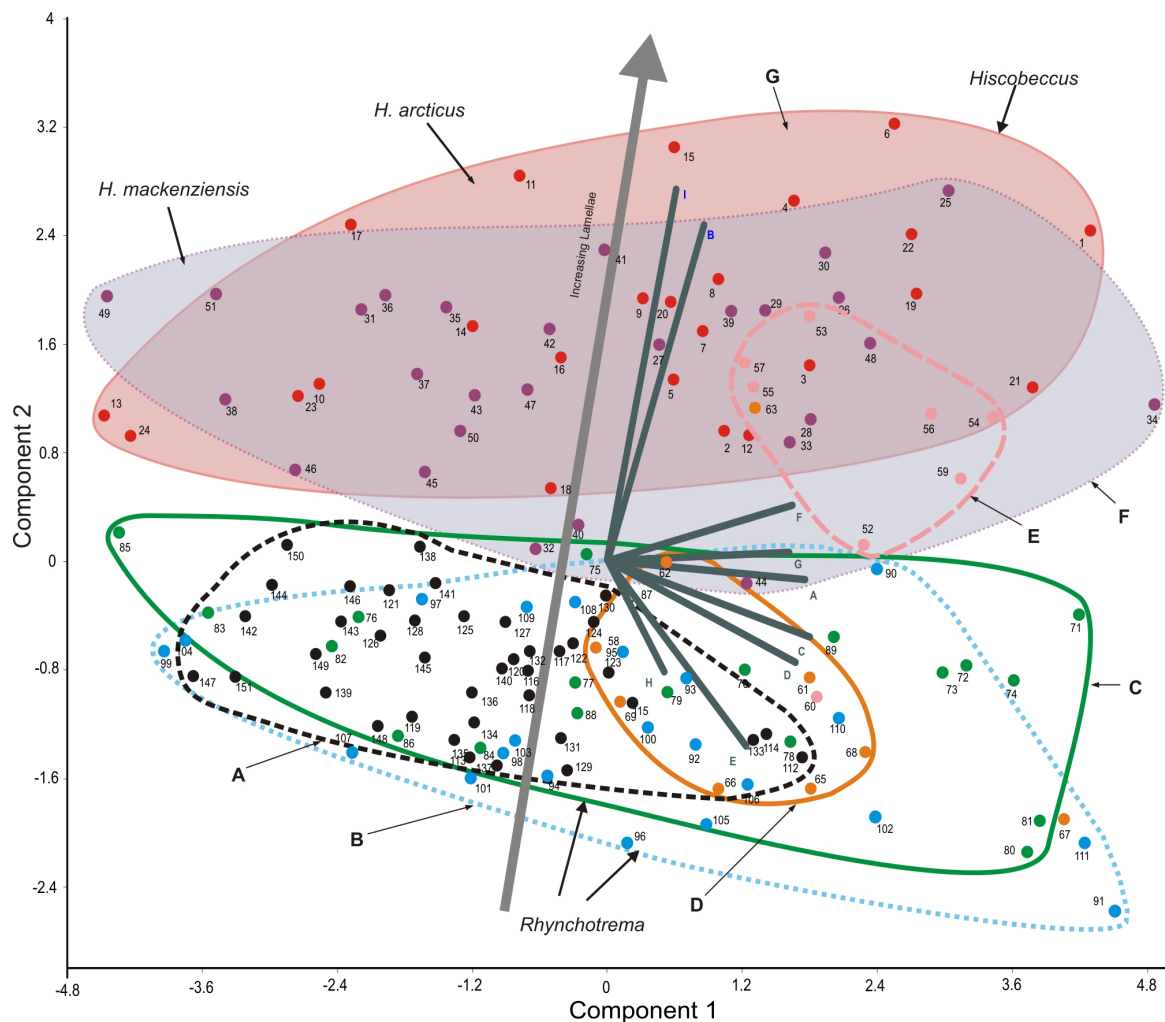


Figure 3.7 Principal component analysis of *Rhynchotrema* and early forms of *Hiscobeccus* association of upper Sandbian to Maysvillian age. Note the morphological overlap between *Hiscobeccus mackenziensis* (sample F) and *Rhynchotrema*.

### 3.4.1 Differentiation of *Rhynchotrema* from *Hiscobeccus*

As is shown in Figure 3.6, the Richmondian (late Katian) forms of *Hiscobeccus* are clearly separated from all the species of *Rhynchotrema*, as well as from the early forms of *Hiscobeccus*. *Hiscobeccus capax*, for example, is characterized by medium-sized, strongly biconvex to globular shells (thicker than wide in some specimens, see Figure 3.8, images A–J). This species is predominant in Richmondian strata of the Cincinnati type area (Howe 1969, 1979; Amsden 1983), Tennessee, Alabama, and Oklahoma (Alberstadt, 1973; Holland and Patzkowsky 2008, 2009); but relatively rare in paleoequatorially located inland seas (Jin and Zhan 2001).

The shells of *H. gigas* from the Stony Mountain Formation of southern Manitoba are typically large (up to 34.5 mm in width, see Figure 3.9, images A–J), but they tend to have a lower degree of globosity (measured by thickness/width ratio) than *H. capax*, the average thickness/width ratio (T/W) being 0.66 mm in *H. gigas*, compared to 0.72 mm in *H. capax*. *Hiscobeccus gigas* occurs predominantly in the Williston and Hudson Bay basins (Macomber 1970; Jin et al. 1997; Jin and Zhan 2001), where about 90% of the *Hiscobeccus* specimens belong to *H. gigas*, whereas *H. capax* and other rhynchonellids (e.g. *Hypsiptycha*, *Lepidocyclus*, *Rhynchotrema*) are relatively rare.

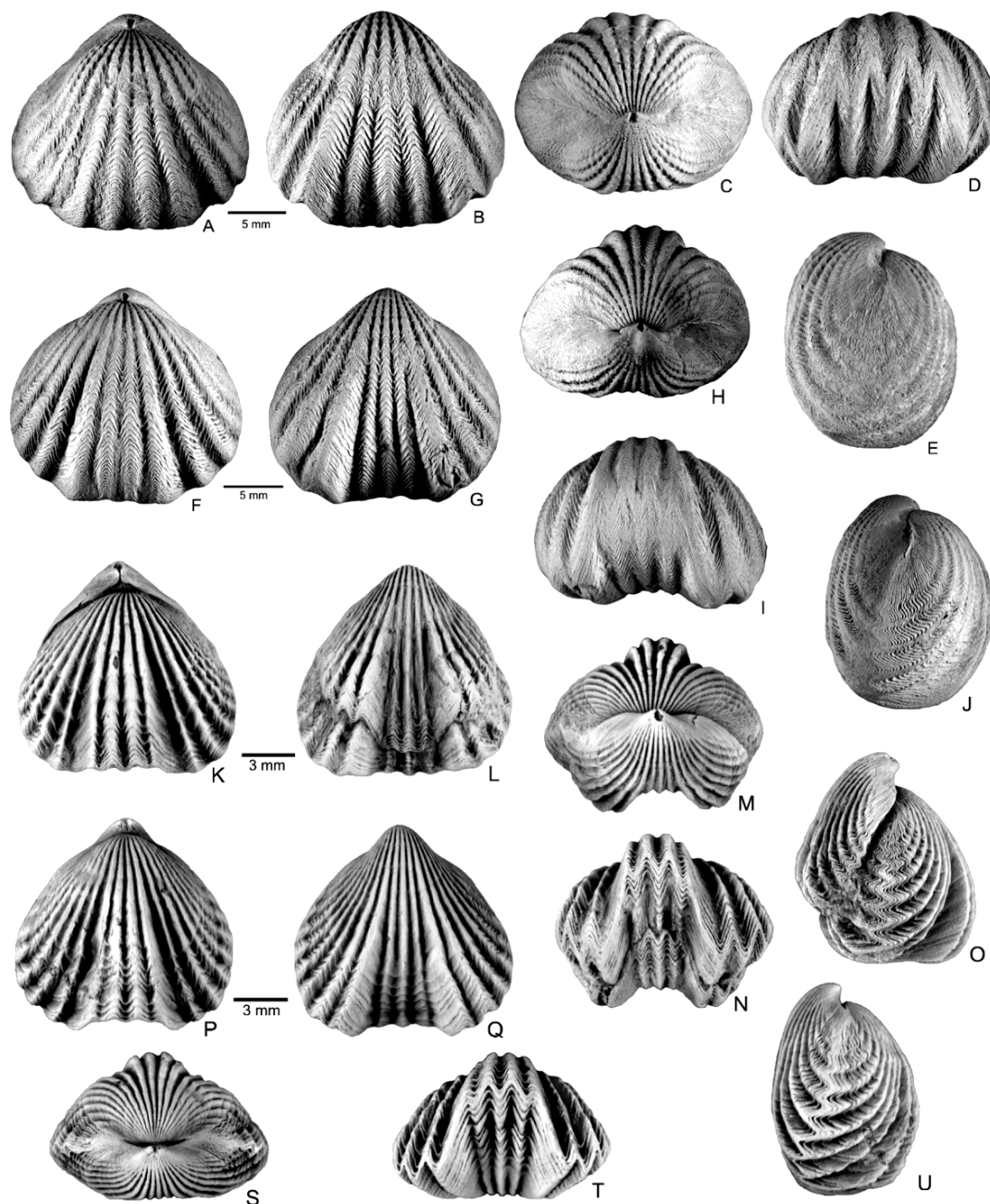


Figure 3.8 Specimens of *Hiscobeccus* and *Rhynchotrema* used for analysis. A–J, two shells of *Hiscobeccus capax* (Conrad 1842), Waynesville Formation, Cincinnati area (locality C-7a-77), showing strong and dense lamellae. K–U, two strongly lamellose shells of *Rhynchotrema increbescens* (Hall 1847), Verulam Formation, Bay of Quinte, southeastern Ontario; GSC 1630 g (K–O) and GSC 1603 (P–U).

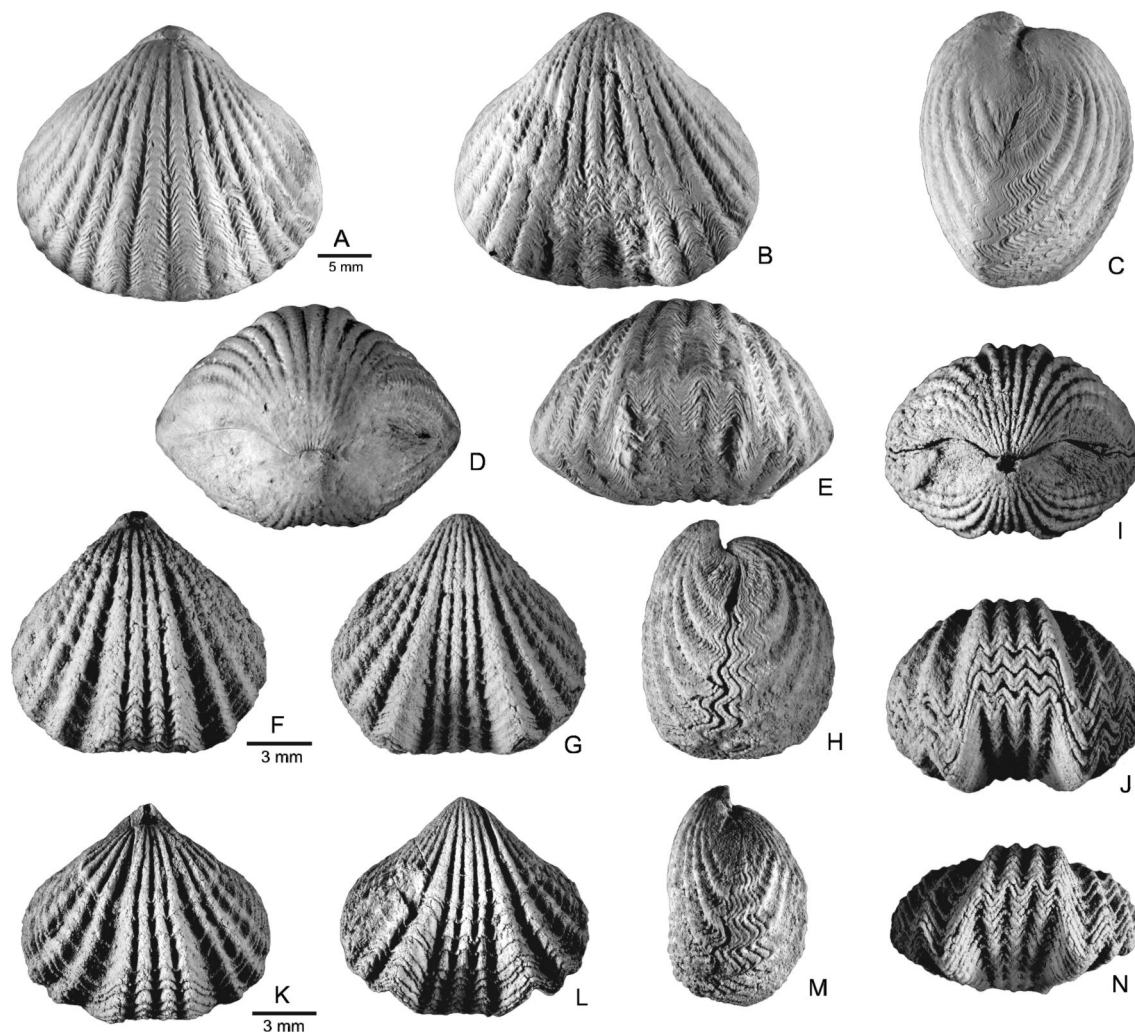


Figure 3.9 Early and late forms of *Hiscobeccus*. A–E, *Hiscobeccus gigas* (Wang 1949), Stony Mountain Formation, southern Manitoba, GSC Loc. C-205929. F–N, two silicified shells of *Hiscobeccus mackenziensis*, Jin and Lenz 1992, Advance Formation, northern Rocky Mountains, British Columbia, GSC Loc. 205924; the oldest known *Hiscobeccus*.

### 3.4.2 Differentiation among early *Rhynchotrema*, late *Rhynchotrema*, and early *Hiscobeccus*

The samples of A, B, C, D, E, F, and G on the left of the PCA plot (Figure 3.6) comprise a mixture of *Rhynchotrema* and *Hiscobeccus* specimens from seven localities. A more detailed plot of these samples is shown in Figure 3.7. The specimens range from old forms of *Rhynchotrema* (Sandbian–early Katian) to younger forms of *Rhynchotrema* and *Hiscobeccus* (Maysvillian–Richmondian). Among the nine vectors (A to G, corresponding to the nine variables) in the PCA plot (Figure 3.7), vectors B and G correspond mainly to the axis of principal component 2 and represent lamella-covered length of shell (L1) and lamella number. As is shown in the scattergram, the lamella - covered length of shell and lamella number increase from the pioneer representatives of *Rhynchotrema* from Minnesota, Ottawa, Lake Simcoe and Cincinnati areas to the younger forms of *Rhynchotrema* from the Bay of Quinte and to early forms of *Hiscobeccus* from the northern Rocky Mountains and Baffin Island. Figure 3.7 shows that the older forms of *Rhynchotrema* have various degrees of overlap among themselves, but they are clearly differentiated from the younger forms of *Rhynchotrema* and *Hiscobeccus*.

To investigate the differentiation among the early and late forms of *Rhynchotrema* and also the early form of *Hiscobeccus*, a number of secondary morphological parameters will be used, as defined below:

Shell convexity index ( $SCI = T/W$ ), measured by the ratio of shell thickness to width.

Shell lamellosity index ( $SLI = L1/L$ ), measured by the ratio of lamella-covered length to total length of the shell.

Shell lamella density ( $SLD = L_n/L_1$ ), measured by the total number of lamellae divided by the lamella-covered length of the shell.

Shell lamella density Index ( $SLDI = (L_1/L) \times L_n$ ), measured by shell lamellosity index multiplied by the total number of lamellae on external shell. This is an average of lamellae-covered shell surface area and lamellar density.

*Rhynchotrema wisconsinense* from the McGregor Member, Platteville Formation, Minnesota, is the oldest form of the genus in North America. As is shown in Figure 3.7, this sample of *Rhynchotrema* (A) is plotted in the lower portion of the PCA scattergram, and characterized by a small, moderately convex shell (length= 9.27 mm, width= 9.89 mm, SCI= 0.63, SLI= 0.17, SLD= 3.05, SLDI= 0.83) (Figure 3.10, images A-J).

There is a notable similarity between the species of *Rhynchotrema wisconsinense* from Minnesota and *R. increbescens* from the Lake Simcoe area, both having the lowest lamellae number, but they are distinct from the slightly younger *R. increbescens* from the Bay of Quinte.

*Rhynchotrema increbescens* of the Lake Simcoe area (sample B) has an average of four lamellae and is characterized by a relatively small shell (length= 10.37 mm, width =11.04 mm, SCI= 0.57, SLI= 0.16, SLD= 2.47, SLDI= 0.71, see Figure 3.10, images K-S).

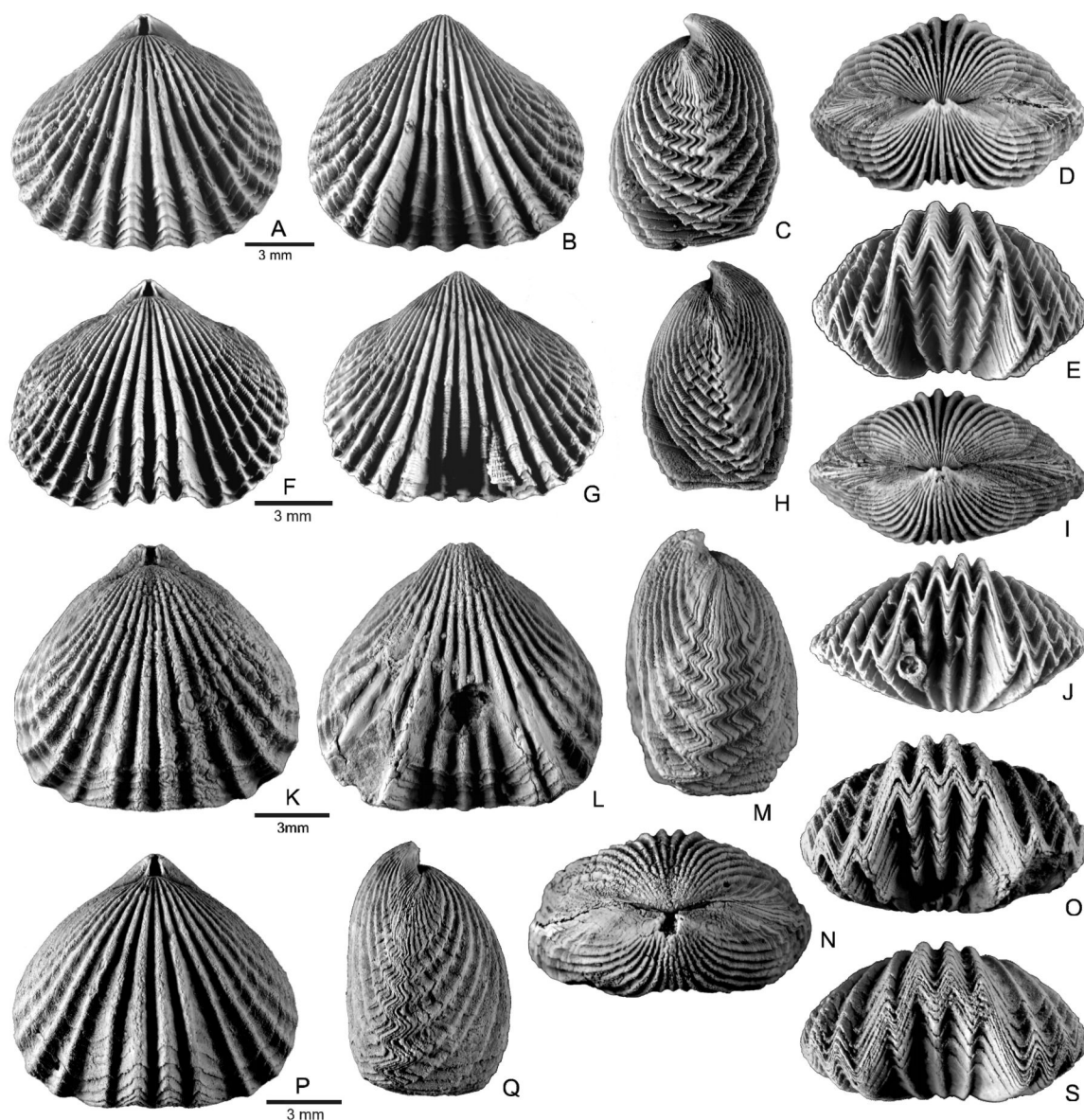


Figure 3.10 Various forms of *Rhynchotrema*. A–J, two shells of *Rhynchotrema wisconsinense* Fenton and Fenton 1922, McGregor Member, Platteville Formation, Minnesota, locality Mn-10. Note the development of both imbricated growth lamellae and finer growth lines. K–S, two partially silicified shells *Rhynchotrema increbescens* (Hall 1847), Verulam Formation, Lake Simcoe area, Ontario, locality Mara-1.

*Rhynchotrema increbescens* from the Verulam Formation of the Ottawa area (sample C) overlaps with samples A, B, and D (Figure 3.7), and is characterized by a slightly higher lamellae number (five on average) and a slightly larger shell (length= 10.16 mm, width= 11.13 mm, SCI= 0.61, SLI= 0.31, SLD= 1.72, SLDI=1.89) (Figure 3.11, images E-L).

*Rhynchotrema increbescens* from the Bromley Member (upper Chatfieldian) of the Lexington Formation, Kentucky (sample D; Figure 3.7), overlaps with the right portion of the plotted fields for the older representatives of *Rhynchotrema* (samples A, B, C) in the scattergram. Compare to samples A, B, and C, the Kentucky form of *R. increbescens* shows an increase in growth lamellae (seven), with a larger shell size (length= 11.47 mm, width= 12.62 mm, SCI= 0.61, SLI= 0.31, SLD= 1.72, SLDI= 2.33, see Figure 3.10, images K-S, Figure 3.11, images E-L).

The shells of *Rhynchotrema increbescens* from the Verulam Formation, Bay of Quinte (sample E) is plotted in the upper right portion of PCA scattergram (Figure 3.7), delimited by an average of nine lamellae, the highest value known for *Rhynchotrema* shells, and by a relatively large shell size for the Ordovician faunas of the genus (length= 11.55 mm, width= 12.02 mm, SCI= 0.71, SLI= 0.36, SLD= 2.40, SLDI= 3.81; Figure 3.8, images K-O).

The oldest form of *Hiscobeccus*, *H. mackenziensis* (sample F) from the Advance Formation (Kirkfieldian–Shermanian), northern Canadian Rocky Mountains, is plotted in the upper portion of the PCA scattergram (Figure 3.6), characterized by a relatively small,



moderately convex shell for the genus but strong growth lamellae (length= 9.91 mm, width= 10.07 mm, SCI= 0.62, SLI= 0.52, SLD= 2.28, SLDI= 6.23; Figure 3.9, images F–N). The lamellae do not extend all the way up to the shell apex, which accounts for its partial overlap with *Rhynchotrema increbescens* from the Bay of Quinte.

Sample G represents the Maysvillian species of *Hiscobeccus*, *H. arcticus*, from the Amadjuak Formation, Baffin Island. These shells are plotted also in the top portion of the PCA scattergram (Figure 3.7), and have the largest lamellae number among all samples (A–G) used for this plot. The shells attain a lamellae number of 15 on average. The strong growth lamellae cover more than half of the shell length. Despite the generally small shell size, the shell convexity is notably higher than *H. mackenziensis* (length= 9.86 mm, width= 10.47 mm, thickness= 7.14 mm, SCI= 0.67, SLI= 0.52, SLD= 2.95, SLDI= 8.45, Figure 3.11, images M–W).

At the generic level, *Rhynchotrema* and *Hiscobeccus* can be differentiated by the development of imbricated growth lamellae, which usually cover less than one-third (SLI from 0.16 to 0.31) of the shell length in *Rhynchotrema*, with the exception of *R. increbescens* from the Bay of Quinte (SLI= 0.36). In the early forms of *Hiscobeccus*, the lamellae covers more than half of the shell length (average value of SLI= 0.52 for samples of *H. mackenziensis* and *H. arcticus*).

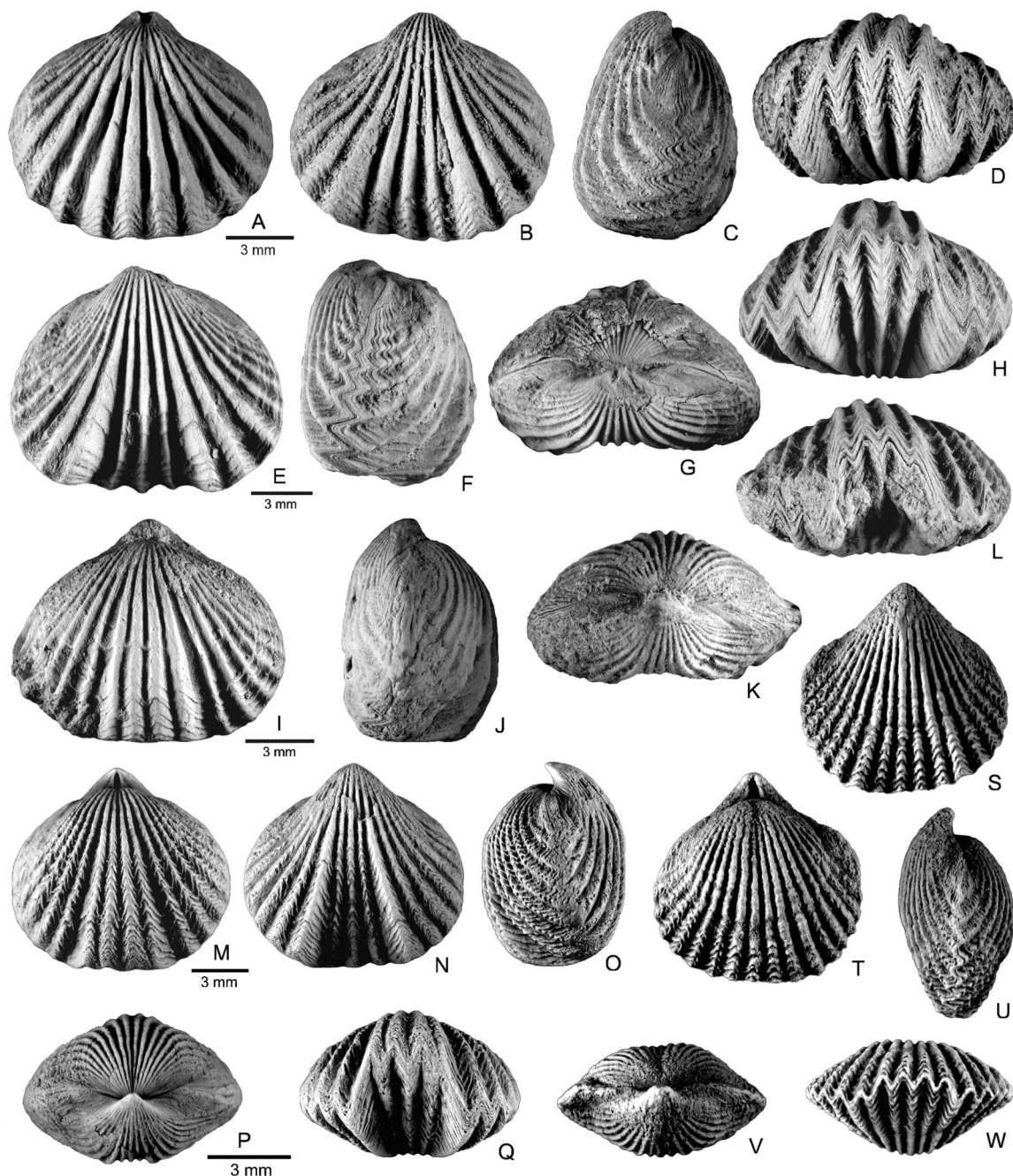


Figure 3.11 Specimens of *Rhynchotrema* and *Hiscobeccus*. A–D, *Rhynchotrema increbescens* (Hall 1847), Bromley Member, Lexington Limestone, Kentucky, locality W (NAPC-9, stop 1B). E–L, two shells of *Rhynchotrema increbescens*, Verulam Formation, Ottawa area; GSC collection. M–W, *Hiscobeccus arcticus* (Roy 1941), Amadjuak Formation, northwest of Silliman's Fossil Mount, Baffin Island (GSC Loc. 113531), two hypotypes, GSC 113533 (M–Q) and GSC 113541 (S–W).

### 3.5 The *Rhynchotrema*–*Hiscobeccus* lineage and implications for Late Ordovician rhynchonellide evolution, paleoecology, and paleobiogeography

The multivariate analysis in this study provided the first strong, quantitative evidence that *Hiscobeccus* evolved from *Rhynchotrema* during late Caradoc (Chatfieldian) time (Figure 3.2), because the early forms of *Hiscobeccus* (*H. mackenziensis*) cluster more closely with *Rhynchotrema* than with younger (Maysvillian–Richmondian) species of *Hiscobeccus* in overall morphology (Figure 3.6). The origin of *Hiscobeccus* appears to have been a cladogenesis because various species of *Rhynchotrema* persisted in North America and other paleogeographical regions throughout the Late Ordovician–Early Silurian epochs, thriving contemporaneously with *Hiscobeccus* during the Late Ordovician. As the ancestral stock of *Hiscobeccus*, *Rhynchotrema* survived into the Early Silurian after the Hirnantian mass extinction event, but *Hiscobeccus* largely became extinct below the Katian–Hirnantian boundary. During the Late Ordovician (mostly Katian), several morphological trends of the *Rhynchotrema*–*Hiscobeccus* lineage may have been controlled by paleoecological and paleobiological factors.

#### 3.5.1 Shell size

The size of a rhynchonellide shell is difficult to quantify precisely because its tapering posterior and usually prominent fold and sulcus make the shell deviate considerably from any geometric shape. In this study a shell size index (SSI, see Figure 3.12) is used as a proxy for the shell volume of *Rhynchotrema* and *Hiscobeccus* specimens, and such a proxy is calculated using the formula:

$$SSI = \frac{4\pi}{3} (LWT)$$

where  $L$  is the shell length,  $W$ , width, and  $T$ , thickness.

As is shown in Figure 3.7, the shell size increases at temporally uneven rates from the older forms of *Rhynchotrema* to the younger forms of *Hiscobeccus*. The oldest *Rhynchotrema*, *R. wisconsinense* from the McGregor Member of Minnesota, has the smallest shell size among the shells of *Rhynchotrema* and *Hiscobeccus* analyzed in this study. In comparison, *Rhynchotrema increbescens* from the Lake Simcoe area, Bay of Quinte, the Ottawa area, and the Cincinnati region show gradual increase in shell size with time (Figure 3.12). An early form of *Hiscobeccus*, *H. mackenziensis* from the Advance Formation of the Rocky Mountains, northeastern British Columbia, has the smallest shell size among all *Hiscobeccus* species. The Richmondian forms of *Hiscobeccus*, *H. capax* from the Cincinnati type area and *H. gigas* from southern Manitoba, attained maximum shell sizes in comparison to the other forms, particularly *H. gigas*, which represents the largest shell size among all the specimens, reaching 34 mm in length and 35 mm in width (Figure 3.12).

The older forms of *Rhynchotrema* have a small and moderately biconvex shell. The early form of *Hiscobeccus*, *H. mackenziensis*, in the mid-late Chatfieldian has an increased size, but rarely exceeds 12 mm in length (average 9 mm), with a moderate biconvex, non-globose profile. By the Late Ordovician (Maysvillian-Richmondian), *Hiscobeccus* became the most widespread and abundant form of rhynchonellides and exhibited gigantism in carbonate depositional environments in the epicontinental seas, especially in the paleoequatorially located Williston and Hudson Bay basins.

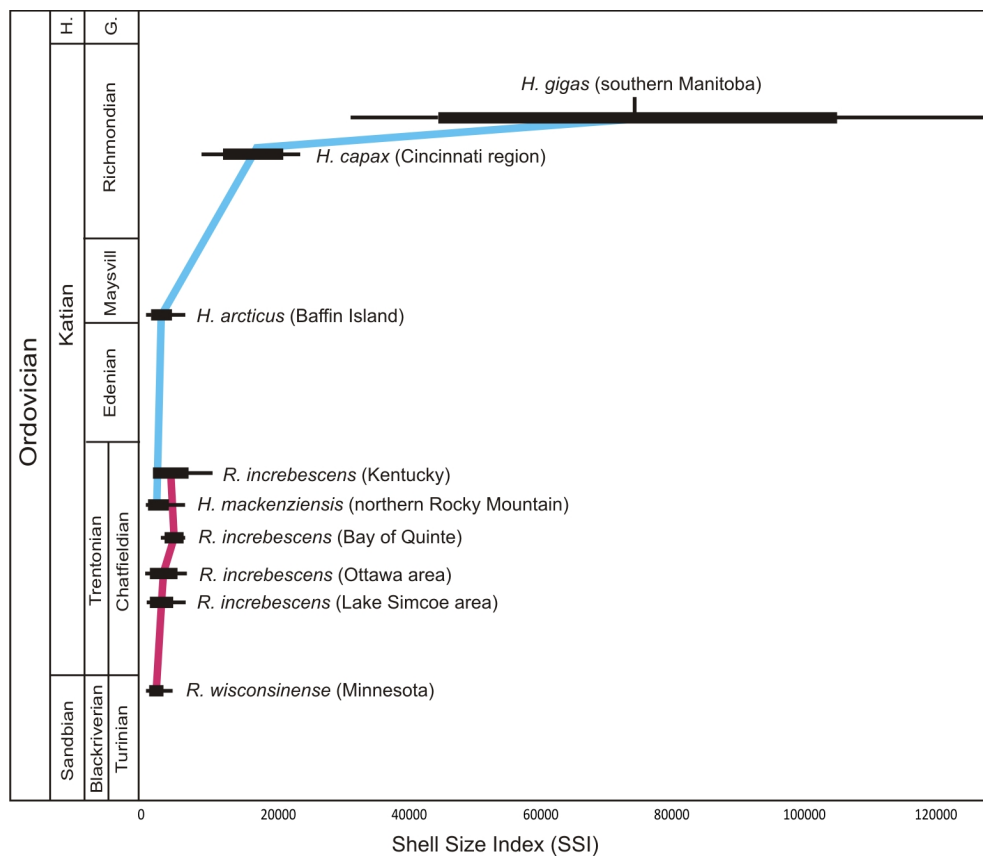


Figure 3.12 Plots of shell size index (SSI) for *Rhynchotrema* and *Hiscobeccus* specimens from nine localities. *Hiscobeccus gigas* has the largest shell size among all specimens.

In the Stony Mountain Formation of southern Manitoba, the common species of *Hiscobeccus*, *H. gigas*, exhibits a pronounced increase in shell size and lamellosity compared to most other congeneric species in other regions of North America. In the Gunn Member of the Stony Mountain Formation, the fossil assemblages (particularly rich in brachiopods and corals) indicate a relatively shallow, subtidal, largely open, tropical marine depositional environment, with a certain amount of fine siliciclastic material input (Young and Elias 1999; Young et al. 2008). During the late Katian (Maysvillian–Richmondian) the shallow, epicontinental, tropical seas appear to have facilitated the development of gigantism not only in brachiopods but in many other organisms, such as receptaculitids, nautiloids, and gastropods (Jin 2001).

The early forms of *Hiscobeccus* originated in the continental-margin basins or platforms of Laurentia, most likely in relatively deep-water (mid- to outer-shelf) settings during the early Katian. By the late Katian (Maysvillian–Richmondian) the newly formed shallow inland seas led to *Hiscobeccus* gigantism long after its origin. The large shell was most likely an adaptation to the shallow, warm epicontinental tropical seas with soft muddy substrates. Supersaturation of the seawater with respect to  $\text{CaCO}_3$  may have been a contributing factor, just as in modern tropical, especially equatorial shallow seas. In such supersaturated environments, the secretion and maintenance of  $\text{CaCO}_3$  shells cost less metabolic energy. Increase in size and volume may also have been associated with an enlargement of the lophophores which are responsible for suspension filter feeding and respiration in brachiopods. An increase in lophophore size and volume was probably an adaptation in order to increase feeding efficiency and oxygen exchange in tropical marine environments, especially in paleoequatorial epicontinental seas, where poor water

circulation, reduced oxygen content, and fluctuating micro-particle food supply were expected to be common. The generally low oxygen content in the paleoequatorial inland seas may have been the result of several factors:

- a) The shallow paleoequatorial intracratonic seas had a warm water mass year round and thus had a generally low oxygen content;
- b) The paleoequatorial zone lacked hurricanes or severe storms to cause effective vertical mixing, leading to low oxygen content even at relatively shallow-water substrate (e.g. 30 m depth);
- c) The vast expanse of shallow epicontinental seas would have poor connection with open-ocean currents, and hence sluggish circulation.

Siliciclastic silts and iron-rich sediment in the Gunn and Penitentiary members indicate a possible change in the epicontinental sea from clear to turbid conditions (Elias 1991; Jin and Zhan 2001; Young et al. 2008). This would have had a negative impact on sunlight penetration and hence on the primary productivity. The increase in the lophophore size of *Hiscobeccus gigas* may have been an adaptation to such paleoecological stressors by increasing feeding efficiency.

### 3.5.2 Shell convexity (T/W)

The shell thickness/width (T/W) ratio is used as a proxy to describe shell convexity. *Hiscobeccus capax* of Richmondian age from the Cincinnati region has the highest convexity among all forms of *Hiscobeccus* and *Rhynchotrema* (Figure 3.13). Despite its large shell size, *Hiscobeccus gigas* from the Stony Mountain Formation of southern Manitoba has a lower convexity index than *H. capax*.

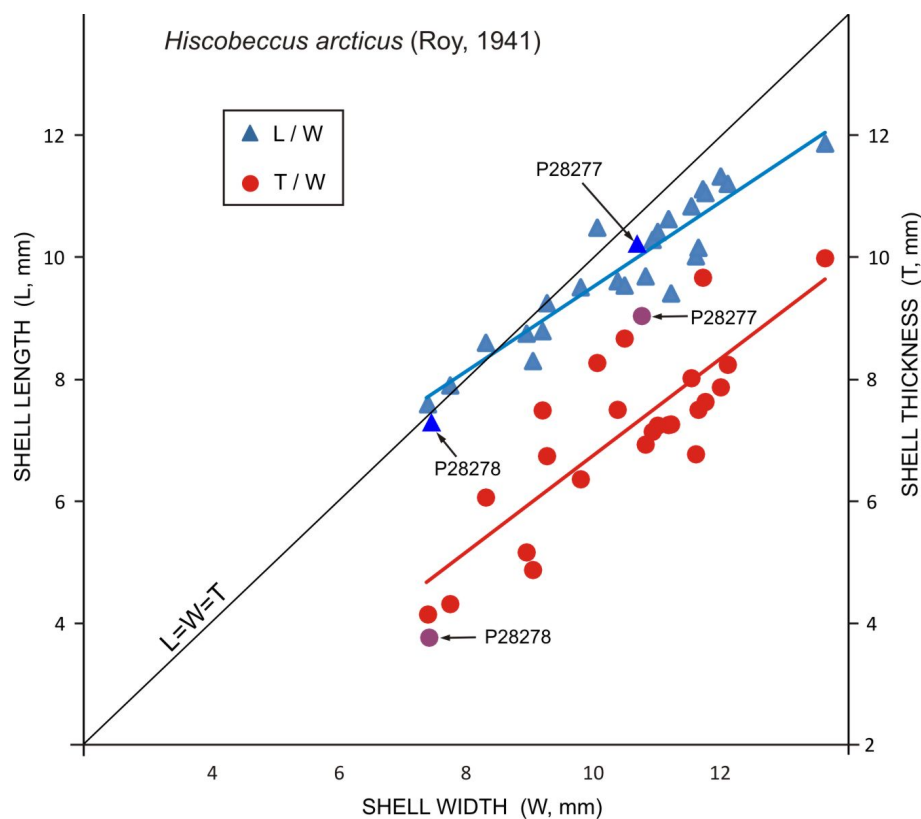


Figure 3.13 Shell dimensions of *Hiscobeccus arcticus* (Roy, 1941), samples (24 specimens) from GSC Loc. 113531, Amadjuak Formation, Silliman's Fossil Mount, Baffin Island, and two holotypes, PE-P28277 (*Rhynchotrema capax arcticum*, Roy 1941), PE-28278 (*Rhynchotrema anticostiense breve*, Roy, 1941) from Silliman's Fossil Mount, Baffin Island.



The older *H. mackenziensis* (Trentonian) has the lowest convexity index. Among the *Rhynchotrema* species, *R. increbescens* from the Trentonian strata in the Bay of Quinte has a relatively high convexity index, some approaching a globular shell.

During the Late Ordovician (middle and late Katian), the Cincinnati region was covered by a shallow epeiric sea, located about 20 degrees south of the equator (Scotese and McKerrow 1991; Cocks and Torsvik 2011). The depositional environment was characterized by a storm-dominated carbonate ramp (Holland 2001, 2008). The Waynesville Formation represents a relatively shallow-water environment (BA2–3) near the Cincinnati Arch and contains abundant *Hiscobeccus capax*. The highly globular shells of *H. capax* may have been the result of adaptation to such a high-energy, storm-dominated environment. Increased globosity in *H. capax* is closely associated with prominent posterior thickening of the shell, to the extent that the dental plates become fused with the posterior shell wall (Amsden 1983; Jin and Lenz 1992). A globular shell, coupled with a strongly weighted posterior, would have improved stability, with a humpty-dumpty effect to maintain its beak-down life position on the sea floor. In comparison, *H. gigas* in the Stony Mountain Formation of southern Manitoba, located within 10° of the Late Ordovician paleoequator, in the hurricane-free zone (Cock and Torsvik 2011; Jin et al. 2011), did not develop an extremely globular shell, despite its unusually large shell size. This corroborates the interpretation of a relationship between shell globosity and water turbulence.

### **3.5.3 Shell lamella density index (“wrinkling index”)**

The shell lamella density index (SLDI) is a morphological parameter used in this study to determine the proportions of lamella-covered shell surface area and lamellar

density. As is shown in Figure 3.14, lamellae increase from older forms of *Rhynchotrema* to early forms of *Hiscobeccus*. The older forms of *Rhynchotrema*, *R. wisconsinense* from Minnesota (late Sandbian) and Lake Simcoe area, have a low SLDI value of 0.71 amongst all species examined in this study, with an average of four lamellae covering 17% of the shell length from anterior margin. There is a slight SLDI increase in the specimens of *Rhynchotrema increbescens* from Trentonian strata of the Ottawa area, Kentucky, and Bay of Quinte. The Ottawa specimens have five lamellae on average, covering 31 % of the shell length, with a SLDI value of 1.89. In the Kentucky forms of *Rhynchotrema*, an average of seven lamella covers 27% of the shell length, with a SLDI value of 2.33. The specimens from the Bay of Quinte have nine lamellae on average, covering 36% of shell length (SLDI = 3.81).

The oldest form of *Hiscobeccus*, *H. mackenziensis*, exhibits strong growth lamellae and an increased lamella density index (value of 6.23) compared to all examined forms of *Rhynchotrema*. It typically has an average of 11 lamellae, covering 52% of the shell length, with only the umbonal areas devoid of lamellae (see Jin and Norford 1996). By Maysvillian time, the lamella density index becomes more pronounced in *H. arcticus* from the Amadjuak Formation of the Baffin Island (Figure 3.14). Despite their relatively small shell size (average 9.8 mm in length), the Baffin species usually has an average of 15 lamellae, covering 52 % of the shell length, with lamella density index value of 8.45. During the Richmondian, *Hiscobeccus* attained a maximum lamella density index, which is particularly evident in *H. capax* and *H. gigas*.

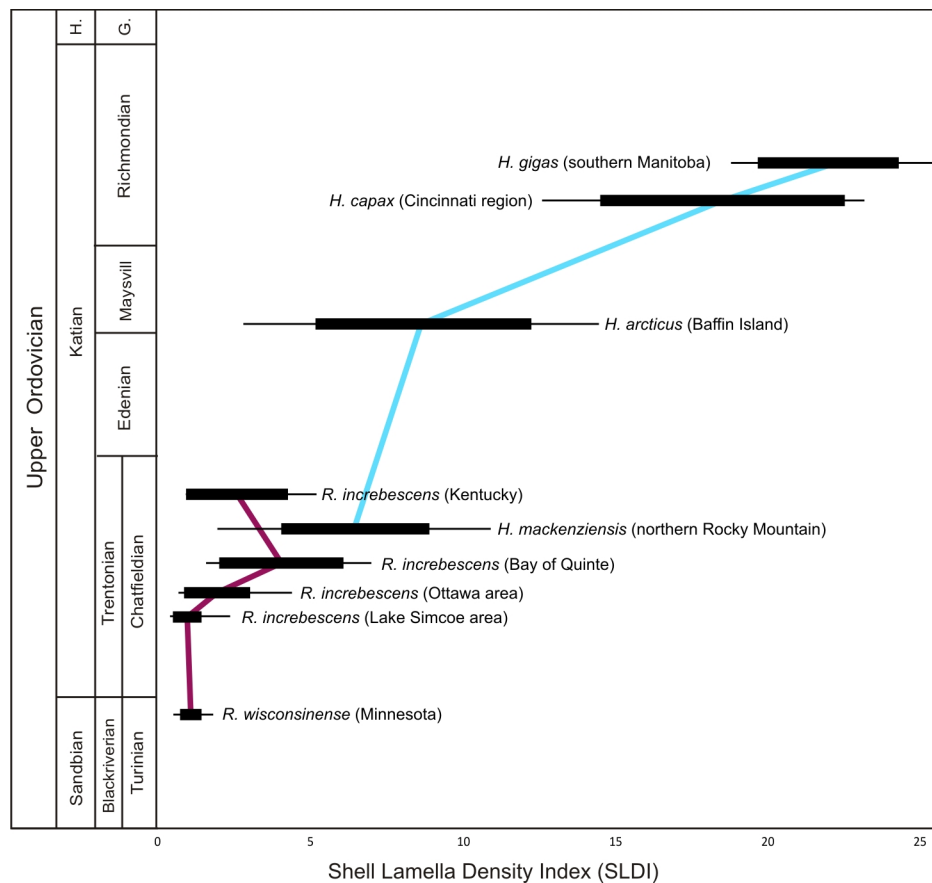


Figure 3.14 Plots of shell lamella density index (SLDI) for *Rhynchotrema* and *Hiscobeccus* from nine localities. The Richmondian forms of *Hiscobeccus* have the highest SLDI value among all specimens.

In the Cincinnati region (Figure 3.14), *H. capax* from the Waynesville Formation was clearly separated from other forms of *Rhynchotrema* and *Hiscobeccus* by developing strong growth lamellae, with up to 25 lamellae extending virtually to the apices of both valves (SLDI=18.68).

The highest lamella density index belongs to *H. gigas* from the Stony Mountain Formation of southern Manitoba (Figure 3.14), with values of 22.10 to 30 lamellae covering 79% of the shell length.

Increased lamellosity in *Hiscobeccus*, especially in such younger forms as *H. capax* and *H. gigas* during Maysvillian–Richmondian time, was likely an adaptation to the shallow, warm epicontinental tropical seas with soft muddy substrates. Within this environment, lamellae would have helped anchor the shell in soft lime mud and reduce their sliding on the sea floor during water turbulence. Similar shell lamellosity is common also in Silurian and Devonian atrypide brachiopods, which preferred muddy bottom depositional settings (Copper 2004).

### 3.6 Systematic paleontology

Order Rhynchonellida Kuhn, 1949

Superfamily Rhynchotrematoidea Schuchert, 1913

Family Rhynchotrematoidea Schuchert, 1913

Genus *Hiscobeccus* Amsden, 1983a

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

Age: Late Trentonian to Richmondian.

*Hiscobeccus arcticus* (Roy, 1941)

Figures 3.11 (images M–W), 3.15, 3.16

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

1941 *Rhynchotrema anticostiense breve* 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 breve* (Roy); Bolton, Pl, 20, fig.19, 24.

*Type specimens.* *Rhynchotrema capax arcticum*, FM P28277, holotype (original of Roy, 1941, p. 100, fig. 66). *Rhynchotrema anticostiense breve*, FM P28278, holotype, original of Roy (1941, p.101, fig. 67); Silliman’s Fossil Mount, Frobisher Bay, Baffin Island.

*Type locality and type stratum.* 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 (Sanford and Grant 2000; Bolton 2000). This should be referred as the type locality and type stratum.

*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, Figure 3.17). 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 3.16, 2.6–2.8 mm from apex; Figure 3.17, E, F), covering more than three-fourths 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 3. 15, images A-L).

*Exterior of ventral valve.* Umbo strongly convex and arched; beak suberect in younger forms, incurved in gerontic forms to become oppressed to umbonal area dorsal valve. 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.

*Interior of ventral valve.* Dental plates low, forming small dental cavities, extending slightly anterior of hinge line (Figure 3.16) Teeth small, weak. Muscle field poorly impressed.

*Exterior of dorsal valve.* 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 3. 11 images M-W).

*Interior of dorsal valve.* Sockets small, shallow. Septalium small, narrow, minute trough-like, anteriorly not extending beyond hinge line (2.5–2.8 mm, Figure 3.16). Septalial plates short, poorly delimited (Figure 3.16). 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.

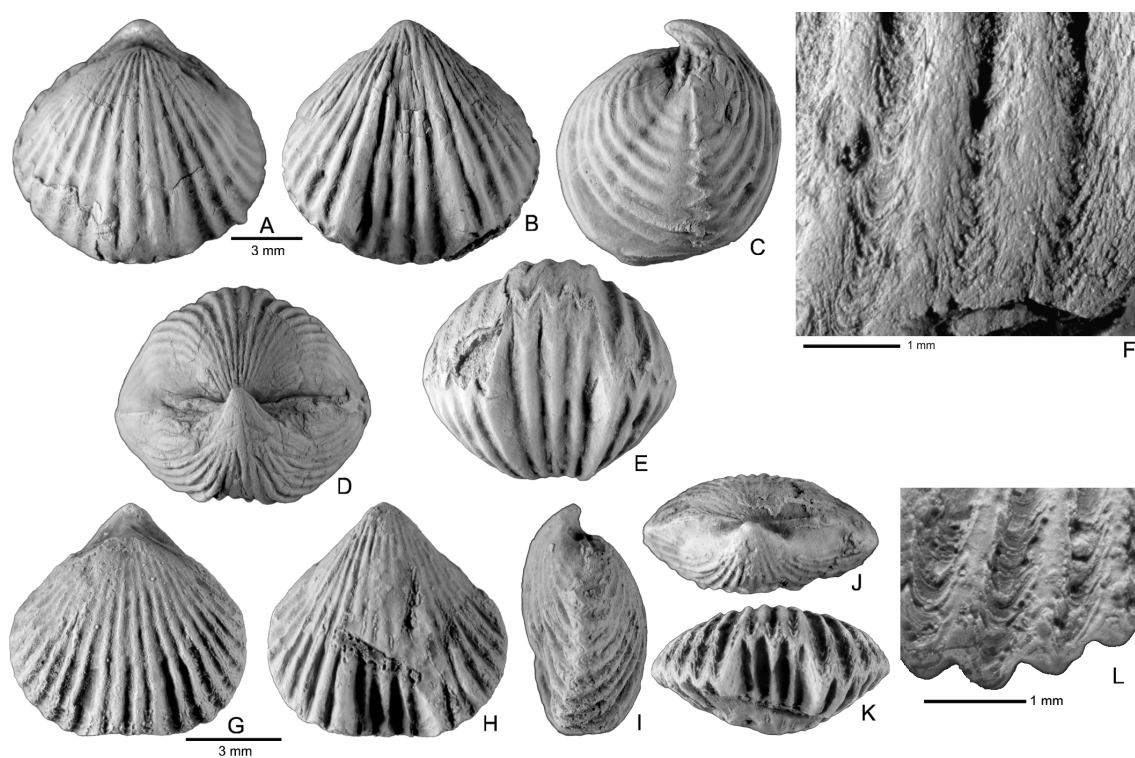


Figure 3.15 Original types of *Hiscobeccus arcticus* (Roy, 1941) from Silliman's Fossil Mount, Baffin Island. A–F, *Rhynchotrema capax arcticum* Roy, 1941, holotype, PE-P28277; G–L, *Rhynchotrema anticostiense breve* Roy, 1941, holotype, PE-P28278.

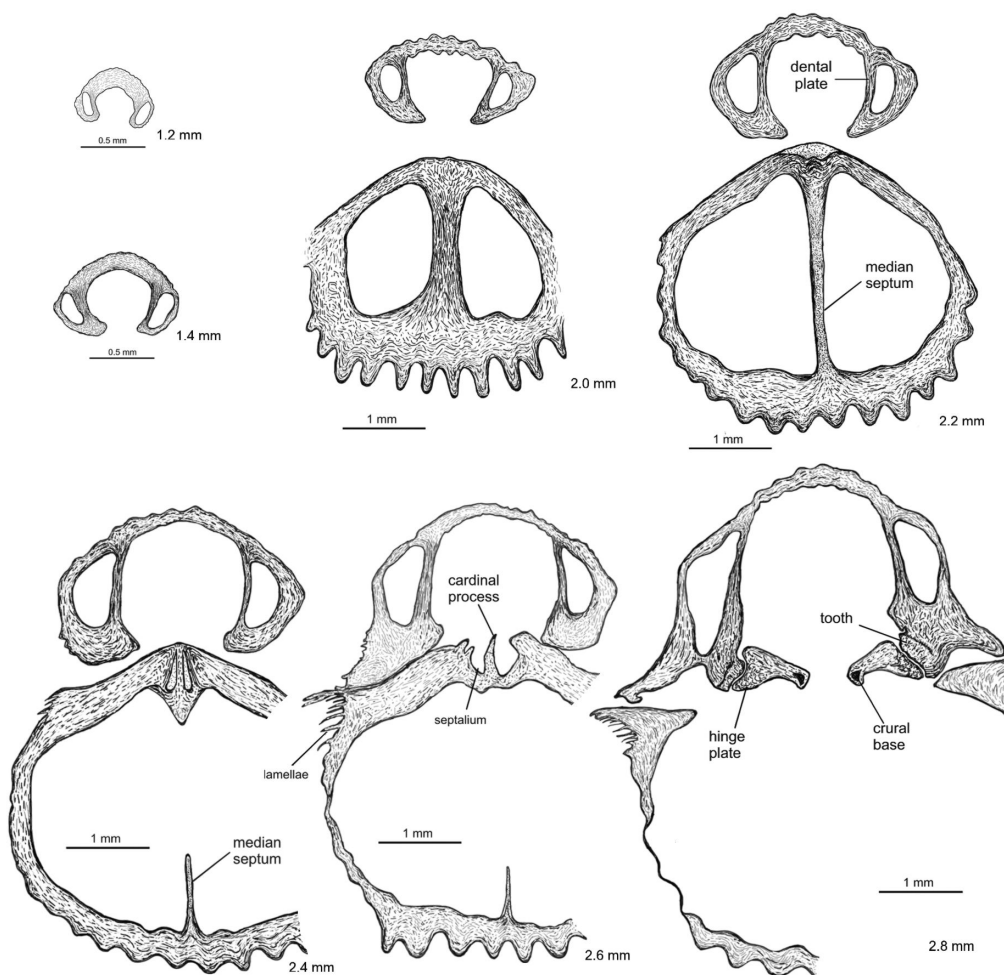


Figure 3.16 Serial sections of *Hiscobeccus arcticus* (Roy, 1941), GSC loc. 0104507, Amadjuak Formation, Silliman's Fossil Mount, Baffin Island. The distance of a section is measured from shell apex.



*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 Fossils 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 *Hiscobeccus* 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 3.16, 2.6 and 2.8 mm from apex; Figure 3.17, E, F) in spite of its smaller shell size. All other species of *Hiscobeccus* 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).

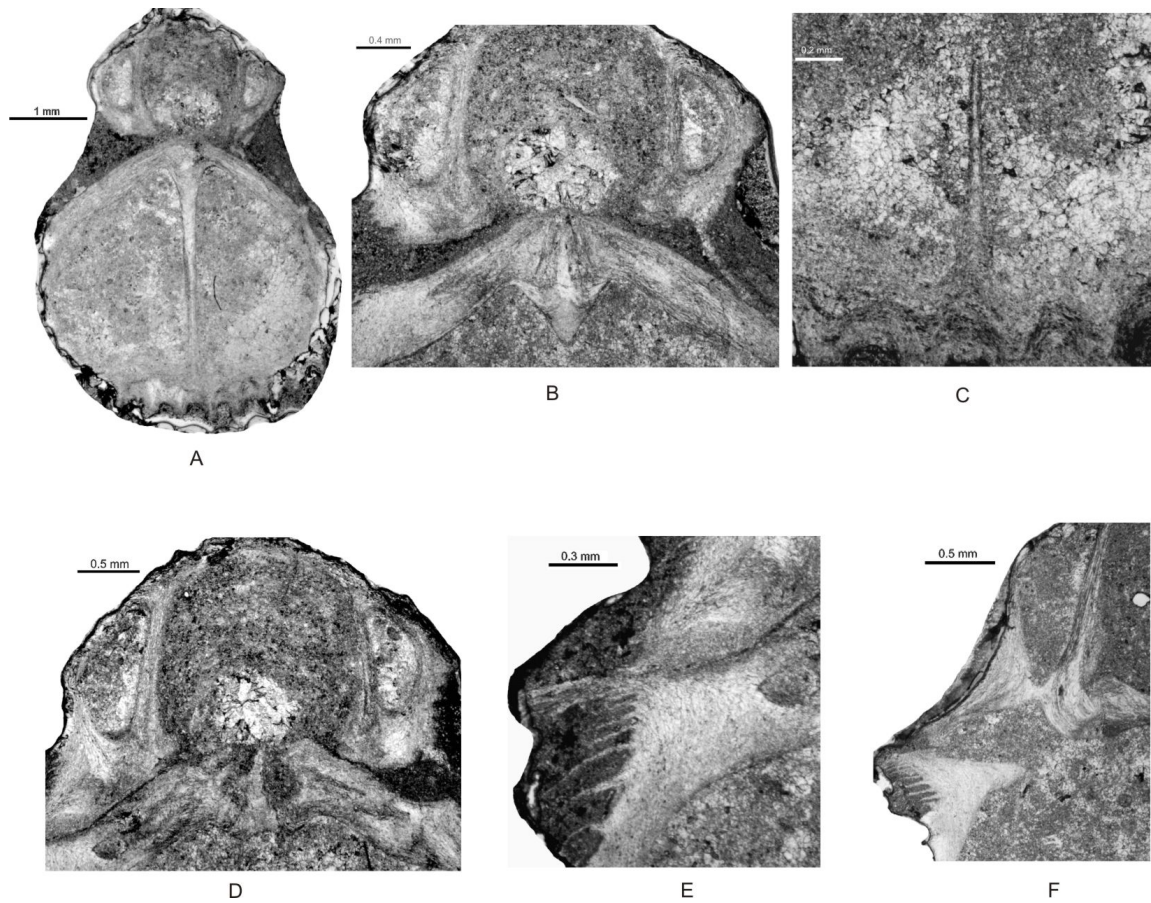


Figure 3.17 *Hiscobeccus arcticus* (Roy, 1941) Topotype, GSC Loc. 0104507, A–D: cardinal process, median septum, septalium, E–F: lamellae, hinge plate; Amadjuak Formation, Silliman’s Fossil Mount, Baffin Island.

### 3.7 Conclusions

Previous qualitative studies have indicated that *Hiscobeccus* most likely evolved from *Rhynchotrema* during the early Katian and developed a large, globular and strongly lamellose shell. The quantitative multivariate analysis in this study, based on 171 rhynchonellide specimens (*Rhynchotrema* and *Hiscobeccus*) from nine upper Sandbian–upper Katian localities in North America, provides strong support for the early hypothesis and demonstrated that the earliest *Hiscobeccus*, *H. mackenziensis*, exhibits transitional characteristics between *Rhynchotrema* and the typical *Hiscobeccus*. The multivariate analysis indicates that the shells of early forms of *Hiscobeccus* (*H. mackenziensis*) cluster more closely with *Rhynchotrema* than with younger species of *Hiscobeccus* of Maysvillian–Richmondian age. The oldest *Hiscobeccus* from the Advance Formation of the northern Rocky Mountains was similar to *Rhynchotrema* in size and convexity except for more extensive development of lamellae.

The secondary parameters derived from primary measurements, such as shell size index (SSI), shell convexity index (SCI), shell lamellosity index (SLI), and shell lamella density (SLD) were used in this study to compare the differences between the early and late forms of *Rhynchotrema* as well as early forms of *Hiscobeccus*.

The older forms of *Rhynchotrema* and *Hiscobeccus* have relatively smaller shells compared to younger forms of *Hiscobeccus*. The shell size increased from the older forms of *Rhynchotrema* (late Sandbian and Trentonian) to the early forms of *Hiscobeccus* (Richmondian). By the Late Ordovician (Maysvillian–Richmondian), large-shelled *Hiscobeccus* became widespread in carbonate deposits of the North American paleocontinent, especially in the paleoequatorial Williston and Hudson Bay basins. The

large and globular shells are interpreted as a reflection of increased lophophore size for more efficient filter feeding and respiration, and adaptation to the generally overheated, poorly circulated, oxygen-poor epicontinental seas, with unstable food supply (e.g. periodic plankton blooms).

The specimens of *Hiscobeccus capax* from the Cincinnati region of Richmondian have the highest globosity index values among all forms of *Hiscobeccus* and *Rhynchotrema*. Other Richmondian forms of *Hiscobeccus* showing gigantism, such as *H. gigas* from southern Manitoba, show a lower globosity compared to *H. capax* of the Cincinnati region. Among all *Hiscobeccus* species, *H. mackenziensis* of Trentonian age has the lowest globosity. Increased shell globosity is noted in both the *Rhynchotrema* and the *Hiscobeccus* stocks, such as the strongly biconvex *Rhynchotrema increbescens* from the Bay of Quinte, which approaches the globular *Hiscobeccus capax*. Increased globosity was more likely an adaptation to the high-energy, storm dominated, high tropical latitude paleoenvironments (e.g. the Cincinnati Arch region) during Richmondian time. A globular shell with thickened umbones would have improved stability for *H. capax* by weighting the posterior part of the shell to maintain a beak-down life position on turbulent substrates.

The number of lamellae increased from the old representatives of *Rhynchotrema* to the early forms of *Hiscobeccus*. They usually cover less than one-third of the shell length in *Rhynchotrema*, but more than one-half of the shell in *Hiscobeccus*. The number of lamellae shows gradational increase from older *Rhynchotrema* to pioneer species of *Hiscobeccus* (e.g. *H. mackenziensis* and *H. arcticus*), whereas in younger forms of

*Hiscobeccus* (*H. capax* and *H. gigas*) the total number of growth lamellae increased drastically, in keeping with accelerated increase in shell size and globosity.

Increased lamellosity in *Hiscobeccus*, particularly in such younger forms as *H. capax* and *H. gigas* during Maysvillian–Richmondian time, was interpreted here as an adaptation to the shallow, warm epicontinental tropical seas with soft muddy substrates. Within this environment, lamellae most likely helped to anchor the shell and prevented it from sliding on the muddy substrate during water turbulence. In addition, lamellosity had an additional function against breakage in maintaining the shell strength in storm environments.

During the late Katian (Maysvillian and Richmondian), *Hiscobeccus* diversified and spread across North America, becoming larger, globular, and developing more strongly lamellose shells, especially in the paleoequatorially located epicontinental seas. *Rhynchotrema* was most common and diverse in basins and platforms in the pericratonic regions of Laurentia (e.g. Anticosti Island and Mackenzie Mountains), but generally rare in epicontinental inland seas (e.g. Williston and Hudson Bay basins).

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## Chapter 4<sup>2</sup> – Global paleobiogeographical patterns of early Katian (Trentonian, Late Ordovician) brachiopod faunas

### 4.1 Introduction

Brachiopods constituted the predominant marine shelly benthos in the Paleozoic and as such have been used extensively for paleobiogeographical analysis and paleogeographical reconstructions (e.g. Boucot 1975; Sheehan and Coorough 1990; Shen and Shi 2000; Cocks 2001). Compared to the commonly used quantitative brachiopod biogeography for the Carboniferous and Permian (e.g. Shi 1993), early Paleozoic brachiopod biogeographical analyses have been largely qualitative or semi-quantitative in approach, and regional in scope. This is particularly true for Late Ordovician brachiopod biogeographical analysis, partly because of the unusually high level of endemism displayed by most brachiopod faunas of this age, which makes it difficult to determine the relative biogeographical affinities among the faunas.

During the Late Ordovician, Laurentia (largely North America and Greenland) and its adjacent plates of Baltica and Siberia were located in the tropical zones (Cocks and Fortey 1982; Cocks 2001; Cocks and Torsvik 2004; Cocks and Trovik 2011; see Figure 4.1). In terms of the major cratonic sequences (Sloss 1963), after the Sauk regression during the Early Ordovician, the Tippecanoe transgression resulted in a protracted phase of gradual inundation of the North American craton during the Middle–Late Ordovician time (Sloss 1963; Levin 1996). By the Late Ordovician (mid-Katian), much of Laurentia was flooded by a shallow epicontinental sea, which resulted in the build-up of vast carbonate platforms in both intracratonic basins and pericratonic shelves (Finnegan et al.

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<sup>2</sup> A shortened version of this chapter has been published online (see Sohrabi and Jin 2013).

2012). Such a major phase of marine transgression and carbonate build-up suggests a general greenhouse episode. Some sedimentological and geochemical data, however, have also been used to hypothesize either a broad trend of cooling or episodic cooling in the Late Ordovician, leading to the Hirnantian icehouse climate (e.g. Page et al. 2007; Trotter et al. 2008; Buggisch et al. 2010). Thus the interpretations of Late Ordovician climate change have been rather controversial, much like the late Katian Boda Event that has been interpreted as either a warming or cooling episode (e.g. Fortey and Cocks 2005; Cherns and Wheeley 2007).

During much of the Early and Middle Ordovician, Baltica was in temperate latitudes, between 30° and 60° in the southern hemisphere. By the Late Ordovician (Katian), however, Baltica had moved to the southern tropics between 35° and the equator (Cocks and Fortey 1982; Cocks and Fortey 1998; Cocks 2001; Cocks and Trosvik 2005). This is reflected by the Late Ordovician brachiopods in predominantly carbonate facies of Baltica, with some taxa in common with Laurentia. The terms ‘facies zone’ (Männil 1966) and ‘confacies belts’ (Jaanusson 1976) have been applied for various litho- and biofacies belts within the Baltica which generally reflect differences in depth. In terms of confacies belts, the Baltic Ordovician is divided into the Central Baltoscandian Confacies Belt, the Scanian Confacies Belt, the Lithuanian Confacies Belt, the North Estonian Confacies Belt, and the Oslo Confacies Belt (Jaanusson 1976).

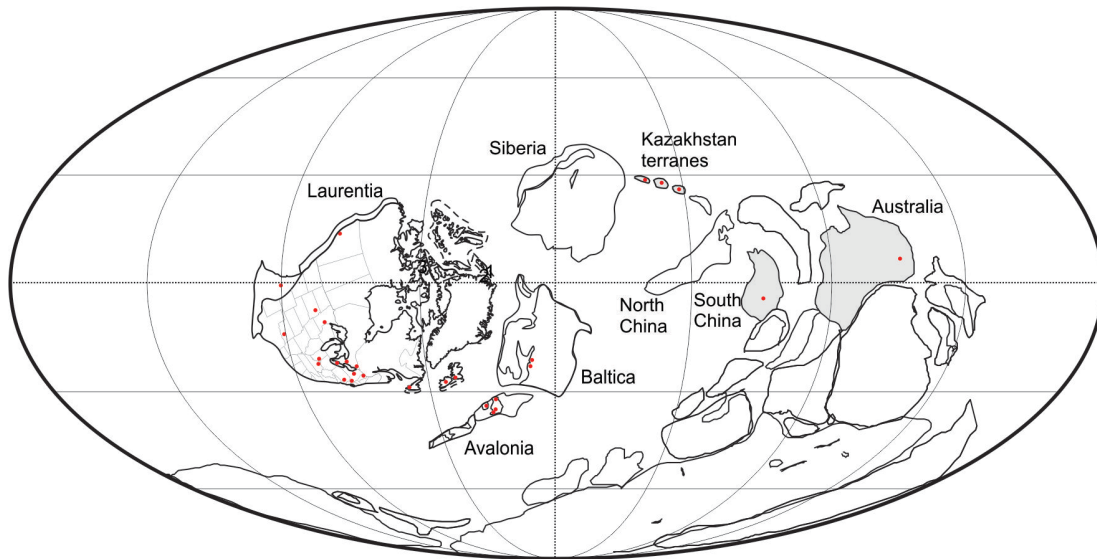


Figure 4.1 Paleogeographical map showing the approximate locations (solid dots) of the 33 early Katian brachiopod faunas from Laurentia, Baltica, Avalonia, Kazakhstan, South China, and Australia. Based map modified from Hints and Eriksson (2007) and Cocks and Torsvik (2011).

Avalonia, which was part of Gondwana during the Cambrian and earliest Ordovician, became separated from Gondwana by the Middle Ordovician (early Darriwilian; see Cocks et al. 1997; Van Staal et al. 1998; Murphy et al. 2006). Eastern Newfoundland, Nova Scotia, New Brunswick, Maine, northern Germany, southeastern Ireland, Wales, England, Belgium, and Holland were parts of Avalonia during the Ordovician Period (Cocks and Torsvik 2004). It has been suggested that some cool-water brachiopods that periodically invaded Laurentia during the Late Ordovician may have been of Avalonian origin (Jin and Zhan 2008).

The supercontinent of Gondwana in the southern hemisphere included most of South America, Africa, Madagascar and Arabia on the west side, and Antarctica, Australia and India on the east side (Cocks 2001; Fortey and Cocks 2003). In general, high-latitude Gondwana brachiopod faunas had little in common with the tropical brachiopod faunas of Laurentia during the Ordovician. The brachiopod faunas from low-latitude Australia (Percival 1991; Percival et al. 2011) are included in this study, although the very small brachiopod fauna from the lower Katian of Tasmania (Laurie 1991) was not used in the multivariate analysis.

There have been several previous studies on Ordovician paleobiogeography that included North American brachiopod faunas (Williams 1969; Jaanusson 1973a, 1973b; Jaanusson and Bergström 1980; Sheehan and Coorough 1990). In most of the previous work, comprehensive global studies of biogeographical patterns of Late Ordovician brachiopod faunas were generally lacking (with exception of the *Hirnantia* fauna), and these studies were either qualitative or semi-quantitative. During the late Middle to early Late Ordovician (late Darriwilian–early Katian), the brachiopod faunas of Laurentia were

semi-cosmopolitan, sharing some brachiopod genera with Siberia, Baltica, and other adjacent tectonic plates or terranes (Jin 1996). By the late Late Ordovician (middle to late Katian), the brachiopod fauna became highly endemic (Sheehan and Coorough 1990; Jin 1996). The transition from the semi-cosmopolitan to endemic brachiopod faunas occurred during the early–middle Katian, although the controlling mechanism for this biogeographical event remains poorly understood. The widely documented “Trentonian brachiopod fauna” in North America (e.g. Wilson 1946; Titus 1982, 1986; Rice 1987), which marks the initial stage of the growing provincialism during the early Katian, is significant for our understanding of this major biogeographical event.

The main objective of this study is to study the early Katian brachiopod faunal biogeography and attempt to shed some light on the changing patterns of brachiopod biogeography.

#### **4.2 Data and methods**

In order to study the global paleogeography and distribution patterns of the early Katian (Trentonian, Chatfieldian) brachiopods the taxonomically well-documented and stratigraphically well-constrained brachiopod faunas from Laurentia, Baltica, Kazakhstan, Avalonia, Australia, and South China are compiled (Figure 4.1). Linguliform and craniiform brachiopods generally make up a very small portion of the brachiopod faunas and their taxonomy is out of date for many regions due to the lack of experts on these groups. As a result, the faunal comparisons in this study are confined to rhynchonelliforms. Most of the brachiopod faunas are from the formations assigned to the Trentonian, Chatfieldian, or upper Caradoc in previous literature. For each fauna, the information on its geographical area, stratigraphical interval, and faunal data sources is

summarized in Table 4.1.

During the Ordovician, Laurentia was the second largest (next to Gondwana) and paleogeographically stable plate, and the largest tropically located plate. As a result of the Late Ordovician marine transgression, brachiopod faunas of Trentonian age (early Katian) were widespread in North America, and well-documented brachiopod faunas from the following regions of Laurentia were selected for biogeographical analysis: western Newfoundland (Port-au-Port Peninsula), Ontario (Ottawa Valley, Lake Simcoe area, and Manitoulin Island), New York, Champlain Valley, Hudson Valley, Appalachian Valley, Kentucky, Indiana, upper Mississippi Valley, Oklahoma, South Dakota, Nevada, California, Northern Rocky Mountains (British Columbia), Girvan (Scotland), and Tyrone (northern Ireland).

During the Late Ordovician (early Katian), Baltica was a tectonic plate with the closest proximity to Laurentia and both had abundant and diverse tropical brachiopod faunas. Brachiopods of the Keila and Oandu stages from the shallow platform facies of East Baltic regions (Estonia and Latvia) were well studied and used for this study (e.g. Öpik 1930, 1932, 1934; Oraspõld 1956; Hints 1973, 1975, 1990, 2010; Rõõmusoks 1964, 1985, 2004; Paškevičius 1994, 2000; Tinn 1998). For comparison, a coeval fauna from the deep-water facies of the Oslo-Asker district of southern Norway (Hansen 2008) is also included in the analysis.

The late Caradoc (early Katian) brachiopod faunas of Avalonia are from the following localities (see compilation by Cocks 2008): Shropshire, Cumbria (England), Powys (Wales), Gwynedd (Wales), Anglesey (Wales), south-eastern Ireland (Wexford, Waterford), and Meath (Eastern Ireland).

The brachiopod faunas of Kazakhstan are from formations of late Caradoc age.



These formations belong to three terranes, the Chu-Ili, Ishim-Selety and Boshchekul (Popov et al. 2000, 2002; Nikitin et al. 2003, 2006). For the Chu-Ili terrane, the brachiopod fauna of the Anderken Formation is slightly older than that from the Dulankara strata and may be latest Sandbian in age. The Anderken fauna is included in the analysis partly because of its similarity to the other Kazakh faunas, and partly because it was used in similar analysis of late Caradoc brachiopod biogeography (e.g. Candela 2006). Its inclusion is useful for comparing results of this study with previous work.

In South China, brachiopods of early Katian age are mainly from the massive bedded limestones of the Pagoda Formation. Due to its hard lithology, it has been difficult to extract brachiopod shells for taxonomic study and thus the faunal data available so far carry a high degree of collection bias (Renbin Zhan, written comm. 2012).

To investigate paleobiogeographical patterns and affinities of the early Katian brachiopod faunas, a binary dataset (presence or absence) was compiled from 33 localities of Laurentia, Baltica, Avalonia, Kazakhstan, and South China, including 225 genera (Appendix 4.2, 4.3). The dataset is subjected to multivariate analyses using the PAST software (Hammer et al. 2001).

For the cluster analysis (CA), the CA dendrogram was generated based on Paired Group method and using the Raup-Crick similarity coefficient. In the principal component analysis (PCA), since the dataset is binary, the variance-covariance algorithm was used to generate the PCA plot. The faunal similarity indices were calculated using Dice, Jaccard, and Simpson coefficients (Appendix 4.3, 4.4, 4.5).

### **4.3 Stratigraphical notes on the brachiopod faunas**

In this study, the dataset is based on the brachiopods from different geographic areas including North America, Wales, eastern and south-eastern Ireland, Scotland, England, Estonia, Kazakhstan and South China (Appendix 4.1, 4.2).

#### **4.3.1 Laurentia**

The Long Point Formation of western Newfoundland consists of a thick sequence of limestones, sandstones and shales (Weerasinghe 1970). This formation is fossiliferous with a relatively rich and diverse brachiopod fauna of Trentonian age (Cooper 1956; Weerasinghe 1970; Bergström 1971a).

The Ottawa Group exposed in Ottawa River valley contains a classic Trentonian brachiopod fauna of North America (Wilson 1946). Much of the Ottawa area is underlain by a sequence of Middle and Upper Ordovician rocks of the Ottawa Group (Williams and Telford 1986), which is stratigraphically equivalent to the Simcoe Group in south-central Ontario and to the Black River and Trenton groups in the New York area. Wilson (1946) subdivided the Ottawa group into the Pamela, Lowville, Leray, Rockland, Hull, Sherman Fall, and Cobourg formations. The Rockland formation (Raymond 1913) is composed of limestones interbedded with shale. The formation contains a typical Trentonian brachiopod fauna (Wilson 1921; Sinclair 1954).

The Black River Group and Trenton Group in New York are subdivided into the Pamela, Lowville, Chaumont, Selby, Napanee, Hull, Sherman Fall, Cobourg, and Collingwood formations (Kay 1937). The brachiopod fauna of northwestern New York State is mainly from the Rockland formation of the Trenton Group.

In western New York the Trenton Group is subdivided, in ascending order, into the Napanee, Kings Falls, Sugar River, Denley, Steuben, and Hillier formations (Titus and Cameron 1976; Titus 1986). The lower Trentonian Napanee Formation contains limestone and interbedded shale. This formation is very fossiliferous including trilobites, echinoderms and brachiopods (Kay 1937). The Kings Falls Formation is composed of limestone with dark to black shales of Kirkfieldian stage in the New York region (Kay 1968). The Sugar River Formation overlies the Kings Falls Formation and contains limestone, interbedded shales, and fine-grainstones, with thin nodular wackestones (Titus and Cameron 1976). The Denley Formation is composed of nodular fine-grained limestones overlying the Sugar River Formation (Kay 1968).

The upper Trentonian strata of western New York State comprise the Steuben and Hillier formations. The Steuben Formation consists of limestones with shale interbeds and is characterized by a resistant, coarse-grained, calcarenite horizon (Kay 1943, 1953). The overlying Hillier Formation was described by Kay (1937) as an argillaceous limestone forming the uppermost unit of the Trenton Group in western New York. These two formations (Steuben and Hillier) indicate the final stage of the Trentonian marine transgression (Titus 1986).

In south-central Ontario, the Simcoe Group traditionally consists of the Black River and Trenton limestones (Liberty 1955) and was divided by Liberty (1969) into in ascending order, the Gull River, Bobcaygeon, Verulam, and Lindsay formations. The Gull River Formation is characterized by peritidal carbonates, with only rare brachiopods.

Region	Area	Stratigraphic Units	References
Western Newfoundland	Port au Port Peninsula	Long Point Formation	Cooper 1956; Weerasinghe 1970; Bergstrom 1971a
Ottawa Valley	Ottawa River valley and vicinity of Ottawa	Ottawa Group; Rockland, Hull, Sherman Fall, Cobourg formations	Wilson 1946
South-central Ontario	Lake Simcoe, Carden Quarry	Babcaeygeon and Verulam	Sinclair et al. 1969; and this study
NY and adjacent areas	western New York	Trenton Group; Napanee, Kings Falls, Denley, Steuben, and Hillier formations	Kay 1937; Titus and Cameron 1976; Titus 1986
Manitoulin Island Region (Cloche Island Formation)	Manitoulin Island, Goat Island	Cloche Island and Verulam formations	Liberty 1969; Cooper 1956; Copper and Long 1993
Champlain Valley	Isle la Motte, Vermont	Isle la Motte Formation	Cooper 1956; Bechtel and Mehrrens 1995
Hudson Valley region	Albany to Poughkeepsie	Rysedorf conglomerate	Cooper 1956
The Appalachians Valley	Pennsylvania, Alabama, Georgia, Tennessee, and Virginia	Ben Hur, Cane Creek, Nealmont, Collierstown, Edinburg, Eggleston, Hardy Creek, Mercersburg, Jacksonburg, Martinsburg, Moccasin, Oranda, Salona formations	Cooper 1956
Tennessee and Kentucky	central basin of Tennessee, High Bridge, Kentucky	Carters, Kimmswick, Tyrone formations	Cooper 1956
Indiana	disturbed area at Kentland	Division 8 of Trentonian age	Cooper 1956
Mississippi Valley	Iowa, Illinois, Minnesota, Wisconsin	Decorah Shale (Spechts Ferry, Guttenberg, and Ion members), Macy Formation, Barnhart Formation,	Ludvigson et al. 1996, 2004; Emerson et al. 2004; Austin 1969; Witzke 1980; Cooper 1956; Rice 1987;

		Plattin Formation	Thompson 1991
Oklahoma	Arbuckle and Wichita Mountains	Viola Formation	Albersttat 1973; Cooper 1956
South Dakota	Black Hills	Whitewood Formation	Cooper 1956
Great Basin	Nevada and California	Dark Shale with Reuschella	Cooper 1956
British Columbia	Northern Rocky Mountain	Advance Formation	Jin and Norford 1996
Shropshire	Holderley, Woolston, Shelve Inlier, Clunbury	Acton Scott, Onny Shale, Cheney Longville, Spy Wood Grit, Holderley Sandstone, Whittery Shale, Hagley Shale, Hoar Edge, Coston, Aldress Shale, Alternata, Harnage Shale, Glenburrell, Smeathen Wood Beds	Cocks 2008
Scotland	Strathclyde, Girvan	Craighead Limestone, Myoch, Albany Mudstone	Cocks 2008
Central Wales	Powys	Llanfawr Mudstone, Allt-yr-Anker, Bryn Siltstone	Cocks 2008
North-west Wales	Gwynedd	Gelli-grîn Group, Cowarch Phosphate, Allt Ddu, Derfel Limestone, Bryn Beds, Nod Glas, Glyn Gower	Cocks 2008
North-west Wales	Anglesey	Garn, Llanbabo, Crewyn formations	Cocks 2008
South-east Ireland	Wexford, Waterford	Duncannon Group, Annestown, Tramore Volcanic, and Grange Hill formations	Cocks 2008
Ireland	Meath	Grangegeeth Volcanic Series, Collon, and Clashford House formations	Cocks 2008
Northern Ireland	Tyrone	Bardahessiagh Formation	Cocks 2008

Cumbria	Melmerby, Dufton	Dufton Shale, Corona beds	Cocks 2008
Chu-Ili	Kazakhstan	Anderken Formation	Popov et al. 2000; Popov et al. 2002
Chu-Ili	Kazakhstan	Dulankara Formation	Popov et al. 2000
Boshchekul	Kazakhstan	Angrensor Formation	Nikitin et al. 2006
Ishim-Selety	Kazakhstan	Tauken Formation	Nikitin et al. 2003
Keila Stage	northern Estonia	Kahula and Vasalemma formations	Hints and Meidla 1997
Oandu Stage	northern Estonia	Vasalemma and Hirmuse formations	Männil and Rõõmusoks 1984; Hints 1998
South China	Yangtze Platform	Pagoda Formation	Zhan and Jin 2007; Bergström et al. 2009
Southern Norway	Oslo-Asker district	upper Arnestad Formation	Hansen 2008
Australia	New South Wales	Billabong and Quondong formations	Percival 1991

Table 4.1 Geographical area, stratigraphical interval, and faunal data sources of the 33 brachiopod faunas used in multivariate analyses of early Katian brachiopod biogeography. For detailed faunal data, see Appendix 4.2.

The Bobcaygeon Formation has been divided into two informal members, a lower member and a middle-upper member (Liberty 1969). The lower member is considered correlative to the Coboconk Formation and the middle-upper member approximately equivalent to the Kirkfield Formation in southwestern Ontario (Liberty 1969; Melchin et al. 1994; Brett and Rudkin 1997; Armstrong and Carter 2006). The Coboconk Member consists mainly of bioclastic and peloidal grainstones, packstones and wackestones. The Kirkfield Member consists of limestone beds with thin shaly interbeds. Fossils are abundant throughout the Bobcaygeon Formation including brachiopods of Trentonian age, such as the characteristic dalmanellid *paucicrura* as well as abundant large colonies of trepostome and parasporid bryzoans.

The Verulam Formation consists mainly of interbedded limestone and shale (Melchin et al. 1994). In the Orillia area the Bobcaygeon Formation is separated from the Verulam Formation by an ash bed (bentonite). The Verulam Formation is fossiliferous and brachiopods are the dominant fossil group. Based on chitinozoan and conodonts, the base of the Verulam Formation coincides with the base of the Shermanian regional stage (Melchin et al. 1994). The Verulam Formation is approximately equivalent to the Sherman Falls Formation in the subsurface of southwestern Ontario (Armstrong and Carter 2006). In the Lake Simcoe area (from Peterborough to Orillia), the formation is composed of thin to medium bedded, fine to medium crystalline limestone, skeletal wackestone and packstone with interbedded grey-green shale. The shell-rich beds often have scoured bases and cross-stratification, suggesting a generally shallow-water, storm-influenced carbonate platform. The formation is richly fossiliferous including common

brachiopods of Trentonian age, such as *Paucicrura*, *Sowerbyella*, *Rafinesquina*, *Parastrophina*, and *Rhynchotrema*.

The brachiopod fauna of Manitoulin Island is based on fossils from the upper Cloche Island Formation (sensu Foerste 1912) and the Verulam Formation. The upper Cloche Island Formation is fossiliferous and contains abundant brachiopods, nautiloids, corals, and stromatoporoids, typical of the North American Trentonian fauna (Foerste 1912; Cooper 1956; Copper and Long 1993).

The Verulam Formation is most accessible around the shoreline of Goat Island just north of Manitoulin Island. In this area, the Verulam Formation contains limestones, micritic mudstone, bryozoan biostroms, and shelly wackestone and packstone shaly partings. Strophomenide and rhynchonellide brachiopods are particularly abundant such as *Rafinesquina* and *Rhynchotrema* characteristic of the Trentonian (Copper and Long 1993).

The brachiopod faunas of British Columbia are from the northern Rocky Mountains. The Advance Formation is a thin stratigraphic unit in the northern Rocky Mountains such as Advance Mountain, Mount Burden and Williston Lake region. This formation contains platy and nodular carbonates and shales (Norford 1996). Brachiopod fauna is abundant and diverse in the Advance Formation and indicates a Caradoc age (see Jin and Norford 1996), which is supported by correlations of other fossils such as corals, trilobites, bryozoans, and gastropods (Bolton 1996; Elias 1996; Rohr 1996).

In eastern United States, brachiopods occur commonly in Trentonian strata in the Champlain, Mohawk and Hudson valleys (Cooper 1956). In the Champlain Valley, the brachiopods are predominantly from carbonate rocks of the Isle la Motte Formation



which was considered coeval to the Rockland of Ontario (Kay 1937; Cooper 1956), although Bechtel et al. (1995) recently interpreted the strata as Blackriverian (upper Sandbian) in age. The brachiopod fauna from the Isle la Motte Formation is included in the analysis in this study because of its overall similarity to other Trentonian faunas.

The Hudson Valley brachiopods included in this study are from the Rysedorf (= Rysedorph) conglomerate of Trentonian age. The pebbles of the conglomerate were sourced from several older rock formations, such as the grey limestone (lower Cambrian), black crystalline limestone and black compact limestone of pre-Katian age (Cooper 1956). This formation contains brachiopod of Trentonian age (Ruedemann 1901b, 1930; Cooper 1956).

The Trentonian strata in the Appalachians are exposed in Alabama, Georgia, Tennessee, and Virginia. In Virginia and Tennessee, the Ben Hur Formation contains the brachiopod fauna of Trentonian age (Miller and Brosge 1950). The formation consists of yellowish-grey limestone and yellow mudstone (Cooper 1956).

In southwestern Virginia and northeastern Tennessee, the Cane Creek Formation is of Trentonian age and comprises grey limestone, greenish mudstone and thin-bedded shale. This formation contains several bentonites and fossils of brachiopods are fairly common in the upper part of the formation (Cooper 1956). The Cane Creek Formation is correlated with the upper member of Carters Limestones of central Tennessee (Cressman and Noger 1976).

In central Pennsylvania, the Nealmont Formation is a sequence of grey limestones of Trentonian age. The formation is separated into three members; Oak Hall, Centre Hall and Rodman (Kay 1944). The Oak Hall Member is composed of medium- to coarse-

grained, heavy-bedded limestone with some layer of dolomites. The Centre Hall Member is distinguished from other members by its thinner-bedded and shaly character. The member is fossiliferous and contains brachiopods of early Trentonian age (Kay 1944; Cooper 1956). The Rodman Member consists of dark, medium –to coarse-grained limestone and is highly fossiliferous with an abundance of brachiopods (Field 1919; Kay 1944; Cooper 1956). According to Young et al. (2005) the Nealmont Formation in Virginia is of Trentonian (Chatfieldian) age.

The Collierstown Formation is exposed in areas west of Lexington, Virginia (Cooper and Cooper 1946). The formation is composed of shell limestone and calcarenite and crowded with brachiopods of Trentonian age (Cooper 1956).

The Edinburg Formation in Virginia includes the Liberty Hall, St. Luke, and Lantz Mills facies (Cooper and Cooper 1946). The Liberty Hall facies contains black limestone, black graptolitic shale and fossils of brachiopods (Cooper and Cooper 1946; Cooper 1956). The St. Luke facies comprises massive limestone beds and calcarenites. Rader (1984) proposed a Late Ordovician age for the Edinburg Formation whereas based on the conodont biostratigraphy, Harris et al. (1994) indicated a Blackriverian age for this formation. Brachiopods and bryozoans are the most common fossil members in this formation (Cooper and Cooper 1946; Cooper 1956; Rader 1984).

The Eggleston Formation appears in southwestern Virginia and East Tennessee. This formation is divided into three informal members: lower, middle, and upper (Nolde 1996). The Eggleston Formation is composed of greenish-grey, calcareous mudstone in the lower member, and platy limestone in the middle and upper members (Noldy 1996;

Cooper 1956). This formation contains fossils including brachiopods. According to Ryder (1996), the Eggleston Formation is of (Trentonian) Rocklandian age.

The Hardy Creek Formation in Virginia contains dense, fine-grained limestone with chert nodules (Miller and Brosge 1950). This formation can be divided into upper and lower limestone units which are separated by a middle argillaceous limestone unit (Harris 1958). Fossils are present in this formation including brachiopods (Cooper 1956). The Hardy Creek Limestone is of Late Ordovician (Trentonian) age (Cooper 1956; Nolde 1996).

The Mercersburg Formation represents the Trentonian strata in the eastern belt of central Pennsylvania (Craig 1949). This formation includes two members; the lower Housum Member and the upper Kauffman Member. The Housum Member is composed of medium-grey, fine-grained limestone. The recorded brachiopods from this member are Trentonian in age such as *Öpikina* and *Sowerbyella* (Craig 1949; Cooper 1956). The Kauffman Member contains platy, bedded limestone and brachiopods of Trentonian age including *Dinorthis*, *Sowerbyella*, *Strophomena*, and *Zygospira* (Craig 1949; Cooper 1956).

In northwestern New Jersey and adjacent Pennsylvania, the Jacksonburg Formation represents the Trentonian (Rocklandian) rocks (Miller 1937; Ray and Gault 1961). This formation consists of calcareous shales, high-grade limestone, and dark blue or black fossiliferous limestones. Brachiopods of Trentonian age are common in this formation including *Dalmanella*, *Rafinesquina*, and *Skenidioides* (Kummel 1908; Miller 1937; Cooper 1956).

In Virginia, the Martinsburg Formation contains a thick mass of silty and arenaceous shale which overlying the Middle Ordovician limestones in the Appalachian Valley (Geiger and Keith 1891; Keith 1894; Cooper 1956). The brachiopod faunas are from the lower Martinsburg (Salona) in Virginia, and the lower Martinsburg (Curdsville) in southwestern Virginia and Tennessee. The Martinsburg Formation is of Chatfieldian age and is equivalent to the Trenton Limestone in Western Virginia (Twenhofel et al. 1954; Leslie and Bergström 1995; Ryder et al. 1996). This formation is fossiliferous and brachiopods of Trentonian (Chatfieldian) age such as *Parastrophina*, *Paucicrura*, *Skenidioides*, and *Dalmanella* are abundant especially from southwestern Virginia and Tennessee (Rodgers 1953; Cooper 1956).

The Moccasin Formation is widespread in southwestern Virginia and northeast and eastern Tennessee (Campbell 1894; Rodgers 1953). This formation is composed of a mainly maroon calcareous shale, siltstone, silty limestone and blue-weathering limestone (Rodgers 1953). The Moccasin Formation underlies the Eggleston Formation and is equivalent to the Nealmont and Edinburg formations (Rader 1984; Cooper 1956). The formation is of Trentonian (Rocklandian) age and contains fossils of brachiopods such as *Zygospira* (Cooper 1956; Calvert 1962; Ryder et al. 1996).

In Virginia, the Oranda Formation is overlain by the Martinsburg Formation and contains argillaceous limestone with metabentonite clays, shales, and ledge-making siltstones (Cooper and Cooper 1946; Kay 1948). The base of the Chatfieldian (Trentonian) in the Shenandoah Valley is the contact between the Oranda and Martinsburg formations which in British terms corresponds to the Burrellian and Cheneyan of the Caradoc Series (Leslie and Bergström 1995; Leslie 2000; Fortey et al. 2000). Fossils are common in the

Oranda Formation including silicified trilobite faunas and brachiopod fauna (*Parastrophina*, *Rafinesquina*, *Sowerbyella*) of Trentonian age (Cooper 1956; Adrain 2005). These brachiopod fauna are similar to the fauna of the lower Edinburg Formation and the Stinchar-Balclatchie Formation of the Girvan District, Scotland (Cooper 1956).

The Salona Formation extends from Pennsylvania into northern Virginia. This formation is composed of black and dark argillaceous limestone and dark calcareous shale (Kay 1944; Cooper 1956). The Salona Formation overlies the Nealmont Limestone and is equivalent to the Eggleston and lowermost Martinsburg formations in southwest Virginia (Kay 1956). Based on stratigraphic position and fossils, the Salona Formation is of Trentonian (Rocklandian) age (Ryder et al. 1992). Fossils are abundant in this formation such as Trentonian age brachiopods *Sowerbyella* and *Rafinesquina* (Kay 1944; Cooper 1956).

In the central basin of Tennessee and High Bridge, Kentucky, the brachiopod faunas are from the formations of Trentonian age. The Carters Formation overlies the Lebanon Limestone and underlies the Hermitage Formation and represents Trentonian strata in the central basin of Tennessee (Safford 1869; Wilson 1949). This formation is divided into lower and upper members (Wilson 1949). The lower member contains calcarenite with some fine-grained layers. The upper member is composed of fine-grained, laminated, argillaceous limestone (Wilson 1949; Cooper 1956). Fossils are common in both members, but fossils of brachiopods are rare in the lower part whereas they are abundant in the upper part (Cooper 1956; Alberstadt et al. 1974; Wahlman 1992). The Carters Formation is equivalent to the Hardy Creek and Cane Creek in Virginia (Cooper 1956).

The Kimmswick Formation in Tennessee and Missouri is mainly composed of coarse calcarenite, and high-calcium limestones (Ulrich 1911; Thompson 1991). The formation is equivalent to the Carters Formation of Trentonian age in the central basin of Tennessee (Wilson 1949; Cooper 1956). In the central basin of Tennessee, the Hermitage Formation overlies the Carters Formation and contains brachiopods of Trentonian age (McFarlan 1931; Wilson 1949). The Kimmswick Formation is fossiliferous including corals, gastropods, bryozoans, trilobites and brachiopods such as *Rhynchotrema* and *Strophomena* (Esker and Levin 1964; Cooper 1965; Nelson et al. 1996)

In High Bridge, central Kentucky, the Tyrone Formation consists of grey limestone and three metabentonite beds (Miller 1905; Cooper 1956). Fossils contained in this formation are mostly nautiloids, cephalopods, gastropods, and brachiopods such as *Strophomena* (Wahlman 1992; Cooper 1956; Frey 1995). The Tyrone Formation is equivalent to the Cane Creek Formation of Virginia and upper Carters of the central basin of Tennessee and is of Trentonian age (Rocklandian to Kirkfieldian) (Huffman 1945; Cooper 1956; Frey 1995).

In Kentland, Indiana, the Ordovician strata are divided into 12 divisions (Shrock 1937). Division 8 is of Trentonian age and contains dolomitic limestone with black or grey carbonate shale (Shrock 1937; Cooper 1956). Fossils are abundant in this division including brachiopods such as *Rafinesquina* and *Hesperorthis* (Cooper 1956).

The Ordovician formations in the Mississippi Valley are well known in two geographic areas; the upper Mississippi Valley and the lower Mississippi Valley. In the upper Mississippi Valley, the Ordovician strata consist of the following formations: St. Peter sandstone, Platteville Formation, Decorah Formation, and Prosser Formation. The

brachiopods of Trentonian age are from the Decorah Formation, which is underlain by the Platteville Formation. In eastern Iowa, the Decorah Formation contains three members including: Spechts Ferry, Guttenberg, and Ion members in ascending order, whereas in Minnesota this formation loses its lithologic distinction and becomes more shale-dominated (Ludvigson et al. 1996, 2004; Emerson et al. 2004). The Decorah Formation is composed of grey-green shale with thin limestone beds and illite with lesser amounts of kaolinite (Parham and Austin 1969; Austin 1969; Witzke 1980). The Spechts Ferry Member represents the basal member of the Decorah Formation and is the most prominent and geographically widespread shale among the Platteville and Decorah shales (Witzke 1980). The brachiopods of Trentonian age such as *Rostricellula* and *Strophomena* have been reported from the Spechts Ferry Member (Cooper 1956).

The Guttenberg Member is characterized by nodular-bedded limestones with organic-rich brown shale in the type area (Ludvigson et al. 1996, 2004). This formation is correlated with the Oranda Formation in the Appalachian Valley and the Carters Formation of Tennessee. Fossils are common in this member, including Trentonian age brachiopods such as *Rafinesquina* and *Rhynchotrema* (Cooper 1956).

The Ion Member is widely distributed in the Upper Mississippi Valley. This member contains shale and limestone with a succession of pyretic and phosphatic hardground surfaces in Minnesota and Iowa (Ludvigson et al. 2004). This member is equivalent to the Kimmswick and Curdsville formations of Tennessee (Kay 1937; Cooper 1956). The common brachiopods in this member are *Rostricellula* and *Zygospira* of Trentonian age (Cooper 1956).

In the upper Mississippi valley, the Prosser Formation overlies the Ion Member and contains fine grained limestone and calcareous shale (Austin 1969; Mossler 1985, 1987). This member is abundant in fossils including brachiopods (e.g. *Parastrophina* and *Rostricellula*).

In the Middle Mississippi Valley, the Macy Formation represents Trentonian strata and contains fine-textured limestone. This formation is divided into two members: the lower Hook Member and the upper Zell Member (Larson 1951; Cooper 1956; Thompson 1991). The Hook Member is composed of yellowish-brown fine calcitite with dolomitic partings, and layers of conglomerate (Larson 1951). Both members contain fossils including brachiopods which are abundant in the Zell Member (e.g. *Hesperorthis*, *Rhynchotrema*, *Sowerbyella*). The Macy Formation correlates with the Carters Formation in the Central Basin of Tennessee and the Spechts Ferry Member of the Decorah Formation. The Zell Member is overlain by the Barnhart Formation in the Middle Mississippi Valley.

The Barnhart Formation is composed of greenish shale with thin limestones (Cooper 1956). The formation is likely an equivalent to the Guttenberg Member of Decorah Formation (Kay 1935; Cooper 1956). Fossils of brachiopods such as *Paucicrura*, *Rafinesquina*, and *Zugospira* are common in this formation (Cooper 1956).

In northern Arkansas, the Plattin Formation is a dense blue-grey limestone (Buckley and Buehler 1904). This formation is correlated with the Decorah and Barnhart formations in Mississippi Valley (Cooper 1956; Nelson 1996). This formation contains Trentonian age brachiopods such as *Rafinesquina*, and *Strophomena* (Cooper 1956).



In Oklahoma, the Viola Formation represents strata of Trentonian age and contains light-grey to dark limestone (Alberstadt 1973). Brachiopods are reported from the lower member of this formation (e.g. *Platystrophia*, *Rafinesquina*, *Rhynchotrema*) which give a middle Trentonian age (Decker 1933; Alberstadt 1973).

The Whitewood Formation is exposed in South Dakota and includes three members. This formation contains grey shale in the lower member, siltstone in the middle member, and dolomite in the upper member (Furnish et al. 1936; McCoy 1952; Cooper 1956). The upper part of the formation contains fossils of cephalopods and brachiopods of Trentonian age (McCoy 1952; Cooper 1956).

The Trentonian strata of Great Basin region in Nevada and California are from the Dark Shale with *Reuschella*. This formation is composed of yellow-weathering limestone and dark shales (Cooper 1956). The formation is abounding in fossils including brachiopods of Trentonian age such as *Hesperorthis*, *Reuschella*, *Rostricellula*, and *Sowerbyella*. The brachiopods listed suggest a correlation with the Oranda Formation.

The brachiopod faunas of Scotland (Caradoc) are in the Girvan region, which was part of Laurentia during the Ordovician. In Girvan, Strathclyde, the listed brachiopods (Cocks 2008) are from the following formations: the Kiln Mudstone Member of the Craighead Limestone (Cheneyan); the Myoch Formation (Streffordian), Whitehouse Bay; the Albany Mudstone Formation (Aurelucian); the Myoch Formation (Streffordian).

Northern Ireland (Tyrone) was also part of Laurentia during the Ordovician, and brachiopods of the Bardahessiagh Formation of Burrellian age (Cocks 2008) are included in this study.

### 4.3.2 Avalonia

In Great Britain and Ireland, the brachiopod faunas are from the strata of late Sandbian–early Katian (late Caradoc; Burrellian–Streffordian) age, including: England, Shropshire, Wales, Ireland, and Scotland.

The brachiopod fauna of central Wales (Powys) are from the strata of Sandbian–early Katian (Caradoc) age including: the Llanfawr Mudstone Formation (Caradoc), Builth; the Allt-yr-Anker Formation (Caradoc), Meifod; the Burrellian-age beds of Llanfyllin; the Bryn Siltstone Formation (Burrellian), Berwyn Hills; the Burrellian age rocks, “Gaerfawr”, near Welshpool; the shales of *gracilis* Zone age (Aurelucian) from Llanfawr Quarry, Llandrindod Wells.

In north-west Wales, Gwynedd, the brachiopod fauna (Cocks 2008) of early Katian (Burrellian–Cheneyan) age are from Gwynedd, including: the Gelli-grîn Group (Burrellian–Cheneyan), Bala area; the Cowarch Phosphate Bed (Burrellian), Bala area; the Allt Ddu Group (Burrellian), Craig-y-Gath; the Allt Ddu Formation (Burrellian), near Fedw Farm, Llangower; the Derfel Limestone Formation (Burrellian), Pont Aberderfel; the Bryn Beds (Burrellian), Bala area; the Nod Glas Formation (Cheneyan), Bala area; the Glyn Gower Formation (Burrellian) at Afon Twrch; the Glyn Gower and the Nant Hir groups (Burrellian), Bala area.

In north-west Wales, Anglesey, the brachiopod fauna contain the formations of Sandbian–early Katian (Caradoc) age including: the Garn Formation (Aurelucian); the Llanbabo Formation (Aurelucian-Burrellian); the Crewyn Formation (Aurelucian).

In Shropshire, the brachiopod fauna are from the strata of Caradoc age (Cocks 2008), including: the Acton Scott Formation (Streffordian); the Onny Shale Formation

(Streffordian); the Crosspipes Member of the Cheney Longville Formation (Cheyneyan); the Spy Wood Grit Formation (Aurelucian) of the Shelve Inlier; the Horderley Sandstone Formation (Burrellian); the Whittery Shale Formation (Burrellian); the Cheney Longville Formation (Cheneyan); the Hagley Shale and Whittery Volcanic formations (Burrellian) of the Shelve Inlier; the Hoar Edge Grit (Aurelucian); the Coston Formation (Aurelucian); the Aldress Shale Formation (Burrellian); the Alternata Limestone (Burrellian), Woolston; the Harnage Shale (Burrellian), Horderley; the Glenburrell Formation (Burrellian), Horderley; the Smeathen Wood Beds (Burrellian), Smeathen Wood, Horderley; the Crosspipes Member of the Acton Scott Formation (Streffordian); the Crosspipes Member of the Cheney Longville Formation (Cheneyan).

The brachiopod fauna (Caradoc) of southern Ireland (Cocks 2008) are from Meath, Wexford, and Waterford areas, including the Burrellian-age localities in the Duncannon Group, the Annestown Formation (Burrellian), the Lower Tramore Volcanic Formation (Burrellian), the Grange Hill Formation (Burrellian), the Upper Tuffs and Shales of the Grangegeeth Volcanic Series (Burrellian), the Collon Formation of Burrellian age, and the Clashford House Formation (Burrellian-Cheneyan).

In northwestern England, Cumbria, the brachiopods of Caradoc (Burrellian) age are from the Dufton Shale Formation (Burrellian) in Melmerby, and the Corona beds (Burrellian) of Pusgill (Dufton).

#### **4.3.3 Kazakh terranes**

During Ordovician time, most parts of the area of what is today Kazakhstan was divided into many separate fragments. Sengor and Natalin (1996) suggested that most of these fragments completed the Kipchak Arc which was composed of an enormous island

arc, stretching from the craton of Baltica to the central Siberian Angaran craton (see Fig. 1.2). Whereas other authors, notably Nikitin have subdivided Kazakhstan with a more conservative paleogeography.

Brachiopod faunas of Kazakhstan are from early Katian (the late Caradoc) formations which belong to the three main terranes; the Chu-Ili terrane, the Boshchekul terrane, and the Ishim-Selety terrane. In southern Kazakhstan, the Chu-Ili terrane contains the Anderken and Dulankara formations (Popov et al. 2000; Popov et al. 2002).

The Anderken Formation is a transgressive sequence of mainly siliciclastic deposits that contain variably developed lens-like carbonate units. The formation is mainly composed of polymict, pebbly conglomerate, sandstone, siltstone and mudstones. The Anderken Formation is Sandbian (Lower to Middle Caradoc) in age and contains fossils of brachiopods (Popov et al. 2002).

The Dulankara Formation of the Chu-Ili Range is divided into three lithostratigraphical units; the Otar, Degers, and Akkol members (Keller 1956; Nikitin 1972, 1973; Popov et al. 2000). The lower Otar Member contains medium to fine grained sandstone and siltstone with polymict conglomerate and limestone beds. The central member, Degers Member, is composed of fine-grained sandstone and siltstone. The upper Akkol Member consists of bioclastic limestone and an overlying argillite bed (Popov et al. 2000).

In Kazakhstan, the Angrensor Formation belongs to the Boshchekul Terrane, which is characterised by a matrix of fine to medium polymict and volcanomict sandstone, siltstones and argillites. This formation is divided into two units; the Koskarasu Beds, and the Odak Beds (Nikitin et al. 2006). The Koskarasu Beds contain several units of bedded

limestone in the lower part. The Odak Beds are composed of carbonate build-ups such as mud-mounds and carbonate olistostromes (Nikitin et al. 2006). The Angren Formation is rich in fossils including brachiopods of early Katian age.

The Tauken Formation is located at one of the volcanic arcs which belong to the Ishim-Selety terrane of upper Caradoc age. In the central part of the Selety Basin, the Tauken Formation contains shallow-water deposits with sandstones and siltstones and also interbeds of andesitic tuff (Nikitin 1972; Nikitin et al. 2003).

#### **4.3.4 Baltica**

The brachiopod faunas of Estonia are from formations of Keila and Oandu stages. Estonia was part of Baltica during the Ordovician and the region of Estonia is divided between the North Estonia and Central Baltoscandian confacies (Jaanusson 1976).

The Keila Stage includes the Kahula and Vasalemma formations. In most parts of northern Estonia, the Keila Stage contains argillaceous bioclastic limestones with intervals of Kahula limestones (Schmidt 1881). In some restricted area in northwestern Estonia, the upper part of the Kahula Formation is replaced by the Vasalemma Formation (Hints and Meidla 1997).

The Keila Stage is subdivided into several members (Jaanusson 1945; Männil 1966) and the lower boundary of the stage is defined on the level of the thickest K-bentonite (Jürgenson 1958; Jaanusson and Martna 1948; Vingisaar 1972). The Kurtna Member represents the lowermost part of the Keila Stage and is characterized by argillaceous limestones (Hints and Meidla 1997). The Pääsküla Member, which is composed of relatively pure limestones overlies the Kurtna Member (Nõlvak 1996; Hints and Meidla 1997).

The younger part of the Keila Stage, the Vasalemma Formation, contains the Saue and Lehtmetsa members with fossiliferous argillaceous limestones (Hints and Meidla 1997). The Vasalemma Formation is composed of several principal lithotypes, but mostly bedded grainstone (Männil 1960; Põlma 1967; Hints 1996).

In northern Estonia, the Oandu Stage includes two different lithofacies, the Vasalemma Formation and the Hirmuse Formation (Hints 1998). In northwestern Estonia, the Vasalemma Formation is composed of fine- to coarse-grained bioclastic limestones with irregular bodies of massive limestones (Schmidt 1881; Hints 1998). Other lithofacies with argillaceous limestones and marls represent the Hirmuse Formation (Männil and Rõõmusoks 1984), which is exposed in northeastern Estonia (Rõõmusoks 1953; Aaloe et al. 1958).

The brachiopod faunas of southern Norway, Oslo-Asker district, are from the formations of Keila and Oandu stages (Hansen 2008). The Keila Stage includes the upper Arnestad Formation which is characterized by shales and limestones (Hagemann and Spjeldnæs 1955; Owen et al. 1990). This formation contains a rich shelly fauna in the Oslo-Asker district including fossils of brachiopods (Owen et al. 1990; Hansen 2008).

The brachiopod faunas of Oandu Stage include the Frognerkilen Formation in the Oslo-Asker district (Hansen 2008). The Frognerkilen Formation consists of bedded limestones and shales with fossils of brachiopods (Harper 1986; Owen et al. 1990; Hansen 2008).

#### **4.3.5 South China**

The brachiopod faunas of South China are from the upper Sandbian and lower Katian successions of the Yangtze Platform, which include the Pagoda Formation (Zhan

and Jin 2007). The Pagoda Formation conformably overlies the Miaopo Formation in the Yangtze Platform. The formation is composed of a light-grey to purple, medium to thick-bedded limestone, with local thin partings of green shale (Bergström et al. 2009). The Pagoda Formation contains a relatively diverse fossil fauna including brachiopods, trilobites, and nautiloid cephalopods (Zhan and Jin 2007; Bergström et al. 2009). The depositional environment of this formation has been variously interpreted shallow subtidal to deep subtidal with water depths of several hundred metres (for a summary, see Zhan and Jin 2007).

#### **4.3.6 Australia**

The brachiopod faunas examined herein from Australia are from New South Wales region (Percival 1991; Candela 2006). The Billabong Creek Limestone includes bioclastic limestone of Late Ordovician age (late Darriwilian to early Estonian; Sherwin 1970; Pickett and Percival 2001). This limestone unit contains brachiopod faunas of early Katian (Estonian) age in New South Wales (Candela 2006).

The Quondong Limestone in New South Wales is composed of thinly bedded grainstone, packstone, wackestone and lime mud (Semeniuk 1973; Percival 1991). This formation is fossiliferous and includes abundant marine invertebrate faunas such as brachiopods (Percival 1991). In Palin Yard Creek the Quondong Formation contains a brachiopod fauna of early Katian age (early Estonian; see Candela 2006).

#### **4.4 Multivariate analyses**

The multivariate analyses (mainly cluster and principal component analyses) are based on occurrence of 225 brachiopod genera of early Katian (Late Ordovician age) from 33 selected localities. In the binary dataset compiled for this study, the localities are treated as cases and the genera as variables (with two states: presence or absence). The dataset was subjected to cluster analysis (CA) and principal component analysis (PCA) to reveal patterns in the distribution of the brachiopod faunas in time and space.

##### **4.4.1 Cluster analysis (CA)**

In the dataset used in this study, there is a large number of genera overall, as well as a large number of endemic genera for many localities. As a result, the dendrogram generated using Paired Group method and the Raup-Crick similarity coefficient appears to show most clearly segregated clusters. At the level of similarity coefficient value 0.75 (total range 0–10), five main clusters (A, B, C, D1 and D2) are clearly recognizable, and four distinct subclusters (A1 and A2, C1 and C2) are also identified within clusters A and C, respectively.

Cluster A includes two subgroups, cluster A1 and A2 (Figure 4.2). Cluster A1 consists of brachiopod faunas from the Keila and Oandu stages in the East Baltic, mainly in the Lithuanian-North Estonian confacies belts, characterized by relatively shallow- and warm-water carbonate depositional environments during the early Katian (late Caradoc). Brachiopods of these two stages are highly similar, with a Raup-Crick index value approaching 1 (Simpson Similarity index = 0.59; see Supplementary Document 2). Cluster A2 contains brachiopod faunas from the western platform settings of the Appalachian Basin and epicontinental Laurentia, including the Champlain Valley, New



York State, Ottawa River Valley, Newfoundland, Oklahoma, Hudson River Valley, South Dakota, upper Mississippi River Valley, Lake Simcoe and Manitoulin Island areas of south-central Ontario, Kentucky, Indiana and Australia (Figure 4.2). Nearly all localities in cluster A2 were in mid- to high-tropical carbonate shelves or platforms in Laurentia; the nine faunas formed a very tightly knit cluster (minimum Raup-Crick index = 0.98; Simpson similarity index mostly greater than 0.5), forming the largest but most homogeneous brachiopod fauna among all the localities analyzed. It is interesting to note that the brachiopod fauna of these localities had a somewhat higher degree of similarity to that of the Lithuanian-North Estonian confacies belt of the East Baltic than to those of other regions of Laurentia. A similar faunal similarity between eastern Laurentia and the North Estonian confacies belt was noted also by Harper and Hints (2001).

Cluster B comprises brachiopod faunas from Shropshire, Cumbria, Meath (southwestern Ireland) and the Wales localities of Anglesey, Powys, and Gwynedd (Figure 4.2). The close affinities of these localities (Raup-Crick Index = 0.78) are due to their Avalonian faunal elements such as *Bellimurina*, *Chonetoidea*, *Clitambonites*, *Kiaeromena*, *Nicolella*, *Onniella*, *Reuschella*, *Salopia*, *Sulevorthis*, and *Vellamo*.

Cluster C is divided into two subclusters C1 and C2 (Figure 4.2). Subcluster C1 comprises brachiopod faunas from southeastern Ireland (Wexford and Waterford), South China, and the Oslo-Asker district (Norway). The brachiopod genera from these three regions are relatively small, and the brachiopods from the Pagoda Limestone of South China remain to be studied systematically. Thus their apparently close faunal affinity to the three Laurentian localities should be viewed with caution. Similarly, the late Caradoc faunas from South China used in Candela (2006) are also small, some containing only

four genera, and their apparent grouping also requires further investigation when better faunal data become available. Eight of twelve genera in the Irish brachiopod fauna occur in the Appalachian fauna, and their close faunal affinity seems convincing during the early Katian. Cluster C2 contains brachiopod faunas from the Great Basin (Nevada-California), Appalachians Basin (from Pennsylvania, Tennessee, to Alabama), British Columbia (Advance Mountains), Girvan (Scotland), and Tyrone (Northern Ireland). These localities represent continental margin to off-shore island settings of Laurentia during the Late Ordovician.

The Appalachian brachiopod fauna, in particular, exhibits very high species diversity. Many taxa, such as *Bimuria*, *Camerella*, *Christiania*, *Chonetoidea*, *Cyclospira*, *Eoplectodonta*, *Glyptorthis*, *Hesperorthis*, *Kullervo*, *Nicolella*, *Oepikina*, *Orthambonites*, *Parastrophina*, *Reuschella*, and *Skenidioides* were cosmopolitan to semicosmopolitan. The three Laurentian localities share a high degree of faunal similarity (Raup-Crick index = 0.96), and the Simpson similarity index between the Appalachian and the Great Basin faunas approaches 1.0. The cluster of Appalachians faunas with Girvan and Tyrone is in agreement with the concept of a Scoto-Appalachian fauna during the Sandbian–early Katian (see Whittington and Williams 1955; Jaanusson 1979).

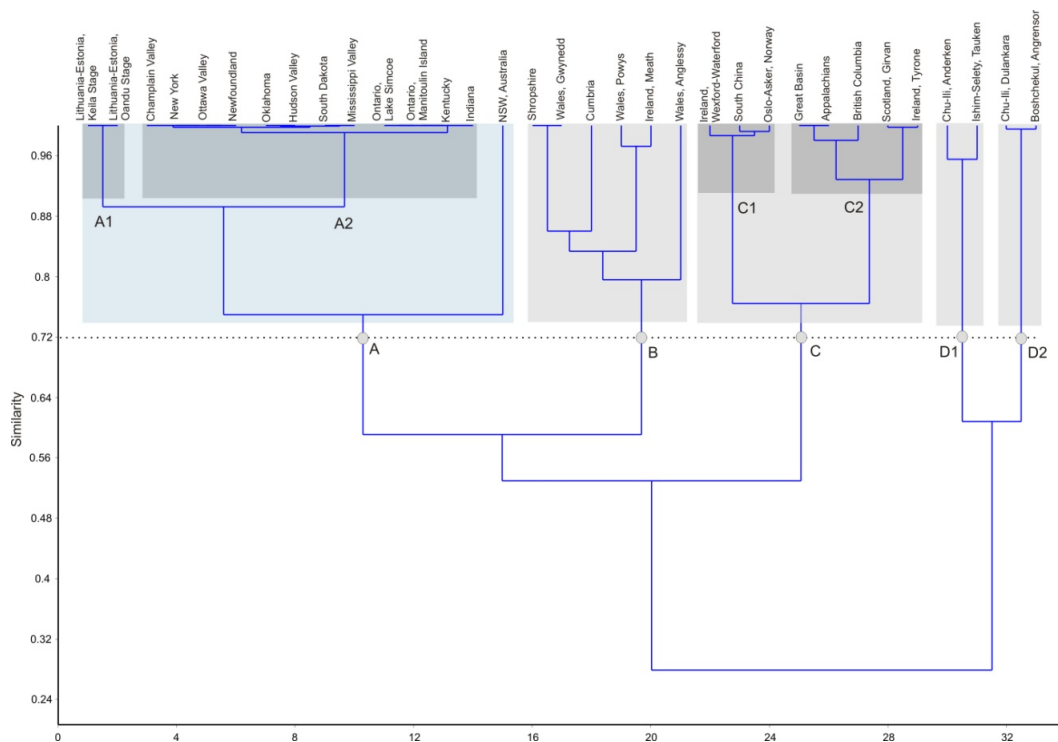


Figure 4.2 Cluster analysis of the 33 early Katian brachiopod faunas from Laurentia, Baltica, Avalonia, Kazakhstan, South China, and Australia, using the PAST software package (Hammer et al. 2001). For details of localities and faunal data, see Appendix 4.1, 4.2.

Clusters D1 and D2 in the CA dendrogram contains brachiopod faunas from three Kazakhstan terranes, the Chu-Ili, Boshchekul, and Ishim-Selety (Fig. 4.1). Brachiopods of the Chu-Ili and Boshchekul terranes were highly diverse and contained a large number of endemic taxa, but shared some genera with Laurentia (e.g. *Glyptorthis*, *Hebertella*, *Dinorthis*, and *Rhynchotrema*) and other regions. This explains its generally low faunal similarity with other regions (Raup-Crick index = 0.28). The faunal similarity within the cluster is very high, with the Dulankara fauna of Chu-Ili and the Angrensor fauna of Boshchekul having a Raup-Crick similarity index of 0.9 and Simpson index of 0.52 (Supplementary Document 2). The Anderken fauna of Chu-Ili and the Tauken fauna of Ishim-Selety also have a high level of similarity (Raup-Crick index = 0.85). The division of the four Kazakhstan faunas into two subclusters may have been their slightly different age, as the Anderken fauna is somewhat older than the Dulankara fauna in Chu-Ili (Popov et al. 2002).

In the current analysis, the four Kazakhstan faunas are shown to be more closely related among themselves than to any faunas elsewhere. This result is fundamentally different from Candela's (2006) CA dendrogram, in which the Kazakhstan faunas did not form a coherent group. In a separate study, however, Percival et al. (2011) also demonstrated the close faunal affinities among the Kazakh terranes.

#### **4.4.2 Principal component analysis (PCA)**

The same dataset used for cluster analysis was subjected also to a principal component analysis (see *Supplementary Document 1*). This binary dataset is suitable for analysis through the variance-covariance algorithm of the PAST PCA software. In the

PCA scatterplot based on principal components 1 (X-axis) and 2 (Y-axis), nearly all the groups in the cluster analysis can be recognized, labelled correspondingly as A1, A2, B, C1, C2, D1 and D2 (Figure 4.3).

Group A includes nearly the same brachiopod faunas from Laurentia (A2) and the East Baltic (A1) as in the CA plot, with the exception that the faunas of the Great Basin (14, Nevada-California) and Advance Mountain (15, Canadian Rocky Mountains, British Columbia) seem to be more closely aligned with those in the pericratonic regions of Laurentia, rather than with the Scoto-Appalachian fauna as in the CA plot (compare Figures 4.2 and 4.3). The close affinity of the East Baltic brachiopod fauna with the Laurentian fauna seems to be corroborated by the PCA plot.

Group B contains brachiopod faunas of mainly Avalonian origin, such as Powys and Anglesey (Wales), south-east Ireland (Wexford, Waterford), Meath (Ireland), and Cumbria (North West England). The tight subgroup of Shropshire and Gwynedd (Wales) within Group B is also reflected by their clustering at a Raup-Crick index close to 1 and a Simpson index 0.57.

Group C in the PCA plot contains two distinct subgroups. Group C2 agrees with a more conventional view of the Scoto-Appalachian fauna, including the well-documented brachiopods from Girvan, Tyrone, and Appalachians, without those from the western margin of Laurentia (Great Basin and Advance Mountain) as in the CA plot.

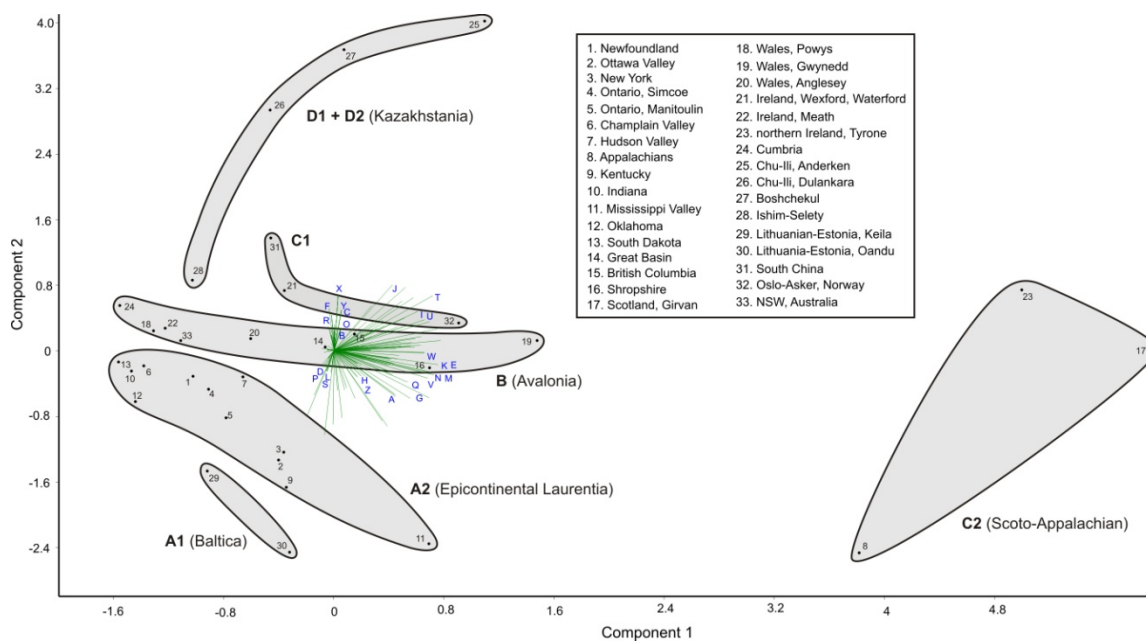


Figure 4.3 Principal component analysis of the 33 early Katian brachiopod faunas from Laurentia, Baltica, Avalonia, Kazakhstan, South China, and Australia, using PAST software (Hammer et al. 2001). Scattergram plotted based on variance-covariance algorithm. For details of localities and faunal data, see Table 4.1, Appendix 4.1.

As is shown in Figure 4.3, the Scoto-Appalachian fauna is most clearly separated not only from the groups from other paleogeographical regions, but also from other faunas within Laurentia. The close faunal link between the Appalachian Basin and the Girvan district of Scotland, for example, is reflected by the large number of characteristic taxa shared by the two regions, such as *Bimuria*, *Christiania*, *Cyrtonotella*, *Dalmanella*, *Dactylogonia*, *Dinorthis*, *Doleroides*, *Eoplectodonta*, *Glyptorthis*, *Laticrura*, *Leptaena*, *Nicolella*, *Oxoplecia*, *Parastrophina*, *Pionodema*, *Ptychoglyptus*, *Ptychopleurella*, *Plectorthis*, *Reuschella*, *Rostricellula*, *Skenidioides*, and *Sowerbyella*. The C1 cluster of three small faunules from southern Ireland (Wexford and Waterford), southern Norway (Oslo-Asker), and South China can be viewed as an outlier of the Avalonian fauna (B) according to the PCA plot, which deviates from the CA result, where it is shown to be more closely related to the Scoto-Appalachian fauna. As discussed earlier, however, the uncertain affinity is most likely the result of the unusually impoverished faunal composition.

Group D1 and D2 in the upper left portion of the scattergram is composed of the four brachiopod faunas of Kazakhstan, from the Chu-Ili, Boshchekul, and Ishim-Selety terranes. The four faunas appear to be widely and evenly spaced, rather than showing two distinct clusters as in the CA plot. Their PCA coordination appears to mimic the faunal distribution along paleogeographical island-chains as depicted in most recent paleogeographical reconstructions (e.g. Candela 2006; Percival et al. 2011).

The affinity indices between the Late Ordovician (early Katian) brachiopod faunas of 31 localities were measured in this study. Appendix 4.3, 4.4, and 4.5 show similarity indices which were calculated from three similarity measures: Dice, Jaccard, and Simpson.

#### **4.5. Paleobiogeography of the early Katian brachiopod fauna**

In the following discussion, the faunal affinities are based on the cluster analysis and principal component analysis, with the additional similarity indices (Simpson, Dice, and Jaccard) calculated using the same PAST software package (Appendix 4.3, 4.4, 4.5).

Both the cluster and principal component analyses indicate that the early Katian brachiopod faunas have a relatively high degree of provincialism, although some of them can be regarded as semi-cosmopolitan.

The Trentonian brachiopod faunas of most of Laurentia (except for the Scoto-Appalachian fauna) were more closely related to those of the North Baltic Confacies belt of Baltica and Avalonia than those of Baltica and South China. In the CA plot, brachiopod faunas of the three Kazakhstan terranes form a conspicuous paleobiogeographical outlier, although they are positioned relatively close to the Avalonian faunas in the PCA scattergram. The distinctness of the Scoto-Appalachian fauna is shown convincingly in both plots, defined by its clear special separation from other faunas in PCA, and by the highest degree of taxonomic homogeneity (high values of Raup-Crick and Simpson similarity indices) in CA.

Despite the early awareness of the high degree of faunal similarity among the Caradoc brachiopod faunas of the Appalachian region, the Girvan district and Northern Ireland (Williams 1962, 1969; Tripp 1962, 1965, 1967; Jaanusson 1973a) the paleogeographical control for the distinctness of this fauna remains poorly known. It is particularly puzzling that the Appalachian fauna was so clearly differentiated from the brachiopod faunas in the adjacent area of western Newfoundland (Port-au-Port Peninsula), western New York State, Kentucky, and Oklahoma.



A similarly distinct Scoto-Appalachian fauna is known to have existed in older strata (especially the Sandbian) of the Appalachians, especially in what was termed the Blount confacies belt by Jaanusson and Bergström (1980). This belt is delimited to the northwest by the Saltville fault and characterized by a high level of biodiversity, with about 60 brachiopod genera, among which 26 were recognized by these authors to be endemic to the Blount belt within eastern Laurentia. Thus the early differentiation of the Scoto-Appalachian fauna can be traced back to the early Sandbian (late Llanvirn, Chazyan). On a global scale, however, many of the diagnostic taxa of this belt were widespread (*Taphrorthis*, *Productorthis*, *Paucicrura*, *Kullervo*, *Anisopleurella*, *Chonetoidea*, *Glyptomena*, and *Christiania*) in Avalonia, Baltica, and Kazakhstan (Jaanusson and Bergström 1980; Nikitina et al. 2006; Cocks 2008). A brachiopod fauna similar to the Scoto-Appalachian fauna occur also in south-western Siberia (Levitskiy 1963).

The “pre-Trentonian” Blount belt brachiopods of the Appalachians had a greater degree of paleobiogeographical affinity to those in Northern Ireland (Tyrone), southern Scotland (Girvan), and the North Estonian Confacies belt of Baltoscandia than to those in the eastern epicontinental seas of Laurentia. Jaanusson and Bergström (1980) proposed multiple paleoecological controlling factors for the provincialism, such as water depth, water temperature, and substrate types. For example, the brachiopod fauna of the North Estonian Confacies lived in warm temperate to marginal subtropical environments during the Middle Ordovician, lacking reef-building corals and stromatoporoids, whereas the counterpart fauna in the Appalachians lived in tropical environments, with common reef-building bryozoans, corals and stromatoporoids. This was regarded by Jaanusson and Bergström (1980) as evidence that the distribution of the Scoto-Appalachian fauna was

not controlled by a single factor (e.g. water temperature).

The Sandbian Scoto-Appalachian Fauna persisted to the early Katian (Trentonian, Chatfieldian), when eastern pericratonic Laurentia and Baltica (Lithuania-Estonia) shared a relatively large number of brachiopod genera, including *Camerella*, *Horderleyella*, *Hesperorthis*, *Kjaerina*, *Leptaena*, *Nicolella*, *Microtrypa*, *Onniella*, *Platystrophia*, *Pionodema*, *Rafinesquina*, *Reuschella*, *Rhynchotrema*, *Rostricellula*, *Rhactorthis*, *Sowerbyella*, *Strophomena*, *Trigrammaria*, *Triplesia*, *Vellamo*, and *Zygospira*. By the Trentonian, however, brachiopods of the Lithuanian-North Estonian confacies belts became much more similar to the epicontinental brachiopod fauna of Laurentia than to the Scoto-Appalachian brachiopod fauna, as is demonstrated by the multivariate analysis of this study (Figure 4.2, 4.3). For example, the brachiopods of the Oandu and Keila regional stages in the Lithuanian confacies (Paškevičius 1994, 2000) form the closest sister group (Raup-Crick index ca. 0.89) with the largely coeval Trentonian brachiopod fauna of south-central Ontario (Ottawa Valley, Lake Simcoe, Manitoulin Island and adjacent areas), upper Mississippi valley (Minnesota-St. Paul area), and the American mid-continent (Kentucky, Indiana, and Oklahoma). In this study, this group of faunas (Clusters A1 and A2) is referred to as the Baltica-epicontinental Laurantia brachiopod (BELB) cluster.

For the Sandbian Scoto-Appalachian fauna, the faunal provincialism was likely controlled by different depositional environments at different paleolatitudes with different water temperature. The Baltoscandian Ordovician carbonates generally lack peloids and ooids, but in the southern and central Appalachians pelletal limestones are relatively common. These sedimentological differences suggest that the Appalachian carbonates accumulated in a warm, tropical to subtropical environment, whereas the Baltoscandian

carbonates represent cool-water carbonates in the warm-temperate climatic zone (Jaanusson 1973b; Jaanusson and Bergström 1980). If this interpretation holds true, the close faunal similarity within the BELB cluster during the late Caradoc (early Katian) would suggest that the area of Baltica had drifted well into the tropical climate zone by that time. This agrees well with the trajectory predicted by the paleogeographical reconstructions of Cocks and Torsvik (2005) for the movement of Baltica during the Ordovician.

The BELB group of faunas has a rather high level of similarity to the coeval fauna of New South Wales, Australia (Percival 1991). Despite its peri-Gondwana paleogeographical affinity, Australia probably straddled the equator during the Late Ordovician (Candela 2006; Percival et al. 2011), much like Laurentia. Its moderate level of faunal exchanges with Laurentia may have been through the equatorial currents of the Panthalassic Ocean to the east, as Australia was located on the eastern margin of the Gondwana landmass (Figure 4.1). To its west, the adjacent plates of Australia, such as South China, North China, and the Kazakh terranes, had much lower levels of faunal similarity with Laurentia than did Australia.

At a somewhat lower level of faunal similarity, the BELB cluster shows a slightly closer affinity to the Avalonia brachiopod fauna than to the Scoto-Appalachian fauna (Raup-Crick index 0.59 compared to 0.53). Shared taxa between the BELB cluster and the Avalonian fauna (e.g. Shropshire, Cumbria, Wales, and southeastern Ireland) are rather numerous, including *Bilobia*, *Bimuria*, *Bellimurina*, *Christiania*, *Dalmanella*, *Dinorthis*, *Dolerorthis*, *Eoplectodonta*, *Hesperorthis*, *Heterorthina*, *Dolerorthis*, *Harknessella*, *Horderleyella*, *Kjaerina*, *Leptaena*, *Leangella*, *Leptellina*, *Mcewanella*, *Nicolella*, *Onniella*, *Oxoplecia*, *Plaesiomys*, *Palaeostrophomena*, *Platystrophia*,

*Plectorthis*, *Reuschella*, *Rhactorthis*, *Rafinesquina*, *Rostricellula*, *Sulevorthis*, *Salopia*, *Skenidioides*, *Sowerbyella*, *Trematis*, *Triplesia*, *Vellamo*, and *Zygospira*.

The brachiopod faunas from the cluster of Kazakhstan terranes (Boshchekul, Chulii, and Ishim-Selety) formed a very cohesive brachiopod faunal province (Clusters D1 and D2), as the two subclusters do not include faunas from any other regions. The Simpson similarity index within the two Kazakh subclusters is quite high, attaining 0.52 and 0.64 respectively (Appendix 4.5). The high degree of endemism of the Kazakh faunas, however, is clearly demonstrated by its low Raup-Crick similarity index (ca. 0.28) relative to the rest of the groups, including the brachiopod faunas of Scoto-Appalachia, epicontinental Laurentia, platform Baltica, and Avalonia (Figure 4.3). The shared brachiopod genera between the entire Laurentia and Kazakhstan terranes are rather limited, including *Bellimurina*, *Bicuspina*, *Christiania*, *Didymelasma*, *Dinorthis*, *Dolerorthis*, *Eoplectodonta*, *Glyptorthis*, *Leangella*, *Leptaena*, *Paracraniops*, *Plaesiomys*, *Plectorthis*, *Pionodema*, *Parastrophina*, *Rhynchotrema*, *Skenidioides*, *Sowerbyella*, *Strophomena*, *Trematis*, and *Triplesia*. Such a high level of faunal provincialism between Laurentia and Kazakhstan was probably attributable to the great paleogeographical distance between the two regions, and temporally unstable faunal compositions in the Kazakhstan terranes, as would be typical of island faunas with high rates of faunal turnovers.

#### **4.5.1 Paleocological control on faunal endemism in Laurentia**

Within Laurentia, it is notable that the early Katian Scoto-Appalachian fauna appears to have been most closely related to the brachiopod faunas along the western margins of Laurentia, such as those of the Great Basin and the northern Canadian Rocky

Mountains in British Columbia (Advance Mountain). This biogeographical pattern in the early Katian is interpreted in this study as the beginning of a clear differentiation between pericratonic (continental-margin) and intracratonic (inland-sea) brachiopod faunas in Laurentia. Through the middle and late Katian (Edenian, Maysvillian, and Richmondian), the pericratonic faunas maintained some, albeit limited, faunal connections with those of Baltica and Avalonia (e.g. Jin and Zhan 2008), whereas the intracratonic fauna became increasingly isolated from not only the faunas of adjacent tectonic plates (e.g. Siberia, Baltica, and Avalonia), but also the pericratonic faunas within Laurentia (Jin et al. 2007).

The differentiation of the Appalachian brachiopod fauna from the epicontinental brachiopod fauna in Laurentia may have been controlled by a number of paleoenvironmental factors, such as plate tectonic effects on migration pathways and barriers, paleolatitude, water depth and temperature, and substrate types.

1) Tectonics. In recent years, improved graptolite biostratigraphy in the Appalachians has led to the recognition of two phases of the Taconic Orogeny (Ganis and Wise 2008). Based on work in Pennsylvania, the classic area of the Taconic Orogeny, these authors proposed that Taconic Phase I (~ 459 to 450 Ma) was a time of thrust faulting, peripheral bulging, and the formation of the Appalachian foreland basin. In comparison, Taconic Phase II (~ 450 to 443 Ma) was characterized by collisional mountain-building and transformation of the foreland basin and adjacent platforms into large nappes. Thus the beginning of Taconic Orogeny corresponded to the Darriwilian-Sandbian transition interval, when the Scoto-Appalachian brachiopod fauna became well defined, and then persisted through the Sandbian and early Katian. Etensohn (2010) suggested that the Taconic Orogeny initiated the Sebree Trough in southeastern Laurentia and facilitated temperate water upwelling and cool-water deposition in the region. Thus

the faunal distinctness of the Appalachian fauna from those in epicontinental regions, where direct tectonic disturbance was minimal, was most likely influenced by the peripheral bulge and its adjacent troughs, as well as other local tectonic elements that had an isolation effect, through either physical barrier or different watermasses, on the sub-basins of the overall foreland basin.

2) Paleolatitude. During the Late Ordovician, Laurentia was rotated nearly 90° relative to its present orientation (Cocks and Torsvik 2011), and the Appalachian belt was largely on the southern margin of Laurentia, located between 20–25° south of the paleoequator. Some of the accreted Appalachian terranes may have been located significantly farther south when restored to their pre-collision positions. Thus the subtropically located Appalachian brachiopods may have experienced a greater degree of faunal exchange with the mid-latitude brachiopod faunas of Avalonia than did the epicontinental brachiopods of Laurentia. During the early Katian, the brachiopod fauna of epicontinental seas (e.g. Ottawa Valley, south-central Ontario, and Minnesota) were located further north and closer to the equator, mostly in mid-tropical latitudes. This probably also contributed to the differentiation between the Appalachian and epicontinental faunas, although in itself the paleolatitudinal difference cannot explain the sharp faunal boundary between the eastern Appalachians (Blount belt) and the epicontinental seas (Jaanusson and Bergström 1980).

3) Substrate type. During the Sandbian and early Katian, black shale and siliciclastic deposits were common to predominant in many areas of the Appalachian Basin, especially in the eastern and central belts. In addition, the basin on the southern margin of Laurentia likely featured relatively deep- and cool-water environmental settings (Herrman et al. 2004; Herrmann and Haupt 2010), whereas the epicontinental seas had

typically shallow water environment and a predominantly carbonate depositional setting, with much less cool-water influence. Periodic cool-water incursions, however, have been proposed for some lower to upper Katian carbonate successions in southeastern Laurentia (e.g. Pope and Steffen 2003; Ettensohn 2010). On a regional scale, however, a much greater influence of deeper and cooler waters and siliciclastic sedimentation must have had a major effect on the faunal composition of Appalachian fauna. The occurrence of thick black shale sequences of early Katian age in the Appalachian foreland basin, such as the lower Utica Shale in New York and the Macasty Shale in the Anticosti Basin in Quebec, is supporting evidence for a suppressed carbonate supply, as well as periodic restriction of the Appalachian Basin. These would have been contributing factors for the isolation of the Appalachian brachiopod fauna from its counterpart in the shallow, open, epicontinental seas of Laurentia.

#### **4.6 Conclusions**

The analyses of 33 early Katian (Chatfieldian, late Caradoc) brachiopod faunas from Laurentia, Avalonia, Baltica, the Kazakhstan terranes, South China, and Australia revealed several paleobiogeographical patterns, with significant paleoenvironmental implications.

With a major onset of the marine transgression to flood the paleocontinent Laurentia during the early Katian, the brachiopod faunas of North America began to show a distinct differentiation between the pericratonic and intracratonic settings.

The Scoto-Appalachian brachiopod fauna in the southeastern margin of Laurentia persisted from Sandbian to early Katian. It had a closer affinity to the faunas of Avalonia and deep-water facies of Baltica than to the intracratonic fauna of Laurentia. Its isolation

was likely controlled by the bulges and troughs related to the Taconic Orogeny, influenced by frequent cool-water incursions along the troughs and the Appalachian foreland basin.

The intracratonic (epicontinental) brachiopod fauna of Laurentia had a much greater degree of faunal similarity to those of the Lithuanian-North Estonian confacies belts and Australia (New South Wales) than to the Scoto-Appalachian brachiopod fauna in the cratonic margin of Laurentia. This paleobiogeographical pattern probably reflected similar shallow and warm-water, platform carbonate depositional environments in the epeiric seas of Laurentia and Baltica.

The early Katian brachiopod faunas marked the beginning of faunal provincialism in Laurentia, with further intensified endemism developing in the middle-late Katian, leading to the insularization and subsequent extinction of the epicontinental brachiopod fauna of Laurentia at the beginning of the Hirnantian glaciation and drawdown of the epicontinental seas.



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## Chapter 5 – Conclusions

### 5.1 Introduction

This thesis project was carried out in several phases: 1) a general review of the Late Ordovician biota, paleoenvironment, paleogeography, and more specifically the evolution of brachiopods during the Great Ordovician Biodiversification Event (GOBE); 2) a broad discussion involving the significance and problems regarding the early Katian (Chatfieldian, Trentonian) brachiopod faunas of Ontario and elsewhere in North America; 3) a compilation of the brachiopod fossil material, locality data, and methods that are used for numerical analyses in order to detect trends of morphological changes in time and space, as well as paleobiogeographical patterns; 4) an in-depth investigation of the Late Ordovician (Katian) *Rhynchotrema-Hiscobeccus* brachiopod evolutionary lineage, and using this widespread lineage as a case study to explore the evolutionary processes and patterns of the marine shelly benthos coincided with a major sea level rising during the Late Ordovician (Sohrabi and Jin 2013a); 5) paleobiogeography of early Katian (Trentonian) brachiopod faunas in North America (Laurentia) and global comparisons with those of Avalonia, Baltica, Kazakhstan, South China, and Australia (Sohrabi and Jin 2013b).

### 5.2 Summary and conclusions

During the Ordovician the major global patterns of marine organisms experienced major evolutionary changes, marked by the Ordovician radiation or the Great Ordovician Biodiversification Event (GOBE), regarded as one of the most drastic biodiversification events in earth history (Sepkoski 1995; Webby et al. 2004a). Brachiopods as one of the most abundant and diverse groups among many other marine animals, underwent several

pulses of diversity increases during this period (Harper and Rong 2001; Harper et al. 2004).

During the Late Ordovician, Laurentia (largely North America and Greenland) was located in the tropical zones, and was flooded by shallow epicontinental seas, resulting in the build-up of massive carbonate platforms in intracratonic basins and pericratonic shelves (Cocks and Torsvik 2004; Cocks and Torsvik 2011; Finnegan et al. 2012), and the creation of expansive new habitats for marine life evolution.

The early Katian (Chatfieldian), historically known as “Trentonian” in North America, is a significant geological time interval. The Trentonian marine transgression, as the regional expression of a major global marine transgression, coincided with the origin of epicontinental fauna especially brachiopods (Fortey 1984; Jin 2001). The brachiopods constituted one of the most abundant and diverse components of the epicontinental faunas evolved during this time. The early Katian (Trentonian) brachiopod faunas of North America, such as those preserved in the Ottawa valley, Lake Simcoe area, and Manitoulin Island, are among the classic Trentonian faunas (e.g. Wilson, 1914, 1946; Foerste 1924). Many brachiopod taxa in the Trentonian brachiopod faunas evolved into predominant components of the epicontinental brachiopod fauna of Laurentia during the middle–late Katian.

### **5.2.1 The *Rhynchotrema*–*Hiscobeccus* evolutionary lineage**

In Chapter 3, multivariate analyses were conducted based on 171 rhynchonellide specimens (*Rhynchotrema* and *Hiscobeccus*) from nine localities (upper Sandbian–upper Katian) in North America. The cluster analysis (CA) and principal component analysis (PCA) in this study provided strong support for the early hypothesis for the origin of

*Hiscobeccus* from *Rhynchotrema* (Amsden 1983; Jin 2001) by quantitatively demonstrate the transitional morphological characters between the early form of *Hiscobeccus*, *H. mackenziensis*, and the typical forms of *Hiscobeccus*. Both analyses (CA and PCA) revealed that the shells of *Hiscobeccus mackenziensis* cluster more closely with *Rhynchotrema* than with younger forms of *Hiscobeccus* of Maysvillian–Richmondian age. In particular, the shell size index (SSI), shell convexity index (SCI), shell lamellosity index (SLI), and shell lamella density index (SLD) all indicated a morphological transition from *Rhynchotrema* to *Hiscobeccus* during the late Sandbian–early Katian.

By the middle–late Katian (Maysvillian–Richmondian), the large-shelled *Hiscobeccus* was most abundant and widespread in the epicontinental inland seas (e.g. Williston and Hudson Bay basins). The large and globular shells of *Hiscobeccus* were likely an adaptation to the shallow, warm epicontinental tropical seas with soft muddy substrates. Increase in size and volume may have been associated with increased lophophore size for more efficient filter feeding and oxygen exchange in generally overheated, poorly circulated, oxygen-poor epicontinental seas, especially in the paleoequatorial zone where hurricanes were largely absent (Jin et al. 2013).

The Richmondian forms of *Hiscobeccus*, *H. capax*, from the Cincinnati region showed the highest globosity index values among all the other forms of *Hiscobeccus* and *Rhynchotrema*. Despite the highest globosity index in *Hiscobeccus capax*, the large shell sized *Hiscobeccus gigas* from the Stony Mountain Formation of southern Manitoba which was located within 10° of paleoequator in the hurricane-free zone during the Late Ordovician (Cock and Torsvik 2011; Jin et al. 2013), did not show an extremely globular shell. Increased globosity in *Hiscobeccus capax* was most likely the result of adaptation

to the high-energy, storm-dominated environment in higher tropics (such as the Cincinnati area; see Holland 2001, 2008). The highly globular shells of *H. capax* was closely associated with prominent posterior thickening of the shell, to improve stability by weighting the posterior part of the shell to maintain a beak-down life position on turbulent substrates (Amsden 1983; Jin and Lenz 1992).

The multivariate analyses in this study also indicated that the number of lamellae increased from the older forms of *Rhynchotrema* to the younger forms of *Hiscobeccus*. Increasing in lamellosity was more pronounced in the younger forms of *Hiscobeccus* such as *H. capax* and *H. gigas*. Increased lamellosity in younger forms of *Hiscobeccus* during Maysvillian–Richmondian time may have been the result of adaptation to the shallow, warm epicontinental tropical seas with soft muddy substrates. Within such environment, increasing in lamellosity most likely aided to anchor the shell and prevented it from sliding on or sinking in the soft lime mud on the sea floor during water turbulence.

During the Maysvillian and Richmondian, *Hiscobeccus* became larger, globular, and developed more strongly lamellose shells in the paleoequatorially located epicontinental seas, whereas *Rhynchotrema* was generally divers and widespread in the pericratonic regions of Laurentia (e.g. Anticosti Island and Mackenzie Mountains) but rare in epicontinental inland seas.

### **5.2.2 Global paleobiogeography of early Katian brachiopods**

Multivariate analyses of early Katian brachiopod faunas from Laurentia, Avalonia, Baltica, Kazakhstan, South China, and Australia indicated several paleobiogeographical patterns, with important paleoenvironmental implications.

Brachiopod faunas of Laurentia that were semi-cosmopolitan during the late

Middle to early Late Ordovician (late Darriwilian–early Katian), show some similarity with those faunas of Siberia, Baltica, and other adjacent tectonic plates or terranes (Jin 1996). During the Trentonian marine transgression, however, the differentiation of brachiopod faunas began to manifest between the pericratonic and intracratonic settings in North America. By the middle to late Katian, the brachiopod fauna of Laurentia were mostly endemic (Sheehan and Coorough 1990; Jin 1996).

Within southeastern margin of Laurentia, the early Katian Scoto-Appalachian brachiopod fauna had a closer affinity to the faunas of Avalonia and deep-water facies of Baltica than to the intracratonic fauna of Laurentia (e.g. Great Basin and the northern Canadian Rocky Mountains in British Columbia). This isolation was likely related to the beginning of a clear differentiation between pericratonic (continental-margin) and intracratonic (inland-sea) brachiopod faunas in Laurentia, which was in turn influenced by the Taconic Orogeny and frequent cool-water incursions along the troughs and the Appalachian foreland basin.

Differentiation of the Appalachian brachiopod fauna from the epicontinental brachiopod fauna in Laurentia more likely triggered by different paleoenvironmental factors such as plate tectonics, paleolatitude, water depth and temperature, and substrate types.

The brachiopod fauna of the intracratonic (epicontinental) of Laurentia shows a close similarity to those of the Lithuanian-North Estonian confacies belts and Australia (New South Wales) than to the Scoto-Appalachian brachiopod fauna in the cratonic margin of Laurentia. This paleobiogeographical pattern likely was related to the shallow

and warm-water, platform carbonate depositional environments in the epeiric seas of Laurentia and Baltica.

During the middle–late Katian, the brachiopod fauna of Laurentia shared very few brachiopod taxa with those of Siberia, Kazakhstan, and South China, especially in terms of newly originated brachiopod genera and species during this interval.

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## Appendices

Appendix 3.1 Biometric measurements of shell morphology for species of *Rhynchotrema* and *Hiscobeccus* from nine localities

Specimen No.	L	L1	W	W1	W2	T	T1	AA	Lamellae No.
15862a	11.89	7.49	13.62	6.28	3.72	10.01	5.41	110.5	21
15862b	10.04	5.78	11.59	5.84	3.29	6.79	4.05	117	13
15862c	10.86	4.64	11.52	5.77	3.45	8.04	4.49	111	18
104507a	10.18	6.88	11.63	5.5	2.93	7.52	5.05	111.5	20
104507b	10.31	4.7	10.91	5.3	3.05	7.16	4.33	108	14
104507c	11.14	6.89	11.7	5.31	2.94	9.69	5.36	107.5	22
104507d	10.65	5.98	11.16	5.55	3.02	7.27	4.25	104	13
104517a	9.43	6.02	11.2	5.52	3.13	7.28	4.83	108	17
104517b	9.63	5.15	10.36	5.12	2.62	7.52	4.52	113	16
104517c	8.77	3.63	8.93	4.38	2.34	5.18	2.31	109	12
104517d	8.81	5.42	9.18	4.32	2.79	7.51	4.42	102	19
104517e	10.44	5.4	10.99	5.99	3.62	7.26	4.17	109.5	13
104517f	7.61	2.79	7.38	3.5	2.21	4.16	2.04	101.5	8
104517g	9.27	4.26	9.25	4.56	2.36	6.76	3.48	107.5	14
104517h	10.51	5.98	10.04	4.95	2.91	8.29	4.22	104	21
104517i	9.53	4.72	9.78	5.06	3.04	6.38	3.72	110	15
104517j	8.62	4.41	8.29	4.27	2.05	6.08	3.34	105.5	16
113531	9.71	4.23	10.8	4.61	2.85	6.95	3.44	114.5	9
113533	11.35	7.42	11.98	6.45	3.61	7.89	4.78	109	17
113534	9.56	4.63	10.47	4.67	2.44	8.69	5.52	108	14
113535	11.23	6.81	12.09	7.42	3.97	8.26	5.79	115	17
113537	11.08	7.16	11.74	6.4	3.76	7.65	4.65	112	22
113540	8.32	3.86	9.03	4.43	2.66	4.89	2.49	103	11
113541	7.92	2.52	7.73	3.93	2.22	4.33	1.72	99	8

Appendix 3.1 Biometric measurements of shell morphology for species of *Rhynchotrema* and *Hiscobeccus* from nine localities (continued)

GSC1	11.85	7.89	12.13	6.48	3.25	9.35	5.26	94	16
GSC2	11.41	7.58	10.96	6.76	4.14	6.28	4.53	96.5	16
GSC3	10.84	6.59	10.99	5.51	3.01	6.52	3.95	99.5	10
GSC4	9.95	5.18	10.99	6.55	3.64	8.12	5.55	99	12
GSC5	10.61	6.05	10.19	6.51	4.02	7.35	4.47	94	16
GSC6	11.29	6.91	11.06	6.55	3.78	7.66	4.24	93.5	17
GSC7	8.24	5.17	8.96	4.91	2.39	5.66	3.17	99.5	11
GSC8	11.33	3.11	9.74	5.34	3.51	6.23	3.27	90	6
GSC9	10.62	5.83	11.89	6.68	3.52	6.76	4.8	103.5	12
GSC10	12.87	7.57	13.61	7.91	4.01	9.23	5.68	102.5	13
GSC11	9.06	4.84	9.01	5.43	2.94	5.78	3.45	92	13
GSC12	9.38	5.38	8.77	5.03	2.97	4.97	2.63	91	12
GSC13	9.14	4.93	8.96	4.82	3.25	5.97	2.87	94	10
GSC14	7.62	3.89	8.15	4.65	2.55	4.38	2.82	94.5	8
GSC15	11.37	5.48	11.86	5.51	2.56	7.12	4.52	103	14
GSC16	9.52	3.64	9.79	5.83	3.74	5.88	4.09	96.5	9
GSC17	9.89	5.94	9.72	5.83	3.31	6.67	4.05	93	16
GSC18	9.41	5.61	9.61	5.29	3.23	6.03	4.51	92	11
GSC19	9.03	4.32	9.33	5.08	3.05	5.46	4.17	98.5	11
GSC20	10.88	4.69	11.44	6.57	4.03	6.13	4.41	100	8
GSC21	9.38	4.33	9.53	5.55	3.06	4.85	2.82	97.5	8
GSC22	8.73	2.72	8.79	4.35	2.77	4.93	2.96	95.5	8
GSC23	8.93	5.09	10.1	5.65	3.23	6.19	3.41	98	11
GSC24	11.13	6.33	11.96	6.59	3.57	8.63	4.79	95.5	13
GSC25	7.65	3.8	7.53	3.43	1.97	4.02	2.26	96.5	10

Appendix 3.1 Biometric measurements of shell morphology for species of *Rhynchotrema* and *Hiscobeccus* from nine localities (continued)

GSC26	9.27	3.06	8.88	5.32	3.02	6.58	3.78	95	11
GSC27	8.19	4.17	7.98	4.21	2.45	4.52	2.37	90	11
1603	11.5	4.21	12.03	6.89	3.88	8.13	4.6	96	9
1603a	12.29	6.39	12.73	5.85	2.94	6.92	4.65	98	13
1603b	11.9	4.19	12.83	6.26	2.32	10.33	7.66	103	10
1603c	11.8	2.42	11.14	4.17	1.84	10.91	6.72	102	10
1603d	11.43	5.37	12.4	6.79	3.41	9.51	5.41	96	11
1603e	11.09	5.32	11.64	6.43	3.23	7.34	4.04	96.5	14
1603f	10.45	2.71	11.07	5.97	3.09	6.3	3.96	102	5
1603g	12.55	4.33	12.64	6.92	3.26	9.51	5.08	100.5	11
1603h	10.98	3.13	11.71	7.46	4.31	8.01	3.47	96.5	6
1	10.56	2.09	11.84	6.66	4.13	7.45	5.28	98	8
2	11.04	3.42	11.58	5.94	4.08	6.25	2.67	98.5	11
3	11.13	4.58	11.74	5.55	2.93	8.14	5.05	101	12
4	14.29	6.56	15.92	8.25	4.39	11.49	5.88	103	10
5	10.59	1.48	12.13	6.79	4.33	7.11	4.54	111.5	8
6	10.92	1.34	11.63	6.47	3.67	6.05	4.43	114.5	6
7	13.18	3.47	13.96	7.68	4.51	6.75	5.73	111	5
8	10.65	3.85	13.29	6.88	3.98	6.78	4.57	119	6
9	10.93	2.51	11.49	5.95	3.65	5.69	3.44	104	5
1	11.56	4.52	11.61	5.97	4.41	6.57	3.27	104	5
2	11.71	6.05	13.78	7.78	4.25	8.85	5.22	110.5	8
3	11.35	3.67	12.65	7.18	4.43	9.11	4.69	107	9
4	11.97	4.23	12.15	7.11	4.11	8.34	5.32	108	6
5	12.65	3.52	13.12	6.59	4.25	10.14	5.04	103	6

Appendix 3.1 Biometric measurements of shell morphology for species of *Rhynchotrema* and *Hiscobeccus* from nine localities (continued)

6	9.83	4.71	9.91	5.75	3.65	6.23	3.58	107.5	7
7	8.39	3.17	9.67	4.92	3.22	4.85	2.43	109.5	6
8	9.88	3.88	10.58	5.83	3.73	6.25	3.07	109	4
9	10.21	2.24	12.59	6.69	3.82	7.59	4.74	105.5	5
10	10.91	2.15	10.96	6.35	3.33	7.68	4.08	100	4
11	11.85	1.76	14.07	7.36	4.09	9.08	6.33	112	4
12	11.31	2.95	13.05	7.41	4.53	9.77	6.13	109.5	3
13	8.41	2.41	9.04	5.24	3.07	4.33	2.75	106.5	4
14	8.86	1.25	9.03	4.03	2.73	4.63	2.18	95	3
15	9.13	1.91	10.29	5.43	3.41	5.92	3.51	106.5	2
16	7.12	3.65	7.49	3.99	2.98	3.81	1.61	103.5	4
17	8.98	1.5	9.62	5.68	3.37	4.62	3.14	102.5	3
18	9.6	4.35	10.89	5.88	3.16	6.54	4.44	105	6
19	9.86	1.39	10.91	5.92	3.54	6.06	4.4	98.5	5
20	9.76	4.2	11.23	7.11	3.86	7.89	5.77	106.5	6
1	11.42	2.98	11.43	6.28	3.61	9.17	6.08	97.5	8
2	12.52	1.63	14.09	8.61	4.94	9.06	5.04	109	5
3	10.42	1.65	11.54	6.65	3.85	6.49	3.96	104.5	6
4	10.41	1.52	11.71	5.92	2.88	8.23	5.03	98.5	3
5	10.15	0.89	10.56	5.97	3.82	5.39	3.96	99	4
6	9.71	1.68	10.71	5.83	3.28	7.14	4.69	99	6
7	9.43	1.42	11.32	6.13	3.89	5.58	4.26	114	3
8	9.55	2.93	9.85	5.32	2.94	5.13	3.47	98	4
9	10.75	0.65	10.92	5.43	3.24	5.41	3.85	95	2
10	8.83	0.91	8.56	4.25	2.55	3.87	2.13	97	2

Appendix 3.1 Biometric measurements of shell morphology for species of *Rhynchotrema* and *Hiscobeccus* from nine localities (continued)

11	10.13	2.53	9.86	6.42	4.38	6.22	3.74	105	6
12	8.86	1.3	10.07	5.4	3.51	5.25	3.94	110.5	3
13	11.05	1.81	12.17	7.27	3.91	7.41	5.65	113.5	5
14	9.99	1.24	10.54	5.84	3.24	5.46	3.78	102	3
15	7.85	1.39	8.23	4.53	2.68	4.01	2.46	102.5	3
16	10.83	1.51	11.94	6.45	3.58	6.67	4.24	112.5	3
17	11.32	1.53	11.33	7.27	3.85	6.49	4.68	97	3
18	8.91	1.15	9.67	5.44	3.39	4.78	2.23	100.5	2
19	10.18	1.65	10.79	5.08	2.69	7.27	4.91	102.5	6
20	10.85	2.51	10.32	4.69	3.42	5.87	3.77	96	5
21	11.67	2.68	13.08	6.28	3.37	7.07	5.83	102	3
22	13.49	2.17	14.24	7.84	4.28	8.53	5.33	104.5	4
MN1	10.6	1.97	11.85	6.28	4.18	7.54	5.12	107.5	6
MN2	8.95	1.09	10.94	5.31	2.91	5.75	3.58	111.5	3
MN3	10.86	1.05	11.58	5.34	3.63	9.29	5.36	104	4
MN4	10.15	1.48	10.9	5.72	3.21	7.74	4.25	108	5
MN5	9.5	1.41	10.21	4.94	3.01	7.78	3.85	106.5	4
MN6	9.74	2.81	10.17	5.48	3.84	6.82	3.4	100.5	5
MN7	10.01	1.42	10.34	4.97	3.22	7.45	3.67	102	4
MN8	8.75	0.72	10.02	5.24	2.87	5.25	3.65	106	3
MN9	9.46	2.18	10.23	5.36	3.09	6.25	4.38	100.5	3
MN10	8.51	1.83	8.91	4.74	2.85	6.36	3.55	106	6
MN11	10.04	2.29	10.5	5.31	3.29	6.78	4.12	104	5
MN12	10.08	1.57	10.6	5.28	3.12	7.68	4.16	110.5	7
MN13	9.89	1.58	10.42	5.3	3.29	7.45	4.09	105.5	8

Appendix 3.1 Biometric measurements of shell morphology for species of *Rhynchotrema* and *Hiscobeccus* from nine localities (continued)

MN14	9.42	1.33	10.13	4.99	2.98	6.21	3.48	103.5	7
MN15	9.49	1.57	9.63	4.21	2.56	5.89	3.81	99.5	3
MN16	9.29	1.86	10.04	4.6	2.86	6.69	4.83	111	6
MN17	8.91	1.53	10.2	4.19	2.84	5.93	3.67	108	6
MN18	9.96	1.17	11.14	5.71	3.25	6.83	3.37	109.5	3
MN19	9.85	2.17	10.03	5.46	3.16	7.8	4.46	104.5	7
MN20	9.8	1.96	10.61	5.67	4.06	5.53	3.72	101	4
MN21	9.58	2.85	10.14	4.96	3.56	6.18	4.15	108	5
MN22	10.9	1.95	11.53	6.3	3.55	8.2	4.48	107.5	4
MN23	9.54	1.15	10.6	5.26	3.17	5.58	3.67	106	4
MN24	9.65	1.02	9.5	5.13	3.77	5.64	3.53	98.5	3
MN25	9.13	1.12	10.17	4.8	3.09	6.39	4.44	105.5	4
MN26	9.29	1.5	10.03	5.49	3.95	5.51	2.85	108.5	5
MN27	8.83	1.35	9.15	4.53	2.69	6.73	4.29	103	8
MN28	8.1	0.93	8.87	4.78	2.95	5.4	3.7	106	4
MN29	9.3	1.61	9.91	4.99	3.3	6.39	4.12	105.5	5
MN30	8.61	1.53	9.15	4.44	2.77	7.4	4.48	103	5
MN31	8.88	1.57	8.57	4.08	2.45	4.67	2.54	108.5	4
MN32	8.34	1.68	8.5	5.3	3.28	5.23	3.33	95.5	5
MN33	8.47	2.23	8.52	4.79	2.86	5.42	2.48	96	4
MN34	8.97	1.8	9.15	5.58	3.36	5.22	3.35	100	5
MN35	9.09	1.71	9.62	4.2	2.38	6.04	3.32	103.5	4
MN36	8.23	1.05	8.72	4.18	2.68	3.76	2.4	101	3
MN37	8.09	1.45	8.51	4.21	4.76	6.24	2.5	101	5
MN38	8.42	1.79	8.83	4.68	3.19	5.37	2.62	108	5



Appendix 3.1 Biometric measurements of shell morphology for species of *Rhynchotrema* and *Hiscobeccus* from nine localities (continued)

MN39	8.23	1.73	8.77	4.5	2.29	5.72	3.46	100	5
MN40	7.97	1.78	8.97	4.5	2.72	4.37	2.81	106	2
ST1	26.15	20.7	28.36	13.54	8.92	19.55	10.43	110.5	25
ST2	30.42	25.86	31.85	16.71	10.28	23.45	10.35	110	27
ST3	29.64	21.33	31.53	17.95	11.31	14.08	11.53	118.5	34
ST4	21.56	17.02	24.42	12.23	8.21	14.72	5.64	114	30
ST5	27.02	21.27	29.52	18.14	10.54	20.07	11.99	119	29
ST6	29.74	20.28	27.48	14.67	8.74	22.06	14.25	111.5	32
ST7	31.51	23.21	35.87	15.7	9.45	25.14	14.62	110	35
ST8	26.98	19.86	28.59	14.62	8.73	20.88	10.65	118	27
ST9	34.49	26.08	39.04	19.84	9.88	23.1	14.07	123	25
ST10	25.74	19.98	28.35	14.91	9.75	18.77	8.95	110	27
1	17.31	10.38	18.87	13.34	7.56	13.75	8.8	110	25
2	18.93	14.89	21.14	12.02	6.88	14.5	9.53	112	26
3	17.77	13.98	19.32	12.24	6.26	14.15	10.3	109	29
4	16.84	13.52	17.45	10.88	6.46	13.31	8.86	113	29
5	15.76	11.55	17.08	9.83	5.83	10.83	6.61	104	18
6	17.78	13.05	17.94	11.28	6.06	13.35	7.95	107.5	28
7	18.57	13.68	19.06	12.89	7.35	14.05	9.57	105	30
8	13.87	9.81	15.74	7.59	4.22	10.12	6.03	112	18
9	16.56	11.86	17.41	10.88	6.27	12.28	7.92	103.5	23
10	16.58	11.98	16.87	10.66	5.29	14.55	10.03	104	28

Appendix 4.1 Brachiopod faunal list from 33 localities used in multivariate analyses in Chapter 4

1. Newfoundland, Western Newfoundland, Port au Port Peninsula, Long Point Formation, sandstones, shales, and limestones:

<i>Camerella</i> aff. <i>C. volborthi</i> Billings =	<i>Glyptorthis bellarugosa</i> (Conrad)
<i>Parastrophina hemiplicata</i> (Hall)	<i>Rafinesquina alternate</i> (Conrad) = <i>R. trentonensis</i> (Conrad)
<i>Dalmanella rogata</i> (Sardeson)	<i>Sowerbyella sericea?</i> (Sowerby)
<i>Dinorthis</i> aff. <i>D. Iphigenia</i> (Billings)	<i>Triplesia extans</i> (Emmons)
<i>Hesperorthis</i> aff.	<i>Valcourea</i> sp.
<i>H. tricenaria</i> (Conrad)	

2. Ottawa Valley, Ottawa River valley and vicinity of Ottawa, Ottawa Group, Rockland Formation, limestone and shale:

<i>Camerella hemiplicata</i> (Hall) =	<i>Ö. rugosa avita</i> Wilson
<i>Parastrophina hemiplicata</i> (Hall)	<i>Ö. septata borealis</i> Wilson
<i>Dalmanella paquettensis</i> (Sinclair) =	<i>Ö. sinclairi</i> Wilson
<i>Onniella paquettensis</i> Sinclair	<i>Ö. subtriangularis</i> Wilson
<i>Dalmanella rogata</i> (Sardeson) =	<i>Ö. transitionalis</i> (Okulitch)
<i>Paucicrura</i>	<i>Ö. tumida</i> Wilson
<i>Didymelasma abruptum</i> Cooper	<i>Platystrophia amoena</i> McEwan
<i>Dinorthis browni</i> n. sp. = <i>Plaesiomys</i>	<i>P. amoena longicardinalis</i> McEwan
<i>D. iphigenia</i> (Billings) = <i>Plaesiomys</i>	<i>P. trentonensis</i> McEwan
<i>D. Iphigenia minor</i> n. var. = <i>Plaesiomys</i>	<i>Plectorthis ottawaensis</i> Wilson
<i>D. pectinella</i> (Emmons)	<i>P. pulchella</i> Wilson
<i>D. cf. D. p. sweeneyi</i> (N.H. Winchell) =	<i>Rafinesquina alternate</i> (Conrad)
<i>Dinorthis</i> cf. <i>D. sweeneyi</i> (N.H. Winchell)	<i>R. a. alata</i> Wilson
<i>D. regularis</i> n.sp. = <i>Plaesiomys</i>	<i>R. a. intermedia</i> Wilson
<i>Doleroides gibbosus</i> (Billings)	<i>R. a. plana</i> Wilson
<i>D. pervetus ottawanus</i> Wilson =	<i>R. a. semiquadrata</i> Wilson
<i>Doleroides ottawansus</i> Wilson	<i>R. a. transversa</i> Wilson
<i>Eichwaldia subtrigonalis</i> Billings	<i>R. hullensis</i> Wilson
<i>Glyptorthis bellarugosa</i> (Conrad)	<i>R. lennoxensis</i> Salmon
<i>Hesperorthis tricenaria</i> (Conrad)	<i>R. opeongoensis</i> Wilson
<i>Microtrypa altilis</i> Wilson	<i>R. orleansensis</i> Wilson
<i>M.? nasuta</i> Wilson	<i>R. patula</i> Wilson
<i>Öpikina ampla</i> Wilson	<i>R. robusta</i> Wilson
<i>Ö. gloucesterensis</i> Wilson	<i>R. subcamerata</i> Wilson
<i>Ö. hemispherica</i> Wilson	<i>R. ottawaensis</i> Wilson
<i>Ö. inquassa</i> (Sardeson)	<i>R. salmon</i> Wilson
<i>Ö. ovalis</i> Wilson	<i>R. sinuate</i> Wilson
<i>Ö. platys</i> Wilson	<i>Rhynchotrema increbescens</i> (Hall)
<i>Ö. rugosa</i> Wilson	<i>R. ottawaense</i> (Billings) =
	<i>Drepanorhyncha ottawaensis</i> (Billings)

*Skenidioides billingsi* Schuchert and Cooper  
*S.? merope* (Billings)  
*Sowerbyella punctostriata* Mather  
*S. sericea* (Sowerby)  
*Strophomena billingsi* Winchell and Schuchert  
*S. filitexta* Hall  
*S. f. obesa* Wilson  
*S. magna* Wilson  
*S.? millionensis affinis* Wilson

*S. rotunda* Wilson  
*S. venustula* Wilson  
*Trigrammaria trigonalis prima* Wilson  
*Triplecia cuspidata* (Hall) = *Triplesia cuspidate* (Hall)  
*T. Extans* (Emmons) = *T. extans* (Emmons)  
*Vellamo trentonensis* (Raymond)  
*Zygospira deflecta* (Hall)  
*Z. recurvirostris* (Hall) = *Anazyga*

Hull Formation, thick and thin-bedded limestone:

*Platystrophia amoena* McEwan  
*Platystrophia amoena longicardinalis* McEwan  
*Dalmanella rogata* (Sardeson) = *Paucicrura*  
*Dinorthis browni* n. sp. = *Plaesiomys*  
*D. iphigenia* (Billings) = *Plaesiomys*  
*D. iphigenia minor* n. var. = *Plaesiomys*  
*D. pectinella* cf. *sweeneyi* (N. H. Winchell)  
*D. regularis* Wilson = *Plaesiomys*  
*D. subquadrata* (Hall) = *Plaesiomys*  
*D. subquadrata alternata* n. var. = *Plaesiomys*  
*Öpikina sinclari* Wilson  
*Sowerbyella sericea* (Sowerby)

*Sowerbyella subovalis* Wilson  
*Rafinesquina alternata* (Conrad)  
*R. alternata intermedia* Wilson  
*R. alternata plana* Wilson  
*R. alternata transversa* Wilson  
*R. semicircularis* Wilson  
*R. opeongoensis* Wilson  
*R. orleansensis* Wilson  
*R. semicircularis minor* Wilson  
*Rhynchotrema increbescens* (Hall)  
*Camerella hemiplicata* (Hall) = *Parastrophina*  
*Strophomena filitexta* Hall  
*Zygospira recurvirostris* (Hall) = *Anazyga*

Sherman Fall Formation, limestone and interbedded shale:

*Plectorthis neglecta* (James)  
*P. ottawaensis* n. sp.  
*P. plicatella laurentina* n. var.  
*Platystrophia amoena* McEwan  
*P. elegantula* McEwan  
*P. extensa* McEwan  
*Dalmanella millipunctata* Wilson  
*D. rogata* (Sardeson) = *Paucicrura*  
*D. whittakeri* Raymond  
*Dinorthis browni* n. sp. = *Plaesiomys*  
*D. caldera* n. sp. = *Plaesiomys*  
*D. dubia* n. sp. = *Plaesiomys*  
*D. iphigenia* (billings) = *Plaesiomys*  
*D. iphigenia media* n. var. = *Plaesiomys*

*D. Iphigenia minor* n. var. = *Plaesiomys*  
*D. meedsi germana* (Winchell and Schuchert) = *Plaesiomys*  
*D. meedsi plana* n. var. = *Plaesiomys*  
*D. pectinella* (Emmons)  
*D. pectinella* cf. *sweeneyi* (N.H. Winchell)  
*D. regularis* n. sp. = *Plaesiomys*  
*D. subquadrata* (Hall) = *Plaesiomys*  
*D. subquadrata alternate* n. var. = *Plaesiomys*  
*Sowerbyella sericea* (Sowerby)  
*S. subovalis* Wilson  
*Rafinesquina alternate* (Conrad)

- R. alternata intermedia* Wilson  
*R. alternata plana* Wilson  
*R. alternata pota* Wilson  
*R. alternata quadrata* Wilson  
*R. carlottina* Wilson  
*R. caldera* Wilson  
*R. orleansensis* Wilson  
*R. patula* Wilson  
*R. prestonensis* Salmon  
*R. robusta* Wilson  
*R. subtrigonalis* Wilson  
*R. declivis* (James) Foerste  
*R. deltoidea* (Conrad)  
*R. gibbosa* Wilson  
*R. miodeltoidea* Wilson  
*R. normalis* Wilson  
*R. normaloides* Wilson  
*R. sardesoni* Salmon?  
*R. semicircularis minor* Wilson

- R. sinuata* Wilson  
*Öpikina tumida* Wilson  
*Strophomena billingsi* W. and S  
*S. filitexta* Hall  
*S. filitexta obesa* Wilson  
*Microtrypa? plana* Wilson  
*M.? tersa* Wilson  
*Clitambonites ottawaensis* Wilson =  
*Vellamo*  
*Vellamo sinclairi* Wilson  
*V. tentonensis* (Raymond)  
*Triplecia extans* (Emmons)  
*Camerella hemiplicata* (Hall) =  
*Parastrophina*  
*Rhynchotrema increbescens* (Hall)  
*R. intermedium* Wilson  
*Zygospira recurvirostris* (Hall) =  
*Anazyga*

Cobourg Formation, coarse-grained, fossiliferous, argillaceous limestone:

- Cornwallia minuta* Wilson?  
*Plectorthis neglecta* (James)  
*P. ottawaensis* n. sp.  
*P. plicatella laurentina* n. var.  
*P. plicatella trentonensis* Foerste  
*P. pulchella* n. sp.  
*Platystrophia amoena* McEwan  
*P. amoena longicardinalis* McEwan  
*P. amoena robusta* McEwan  
*P. elegantula* McEwan  
*P. extensa* McEwan  
*P. hermitagensis* McEwan  
*P. precedens* McEwan  
*P. preponderosa* McEwan  
*P. trentonensis* McEwan  
*P. uniplicata* McEwan  
*P. sp.*  
*Hesperorthis tricenaria* (Conrad)  
*Glyptorthis insculpta* (Hall)  
*Dalmanella millipunctata* Wilson  
*Dalmanella rogata* (Sardeson) =  
*Paucicrura*  
*D. whittakeri* Raymond  
*Dinorthis browni* n. sp. = *Plaesiomys*  
*D. iphigenia* (Billings) = *Plaesiomys*  
*D. iphigenia minor* n. var. = *Plaesiomys*  
*D. meedsi germana* (W. and S.) =  
*Plaesiomys*  
*D. meedsi plana* n. var. = *Plaesiomys*  
*D. ottawaensis* n. sp. = *Plaesiomys*  
*D. subquadrata* (Hall)  
*D. subquadrata alternate* n. var.  
*Doleroides gibbosus* (Billings)  
*Sowebyella? minuta* n. sp.  
*S. sericea* (Sowerby)  
*S. subovalis* Wilson  
*Leptaena affinis* n. sp.  
*L.? diminuta* n. sp.  
*L. trentonensis* Wilson  
*Rafinesquina alternate* (Conrad)  
*R. alternata plana* Wilson  
*R. alternata platys* Wilson  
*R. alternata pota* Wilson  
*R. carlottina* Wilson  
*R. apicalis* Wilson  
*R. caldera* Wilson  
*R. equipunctata* Wilson  
*R. esmondensis borealis* Wilson  
*R. hullensis* Wilson  
*R. orleansensis* Wilson

<i>R. patula</i> Wilson	<i>S. filitexta obesa</i> Wilson
<i>R. prestonensis</i> Salmon	<i>S. irregularis</i> Wilson
<i>R. robusta</i> Wilson	<i>Trigrammaria pulchra</i> Wilson
<i>R. rotunda</i> Wilson	<i>T. trigonalis</i> Wilson
<i>R. subtrigonalis</i> Wilson	<i>T. trigonalis parva</i> Wilson
<i>R. cf. deerensis</i> Salmon	<i>T. tumida</i> Wilson
<i>R. deltoidea</i> (Conrad)	<i>Microtrypa? modesta</i> Wilson
<i>R. gibbosa</i> Wilson	<i>M.? nitida</i> Wilson
<i>R. laurentina</i> Wilson	<i>M.? plana</i> Wilson
<i>R. miodeltoidea</i> Wilson	<i>M.? tersa</i> Wilson
<i>R. normalis</i> Wilson	<i>Clitambonites ottawaensis</i> Wilson =
<i>R. normaloides</i> Wilson	<i>Vellamo</i>
<i>R. okulitchi</i> Wilson	<i>Vellamo sinclairi</i> Wilson
<i>R. praedeltoidea</i> Wilson	<i>V. trentonensis</i> (Raymond)
<i>R. sardesoni</i> Salmon?	<i>Triplecia extans</i> (Hall)
<i>R. semicircularis</i> Wilson	<i>T. nuclea</i> (Hall)
<i>R. semicircularis minor</i> Wilson	<i>T. duplicata</i> Wilson?
<i>R. sinuate</i> Wilson	<i>Camerella hemiplicata</i> (Hall) =
<i>R. camerata</i> (Conrad)	<i>Parastrophina</i>
<i>Öpikina auriculata</i> Wilson	<i>Rhynchotrema increbescens</i> (Hall)
<i>Ö. sinclari</i> Wilson	<i>R. intermedium</i> Wilson
<i>Ö. pikinella affinis</i> Wilson	<i>Zygospira deflecta</i> (Hall)
<i>Ö. salmon</i> Wilson	<i>Z. recurvirostris</i> (Hall) = <i>Anazyga</i>
<i>Strophomena extensa</i> Wilson	<i>Cylclospira bisulcata</i> (Emmons)
<i>S. filitexta</i> Hall	

3. New York and adjacent areas. North-west of New York, Trenton Group, Selby Formation, dark-grey to black, medium to fine textured limestone:

<i>Dalmanella rogata</i> (Sardeson) =	<i>Rafinesquina alternata</i> (Conrad)
<i>Paucicrura rogata</i> (Sardeson)	<i>Rhynchotrema</i> sp.
<i>Doleroides ottawanus</i> Wilson	<i>Sowerbyella curdsvillensis</i> (Foerste)
<i>D. pervetus</i> (Conrad)	<i>Strophomena</i> sp.
<i>Hesperorthis tricenaria</i> (Conrad)	

Napanee Formation, limestone with interbedded shale, packstone and wackestone:

<i>Camerella obesa</i> Cooper	<i>"R." inquassa</i> (Sardeson) = <i>Öpikina</i>
<i>C. volborthi</i> Billings	<i>inquassa</i> (Sardeson)
<i>Dalmanella rogata</i> (Sardeson) =	<i>R. lennoxensis</i> Salmon
<i>Paucicrura rogata</i> (Sardeson)	<i>R. olliformis</i> Salmon
<i>Hesperorthis tricenaria</i> (Conrad)	<i>Sowerbyella punctostriata</i> (Mather)
<i>Parastrophina hemiplicata</i> (Hall)	<i>Strophomena filitexta</i> (Hall)
<i>Protozyga exigua</i> (Hall)	<i>Trigrammaria wilsonae</i> Cooper
<i>Rafinesquina alternata</i> (Conrad)	<i>Triplexia cuspidate</i> (Hall)

Kings Fall Formation, Western New York, limestone with dark to black shales:

*Doleroides pervetus*  
*Dinorthis Iphigenia*  
*D. pectinella*  
*D. sp.*  
*Hesperorthis tricenaria*  
*Paucicrura rogata*  
*Platystrophia amoena*  
*P. longicardinalis*  
*Plectorthis plicatella*  
*Triplesia cuspidate*  
*Öpikina inquassa*  
*Ö. transitionalis*  
*Ö. wagneri*  
*Plectambonites sp.*  
*Rafinesquina lennoxensis*

*R. praecursor*  
*R. prestonensis*  
*R. trentonensis*  
*Sowerbyella minnesotensis?*  
*Sowerbyella sericea*  
*Strophomena conradi*  
*S. diagnata*  
*S. filitexta crenulata*  
*S. foveata*  
*Trigrammaria trigonalis*  
*Parastrophina hemiplicata*  
*Rhynchotrema increbescens*  
*Anazyga recurvirostris*  
*Protozyga exigua*

Sugar River Formation, limestone, grainstones, wackestones:

*Doleroides pervetus*  
*Dinorthis Iphigenia*  
*D. pectinella*  
*D. sp.*  
*Hesperorthis tricenaria*  
*Paucicrura rogata*  
*Platystrophia amoena*  
*P. longicardinalis*  
*Plectorthis plicatella*  
*Triplesia cuspidate*  
*Öpikina inquassa*  
*Ö. transitionalis*  
*Ö. wagneri*  
*Plectambonites sp.*  
*Rafinesquina lennoxensis*

*R. praecursor*  
*R. prestonensis*  
*R. trentonensis*  
*Sowerbyella minnesotensis?*  
*Sowerbyella sericea*  
*Strophomena conradi*  
*S. diagnata*  
*S. filitexta crenulata*  
*S. foveata*  
*Trigrammaria trigonalis*  
*Parastrophina hemiplicata*  
*Rhynchotrema increbescens*  
*Anazyga recurvirostris*  
*Protozyga exigua*

Denly Formation, Poland Member and Russia Member, nodular fine-grained limestones:

*Dinorthis Iphigenia*  
*D. pectinella*  
*Paucicrura rogata*  
*P. whittakeri*  
*Platystrophia amoena*  
*P. longicardinalis*  
*P. robusta*  
*Plectorthis plicatella*  
*Triplesia cuspidate*  
*Rafinesquina camerata*  
*R. deltoidea*

*R. praecursor*  
*R. prestonensis*  
*R. trentonensis*  
*Sowerbyella sericea*  
*S. subovalis*  
*Strophomena conradi*  
*S. filitexta crenulata*  
*Parastrophina hemiplicata*  
*Rhynchotrema increbescens*  
*Anazyga recurvirostris*

Steuban Formation, limestones and shale:

<i>Dinorthis Iphigenia</i>	<i>R. robusta</i>
<i>Paucicrura rogata</i>	<i>R. trentonensis</i>
<i>Platystrophia amoena</i>	<i>Sowerbyella minuta</i>
<i>P. longicardinalis</i>	<i>Sowerbyella sericea</i>
<i>P. robusta</i>	<i>S. subovalis</i>
<i>Plectorthis plicatella</i>	<i>S. sp.</i>
<i>Triplesia cuspidate</i>	<i>Strophomena conradi</i>
<i>Rafinesquina camerata</i>	<i>S. trilobite</i>
<i>R. deerensis</i>	<i>Parastrophina hemiplicata</i>
<i>R. deltoidea</i>	<i>Rhynchotrema increbescens</i>
<i>R. minuta</i>	<i>Anazyga deflecta</i>
<i>R. normalis?</i>	<i>Cyclospira bisulcata</i>
<i>R. ottawaensis</i>	<i>Protozyga exigua</i>
<i>R. praecursor</i>	

Hillier Formation, argillaceous limestone:

<i>Dinorthis Iphigenia</i>	<i>R. robusta</i>
<i>Paucicrura rogata</i>	<i>R. trentonensis</i>
<i>Platystrophia amoena</i>	<i>Sowerbyella minuta</i>
<i>P. longicardinalis</i>	<i>Sowerbyella sericea</i>
<i>P. robusta</i>	<i>S. subovalis</i>
<i>Plectorthis plicatella</i>	<i>S. sp.</i>
<i>Triplesia cuspidate</i>	<i>Strophomena conradi</i>
<i>Rafinesquina camerata</i>	<i>S. trilobite</i>
<i>R. deerensis</i>	<i>Parastrophina hemiplicata</i>
<i>R. deltoidea</i>	<i>Rhynchotrema increbescens</i>
<i>R. minuta</i>	<i>Anazyga deflecta</i>
<i>R. normalis?</i>	<i>Cyclospira bisulcata</i>
<i>R. ottawaensis</i>	<i>Protozyga exigua</i>
<i>R. praecursor</i>	

4. South central Ontario, Carden Quarry, Babcoygeon Formation, lower member grainstones, packstones and wackestones; Upper member limestone and shaly interbeds:

<i>Paucicrura</i>	<i>Strophomena</i>
<i>Hesperorthis</i>	<i>Sowerbyella</i>
<i>Tetraphalerella</i>	<i>Drepanorhycha</i>
<i>Rafinesquina</i>	<i>Idiospira</i>

Peterborough area, Sherman Fall limestone and interbedded shale:

<i>Paucicrura</i>	<i>Strophomena</i>
<i>Onniella</i>	<i>Sowerbyella</i>

*Plaesiomys*  
*Zygospira*  
*Parastrophina*

*Rafinesquina*  
*Rhynchotrema*

Central Ontario, Coboconk Formation, moderately heavy-bedded to fine-grained limestone:

*Leptaena* cf. *radialis* Okulitch =  
*Cyphomena* cf. *C. radialis* (Okulitch)  
*Rafinesquina alternata* (Conrad) =  
*Rafinesquina trentonensis* (Conrad)  
*R. clara* Okulitch = *Öpikina clara*  
 (Okulitch)

*R. minnesotensis* (N.H. Winchell) = *Ö. minnesotensis* (N.H. Winchell)  
*Strophomena* cf. *corrugate* Okulitch  
*S. filitexta* Hall  
*Zygospira recurvirostris* (Hall)

5. Manitoulin Island Region, Cloche Island Formation, limestone and shale:

*Camerella panderi* Billings = *Idiospira panderi* (Billings)  
*Dalmanella rogata* (Sardeson) =  
*Paucicrura rogata* (Sardeson)  
*Dinorthis sweeneyi* (N.H. Winchell)  
*Doleroides pervetus* (Conrad)  
*Glyptorthis bellarugosa* (Conrad)  
*Hallina* sp.

*Hesperorthis tricenaria* (Conrad)  
*Rafinesquina alternata* (Conrad) =  
*Rafinesquina trentonensis* (Conrad)  
*Rhynchotrema increbescens* (Hall)  
*Rostricellula rotundata* Cooper  
*Sowerbyella punctostriata* (Mather)  
*Strophomena* sp. *S. emaciate* Winchell  
 and Schuchert

Goat Island, Verulam Formation, limestones, micrite units interbedded by shaly parting:

*Rafinesquina*  
*Rhynchotrema*

*Anazyga*  
*Idiospira*

6. Northern Rocky Mountains, British Columbia, Advance Formation, thinly bedded, nodular limestone and shale:

*Anazyga bellicostata* n. sp.  
*Bimuria* cf. *B. supreba*  
*Christiania subquadrata*  
*Eoplectodonta (Eoplectodonta) alternata*  
*Dinorthis* cf. *D. holdeni*  
*Glyptambonites musculosus*  
*Glyptorthis assimilis*  
*Hiscobeccus mackenziensis*  
*Leangella (Leangella) biseptata* n. sp.  
*Murinella* cf. *M. biconvexa*  
*Oepikina* sp.

*Oxoplecia globularis*  
*Parastrophina* sp.  
*Platystrophia colbiensis*  
*Paurorthis ponderosa*  
*Paucicrura rogata*  
*Plaesiomys meedsi*  
*Rafinesquina praecursor*  
*Scaphorthis perplexa*  
*Strophomena* cf. *S. planumbona*  
*Thaerodonta redstonensis*

7. Champlain Valley, Isle la Motte Formation, gray-weathering, heavy-bedded limestone:

*Dalmanella testudinaria* = *Paucicrura*

*Dinorthis pectinella* (Emmons)



*Rafinesquina alternate* (Conrad) =  
*Rafinesquina trentonensis* (Conrad)  
*Strophomena incurvata* (Shepard)

*Triplecia extans* (Emmons) = *Triplecsia*  
*cuspidata* (Hall)  
*Zygospira*

8. Hudson Valley Region, Albany to Poughkeepsie, Rysedorf Formation, conglomerate with black compact limestone:

*Christiania trentonensis* Ruedemann  
*Dalmanella testudinaria* (Dalman) =  
*Paucicrura*?  
*Leptaena rhomboidalis* Wilckens = *L.*  
*ordovicica* Cooper  
*Orthis tricenaria* Hall (sic) =  
*Hesperorthis* sp.  
*Platystrophia biforata* (Schlotheim)  
*Plectambonites sericeus* (Sowerby)  
*P. pisum* Ruedemann = *Bilobia pisum*  
(Ruedemann)  
*Rafinesquina alternata* (Emmons) =  
*Macrocoelia ruedemanni* (Salmon)  
*Dalmanella testudinaria* (Dalman)  
*Dinorthis pectinella* (Emmons)

*Leptaena rhomboidalis* Wilckens = *L.*  
*ordovicica* Cooper  
*Orthis tricenaria* Conrad = *Hesperorthis*  
*tricenaria* (Conrad)  
*Parastrophia hemiplicata* Hall =  
*Parastrophina hemiplicata* (Hall)  
*Plectambonites ruedemanni* Raymond  
*P. pisum* Ruedemann = *Bilobia pisum*  
(Ruedemann)  
*Plectorthis plicatella* Hall  
*Protozyga exigua* (Hall)  
*Rafinesquina alternate* (Conrad)  
*R. deltoidea* (Conrad)  
*Triplecia nucleus* Hall  
*Zygospira recurvirostris* (Hall)

9. Appalachians Valley, Pennsylvania, Alabama, Georgia, Tennessee, and Virginia, Ben Hur Formation, yellowish-greylimestone and yellow mudstone:

*Pionodema minuscula* (Willard)  
*Strophomena* sp.

*Zygospira* sp.

Cane Creek Formation, greylimestone, greenish mudstone and thin shale:

*Chaulistomella lebanonensis* Cooper  
*Doleroides tennesseensis* Cooper  
*Öpikina* sp.

*Pionodema sulcata* Cooper  
*Strophomena* sp.  
*Zygospira* sp.

Nealmont Formation, Oak Hall, Centre Hall and Rodman members, limestones and shale:

*Ancistrohyncha australis* (Foerste)  
*Ancistrohyncha* sp.  
*Doleroides pervetus* (Conrad)  
*Camarotoechia* sp. = *Rostricellula* sp.  
*Glassia* sp.  
*Glyptorthis* sp. cf. *G. bellarugosa*  
(Conrad)  
*Hesperorthis tricenaria* (Conrad)  
*Leptaena* (?) sp. cf. *L. charlottae*  
Winchell and Schuchert = *Bellimurina*

*Leptaena* sp. cf. *L. charlottae* Winchell  
and Schuchert = *Limximurina*  
*Öpikina inquassa* (Sardeson)  
*Ö. minnesotensis* (N.H. Winchell)  
*Ö. wagneri* (Okulitch)  
*Parastrophina hemiplicata* (Hall)  
*Pionodema sulcata* Cooper  
*Rhynchotrema* sp.  
*Sowerbyella punctostriata* (Mather)  
*Strophomena* sp. cf. *S. filitexta* (Hall)  
*Strophomena* sp.

*Valcourea* sp. cf. *V. loricula* (Hall)  
*Zygospira elongate* Cooper

*Zygospira recurvirostris* (Hall)

Collierstown Formation, shell limestone and calcarenite:

*Cyclospira* sp.  
*Doleroides* sp.

*Rafinesquina trentonensis* (Conrad)  
*Zygospira* sp

Virginia, Edinburg Formation, Limestone and shale:

*Bilobia virginiensis* Cooper  
*Bimuria parvula* Cooper  
*Camerella leiorhynchoidea* Cooper  
*Christiania platys* Cooper  
*C. subquadrata* (Hall)  
*Cristiferina cristata* Cooper  
*Cyphomena angulate* Cooper  
*Chonetoidea virginica* Cooper  
*Cyclospira quadrata* Cooper  
*Dactylogonia strasburgensis* Cooper  
*Dinorthis transversa* Willard  
*Doleroides* sp.  
*E. rotundata* Cooper  
*Eoplectodonta* sp. 1  
*Eoplectodonta? dubia* Cooper  
*Glyptambonites glyptus* Cooper  
*Hesperorthis* sp. 2  
*Kullervo parva* Cooper  
*Laticrura pionodema* Cooper  
*Leptaena ordovicica* Cooper  
*Leptellina* sp. 1  
*Limbimurina brevilimbata* Cooper  
*Oligorhynchia bifurcate* Cooper

*Öpikina* sp.  
*Öpikina bellula* Cooper  
*Öpikina alata* Cooper  
*Ö. dorsatiformis* Cooper  
*Orthambonites bielsteini* Cooper  
*Oxoplecia multicostellata* Cooper  
*Oxoplecia holstonensis* Willard  
*Paurorthis spinosa* Cooper  
*Paucicrura matutina* Cooper  
*Paucicrura virginica* Cooper  
*Phragmorthis buttsi* Cooper  
*Ptychoglyptus virginiensis* Willard  
*Perimecocoelia semicostata* Cooper  
*Plectocamara transversa* Cooper  
*Plectocamara magna* Cooper  
*Ptychoglyptus virginiensis* Willard  
*Rostricellula* sp.  
*Scaphorthis kayi* Cooper  
*Sowerbyella aequicostellata* Cooper  
*Skenidioides obtusus* Cooper  
*Skenidioides costatus* Cooper  
*Sowerbyella aequicostellata* Cooper  
*Zygospira* sp.

Eggleston Formation, limestone and dark-grey calcareous mudrocks:

*Dalmanella rogata* (Sardeson) =  
*Paucicrura rogata* (Sardeson)  
*Rafinesquina alternate* (Conrad) =  
*Rafinesquina trentonensis* (Conrad)

*R. minnesotensis* (N.H. Winchell) =  
*Öpikina minnesotensis* (N.H. Winchell)  
*Strophomena incurvata* (Shepard)  
*Zygospira recurvirostris* (Hall)

Hardy Creek Formation, dense, fine-grained limestone with chert nodules:

*Campylorthis* sp.  
*Öpikina* sp.  
*Pionodema minuscula* Willard

*Strophomena* sp.  
*Zygospira recurvirostris* (Hall)

Housum Member, Mercersburg Formation; medium-gray, fine-grained limestone:

*Leptaena* sp. cf. *L. charlottae* Winchell  
and Schuchert

*Öpikina* aff. *O. ruedemanni* Salmon  
*Sowerbyella* cf. *S. punctostriata* (Mather)

Kauffman Member, Mercersburg Formation, platy, bedded limestone:

*Dinorthis* sp. cf. *D. pectinella* (Conrad)  
*Doleroides* sp. cf. *D. pervetus* (Conrad)  
*Glyptorthis* sp. cf. *G. bellarugosa*  
(Conrad)  
*Leptaena* sp. cf. *L. charlottae* Winchell  
and Schuchert = *Limbimurina*

*Sowerbyella* sp. cf. *S. punctostriata*  
(Mather)  
*Strophomena* 2 sp.  
*Zygospira recurvirostris* (Hall)

Jacksonburg Formation, Northwestern New Jersey and adjacent Pennsylvania, calcareous shales, high-grade limestone, dark blue or black fossiliferous limestones, Lower part:

*Camarella inornata* Weller = *Idiospira*  
*inornata* (Weller)  
*Dalmanella subaequata* (Conrad) =  
*Pionodema subaequata* (Conrad)  
*Lingula* sp. = *Skenidioides* sp.

*Rafinesquina alternata* (Emmons) = *R.*  
*trentonensis* (Conrad)  
*Scenidium anthonensis* Sardeson =  
*Skenidioides* sp.  
*Strophomena conradi* Hall and Clarke  
*Strophomena* sp.

Jacksonburg Formation, Upper part:

*Dalmanella subaequata* (Conrad)  
*D. testudinaria* (Dalman) = *Paucicrura*  
sp. 2  
*Dinorthis pectinella* (Emmons)  
*Orthis tricenaria* Conrad  
*Parastrophina hemiplicata* (Hall)  
*Platystrophia biforata* (Schlotheim) =  
*Oxoplecia*?  
*Plectambonites sericeus* (Sowerby)  
*Plectorthis plicatella* (Hall)  
*P. (Austinella) whitfieldi* (N.H. Winchell)

*Rafinesquina alternate* (Emmons)  
*Reuschella americana* Cooper  
*Rhynchotrema dentata* (Hall)  
*R. inaequalvis* (Castelnau)  
*Strophomena conradi* Hall and Clarke  
*Strophomena incurvata* (Shepard)  
*Zygospira nicolleti* (Winchell and  
Schuchert) = *Protozyga nicolletti*  
(Winchell and Schuchert)  
*Z. recurvirostris* (Hall)

Lower Martinsburg Formation, Virginia, Green Mount Church, shale and limestone:

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

*Parastrophina hemiplicata* (Hall)  
*Parastrophina* sp. I  
*Paucicrura subplana* Cooper  
*Phragmorthis crassa* Cooper  
*Plectorthis ponderosa* Cooper  
*Skenidioides elongates* Cooper  
*Sowerbyella cava* Cooper  
*S. eximia* Cooper  
*Strophomena bellilineata* Cooper

Lower Martinsburg Formation, Southwestern Virginia and Tennessee:

<i>Dalmanella rara</i> Cooper	<i>Rafinesquina trentonensis</i> (Conrad)
<i>Dinorthis pectinella</i> (Emmons)	<i>Rhynchotrema</i> sp.
<i>Hesperorthis tricenaria</i> (Conrad)	<i>Sowerbyella curdsvillensis</i> (Foerste)
<i>Onniella fertilis</i> (Ulrich)	<i>Zygospira</i> sp.

Pennsylvania, base of Martinsburg Formation:

<i>Christiania lamellose</i> Bassler = <i>Bimuria lamellose</i> (Bassler)	<i>Leptaena tenuistriata</i> Sowerby var. = <i>L. ordovicica</i> Cooper
<i>Dalmanella edsoni</i> Bassler = <i>Reuschella americana</i> Cooper	<i>Strophomena sculpturata</i> Bassler = <i>S.?</i> <i>sculpturata</i> Bassler
<i>D. testudinaria</i> (Dalman) var. = <i>D. sculpta</i> Cooper	<i>Triplecia</i> ( <i>Cliftonia</i> ) <i>simulatrix</i> Bassler = <i>Oxoplecia simulatrix</i> (Bassler)

Moccasin Formation, Southwestern Virginia and northeast Tennessee, reddish argillaceous limestone:

*Zygospira lebanonensis* Cooper

Oranda Formation, Virginia, limestone, shale, siltstone:

<i>Bilobia hemispherica</i> Cooper	<i>Leptellina abbreviate</i> Cooper
<i>Bimuria lamellosa</i> (Bassler)	<i>Nicolella strasburgensis</i> (Butts)
<i>Chaulistomella</i> sp. 2	<i>Orthambonites bielsteini</i> Cooper
<i>Christiania auriculata</i> Cooper	<i>O. multcostellatus</i> Cooper
<i>Cristiferina cristifera</i> Cooper	<i>Oxoplecia simulatrix</i> (Bassler)
<i>Cyphomena homostriata</i> (Butts)	<i>Parastrophina</i> sp. 2
<i>Dalmanella costellata</i> Cooper	<i>Ptychopleurella sulcata</i> Cooper
<i>Eoplectodonta alternate</i> (Butts)	<i>Rafinesquina planulata</i> Cooper
<i>E.?</i> <i>triradiata</i> (Butts)	<i>Reuschella americana</i> Cooper
<i>Furcitella plicata</i> Cooper	<i>Skenidioides rectangulatus</i> Cooper
<i>Glyptambonites musculosus</i> Cooper	<i>Sowerbyella cava</i> Cooper
<i>Hesperorthis virginiensis</i> Cooper	<i>S. eximia</i> Cooper
<i>Laticrura magna</i> Cooper	<i>Strophomena bellilineata</i> Cooper
<i>Leptaena ordovicica</i> Cooper	

Salona Formation, Pennsylvania- northern Virginia, dark argillaceous limestone, calcareous shale:

<i>Colaptomena leptostrophoidea</i> Cooper	<i>Oxoplecia</i> sp. cf. <i>simulatrix</i> (Bassler) =
<i>Dalmanella</i> sp.	<i>O. pennsylvanica</i> Cooper
<i>Leptaena</i> sp. aff. <i>L. rhomboidalis</i> (Wilckens) = <i>L. ordovicica</i> Cooper	<i>Parastrophina hemiplicata</i> (Hall)
<i>Leptelloidea pisum</i> (Ruedemann) =	<i>Porambonites</i> sp. = <i>Porambonites</i> sp. 4
<i>Bilobia hemispherica</i> Cooper	<i>Salonia magnaplicata</i> Cooper and Whitcomb

*Sowerbyella cava* Cooper  
*Sowerbyella* sp.

*Strophomena* sp.  
*Rafinesquina* sp.

10. Central basin of Tennessee, Wells Creek basin and High Bridge, Kentucky, Carters Formation, lower calcarenite with fine-grained layers, upper thin-bedded limestone and thin sale partings:

*Camerella bella* Fenton  
*Chaulistomella lebanonensis* Cooper  
*Chaulistomella* sp. I  
*Doleroides tennesseensis* Cooper  
*Fascifera sulcata* Cooper  
*Hesperorthis tricenaria*  
*Öpikina varia* Cooper

*Oxoplecia planulata* Cooper  
*Sowerbyella subcarinata* (Ulrich)  
*Strophomena filitexta* = *S. auburnensis*  
*nasuta* Cooper  
*S. platyumbona* Cooper  
*Zygospira circularis* Cooper

Kimmswick limestone, Tennessee, Giles County, coarse calcarenite:

*Rafinesquina* cf. *R. minnesotensis*  
*Rhynchotrema minnesotensis*

*Strophomena* cf. *S. Scofieldi* = *Furcitella scofieldi* (Winchell and Schuchert)

Hermitage Formation, Central basin of Tennessee, nodular, argillaceous limestone with shale:

*Dalmanella crassicostellata* Cooper  
*D. sulcata* Cooper  
*Dinorthis? pectinella* (Emmons)  
*Onniella? americana* Cooper  
*O.? planoconvexa* Cooper  
*Pionodema tennesseensis* Cooper

*Platystrophia extensa* McEwen  
*Rafinesquina hermitagensis* Bassler = *R. trentonensis* (Conrad)?  
*Rhynchotrema* “*increbescens*”  
*Rostricellula minuta* Cooper  
*Zygospira* “*recurvirostris*” (Hall)

Tyrone Formation, Central Kentucky, High Bridge, greylimestone and three metabentonites:

*Idiospira panderi* (Billings)  
*Strophomena auburnensis nasuta*  
 Cooper

*Strophomena* cf. *S. dignata* Fenton  
*S.* cf. *S. plattinensis* Fenton  
*Zygospira* sp.

11. Indiana, disturbed area at Kentland, Division 8 dolomitic limestone with black or greycarbonate shale:

*Glyptorthis bellarugosa* = *G. bellarugosa* (Conrad)  
*Hesperorthis tricenaria* = *H. tricenaria* (Conrad)  
*Leptaena charlottae* = *Bellimurina charlottae* (Winchell and Schuchert)  
*Rafinesquina* cf. *hermitagensis* = *R. trentonensis* (Conrad)

*R. minnesotensis* = *Öpikina minnesotensis* (N. H. Winchell)  
*Rhynchotrema minnesotensis* = *Rostricellula minnesotensis* (Sardeson)  
*Strophomena trentonensis* Winchell and Schuchert  
*Zygospira recurvirostris* (Hall)

12. Mississippi Valley, Upper Mississippi Valley, St. Paul, Minnesota, Decorah Formation, shale dominated limestone:

<i>Bellimurina charlottae</i>	<i>Rhynchotrema ainsliei</i>
<i>Dalmanella sculpta?</i>	<i>Rhynchotrema wisconsinense</i>
<i>Dinorthis pectinella</i>	<i>Rostricellula minnesotensis</i>
<i>Doleroides pervetus</i>	<i>Sowerbyella curdsvillensis</i>
<i>Glyptorthis bellarugosa</i>	<i>Sowerbyella minnesotensis</i>
<i>Hesperorthis tricenaria</i>	<i>Strophomena billingsi</i>
<i>Öepikina inquassa</i>	<i>Strophomena filitexta</i>
<i>Öepikina minnesotensis</i>	<i>Strophomena septata</i>
<i>Pionodema subaequata</i>	<i>Skenidioides anthonense</i>
<i>Plaesiomys meedsi</i>	<i>Paucicrura rogata</i>
<i>Platystrophia amoena</i>	<i>Vellamo Americana?</i>
<i>Protozyga nicolleti</i>	<i>Zygospira plinthii</i>
<i>Rafinesquina sp.</i>	<i>Zygospira recurvirostris</i>
<i>Rafinesquina trentonensis</i>	

Decorah Formation, Eastern Iowa, grey-green shale with thin limestone beds, Spechts Ferry Member, basal member and shale dominated:

<i>Dalmanella perveta</i> (Conrad) =	<i>Pionodema uniplicata</i> Cooper
<i>Doleroides pervetus</i> (Conrad)	<i>Plectambonites sericea</i> (Sowerby) =
<i>D. subaequata</i> (Conrad) = <i>Pionodema</i>	<i>Sowerbyella</i> (not seen)
<i>subaequata</i> (Conrad)	<i>Rostricellula ainsliei</i> (N.H. Winchell)
<i>Doleroides gibbosus</i> (Billings)	<i>R. minnesotensis</i> (Sardeson)
<i>D. medius</i> (Winchell) = <i>D. winchelli</i>	<i>Strophomena incurvata</i> (Shepard) = <i>S.</i>
Cooper	<i>auburnensis</i> Fenton
<i>Orthis tricenario</i> (Conrad) =	<i>T. minnesotensis</i> Sardeson
<i>Hesperorthis sp.</i>	<i>Zygospira recurvirostris</i> (Hall) (not seen)

Decorah Formation, Guttenberg Member, nodular-bedded limestones, organic-rich brown shale:

<i>Dalmanella hamburgensis</i> Winchell and Schuchert = <i>D. winchelli</i> Cooper	<i>Pionodema subaequata</i> (Conrad)
<i>Idiospira panderi</i> (Billings)	<i>P. uniplicata</i> Cooper
<i>Leptaena charlottae</i> Winchell and Schuchert = <i>Bellimurina charlottae</i> (Winchell and Schuchert)	<i>Plectambonites sericea</i> Sowerby =
<i>Orthis tricenaria</i> Conrad = <i>Hesperorthis tricenaria</i> (Conrad)	<i>Sowerbyella punctostriata</i> (Mather)
<i>O. (Dalmanella) subaequata perveta</i> Conrad = <i>Doleroides pervetus</i> (Conrad)	<i>Rafinesquina minnesotensis inquassa</i>
<i>O. (Hebertella) bellarugosa</i> Conrad =	Sardeson = <i>Öpikina inquassa</i> (Sardeson)
<i>Glyptorthis bellarugosa</i> (Conrad)	<i>R. prestonensis</i> Salmon
	<i>R. sinclairi</i> Salmon
	<i>R. trentonensis</i> (Conrad)
	<i>Rhynchotrema ainsliei</i> N.H. Winchell =
	<i>Rostricellula ainsliei</i> (N.H. Winchell)

*R. minnesotensis* Sardeson =  
*Rostricellula minnesotensis* (Sardeson)  
*Rostricellula pulchra* Cooper  
*Strophomena delicatula* Fenton

*S. dignata* Fenton  
*S. incurvata* (Shepard) = *S. auburnensis*  
 Fenton  
*Zygospira recurvirostris* (Hall)

Decorah Formation, Ion Member, shale and limestone:

*Dinorthis sweeneyi* (Winchell)  
*Glyptorthis subcircularis* Cooper  
*Orthis tricenaria* Conrad = *Hesperorthis*  
*colei* Cooper  
*O. (Dalmanella) hamburgensis?* Walcott  
 = *D. winchelli* Cooper  
*O. (D.) testudinaria* Dalman =  
*Paucicrura rogata* (Sardeson)  
*O. (D.) subaequata circularis* N.H.  
 Winchell = *Pionodema circularis* (N.H.  
 Winchell)  
*O. (Hebertella) bellarugosa* Conrad =  
*Glyptorthis bellarugosa* (Conrad)  
*Pionodema minnesotensis* Cooper  
*P. uniplicata* Cooper

*Plectambonites sericea* Sowerby =  
*Sowerbyella monilifera* Cooper  
*Rafinesquina alternate* Conrad = *R.*  
*trentonensis* (Conrad)  
*R. minnesotensis inquassa* Sardeson =  
*Öpikina lirata* Cooper  
*Rhynchotrema inaequivalvis* Castelnau =  
*R. wisconsinense* Fenton and Fenton  
*Rostricellula colei* Cooper  
*Scenidium anthonensis* Sardeson =  
*Skenidioides anthonensis* (Sardeson)  
*Strophomena incurvata* (Shepard) =  
*Skenidioides anthonensis* (Sardeson)  
*S. septata* Winchell and Schuchert  
*S. trentonensis* Winchell and Schuchert  
*Zygospira recurvirostris* (Hall)

Prosser Formation, fine grained limestone and calcareous shale:

*Parastrophina bernensis* (Sardeson)  
*P. rotundiformis* Willard

*Rostricellula acutiplicata* Cooper  
*Rostricellula* sp.3

Macy Formation, Middle Mississippi Valley, Hook Member, fine calcitite with dolomitic partings, layers of conglomerate:

*Campylorthis deflecta* (Conrad)  
*Hesperorthis tricenaria* (Conrad)  
 Macy Formation, Zell Member, fine-  
 textured limestone: *Ancistrorhyncha* sp.  
*Camerella bella* Fenton  
*C. gregeri* Cooper  
*Campylorthis deflecta* (Conrad) = *C.*  
*subplana* Cooper  
*Doleroides gibbosus* (Billings)  
*D. cf. D. pervetus* (Conrad) = *D.*  
*missouriensis* Cooper  
*Glyptorthis bellarugosa* (Conrad)  
*Hesperorthis tricenaria* (Conrad)  
*Öpikina septata?* Salmon  
*Ö. transitionalis* (Okulitch)

*Öpikina* sp.  
*Öpikina* sp.  
*Pionodema 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. inconsueta* Fenton  
*S. musculosa* Fenton  
*S. plattinensis* Fenton

*S. winchelli* Hall and Clarke  
*Strophomena* sp.  
*Zygospira recurvirostris* (Hall)  
*Z. variabilis* Fenton

Barnhart Formation, greenish shale with thin limestone; Auburn Formation, chert:

*Dalmanella subaequata* (Conrad) =  
*Pionodema subaequata* (Conrad)  
*D. testudinaria* (Dalman) = *Paucicrura*  
*rogata* (Sardeson)  
*Campylorthis subplana* Cooper  
*Hallina globularis* Cooper  
*Hesperorthis tricenaria* (Conrad)  
*Idiospira panderi* (Billings)  
*Orthis tricenaria* Conrad = *Hesperorthis*  
*tricenaria* (Conrad)  
*Paucicrura rogata* (Sardeson)  
*Pionodema subaequata* (Conrad)  
*Protozyga rotunda* Cooper  
*P. superba* Cooper  
*Rafinesquina sinclairi* Salmon

*Rafinesquina minnesotensis* (N.H.  
Winchell) = *Öpikina*  
*R. sinclairi* Salmon  
*Rostricellula cuneiformis* (Fenton and  
Fenton)  
*R. missouriensis* (Fenton and Fenton)  
*Sowerbyella* sp.  
*Strophomena delicatula* Fenton  
*Strophomena incurvata* (Shepard) = *S.*  
*auburnensis* Fenton  
*S. dignata* Fenton  
*Zugospira* sp.  
*Z. lebanonensis* Cooper  
*Z. recurvirostris* (Hall)  
*Z. nicolleti* Winchell and Schuchert =  
*Protozyga superba* Cooper

Northern Arkansas, Plattin Formation, dense blue-grey limestone:

*Ancistrorhyncha costata* Ulrich and  
Cooper  
*Camerella* aff. *C. panderi* Billings

*Rafinesquina* aff. *R. alternate* (Emmons)  
*Strophomena* cf. *incurvata* (Shepard)  
*Zygospira* aff. *Z. recurvirostris* (Hall)

13. Oklahoma, Arbuckle and Wichita Mountains, Viola Formation, light-grey to dark limestone:

*Dalmanella hamburgensis*  
*Dinorthis pectinella*  
*Platystrophia* sp.  
*Plectambonites sericeus*

*Rafinesquina deltoidea*  
*Rhynchotrema increbescens*  
*Strophomena filitexta*  
*Zygospira recurvirostris*

14. South Dakota, Black Hills, Whitewood Formation, grey shale in the lower member, siltstone in the middle member, and dolomite in the upper member:

*Dalmanella?* cf. *D. hamburgensis*  
(Winchell, not Walcott) = *Dalmanella*  
*winchelli* Cooper  
*Rafinesquina* sp.

*Rhynchotrema* cf. *R. minnesotense*  
(Sardeson)  
*Sowerbyella* sp.  
*Strophomena* sp.  
*Zygospira*



15. Great Basin, Nevada and California, Dark Shale with *Reuschella*, yellow-weathering limestone and dark shales:

<i>Bilobia hemispherica</i> Cooper	<i>Oxoplectia nevadensis</i> Cooper
<i>Bimuria</i> sp. I	<i>Paurorthis gigantean</i> Cooper
<i>Cristiferina cristifera</i> Cooper	<i>Plectorthis obesa</i> Cooper
<i>Eoplectodonta alternate</i> (Butts)	<i>Reuschella vespertina</i> Cooper
<i>Glyptorthis</i> sp. I	<i>Rostricellula angulate</i> Cooper
<i>Hesperorthis antelopensis</i> Cooper	<i>Sowerbyella merriami</i> Cooper
<i>Leptaena ordovicica</i> Cooper	<i>Sowerbyella</i> sp. I and 2
<i>Leptellina incompta</i> Cooper	<i>Strophomena</i> sp. I

16. Central Wales, Powys, Llanfawr Mudstone Formation, Builth; Allt-yr-Anker Formation, Meifod; Bryn Siltstone Formation, Berwyn Hills; Burrellian age rocks, "Gaerfawr", near Welshpool; shales of gracilis Zone age (Aurelucian) from Llanfawr Quarry, Llandrindod Wells:

<i>Kiaeromena</i> cf. <i>kjerulfi</i> (Holtedahl, 1916)	<i>Bicuspina</i> sp.
<i>Leptaena</i> ( <i>Leptaena</i> ) <i>tenuistriata</i> J. de C. Sowerby, 1839	<i>Hesperorthis</i> sp.
<i>Colaptomena expansa</i> (J. de C. Sowerby, 1839)	<i>Platystrophia elevata</i> Harper and Brenchley, 1993
<i>Leangella</i> ( <i>Leptestiina</i> ) <i>oepiki oepiki</i> (Whittington, 1938)	<i>Plaesiomys multiplicata</i> Bancroft, 1945
	<i>Reuschella</i> sp.

17. Wales, Gwynedd, Bala area, Gelli-grîn Group, Cowarch Phosphate Bed, Allt Ddu Group, Allt Ddu Formation, Llangower area, Derfel Limestone Formation, Bryn Beds, Nod Glas Formation, Glyn Gower Formation, Glyn Gower Group, Nant Hir Group:

<i>Bellimurina incommoda</i> Williams, 1963	<i>Anisopleurella multiseptata</i> (Williams, 1955)
<i>Oslomena</i> cf. <i>osloensis</i> Spjeldnaes, 1957	<i>Eoplectodonta</i> ( <i>Eoplectodonta</i> ) <i>lenis</i> (Williams, 1955)
<i>Colaptomena prolata</i> (Williams, 1963)	<i>Sowerbyella</i> ( <i>Sowerbyella</i> ) <i>musculosa</i> Williams, 1963
<i>Hedstroemina</i> sp.	<i>Sowerbyella</i> ( <i>Sowerbyella</i> ) <i>sericea permixta</i> Williams, 1963
<i>Kiaeromena</i> cf. <i>kjerulfi</i> (Holtedahl, 1916)	<i>Bicuspina spiriferoides</i> (M'Coy, 1851)
<i>Bimuria?</i> <i>dyfiensis</i> Lockley, 1980	<i>Caeroplecia mutabilis</i> Williams, 1955
<i>Palaeostrophomena canalis</i> Lockley, 1980	<i>Oxoplectia</i> sp.
<i>Palaeostrophomena magnifica</i> Williams, 1955	<i>Triplesia maccoyana</i> Davidson, 1860
<i>Leangella</i> ( <i>Leptestiina</i> ) <i>derfelensis</i> (Jones, 1928)	<i>Vellamo</i> sp.
<i>Chonetoidea abdita complicata</i> (Lockley, 1980)	<i>Kullervo</i> aff. <i>panderi</i> (Öpik, 1930)
<i>Chonetoidea</i> sp.	<i>Skenidioides costatus</i> Cooper, 1956

*Sulevorthis cessatus* (Williams, 1963)  
*Dolerorthis duftonensis prolixa* Williams, 1963  
*Dolerorthis* sp.  
*Dinorthis berwynensis angusta* Williams, 1963  
*Plaesiomys multifida* (Salter, 1866)  
*Nicolella actoniae obesa* Williams, 1963  
*Nicolella humilis* Williams, 1955  
*Cremnorthis parva* Williams, 1963  
*Platystrophia* cf. *sublimis* Öpik, 1930  
*Platystrophia* sp.  
*Bancroftina* sp.  
*Dalmanella modica* Williams, 1963  
*Howellites antiquior* (M'Coy, 1852)  
*Howellites intermedius* Bancroft, 1945  
*Howellites striatus* Bancroft, 1945

*Howellites ultimus* Bancroft, 1945  
*Reuschella horderleyensis*  
*horderleyensis* Bancroft, 1928  
*Reuschella horderleyensis undulata* Williams, 1963  
*Heterorthis retrorsistria* (M'Coy, 1851)  
*Salopia?* *globosa* (Williams, 1949)  
*Salopia salteri gracilis* Williams, 1955  
*Salopia* sp.  
*Parastrophinella brenchleyi* Lockley, 1980  
*Rostricellula sparsa* Williams, 1963  
*Cyclospira musculosa* (Lockley, 1980)  
*Cyclospira* sp.  
*Leptaena (Leptaena) ventricosa* Williams, 1963  
*Onniella soudleyensis* (Bancroft, 1945)  
*Rhactorthis crassa* Williams, 1963

18. North-west Wales, Anglesey, Garn Formation, Llanbabo Formation, Crewyn Formation:

*Kiaeromena (Kiaeromena)* sp.  
*Leptaena (Leptaena)* sp.  
*Palaeostrophomena* sp.  
*Bilobia* aff. *musca* (Öpik, 1930)  
*Ptychoglyptus* sp.  
*Clitambonites?* sp.  
*Ilmarinia* sp.  
*Kullervo* aff. *panderi* (Öpik, 1930)  
*Paralenorthis* sp.

*Dolerorthis tenuicostata* Williams, 1955  
*Ptychopleurella* sp.  
*Plaesiomys robusta* Bancroft, 1945  
*Dalmanella* sp.  
*Onniella* sp.  
*Harknessella* sp.  
*Horderleyella* sp.  
*Camerella* sp.

19. Shropshire, Horderley, Woolston, Shelve Inlier, Clunbury, Acton Scott Formation, Onny Shale Formation, Cheney Longville Formation, Spy Wood Grit Formation, Horderley Sandstone Formation, Whittery Shale Formation, Hagley Shale Formation, Hoar Edge Grit Formation, Coston Formation, Aldress Shale Formation, Alternata Limestone, Harnage Shale, Glenburrell Formation, Smeathen Wood Beds:

*Palaeoglossa lockleyi* Hurst, 1979  
*Dactylogonia?* *callawayiana* (Davidson, 1883)  
*Furcitella* sp.  
*Kjaerina complanata* (J. de C. Sowerby, 1839)  
*Kjaerina geniculata* Bancroft, 1929  
*Kjaerina hedstroemi* Bancroft, 1929  
*Kjaerina horderleyensis* Bancroft, 1929  
*Kjaerina jonesi* Bancroft, 1929

*Kjaerina latericostata* Bancroft, 1929  
*Kjaerina typa* Bancroft 1929  
*Rafinesquina?* sp.  
*Kiaeromena* cf. *kjerulfi* (Holtedahl, 1916)  
*Leptaena (Leptaena) salopiensis* Williams, 1963  
*Leptaena (Leptaena) ventricosa* Williams, 1963  
*Bystromena perplexa* Williams, 1974  
*Christiania hollii* (Davidson, 1871)

- Palaeostrophomena* sp.  
*Leangella* (*Leptestiina*) sp.  
*Sowerbyella* (*Sowerbyella*) *multipartita* Williams, 1978  
*Sowerbyella* (*Sowerbyella*) *sericea sericea* (J. de C. Sowerby, 1839)  
*Sowerbyella* (*Sowerbyella*) *soudleyensis* Jones, 1928  
*Bicuspina modesta* Williams, 1974  
*Bicuspina subquadrata* Williams, 1974  
*Bicuspina* sp.  
*Caeroplecia plicata* Williams, 1974  
*Triplesia* sp.  
*Skenidioides costatus* Cooper, 1956  
*Sulevorthis exopunctatus* (Williams, 1974)  
*Glyptorthis viriosa* Williams, 1974  
*Dolerorthis tenuicostata* Williams, 1955  
*Dolerorthis virgata* (J. de C. Sowerby, 1939)  
*Dinorthis berwynensis berwynensis* (Whittington, 1938)  
*Dinorthis flabellulum* (J. de C. Sowerby, 1839)  
*Dinorthis* sp.  
*Plaesiomys robusta* Bancroft, 1945  
*Nicolella actoniae actoniae* (J. de C. Sowerby, 1839)  
*Whittardia paradoxica* Williams, 1974  
*Plectorthis whitteryensis* Williams, 1974  
*Plectorthis* sp.  
*Gelidorthis* sp.  
*Mcewanella* sp.  
*Platystrophia caelata* Williams, 1974  
*Platystrophia major* Williams, 1955  
*Platystrophia* sp.  
*Salacorthis costellata* Williams, 1974  
*Rhactorthis actoniae* Hurst, 1979  
*Rhactorthis grandis* Hurst, 1979  
*Bancroftina typa* (Whittington, 1938)  
*Cryptothyris paracyclica* (Bancroft, 1928)  
*Dalmanella horderleyensis* (Whittington, 1938)  
*Dalmanella indica* Whittington, 1938  
*Dalmanella multiplicata multiplicata* (Bancroft, 1928)  
*Dalmanella multiplicata prima* Hurst, 1979  
*Dalmanella salopiensis gregaria* Williams, 1974  
*Dalmanella salopiensis transversa* Williams, 197  
*Dalmanella unguis ultima* Hurst, 1979  
*Dalmanella wattsi* (Bancroft, 1928)  
*Onniella avelinei* Bancroft, 1928  
*Onniella broeggeri* Bancroft, 1928  
*Onniella depressa* Bancroft, 1945  
*Onniella ostentata lepida* Williams, 1974  
*Onniella reuschi* Bancroft, 1928  
*Onniella soudleyensis* (Bancroft, 1945)  
*Harknessella jonesi* Bancroft, 1928  
*Harknessella subplicata* Bancroft, 1928  
*Harknessella subquadrata* Bancroft, 1928  
*Horderleyella corrugata* Bancroft, 1945  
*Horderleyella plicata* Bancroft, 1928  
*Reuschella bilobata* (J. de C. Sowerby, 1839)  
*Reuschella horderleyensis horderleyensis* Bancroft, 1928  
*Reuschella horderleyensis carinata* Williams, 1974  
*Smeathenella harnagensis* Bancroft, 1928  
*Smeathenella strophomenoides* Bancroft, 1945  
*Heterorthina praeculta* Bancroft, 1928  
*Heterorthis alternata* (J. de C. Sowerby, 1839)  
*Heterorthis patera* (Davidson, 1869)  
*Heterorthis* sp.  
*Marionites typus* (Bancroft, 1928)  
*Destombesium* sp.  
*Drabovia* cf. *fascicostata* Havlíček, 1950  
*Drabovia* sp.  
*Salopia salteri salteri* (Davidson, 1869)  
*Salopia triangularis* (J. de C. Sowerby, 1839)  
*Salopia* sp.  
*Zygospira?* *similis* (Reed, 1897)

20. Scotland, Strathclyde, Girvan, Kiln Mudstone Member of the Craighead Limestone;  
Myoch Formation; Albany Mudstone Formation; Myoch Formation:

- 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. *strandii* 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.

- Sivorthis? ardmillanensis* (Reed, 1917)  
*Sulevorthis humilidorsatus primadventus*  
 (Harper, 1984)  
*Sulevorthis playfairi* (Reed, 1917)  
*Taphrorthis bellatrix* (Reed, 1917)  
*Glyptorthis balcletchiensis* (Davidson,  
 1883)  
*Dolerorthis duftonensis duftonensis*  
 (Reed, 1910)  
*Dolerorthis rankini* (Davidson, 1883)  
*Dolerorthis* sp.  
*Hesperorthis craigensis* (Reed, 1917)  
*Ptychopleurella lapworthi* (Davidson,  
 1883)  
*Chaulistomella* sp.  
*Dinorthis carrickensis* Reed, 1917  
*Dinorthis? subplicatellus* (Reed, 1917)  
*Dinorthis* sp.  
*Valcourea* sp.  
*Nicolella actoniae actoniae* (J. de C.  
 Sowerby, 1839)  
*Doleroides* cf. *tennessensis* Cooper,  
 1956  
*Mimella* sp.  
*Plectorthis scotica* (M'Coy, 1851)  
*Plectorthis* sp.  
*Phragmorthis* sp.  
*Platystrophia scotica* Williams, 1962  
*Dalmanella cheesemani* Williams, 1962  
*Dalmanella federata* Reed, 1917  
*Eremotrema gracile* (Reed, 1917)  
*Onniella williamsi* Harper, 1986  
*Paucicrura cristata* (Cooper, 1956)  
*Paucicrura eximia* Williams, 1962  
*Paucicrura sila* Williams, 1962  
*Paucicrura* sp.  
*Dedzetina albadomus* Harper, 1989  
*Reuschella americana* Cooper, 1956  
*Diorthelasma* cf. *parvum* Cooper, 1956.  
*Fascifera? carrickensis* (Reed, 1917)  
*Pionodema girvaniensis* (Davidson,  
 1869)  
*Pionodema* cf. *subaequata* (Conrad,  
 1843)  
*Pionodema* sp.  
*Laticrura inconstans* (Reed, 1917)  
*Laticrura* sp.  
*Porambonites acutiplicatus* Reed, 1917  
*Camerella peachi* (Davidson, 1883)  
*Camerella* sp.  
*Parastrophina balcletchiensis* (Davidson,  
 1883)  
*Parastrophina? scotica* (Davidson, 1883)  
*Parastrophinella youngi* (Reed, 1917)  
*Metacamarella balcletchiensis*  
 (Davidson, 1883)  
*Drepanorhyncha calva* Williams, 1962  
*Drepanorhyncha? trigonalis* Williams,  
 1962  
*Oligorhynchia bifurcata* Cooper, 1956  
*Oligorhynchia conybeari* (Reed, 1917)  
*Rostricellula ardmillanensis* (Reed, 1917)  
*Rostricellula lapworthi* (Davidson, 1883)  
*Orthorhynchuloides nasutus* (M'Coy,  
 1851)  
*Anazyga? orbis* (Reed, 1917)  
*Catazyga arcana* Williams, 1962  
*Idiospira carrickensis* (Reed, 1917)  
*Idiospira? cuneatella* (Davidson, 1883)  
*Idiospira* cf. *longa* (Cooper, 1956)  
*Idiospira? sulcata* (Williams, 1962)  
*Idiospira thomsoni* (Davidson, 1869)  
*Manespira? diversa* (Reed, 1917)  
*Aulidospira trippi* Williams, 1962

21. Ireland, Wexford, Waterford, Duncannon Group, Annestown Formation, Wexford;  
 Lower Tramore Volcanic Formation, Waterford; Grange Hill Formation, Waterford:

- Colaptomena pseudopecten* (M'Coy,  
 1846)  
*Bimuria* sp.  
*Chonetoidea abdita abdita* (Williams,  
 1955)  
*Ptychoglyptus* sp.  
*Glyptorthis crispa* (M'Coy, 1846)  
*Nicolella* sp.  
*Reuschella* sp.  
*Oanduporella* cf. *reticulata* Hints, 1975  
*Salopia* sp.  
*Bimuria? dyfiensis* Lockley, 1980

*Leptellina (Leptellina) llandeiloensis*  
(Davidson, 1883)  
*Leangella (Leptestiina) oepiki ampla*  
(Parkes, 1994)  
*Anisopleurella multiseptata* (Williams,  
1955)

*Nicolella? calcarata* (M'Coy, 1846)  
*Leangella (Leptestiina) oepiki oepiki*  
(Whittington, 1938)  
*Kullervo hibernica* Harper, 1952  
*Skenidioides costatus* Cooper, 1956  
*Saukrodictya* sp.

22. Ireland, Meath, Upper Tuffs and Shales of the Grangegeeth Volcanic Series; Collon Formation; Clashford House Formation:

*Oepikina celtica* Harper, 1952  
*Kiaeromena (Kiaeromena)* sp.  
*Leptestia jukesii* (Davidson, 1869)  
*Chonetoidea abdita abdita* (Williams,  
1955)

*Plaesiomys multiplicata* Bancroft, 1945  
*Productorthis mitchelli* Williams, 1956  
*Oanduporella cf. reticulata* Hints, 1975  
*Cremnorthis* sp.

23. Northern Ireland, 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.  
*Cathrynina puteus* Candela, 1999  
*Anoptambonites* sp.  
*Anisopleurella* sp.  
*Eochonetes cf. aspera* (Wang, 1949)  
*Eochonetes celticus* Mitchell, 1977  
*Eoplectodonta (Eoplectodonta) cf. alternata* (Butts, 1942)  
*Eoplectodonta (Eoplectodonta)* sp.  
*Sowerbyella (Sowerbyella) cf. monilifera*  
Cooper, 1956  
*Bicuspina subquadrata* Williams, 1974  
*Caeroplecia tenuis* Candela, 2003  
*Oxoplecia* sp.  
*Triplexia* 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, 195  
*Paurorthis catawbensis* Cooper, 1956  
*Fascifera* sp.  
*Pionodema* cf. *subaequata* (Conrad, 1843)  
*Oanduporella* cf. *reticulata* Hints, 1975  
*Salopina ordovicica* Mitchell, 1977  
*Laticrura* cf. *heteropleura* Cooper, 195  
*Camerella* sp  
*Liostraphia* sp.  
*Parastrophina* sp.  
*Drepanorhyncha* sp.  
*Rostricellula simulata* (Reed, 1952)  
*Idiospira plicata* (Mitchell, 1977)  
 "Protozyga" sp.  
*Cyclospira* sp.

24. Cumbria, Dufton Shale Formation, Melmerby, Cumbria Corona beds of Pusgill, Dufton:

*Dolerorthis duftonensis duftonensis*  
 (Reed, 1910)

*Hesperorthis? equivocalis* (Reed, 1910)  
*Rhactorthis melmerbiensis* (Reed, 1910)

25. Chu-Ili Terrane, Anderken formation, pebbly conglomerate, sandstone, siltstone, mudstones:

*Longvillia lanx* (Popove, 1985)  
*Bellimurina* (*Bellimurina*) *sarytumensis*  
 sp.  
*Teratelasmella chugaevae* sp. nov.  
*Glyptomena onerosa* Popove, 1980  
*Limbimurina?* Sp.  
*Christiania egregia* Popove, 1985  
*Christiania* aff. *Sulcata* Williams, 1962  
*Foliomena prisca* sp. nov.  
*Isophragma imperator* Popove, 1980  
*Craspedelia tata* Popove, 1980  
*Acculina kulanketpesica* sp. nov.  
*Dulankarella larga* sp. nov.  
*Kajnaria rugosa* sp. nov.  
*Mabella conferta* (Popove, 1985)  
*Shlyginia fragilis* (Rukavishnikova, 1956)  
*Glyptambonites* sp.  
*Tesikella necopina* (Popove, 1980)  
*Chonetoidea* sp.  
*Anoptambonites convexus* sp. nov.

*Anoptambonites orientalis* Popove, 1980  
*Kassinella* (*Kassinella*)? Sp.  
*Sowerbyella* (*Sowerbyella*)  
*rukavishnikovaen* Popove, 1980  
*Sowerbyella* (*Sowerbyella*) aff. *Ampla*  
 (Nikitin and Popove)  
*Anisopleurella* sp.  
*Olgambonites insolita* sp. nov.  
*Zhilgyzambonites extenuate* sp. nov.  
*Gacella institata* sp. nov.  
*Triplesia* sp.  
*Triplesia* aff. *Subcarinata* Cooper, 1956  
*Bicuspina rukavishnikovae* Klenina,  
 1984  
*Grammoplecia wright* sp. nov.  
*Placotriplesia spissa* sp. nov.  
*Skenidioides* sp.  
*Dolerorthis expressa* Popove, 1980  
*Dolerorthis pristina* sp. nov.  
*Glyptorthis* sp.

*Austinella sarybulakensis* sp. nov.  
*Plectorthis? Burultasica* sp. nov.  
*Phaceloorthis?* sp.  
*Bowanorthis? devexa* sp. nov.  
*Eodalmanella extera* Popove, 1985  
*Phragmorthis conciliate* Popove, 1985  
*Pionodema opima* sp. nov.  
*Parastrophina iliana* sp. nov.  
*Parastrophina plena* Sapelnikov and  
 Rukavishnikova, 1975  
*Ilistrophina tesikensis* sp. nov.

*Liostrophia pravula* sp. nov.  
*Plectosyntrophia unicostata* sp. nov.  
*Schizostrophina margarita* Fu, 1982  
*Didymelasma cf. transversa* Fu, 1982  
*Rhynchotrema akchokense* sp. nov.  
*Pectenospira pectenata* Popove, Nikitin  
 and Sokiran, 1999  
*Kellerella Misiusi* Popov, Nikitin and  
 Sokiran, 1999  
*Nikolaispira guttula* sp. nov.

26. Chu-Ili Terrane, Dulankara Formation, Otar, Degers, and Akkol members; Otar Member, sandstone and siltstone with polymict conglomerate and limestone beds:

*Acrosaccus* sp.  
*Strophomena (Strophomena)*  
*orthonurensis* Misius, 1986  
*Holtedahlinia orientalis* sp. nov.  
*Rhipidomena* sp.  
*Glyptomenoides girvanensis* (Salmon,  
 1942)  
*Glyptomenoides?* sp.  
*Platymena tersa* sp. nov.  
*Christiania proclivis* sp. nov.  
*Bandaleta cf. plana* Nikitin and Popov,  
 1996  
*Glyptambonites aff. musculosus* Cooper,  
 1956  
*Nikitinamena bicostata* sp. nov.  
*Dulankarella cf. magna* Rukavishnikova,  
 1956  
*Shlyginia extraordinaria*  
 (Rukavishnikova, 1956)  
*Leangella (Leangella) paletsae* sp. nov.  
*Anoptambonites kovalevskii* Popov,  
 Nikitin and Cocks, 2000  
*Metambonites subcarinatus* sp. nov.  
*Sowerbyella (Sowerbyella)*  
*akdombakensis* Klenina, 1984

*Sowerbyella (Sowerbyella) ampla*  
 (Nikitin and Popov, 1996)  
*Sowerbyella (Rugosowerbyella)* sp.  
*Gunningblandella* sp.  
*Placotriplezia* sp.  
*Grammoplecia subcraegensis*  
 (Rukavishnikova, 1956)  
*Ogmoplecia nesca* sp. nov.  
*Dolerorthis* sp.  
*Ptychopleurella?* sp.  
*Plectorthis licta* sp. nov.  
*Weberorthis brevis* (Rukavishnikova,  
 1956)  
*Phragmorthis* sp.  
*Bokotorthis kasachstanica*  
 (Rukavishnikova, 1956)  
*Epitomyonia* sp.  
*Dalmanelloidea* gen. et sp. indet.  
*Altaethyrella otarica* (Rukavishnikova,  
 1956)  
*Eospirigerina pennata* (Rukavishnikova,  
 1956)  
*Qilianotryma suspectum* (Popov, in  
 Nikiforova et al. 1982)  
*Schachriomonina parva* (Rukavishnikova,  
 1956)

27. Boshchekul Terrane, Angrensor Formation, fine to medium polymict and volcanomict sandstone, siltstones and argillites, Odak bed, carbotaes build-ups such as mud-mounds and carbonate olistostromes:

*Phaceloorthis recondita* sp. nov.



- Hebertella? brevis* (Rukavishnikova, 1956)  
*Plaesiomys fidelis* sp. nov.  
*Bokotorthis kasachstanica* (Rukavishnikova, 1956)  
*Dinorthis kassini* Rukavishnikova, 1956  
*Grammoplectia subcraegensis* (Rukavishnikova, 1956)  
*Dulankarella magna* Rukavishnikova, 1956  
*Shlyginia extraordinaria* (Rukavishnikova, 1956)  
*Anoptambonites kovalevskii* sp. nov.  
*Sowerbyella akdombakensis* Klenina, 1984  
*Strophomena cf. orthonurensis* Misius, 1986  
*Karomena squalida* sp. nov.  
*Dzhebaglina plicata* sp. nov.  
*Christiania* sp.  
*Altaethyrella otarica* (Rukavishnikova, 1956)  
*Paraoligorhyncha reducta* Popov, in Nikiforova and Popov, 1981  
*Nalivkinia (Pronalivkinia) rudis* (Rukavishnikova, 1956)  
*Sulcatospira prima* Popov, Nikitin and Sokiran, 1999  
*Actinomena? Sp.*  
*Gunnarella? Sp.*  
*Bellimurina? Sp.*  
*Dzhebaglina? sp.*  
*Holtehdahlina? sp.*  
*Strophomenidae* gen. et sp. indet  
*Glyptomenidae* gen. et sp. indet  
*Christiania* sp.

Koskarasu Beds, several units of bedded limestone,

- Glyptomenidae* gen. et sp. indet  
*Anoptambonites perforates* sp. nov.  
*Triplexia shansorensis* sp. nov.  
*Dolerorthis? sp.*  
*Glyptorthis cf. maritime* Wright, 1964  
*Dicoelosia* sp.  
*Parastrophina asymmetrica* sp. nov.
- Leptaena (Ygdrasilomena) reticulate* sp. nov.  
*Cooperia aurita* sp. nov.  
*Shlyginia? Sp.*  
*Dulankarella* sp.  
*Leangella rugellosa* sp. nov.  
*Synambonites ricinium* sp. nov.  
*Sortanella aequabilis* sp. nov.  
*Sowerbyella? aff. ampla* (Nikitin and Popov, 1996)  
*Eoplectodonta oroensis* sp. nov.  
*Grammoplectia bulygi* sp. nov.  
*Placotriplesia cristata* sp. nov.  
*Dolerorthis fasciculate* sp. nov.  
*Glyptorthis? Sp.*  
*Plectorthis* sp.  
*Orthidiellidae* gen. et sp. indet.  
*Mirorthis? antecedens* (Klenina, 1984)  
*Epitomyonia cf. glypha* Wright, 1968  
*Parastrophina asymmetrica* sp. nov.  
*Parastrophina tersa uniplicata* subsp. Nov.  
*Parastrophina? Quinquecostata* sp. nov.  
*Illostrophina keregetasica* sp. nov.  
*Liostrophia lenticular* sp. nov.  
*Altaethyrella otarica* (Rukavishnikova, 1956)  
*Eospirigerina milleri* sp. nov.  
*Euroatrypa aitenensis* sp. nov.  
*Qilianotrypa suspectum* (Popov, 1982)  
*Pectenospira aff. pectenata* Popov, Nikitin, and Sokiran, 1999  
*Kellerella pilata* sp. nov.  
*Nikolaispira tripartita* sp. nov.  
*Odakella odakensis* sp. nov.
- Parastrophina tersa tersa* Nikitin and Popov, 1996  
*Parastrophina* sp.  
*Liostrophia lenticular* sp. nov.  
*Altaethyrella otarica* (Rukavishnikova, 1956)  
*Eospirigerina milleri* sp. nov.  
*Euroatrypa aitenensis* sp. nov.

Sulcatospira prima Popov, Nikitin, and

Sokiran, 1999

28. Ishim-Selety terrane, Tauken Formation, sandstones and siltstones and also interbeds of andesitic tuff:

*Tetraphalerella bestiubensis* sp. nov.

*Skenidioides* sp.

*Anoptambonites* sp.

*Dinorthis taukensis* sp. nov.

*Sowerbyella sinensis* Wang in Wang and Jin, 1964

*Rhynchotrema seletensis* sp. nov.

*Triplesia?* sp.

*Nalivkinia (Pronalivkinia) zvonstovi* sp.

29. Keila Stage, Estonia, Kahula Formation, argillaceous bioclastic limestones; Vasalemma Formation, fossiliferous argillaceous limestones:

*Actinomena asmussi* (Verneuil)

*Longvillia asmusi* (Verneuil, 1845)

*Actinomena orta* (Öpik), 1930

*Oepikina anijana grandis* (Alichova)

*Actinomena cf. luna* Törnquist

*Onniella* sp. A Hints, 1975

*Apatorthis punctata* Öpik

*Platystrophia rara* Männil

*Bassettella alata* Hints, L. 2010

*Platystrophia lynx* (Eichwald, 1830)

*Clinambon anomalus* (Schlotheim, 1822)

*Platystrophia lynx lynx* (Eichwald, 1830)

*Clitambonites schmidti* (Pahlen, 1877)

*Platystrophia* sp.

*Dalmanella kegelensis* Alichova, 1954

*Platystrophia dentata* (Pander, 1830)

*Dalmanella testudinaria* (Dalman, 1828)

*Platystrophia attenuata* McEwan, 1919

*Estlandia marginata* Pahlen, 1877

*Platystrophia crassoplicata* Alichova, 1951

*Estlandia pyron* Eichwald, 1840

*Platystrophia galri* Männil

*Glossorthis tacens* Öpik, 1930

*Platystrophia crassoplicata*

*Haljalanites grandis* (Alichova, 1951)

*crassoplicata* Alichova

*Hesperorthis pljussensis* Alichova, 1951

*Porambonites ventricosus* Kutorga

*Hesperorthis aff. inostrancevi*

*Porambonites* sp.

Wysogorski

*Parabekkerina grandis* (Alichova, 1951)

*Horderleyella kegelensis* (Alichova, 1953)

*Porambonites baueri* Noetling

*Horderleyella* sp. Hints, 1975

*Porambonites schmidti* Noetling

*Hordeleyella* (Dalmanella) oanduensis, Hints, 1975

*Parabekkerina grandis* (Alichova, 1951)

*Keilamena occidens* (Oraspöld, 1956)

*Porambonites schmidti* Noetling

*Kiaeromena cryptoides* (Oraspöld)

*Platystrophia galri* Männil

*Kierulfina ocsidens* (Verneuil)

*Rhactorthis kaagverensis* Hints, 1973

*Kjaerina orvikui* (Oraspöld, 1956)

*Sowerbyella (Sowerbyella) forumi*

*Kurnamena rugosoides* (Oraspöld, 1956)

Rõõmusoks

*Kurnamena laterorugata* Rõõmusoks, 1989

*Sowerbyella* sp.

*Leptaena rugosoides* Oraspöld, 1956

*Sowerbyella (Sowerbyella) trivia*

*Leptaena* sp.

Rõõmusoks, 1959

*Leptelloidea leptelloides* (Bekker, 1922)

*Sowerbyella (Sowerbyella) oepiki*

*Leptaena rhomboidalis* (Wahlenberg, 1818)

Rõõmusoks

*Septomena cf. alliku* (Oraspöld, 1956)

*Septomena cryptoides* (Oraspöld, 1956)

*Saukrodictya oblongatopora* Hints, 1979

*Septomena cf. alliku* (Oraspöld, 1956)  
*Sowerbyella* (*Sowerbyella*) *liliifera* Öpik,  
 1930  
*Strophomena asmussi* Verneuil  
*Sowerbyella* (*Sowerbyella*) sp.  
*Strophomena* (*Actinomena*) sp.  
*Triplesia* sp.  
*Vellamo magna* Öpik, 1934

*Vellamo magna wesenbergensis* Öpik,  
 1934  
*Vellamo phrygia* Öpik, 1934  
*Vellamo magna* Öpik, 1934  
*Vellamo ambisulcata* Öpik, 1934  
*Vellamo verneuili* (Eichwald, 1843)  
*Vellamo* sp.

30. Oandu Stage, Vasalemma Formation, bioclastic limestones; Hirmuse Formation, argillaceous limestones and marls:

*Actinomena orta* (Öpik, 1930)  
*Apatorthis inflata* Öpik  
*Camerella dura* Oraspöld, 1956  
*Clinambon anomalus* (Schlotheim, 1822)  
*Clinambon anomalus postumus* Öpik  
*Dactylogonia luhai* (Sokolskaja)  
*Dalmanella kegelensis* Alichova  
*Dalmanella* sp.  
*Hesperorthis pljussensis* Alichova, 1951  
*Howellites wesenbergensis* (Alichova,  
 1951)  
*Horderleyella kegelensis* (Alichova,  
 1953)  
*Holtedahlina sakuensis* Oraspöld, 1956  
*Holtedahlina* sp.  
*Ilmarinia dimorpha* Öpik, 1934  
*Kjerina poljensis* (Alichova, 1951)  
*Kjaerina orvikui* (Oraspöld, 1956)  
*Kjerina? sakuensis* Rõõmusoks  
*Kjaerina* sp.  
*Kurnamena palmrei* Rõõmusoks, 2004  
*Laticrura* sp. Hints, 1975  
*Leptaena rugosoides* Oraspöld, 1956  
*Leptaena fluviatilis* Oraspöld 1956  
*Macrocoelia* sp.  
*Nicolella aff. oswaldi oswaldi* (Buch,  
 1839)  
*Onniella longa* Hints, 1975  
*Oandumena fluviatilis* (Oraspöld, 1956)  
*Oanduporella reticulata* Hints, 1975  
*Onniella bancrofti* Lindström, 1953  
*Onniella* sp. B Hints, 1975  
*Oandumena fluviatilis* Rõõmusoks  
*Pionodema dubia* Hints, 1975

*Platystrophia dentata* triata Orspöld,  
 1956  
*Platystrophia crassoplicata* Alichova,  
 1951  
*Platystrophia lynx lynx* (Eichwald, 1830)  
*Platystrophia crassoplicata Alichova var*  
*rava* Oraspöld, 1956  
*Platystrophia dentata* (Pander) *var evari*  
 Oraspöld, 1956  
*Porambonites* sp.  
*Pseudostrophenomena reclinis* Rõõmusoks,  
 1963  
*Pseudostrophenomena* sp.  
*Rafinesquina* (*Rafinesquina*) *orvikui*  
 Oraspöld, 1956  
*Rafinesquina* (*Rafinesquina*) *poljensis*  
 Alichova  
*Rafinesquina* (R.) *orvikui* Männil (in coll)  
 "Rafinesquina" *poljensis* Alichova, 1951  
*Rafinesquina* sp.  
*Rafinesquina poljensis* (Alichova, 1951)  
*Rakverina inaequiclina* (Alichova)  
*Rakverina oanduensis* (Oraspöld, 1956)  
*Rakverina* sp. (*Rafinesquina* sp.)  
*Reuschella magna* Hints, 1975  
*Rhactorthis kaagverensis* Hints, 1973  
*Rhynchotrema nobilis* Oraspöld, 1956  
*Rhynchotrema parva* Oraspöld, 1956  
*Rostricellula nobilis* (Oraspöld)  
*Rostricellula nobilis* (Oraspöld, 1956)  
*Sakunites luhi* (Sokolskaya, 1954)  
*Saukrodictya rotundopora* Hints, 1979  
*Saukrodictya oblongatopora* Hints, 1979  
*Sampo* sp.  
*Sampo cf. identata Spjeldnaes*

<i>Similoleptaena?</i> crassorugata Rõõmusoks, 2004	<i>Trigrammaria?</i> minima (Rõõmusoks, 1985)
<i>Sowerbyella</i> ( <i>Sowerbyella</i> ) tenera Rõõmusoks, 1959	<i>Trigrammaria estonica</i> (Rõõmusoks, 1985)
<i>Sowerbyella</i> n. sp. sericea (Sowerby, 1839)	<i>Vellamo oandoensis</i> Öpik, 1934
<i>Sowerbyella</i> sp.	<i>Vellamo</i> sp.
<i>Sowerbyella</i> aff. sericea (Sowerby, 1839)	<i>Virunites orvikui</i> (Oraspõld, 1956)
<i>Strophomena</i> sp.	<i>Vellamo defecta</i> Öpik, 1934
	<i>Vellamo oandoensis</i> Öpik, 1934
	<i>Zygospira gutta</i> Oraspõld, 1956

31. Pagoda Formation, South China, medium to thick-bedded limestone and green shale:

<i>Petrocrani</i>	<i>Eoplectodonta</i>
<i>Glyptorthis</i>	<i>Foliomena</i>
<i>Epitomyonia</i>	<i>Cyclospira</i>
<i>Kenidioidea</i>	<i>Chonetoidea</i>
<i>Leangella</i>	<i>Christiania</i>
<i>Anisopleurella</i>	<i>Nubialba</i>

32. Oslo-Asker District-Norway, Keila stage, Upper Arnestad Formation:

<i>Acrosaccus?</i> sp.	<i>Osloella</i> sp.
<i>Anisopleurella karina</i>	<i>Osloella lata</i>
<i>Chonetoidea gamma</i>	<i>Oslomena osloensis</i>
<i>Christiania holtedahli</i>	<i>Oxoplecia tenuifilata</i>
<i>Cremnorthis parva</i>	<i>Paucicrura</i> cf. <i>Navis</i>
<i>Diambonia anatoli</i>	<i>Platyctrophia</i> cf. <i>Lynx</i>
<i>Eoplectodonta</i> (E.) <i>acuminata</i>	<i>Porambonites</i> sp.
<i>Glyptorthis alata</i>	<i>Pseudopholidops stolleyana</i>
<i>Gunnarella alpha</i>	<i>Ptychoglyptus valdari</i>
<i>Gunnarella beta</i>	<i>Sivorthis magna</i>
<i>Kullervo</i> cf. <i>Hibernica</i>	<i>Skenidioidea costatus</i>
<i>Leangella</i> (L.) <i>spjeldnaesi</i>	<i>Strophomena</i> (K.) <i>norvegica</i>
<i>Leptaena</i> (L.) <i>enessbe</i>	<i>Trematis concentric</i>
<i>Nicolella actoniae</i>	<i>Veliseptum?</i> sp.
<i>Onniella bancrofti</i>	

Oandu stage, Frognerkilen Formation:

<i>Acanthambonia ildjernensis</i>	<i>Glyptorthis alata</i>
<i>Anisopleurella karina</i>	<i>Gunnarella alpha</i>
<i>Chonetoidea gamma</i>	<i>Gunnarella beta</i>
<i>Cremnorthis parva</i>	<i>Iberomena nakkholmiensis</i>
<i>Dalmanelloidea</i> indet.	<i>Kiaeromena kjerulfi</i>
<i>Eoplectodonta</i> (E.) <i>acuminata</i>	<i>Kullervo</i> cf. <i>Hibernica</i>
<i>Eoplectodonta</i> (E.) <i>precedens</i>	<i>Lacunatella concentrica</i>

*Leangella* (L.) *indentata*?  
*Leangella* (L.) *spjeldnaesi*  
*Leptaena* (L.) *indigena*  
*Mytoella*? *robusta*  
*Nicolella actoniae*  
*Nicolella*? sp.  
*Onniella bancrofti*  
*Onniella longa*  
*Orthida* indet.  
*Oslella lata*  
*Oxoplecia tenuifilata*

*Paucicrura* cf. *Navis*  
*Platystrophia* cf. *Lynx*  
*Plectambonitoidea* indet.  
*Porambonites* sp.  
*Porambonites* (P.) *kjerulfi*  
*Protozyga norvegica*  
*Pseudopholidops stolleyana*  
*Skenidioides costatus*  
*Triplesia* sp.  
*Veliseptum*? Sp.

33. Australia, New South Wales, Billabong Creek, Billabong Creek limestone: Member:

*Anoptambonites*  
*Australispira*  
*Bowanorthis*  
*Didymelasma*  
*Dinorthis*  
*Doleroides*  
*Eridorthis*  
*Paraonychoplecia*

*Protozyga*  
*Quondongia*  
*Rhynchotrema*  
*Sowerbyella*  
*Sowerbyites*  
*Trigrammaria*  
*Wiradjuriella*  
*Zygospira*

Palin Yard Creek, Quondong Limestone

*Australispira*  
*Bowanorthis*  
*Hesperorthis*  
*Molongcola*  
*Phaceloorthis*

*Ptychopleurella*  
*Trigrammaria*  
*Tylambonites*  
*Wiradjuriella*  
*Zygospira*













































## Appendix 4.3 Dice similarity index

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33			
1- New foundland	1	0.5	0.5	0.3	0.5	0.5	0.4	0.3	0.4	0.4	0.3	0.4	0.4	0.3	0.2	0.2	0.2	0.1	0.2	0.1	0	0.1	0.1	0.2	0.1	0.1	0.1	0.3	0.2	0.2	0.1	0.1	0.2			
2- Ottawa Valley, Ottawa	0.5	1	0.7	0.3	0.5	0.4	0.4	0.4	0.6	0.5	0.6	0.5	0.4	0.3	0.2	0.3	0.3	0.1	0.3	0.2	0.1	0.1	0.2	0.1	0.2	0.1	0.2	0.3	0.4	0.2	0.2	0.4	0.2			
3- NY and adjacent areas	0.5	0.7	1	0.4	0.6	0.4	0.5	0.4	0.6	0.3	0.5	0.5	0.3	0.2	0.3	0.2	0.3	0.1	0.2	0.1	0	0.1	0.3	0.1	0.1	0.1	0.2	0.3	0.3	0.1	0.2	0.3	0.1	0.2		
4- Ontario (Lake Simcoe)	0.3	0.3	0.4	1	0.5	0.3	0.2	0.4	0.5	0.4	0.3	0.3	0.3	0.3	0.3	0.2	0.2	0.1	0.2	0.1	0.2	0.2	0.2	0.1	0.1	0.1	0.2	0.2	0.3	0.3	0	0.2	0.2			
5- Manitoulin Island	0.5	0.5	0.6	0.5	1	0.3	0.2	0.3	0.6	0.5	0.6	0.3	0.4	0.3	0.3	0.2	0.2	0.1	0.1	0.1	0	0.1	0.2	0.1	0.1	0.1	0.1	0.2	0.2	0.3	0.1	0.1	0.1	0.2		
6- Champlain Valley	0.5	0.4	0.4	0.3	0.3	1	0.5	0.2	0.4	0.5	0.2	0.7	0.5	0.1	0.2	0.2	0.1	0	0.1	0.1	0	0.1	0.1	0	0	0.1	0.1	0.2	0.2	0.2	0	0.2	0.1	0.2		
7- Hudson Valley	0.4	0.4	0.5	0.3	0.2	0.5	1	0.3	0.3	0.4	0.6	0.3	0.1	0.3	0.3	0.2	0.1	0.2	0.1	0	0.1	0.2	0.1	0	0	0.1	0.1	0.2	0.2	0.2	0.1	0.3	0.2	0.2		
8- The Appalachians	0.3	0.4	0.4	0.2	0.3	0.2	0.3	1	0.4	0.2	0.6	0.2	0.2	0.4	0.3	0.3	0.6	0.1	0.4	0.2	0.2	0.1	0.5	0	0.2	0.2	0.2	0.1	0.2	0.4	0.2	0.4	0.2	0.2		
9- Tennessee, Kentucky	0.4	0.6	0.6	0.4	0.6	0.4	0.3	0.4	1	0.4	0.6	0.5	0.4	0.3	0.2	0.3	0.1	0.3	0.1	0.3	0.1	0	0.1	0.2	0.1	0.1	0.1	0.2	0.3	0.4	0	0.2	0.3	0.2		
10- Indiana	0.4	0.5	0.3	0.5	0.5	0.3	0.2	0.4	1	0.3	0.5	0.5	0.4	0.2	0.2	0.1	0.1	0	0.1	0	0.1	0.2	0.1	0.2	0.1	0.1	0.1	0.1	0.2	0.3	0.1	0.1	0.2	0.1	0.2	
11- Mississippi Valley	0.3	0.6	0.5	0.4	0.6	0.2	0.4	0.6	0.6	0.3	1	0.4	0.3	0.2	0.3	0.3	0.3	0.2	0.3	0.2	0.2	0	0.2	0.4	0.1	0.2	0.1	0.2	0.2	0.3	0.4	0.1	0.3	0.3	0	
12- Oklahoma (Viola Fm)	0.4	0.5	0.5	0.3	0.3	0.7	0.6	0.2	0.5	0.5	0.4	1	0.6	0.1	0.3	0.2	0.1	0.1	0.1	0.1	0.1	0	0.1	0.1	0	0	0.1	0	0.2	0.2	0	0.1	0.2	0.1	0.2	
13- South Dakota	0.4	0.4	0.3	0.3	0.4	0.5	0.3	0.2	0.4	0.5	0.3	0.6	1	0.1	0.1	0.2	0.1	0	0.1	0.1	0	0.1	0.1	0	0.1	0	0.1	0.1	0	0.3	0.2	0.2	0	0.1	0.2	
14- Nevada and California	0.3	0.3	0.2	0.3	0.3	0.1	0.1	0.4	0.3	0.4	0.2	0.1	0.1	1	0.3	0.2	0.3	0.2	0.3	0.1	0.2	0.1	0.3	0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.2	0.3	0.1	0.1	0.2	
15- British Columbia	0.2	0.2	0.3	0.3	0.3	0.2	0.3	0.2	0.3	0.2	0.3	0.3	0.1	0.3	1	0.2	0.3	0.1	0.2	0.1	0.2	0.1	0.2	0.3	0	0	0.1	0.2	0.2	0.1	0.1	0.3	0.3	0	0	
16- Shropshire	0.2	0.3	0.2	0.2	0.2	0.2	0.3	0.3	0.2	0.2	0.2	0.2	0.2	0.2	0.2	1	0.3	0.2	0.5	0.3	0.2	0.2	0.3	0.1	0.2	0.1	0.2	0.2	0.3	0.2	0.3	0.2	0.3	0.1	0.1	0.2
17- Scotland, Girvan	0.2	0.3	0.3	0.2	0.2	0.1	0.2	0.6	0.3	0.1	0.3	0.1	0.1	0.3	0.3	0.3	1	0.1	0.4	0.2	0.2	0.1	0.6	0.1	0.3	0.2	0.1	0.2	0.1	0.2	0.3	0.2	0.3	0.2	0.3	0.1
18- Wales, Powys	0.1	0.1	0.1	0.2	0.2	0	0.1	0.1	0.1	0.1	0.2	0.1	0	0.2	0.1	0.2	0.1	1	0.2	0.2	0.1	0.3	0.1	0.2	0	0	0	0	0	0.1	0.1	0	0.1	0.1	0.1	
19- Wales, Gwynedd	0.2	0.3	0.2	0.1	0.1	0.1	0.2	0.4	0.3	0	0.3	0.1	0.1	0.3	0.2	0.5	0.4	0.2	1	0.3	0.3	0.3	0.4	0.1	0.2	0.1	0.2	0.2	0.3	0.3	0.3	0.3	0.5	0.1	0.1	
20- Wales, Anglesey	0.1	0.2	0.1	0.2	0.1	0.1	0.1	0.2	0.1	0.1	0.2	0.1	0.1	0.1	0.1	0.3	0.2	0.2	0.3	1	0.1	0.2	0.2	0.1	0	0.1	0.1	0	0.2	0.2	0	0.2	0.2	0	0.2	0.1
21- Ireland	0	0.1	0	0	0	0	0	0.2	0	0	0	0	0	0.2	0.1	0.2	0.1	0.3	0.1	1	0.2	0.2	0	0	0.1	0	0	0.1	0.1	0.2	0.3	0.3	0	0	0	
22- Ireland, Meath	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.2	0.2	0.1	0.3	0.3	0.2	0.2	1	0.2	0.1	0	0	0	0	0	0.2	0.1	0.1	0.2	0	0	
23- Northern Ireland, Tyrone	0.1	0.2	0.3	0.2	0.2	0.1	0.2	0.5	0.2	0.1	0.4	0.1	0.1	0.3	0.3	0.6	0.1	0.4	0.2	0.2	0.2	1	0	0.3	0.2	0.3	0.2	0.1	0.2	0.2	0.3	0.2	0.3	0.2	0.2	0.2
24- Cumbria	0.2	0.1	0.1	0.1	0.1	0	0	0	0.1	0.2	0.1	0	0	0.1	0	0.1	0.1	0.2	0.1	0.1	0	0.1	0	1	0	0.1	0	0	0.1	0	0.1	0	0	0	0	0.1
25- Chu-ili, Anderken	0.1	0.2	0.1	0.1	0.1	0	0.1	0.2	0.1	0.1	0.2	0	0.1	0.1	0.1	0.2	0.3	0	0.2	0	0.1	0	0.3	0	1	0.3	0.4	0.2	0.1	0.1	0.2	0.1	0.1	0.2	0.1	0.2
26- Chu-ili, Dulankara	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.2	0	0.1	0.1	0	0	0.2	0.1	0.3	1	0.5	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
27- Boshchekul Terrane	0.1	0.2	0.2	0.2	0.1	0.1	0.2	0.2	0.1	0.1	0.2	0	0	0.2	0.2	0.2	0	0.2	0.1	0	0.2	0.1	0	0.3	0	0.4	0.5	1	0.2	0.1	0.1	0.2	0.2	0.1	0.2	0.1
28- Ishim-Seley terrane	0.3	0.3	0.3	0.2	0.2	0.2	0.2	0.1	0.2	0.1	0.2	0.2	0.3	0.1	0.1	0.2	0.1	0	0.2	0	0.1	0	0.2	0	0.2	0	0.2	0.1	0.2	1	0.1	0.1	0.1	0.1	0.3	
29- Keila Stage:	0.2	0.4	0.3	0.3	0.2	0.2	0.2	0.2	0.3	0.2	0.3	0.2	0.2	0.1	0.3	0.2	0.1	0.3	0.2	0.1	0.3	0.2	0.1	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.5	0	0.3	0.1	
30- Qandu Stage:	0.2	0.4	0.3	0.3	0.3	0.2	0.2	0.4	0.3	0.4	0.2	0.2	0.2	0.1	0.3	0.3	0.1	0.3	0.3	0.1	0.3	0.2	0.1	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.5	1	0	0.2	
31- South China	0.1	0.2	0.1	0	0.1	0	0.1	0.2	0	0.1	0.1	0	0	0.2	0.3	0.2	0.2	0	0.3	0	0.3	0.1	0.2	0	0	0.2	0.1	0.2	0.1	0	0	0.1	0.2	0.1	0	0
32- Oslo, Asker District, Norway	0.1	0.2	0.2	0.2	0.1	0.2	0.3	0.4	0.2	0.1	0.3	0.1	0.1	0.2	0.3	0.3	0.3	0.1	0.5	0.2	0.3	0.2	0.3	0	0.1	0.1	0.1	0.2	0.1	0.3	0.2	0.3	1	0	0	
33- New South Wales, Australia	0.2	0.4	0.3	0.2	0.2	0.1	0.2	0.2	0.3	0.2	0.3	0.2	0.2	0.1	0	0.1	0.1	0.1	0.1	0.1	0	0	0.2	0.1	0	0.2	0.1	0.2	0.1	0.1	0.3	0.1	0.2	0	0	0



## Appendix 4.5 Simpson similarity index

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	
1- New foundland	1	0.9	0.8	0.3	0.7	0.7	0.4	1	0.7	0.4	0.8	0.4	0.6	0.3	0.3	0.7	0.9	0.1	0.4	0.1	0	0.1	0.6	0.3	0.3	0.1	0.3	0.3	0.6	0.1	0.3	0.3		
2- Ottawa Valley, Ottawa a	0.9	1	0.8	0.5	0.6	1	0.6	0.8	0.6	1	0.7	0.9	1	0.4	0.2	0.5	0.6	0.3	0.4	0.2	0.1	0.1	0.5	0.3	0.3	0.1	0.3	0.5	0.4	0.5	0.3	0.3	0.4	
3- NY and adjacent areas	0.8	0.8	1	0.5	0.7	0.8	0.7	0.9	0.6	0.6	0.8	0.9	0.8	0.3	0.4	0.4	0.7	0.3	0.3	0.1	0	0.1	0.6	0.3	0.3	0.2	0.3	0.4	0.4	0.5	0.1	0.3	0.4	
4- Ontario (Lake Simcoe)	0.3	0.5	0.5	1	0.5	0.5	0.3	0.7	0.5	0.7	0.8	0.4	0.6	0.3	0.4	0.5	0.7	0.3	0.2	0.2	0	0.2	0.6	0.3	0.2	0.2	0.3	0.2	0.5	0	0.3	0.2		
5- Manitoulin Island	0.7	0.6	0.7	0.5	1	0.5	0.2	0.7	0.7	0.7	0.9	0.5	0.8	0.3	0.4	0.3	0.7	0.3	0.2	0.1	0	0.1	0.6	0.3	0.3	0.1	0.3	0.2	0.3	0.5	0.1	0.2	0.3	
6- Champlain Valley	0.7	1	0.8	0.5	0.5	1	0.8	1	0.8	0.5	0.8	0.8	0.6	0.2	0.5	0.8	0.7	0	0.5	0.2	0	0.2	0.7	0	0.2	0.2	0.3	0.3	0.7	0	0.5	0.3		
7- Hudson Valley	0.4	0.6	0.7	0.3	0.2	0.8	1	0.9	0.4	0.4	0.8	0.8	0.6	0.2	0.4	0.7	0.7	0.1	0.4	0.2	0	0.2	0.6	0	0.3	0.2	0.4	0.2	0.4	0.4	0.1	0.5	0.2	
8- The Appalachians	1	0.8	0.9	0.7	0.7	1	0.9	1	0.9	1	0.8	1	1	1	0.7	0.4	0.6	0.4	0.5	0.5	0.7	0.3	0.5	0.3	0.3	0.2	0.2	0.5	0.3	0.4	0.5	0.5	0.3	
9- Tennessee Kentucky	0.7	0.6	0.6	0.5	0.7	0.8	0.4	0.9	1	0.7	0.8	0.9	1	0.3	0.3	0.4	0.7	0.3	0.4	0.1	0	0.1	0.5	0.3	0.2	0.1	0.1	0.3	0.4	0.6	0	0.3	0.3	
10- Indiana	0.4	1	0.6	0.7	0.7	0.5	0.4	1	0.7	1	0.6	0.6	0.6	0.4	0.6	0.6	0.6	0.1	0.1	0.1	0	0.3	0.4	0.3	0.3	0.1	0.4	0.1	0.6	0.9	0.1	0.4	0.4	
11- Mississippi Valley	0.8	0.7	0.8	0.8	0.9	0.8	0.8	0.8	1	1	1	1	1	0.4	0.4	0.3	0.5	0.5	0.3	0.2	0.1	0.3	0.5	0.3	0.2	0.1	0.2	0.4	0.3	0.4	0.2	0.3	0.3	
12- Oklahoma (Viola Fm)	0.4	0.9	0.9	0.4	0.5	0.8	0.8	1	0.9	0.6	1	1	0.8	0.1	0.5	0.6	0.5	0.1	0.4	0.1	0	0.1	0.4	0	0.1	0.1	0.1	0.1	0.3	0.5	0.8	0	0.4	0.4
13- South Dakota	0.6	1	0.8	0.6	0.8	0.6	0.6	1	1	0.6	1	0.8	1	0.2	0.2	0.8	0.6	0	0.4	0.2	0	0.2	0.4	0	0.4	0	0.4	0.2	0.4	0.6	1	0	0.2	0.6
14- Nevada and California	0.3	0.4	0.3	0.3	0.3	0.2	0.2	1	0.3	0.6	0.4	0.1	0.2	1	0.4	0.3	0.8	0.3	0.5	0.1	0.3	0.1	0.7	0.3	0.2	0.2	0.4	0.1	0.3	0.4	0.2	0.3	0.1	
15- British Columbia	0.3	0.2	0.4	0.4	0.4	0.5	0.4	0.7	0.3	0.4	0.4	0.5	0.2	0.4	1	0.3	0.6	0.3	0.3	0.1	0.2	0.3	0.7	0	0.2	0.2	0.3	0.1	0.2	0.1	0.4	0.4	0	
16- Shropshire	0.7	0.5	0.4	0.5	0.3	0.8	0.7	0.4	0.4	0.6	0.3	0.6	0.8	0.3	0.3	1	0.4	0.5	0.6	0.5	0.3	0.4	0.4	0.7	0.2	0.2	0.2	0.4	0.3	0.3	0.4	0.3	0.1	
17- Scotland, Girvan	0.9	0.6	0.7	0.7	0.7	0.7	0.7	0.6	0.7	0.6	0.5	0.5	0.6	0.8	0.6	0.4	1	0.6	0.6	0.5	0.8	0.3	0.6	0.7	0.4	0.3	0.3	0.5	0.3	0.4	0.7	0.5	0.3	
18- Wales, Powys	0.1	0.3	0.3	0.3	0.3	0	0.1	0.4	0.3	0.1	0.5	0.1	0	0.3	0.3	0.5	0.6	1	0.6	0.3	0.1	0.4	0.3	0.3	0.1	0	0.1	0	0.4	0.4	0	0.3	0.1	
19- Wales, Cwynedd	0.4	0.4	0.3	0.2	0.2	0.5	0.4	0.5	0.4	0.1	0.3	0.4	0.4	0.5	0.3	0.6	0.6	1	0.4	0.7	0.5	0.6	0.7	0.2	0.1	0.2	0.4	0.3	0.3	0.5	0.5	0.1		
20- Wales, Anglesey	0.1	0.2	0.1	0.2	0.1	0.2	0.2	0.5	0.1	0.1	0.2	0.1	0.2	0.1	0.1	0.5	0.5	0.3	0.4	1	0.2	0.2	0.5	0.3	0.1	0.1	0.1	0	0.4	0.3	0	0.4	0.1	
21- Ireland	0	0.1	0	0	0	0	0	0.7	0	0	0.1	0	0	0.3	0.2	0.3	0.8	0.1	0.7	0.2	1	0.3	0.7	0	0.3	0.1	0.1	0.1	0.2	0.3	0.4	0.6	0	
22- Ireland, Meath	0.1	0.1	0.1	0.2	0.1	0.2	0.2	0.3	0.1	0.3	0.3	0.1	0.2	0.1	0.3	0.4	0.3	0.4	0.5	0.2	0.3	1	0.4	0.3	0.1	0	0.1	0	0.4	0.3	0.1	0.3	0	
23- Northern Ireland, Tyrone	0.6	0.5	0.6	0.6	0.6	0.7	0.6	0.5	0.5	0.4	0.5	0.4	0.4	0.7	0.7	0.4	0.6	0.3	0.6	0.5	0.7	0.4	1	0.3	0.3	0.3	0.4	0.5	0.2	0.3	0.7	0.5	0.4	
24- Cumbria	0.3	0.3	0.3	0.3	0.3	0	0	0.3	0.3	0.3	0.3	0	0	0.3	0	0.7	0.7	0.3	0.7	0.3	0	0.3	0.3	1	0.3	0.3	0	0.7	0	0	0.3	0		
25- Chu-ll, Anderken	0.3	0.3	0.3	0.2	0.3	0.2	0.3	0.2	0.3	0.2	0.3	0.2	0.1	0.4	0.2	0.2	0.2	0.4	0.1	0.2	0.1	0.3	0.1	0.3	0.3	1	0.4	0.5	0.6	0.1	0.1	0.5	0.2	0.3
26- Chu-ll, Dulankara	0.1	0.1	0.2	0.2	0.1	0.2	0.2	0.2	0.1	0.1	0.1	0.1	0.2	0.2	0.2	0.2	0.3	0	0.1	0.1	0.1	0	0.3	0.3	0.4	1	0.5	0.2	0.1	0.1	0.3	0.1	0.1	
27- Boshchekul terrane	0.3	0.3	0.3	0.3	0.3	0.3	0.4	0.2	0.1	0.4	0.2	0.1	0.2	0.4	0.3	0.2	0.3	0.1	0.2	0.1	0.1	0.1	0.4	0.3	0.5	0.5	1	0.5	0.1	0.1	0.5	0.2	0.1	
28- Ishim-Seley terrane	0.3	0.5	0.4	0.2	0.2	0.3	0.2	0.5	0.3	0.1	0.4	0.3	0.4	0.1	0.1	0.4	0.5	0	0.4	0	0.1	0	0.5	0	0.6	0.2	0.5	1	0.2	0.2	0.1	0.2	0.4	
29-Keila Stage:	0.6	0.4	0.4	0.5	0.3	0.7	0.4	0.3	0.4	0.6	0.3	0.5	0.6	0.3	0.2	0.3	0.3	0.4	0.3	0.4	0.2	0.4	0.2	0.7	0.1	0.1	0.1	0.2	1	0.6	0	0.3	0.1	
30-Oandru Stage:	0.6	0.5	0.5	0.5	0.5	0.7	0.4	0.4	0.6	0.9	0.4	0.8	1	0.4	0.1	0.3	0.4	0.4	0.3	0.3	0.3	0.3	0.3	0.7	0.1	0.1	0.1	0.2	0.6	1	0	0.2	0.2	
31-South China	0.1	0.3	0.1	0	0.1	0	0.1	0.5	0	0.1	0.2	0	0	0.2	0.4	0.4	0.7	0	0.5	0	0.4	0.1	0.7	0	0.5	0.3	0.5	0.1	0	0.1	0.6	0		
32- Oslo, Asker District, Nonw ay	0.3	0.3	0.3	0.3	0.2	0.5	0.5	0.5	0.3	0.4	0.3	0.4	0.2	0.3	0.4	0.3	0.5	0.3	0.5	0.4	0.6	0.3	0.5	0	0.2	0.1	0.2	0.2	0.3	0.2	0.6	1	0	
33- New South Wales, Australia	0.3	0.4	0.4	0.2	0.3	0.3	0.2	0.3	0.3	0.4	0.3	0.4	0.6	0.1	0	0.1	0.3	0.1	0.1	0.1	0	0	0.4	0.3	0.3	0.1	0.1	0.4	0.1	0.2	0	0	1	

## **Curriculum Vitae**

**Akbar Sohrabi**

### **Education**

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- Ph.D. Western University, London, Canada , Paleontology, 2013
- M.Sc. Shahid Beheshti University, Tehran, Iran, Stratigraphy and Paleontology, 2008
- B.Sc. University of Tabriz, Tabriz, Iran, Geology, 2005

### **Employment History**

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- Sept 2009- December 2009. Teaching Assistant, Paleobiology and Paleoecology, UWO
- January 2010- April 2010. Teaching Assistant, Catastrophic Events in Earth History,UWO
- Sept 2010- December 2010. Teaching Assistant, Paleobiology and Paleoecology, UWO
- January 2011- April 2011. Teaching Assistant, Vertebrate Paleontology, UWO
- Sept 2011- December 2011. Teaching Assistant, Paleobiology and Paleoecology, UWO
- January 2012- April 2012. Teaching Assistant, Catastrophic Events in Earth History, UWO
- May 2012- August 2012. Research and field work for PhD thesis, Lake Simcoe area, Ontario
- Sept 2012- December 2012. Teaching Assistant, Paleobiology and Paleoecology, UWO
- January 2013- April 2013. Teaching Assistant, Vertebrate Paleontology, UWO

## Publications

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Sohrabi, A., and Jin, J. 2013a. Evolution of the *Rhynchotrema*–*Hiscobeccus* lineage: implications for the diversification of the Late Ordovician epicontinental brachiopod fauna of Laurentia. *Lethaia*, 46(2): 188-210.

Sohrabi, A. and Jin, J. 2013b (published online). Global palaeobiogeography of brachiopod faunas during the early Katian (Late Ordovician) greenhouse episode. *Palaeogeography, Palaeoclimatology, Palaeoecology*. Doi 10.1016/j.palaeo.2013.02.027.

## Conference Presentations

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**Sohrabi, A.**, and Jin, J. 2011. Evolution of the Late Ordovician *Rhynchotrema*–*Hiscobeccus* lineage in North America. Canadian Paleontology Conference, Vancouver.

**Sohrabi, A.**, and Jin, J. 2012. Evolution and extinction of the *Rhynchotrema*–*Hiscobeccus* lineage across the Ordovician–Silurian boundary in North America. International Geoscience Programme (IGCP) Project 591, 2nd Annual Meeting and 1st Foerste Symposium, Cincinnati, USA.

**Sohrabi, A.**, Sproat, C.D, and Jin, J. 2012. Latitudinal gradients and development of endemism in Late Ordovician brachiopods of Laurentia: examples from the *Hiscobeccus*–*Rhynchotrema* and *Dinorthis*–*Plaesiomys* lineages. Canadian Paleontology Conference, Toronto.

## Awards

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- Graduate Teaching Assistantship (GTA), Western University, 2009
- Western Graduate Research Scholarship (WGRS), Western University, 2009