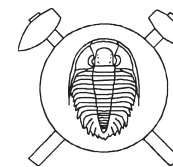


## Paleoecology and paleobiogeography of Wenlockian (Silurian) brachiopods of the Cape Phillips Formation from Baillie Hamilton Island, Arctic Canada



### Paleoekologie a paleobiogeografie wenlockých (silur) brachiopodů souvrství Cape Phillips z ostrova Baillie Hamilton a arktické Kanadě

(3 tables)

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The Baillie Hamilton fauna contains a mixture of both shallow water and deep water brachiopods brought together in debris flows. By using criteria such as taphonomy, abundance distribution, and the community framework concept, a total of 10 communities are recognized from the collection. These communities represent the northern end of the Wenlockian Cordilleran faunal belt. The Baillie Hamilton fauna belongs to the Uralian-Cordilleran Region. The high Affinity Index shared by the fauna and the coeval Eastern Great Basin fauna indicates that a gradual environmental gradient separates the Uralian-Cordilleran Region from the North American Province.

*Key words:* Silurian, Wenlockian, brachiopods, paleoecology, paleobiogeography, community

### Introduction

The Baillie Hamilton fauna (B-H fauna for short) is a diverse brachiopod fauna collected from the Wenlockian part of the Cape Phillips Formation from the south coast of Baillie Hamilton Island, District of Franklin, Arctic Canada. The complete description of the fauna is contained in a three part publication by Zhang (1989a–c). The B-H fauna consists of nearly 50,000 specimens of 87 brachiopod species. This large collection yields rich information for the study of the Early Silurian benthic community and marine biogeography. This study relies on the Benthic Assembly and community framework developed by Boucot (1975, 1999) for community assignment. The community study is based on taxa including both genera and species while biogeographical analysis is based on taxa at the generic level.

### Paleoecology

The Baillie Hamilton fauna was recovered from the distal phase of debris flows deposits. Down slope transportation must have resulted in considerable mixing of brachiopods from various communities. It is possible, however, to reconstruct some of the communities on the basis of careful evaluation of the following criteria:

**Morphology:** Shell morphology commonly correlates with certain environmental gradients. The study by Faber – Vogel – Winter (1977) shows that large brachiopods with stronger external ornamentation generally co-occur with coarse grain size, typically shallow-water deposits, while small, smooth forms with a high articulation ratio are found in more offshore fine grained deposits. The B-H fauna contains two groups of brachiopods. The dominant group consists of small, thin-shelled brachiopods with a relatively low disarticulation ratio. It characterizes an offshore, low energy environment. The oth-

er group includes medium size and often thick-shelled forms. They are mostly disarticulated and not well preserved, indicating a shallow-water environment with relatively high energy.

**Taphonomy:** Disarticulation and shell fragmentation can be used as a measure of the distance and mode of transportation. The small, thin-shelled brachiopods in the B-H fauna rarely show shell damage and usually have a relatively high articulation ratio even among forms with a weak deltidodont type articulating mechanism. The relatively undisturbed nature of these species suggests that they are derived from a nearby source. They probably colonized slope and basinal environments close to the final burial site. These small shells are likely to be held in suspension in the fluid head portion of a debris flows during down slope transportation; thus they suffered little shell damage. The larger, thick-shelled brachiopods on the other hand are mostly disarticulated and fragmentary. They bear the evident marks of more abrasive shallow-water and down slope transportation.

**Abundance distribution among samples:** Each of the five samples contains fossils brought together by a debris flows on its path to the depositional site. Because of their time and spatial proximity, it is assumed that these debris flows had swept each time through the same ring of communities that roughly correlate with depth zones. Consequently, the abundance distribution of species may provide clues to their original distribution in communities. Species with an even distribution in all five samples are most likely to have come from a closer source or are abundant and widespread. On the other hand, species that show erratic distributions are either from a more distant shallow-water community or have fluctuating population densities. Furthermore, species with a similar abundance distribution pattern are assumed to have come from a common source.

Comparison with model communities: Boucot (1975, 1999) has defined an array of Silurian brachiopod communities. Many of these communities reoccur in places, and thus can serve as models for community study. It is relatively easy to compare low diversity communities with the model. High diversity communities, such as the *Dicoelosia-Skenidioides* Community, often vary in both composition and relative abundance of species from one area to another. One has to make judgment call in employing a high diversity community model. This study relies primarily on the low diversity community models summarized by Boucot (1975, 1999, see also Johnson et al. 1976; Boucot et al. 1988).

Used alone, any one of the above criteria may not be adequate for community assignment, but together they can provide enough clues for the reconstruction of some communities. The notion that communities can be recognized from transported assemblages is based on the principles borrowed from the botanists of the Braun-Blanquet school, who employ the so-called Braun-Blanquet table to classify plant communities. To paraphrase Gauch (1982): “the Braun-Blanquet approach is founded on three principal ideas. (1) Plant communities are recognizable by their taxic composition apart from environmental information. (2) The stenotopic species of a community are diagnostic or indicator species and are emphasized in Braun-Blanquet analysis. (3) The species associations form building blocks of communities.” The first two principals can be readily applied to fossil communities. As to the last principal, fossil data are commonly insufficient for hierarchical community classification.

The foregoing discussion leads to the recognition of the following brachiopod communities in the B-H fauna. *Trimerella* Community: *Trimerella* commonly forms a high dominance community in turbulent waters at a BA 3 position. The genus is represented by 12 fragmentary valves from two separate samples. The abundance distribution of the genus does not correlate with that of other platform taxa such as the pentamerids in the collection. A typical *Trimerella* Community situated in the platform interior is the most likely source for the uncommon *Trimerella* specimens in the B-H collection.

*Rhipidium-Lissocoelia?* Community: The *Rhipidium* Community has been found in several localities in the North Atlantic Region. Boucot (1999) defines the community as a BA 3 rough water community. *Rhipidium* and *Lissocoelia?* co-occur in three of the five samples from the B-H collection. The shells of both genera are relatively large and thick, and are disarticulated and fragmentary. The valves of both genera are likely derived from a distant shallow-water community. The presence of a platform pentamerid community is further supported by Sodro and Hobson’s findings (1979). These Canadian geologists reported pentamerids associated with reef communities in the Wenlockian part of the Allen Bay carbonates on adjacent Cornwallis Island.

*Gracianella* Community: The *Gracianella* Community was noted first by Boucot (1975) and later

described by Johnson et al. (1976) from the Roberts Mountains Formation of central Nevada. It is a low diversity, high dominance community with abundant articulated *Gracianella*. Boucot (1999) has proposed a BA 2–4 spread in a quiet water environment for the community.

In the B-H collection *Gracianella* is abundant in three of the five samples. About one third of the specimens are disarticulated valves consisting of nearly equal numbers of dorsal and ventral valves. A relatively short distance of post-mortem transportation may have caused the disarticulation. It is assumed here that a quiet-water BA 4 *Gracianella* Community, probably situated on the upper slope, provided the source for the abundant *Gracianella* in the collection.

*Liljevallia*-Stromatoporoid Community: This community is described here for the first time. *Liljevallia* is a small, cemented brachiopod. In-situ samples from the Upper Visby Marl of Gotland show that *Liljevallia* attaches to the undersides of stromatoporoids, as well as some coexisting corals. The latter two organisms form both patchy reef and level bottom communities in the Upper Visby. Kershaw (1980) described the environment of the Upper Visby stromatoporoid communities as “a relatively deep and quiet environment subject to periodic turbulence caused by activities such as a storm”. In Gotland, only the attached ventral valves of *Liljevallia* are found. The dorsal valves are presumably washed away by scouring currents. Since the cemented brachiopod depended on stromatoporoids as substrate, this special association can be recognized as a fossil community. In Gotland the community can be assigned to BA 3 in a moderately turbulent environment. The community group assignment is uncertain.

In the B-H fauna, *Liljevallia* is mostly disarticulated and its dorsal valves are eight times more abundant than ventral valves. This lopsided ratio of opposite valves is consistent in all five samples, which is unique in the collection. It is reasonable to conclude that the Baillie Hamilton *Liljevallia* had a habitat similar to that of the Gotland species. Because ventral valves are usually cemented firmly to stromatoporoids, only dorsal valves can be readily freed by currents and transported any distance. For a shallow-water origin, *Liljevallia* has a rather even distribution in all five samples, suggesting the vast areal extent of the community. The presence of an extensive stromatoporoid community on the coeval shelf has been substantiated by Sodro – Hobson (1979).

*Vosmiverstum-Conchidium* Community: Subrianid communities are common in the Uralian-Cordilleran Region. They are commonly characterized by low diversity, high dominance and crowding. Boucot (1975, 1999) assigned a BA 3 moderately turbulent environment for these communities. Five subrianid genera are present in the B-H fauna. The three larger genera, *Vosmiverstum*, *Conchidium*, and *Cymbidium* are present in only two samples, while the smaller genera *Severella* and *Spondylopyxis* occur in four and all five samples respectively. For this reason, the smaller subrianids are con-

sidered to be derived from a community separate from the larger one's (see below). Many valves of these subrianids show growth deformation induced by crowding. The original community is postulated to have been dominated by dense populations of *Vosmiverstum* and *Conchidium* with a subordinate number of *Cymbidium*. Among a total of 1683 specimens, only two are articulated. This correlates well with a BA 3 rough water environment typical for subrianid communities elsewhere.

***Severella-Spondylopyxis* Community:** Boucot (1999) describes the *Severella* Community as a high dominance community and he assigns it to a BA 3 rough water environment based on disarticulated valves of the nominal genus. In the B-H fauna, *Severella* and *Spondylopyxis* are disarticulated. The two genera have a similar distribution. Both are smaller and have thinner shells than the coexisting *Conchidium* or *Vosmiverstum*. They probably lived in an environment deeper than the *Vosmiverstum-Conchidium* Community. A BA 4 or lower BA 3 position on the upper slope is a reasonable assignment for the community. Larger valves of the both species show the kind of deformation that indicates crowding.

***Janius* Community:** Boucot (1999) has redefined the *Janius* Community based on collections from the Eke Marl on Gotland. It is a high diversity community consisting of abundant orthids, strophomenids, rhynchonellids, atrypids, and spiriferids. The community is assigned to a BA 3 position in a normal current environment.

In the B-H fauna, several species may have been derived from a shallow-water *Janius* Community. These are *Janius occidentalis*, *Amphistrophia* sp., *Leptaena* sp., *Howellella* sp., *Flabellitesia kessei*, and *Pseudomendacella boucoti*. They are mostly disarticulated, and have larger and thicker valves than most members of the fauna. The larger valves are noticeably fragmentary, indicating a shallow water origin. Along with these larger species, a group of small species may also be from the same community because of their similar distribution with *Janius* and their high disarticulation ratio. The small species include *Amsdenina amsdeni*, *Arcuella jinni*, *A. walmsleyi*, *A. sulcata boreaina*, *Hedeina* sp., *Hirnantia* cf. *sagittifera*, *Morinorhynchus miniparvicostellus*, *Ptychopleurelia lenzi*, *Stegerhynchus angaciensis*, *Plectatrypa unicosta*, *Fascizetina rohri*, *Plicoplasia* cf. *acutiplicata*, and *Thebesia* cf. *thebesensis*. The taxic makeup of these two groups of species is compatible with the composition of a typical *Janius* Community.

***Spirinella* Community:** Sheehan (1980) described the *Spirinella* Community as a community characterized by abundant *Spirinella* in a BA 3 quiet-water environment. The abundant, mostly disarticulated, *Spirinella* in the B-H collection may have been derived from a typical *Spirinella* Community. Post-mortem transportation may have caused the high rate of disarticulation.

***Dicoelosia-Epitomyonia* Community** (Tab. 1): The B-H collection contains a large number of excellently preserved small brachiopods. These

small brachiopods are mostly articulated regardless of their weak hinge mechanism. In addition, the abundance occurrence of each species is evenly distributed among all samples. This group of brachiopods is most likely derived from a very close source. *Dicoelosia* and *Epitomyonia* are the most abundant members of the group. The *Dicoelosia-Epitomyonia* Community is named here to include this diverse group of small-sized brachiopods. The evidence suggests that the community is the most seaward community of the B-H fauna. It is defined here as a BA 5 community in a quiet water environment.

The Cordilleran *Dicoelosia* species such as *Dicoelosia bailliehamiltonensis* and *D. parvifrons* are distinct from the *D. biloba* group. The former tend to have a pair of long lobes with a centrally crested costa on each lobe. They are found in a deeper and less turbulent environment than the *D. biloba* group. The *Dicoelosia-Epitomyonia* Community represents a more seaward position than a typical *Dicoelosia-Skenidioides* Community. It is a unique community that colonized the slopes of a vast Cordilleran graptolitic basin. Abundant *Skenidioides* specimens are also found in the collection. However, these specimens consist of mostly disarticulated valves. They are more likely to be derived from a community that is further landward than the *Dicoelosia-Epitomyonia* Community.

***Skenidioides* Community:** A group of small brachiopods typically with less than 10 % articulation ratio is assumed to have derived from a deep-water community more landward than the *Dicoelosia-Epitomyonia* Community. The *Skenidioides* Community is named here as the source community for these specimens. The shell morphology and the diversity of the community suggest a BA 3–4 position with normal current activity. The community is composed of *Cliftonia contoria*, *Clo-rinda* sp., *Cyrtia alatiformis*, *Dalejina parahanusii*, *Plicocyrtia jonesi*, *Salopina carinata*, *Skenidioides operosa*, *Spurispirifer hughsi*, *Wangyuia thorsteinssoni*.

The remaining species of the B-H fauna are not assigned to any communities at present. These species can be divided into two groups on the basis of their abun-

Table 1 Brachiopods of the *Dicoelosia-Epitomyonia* Community.

Species	Total	%
<i>Aegiria grayi</i>	618	3.6
" <i>Ancillotoechia</i> " <i>sheehani</i>	198	1.1
<i>Chonetoidea? cocksi</i>	374	2.2
<i>Dicoelosia bailliehamiltonensis</i>	6233	36.2
<i>Eospinatrypa bassetti</i>	2381	13.8
<i>Eospinatrypa sagana</i>	336	1.9
<i>Epitomyonia amplissima</i>	265	1.5
<i>Epitomyonia clausula</i>	2435	14.1
<i>Glassia? sp. 1</i>	69	0.4
<i>Lissatrypa cf. atheroidea</i>	1912	11.1
<i>Nucleospira cf. raritas</i>	377	2.2
<i>Paranisopleurella cooperi</i>	804	4.7
<i>Reticulatrypa blodgetti</i>	418	2.4
<i>Stegerhynchus estonicus cordillerus</i>	599	3.5
<i>Visbyella visbyensis</i>	192	1.1
<i>Zygatrypa stenoparva</i>	22	0.1

dance distribution. The first group contains those species that are present in only one or two samples, the second group contains species that are either conspicuously absent in one of the two largest samples or present in abundance in a small sample. The first group include “*Anciloteochia*” cf. *pentaforma*, *Antirhynchonella* sp., *Clorinda geniculata*, *Clorinda* ? sp., *Dicoelospirifer dicoelospirifer*, *Drabovia* ? sp., *Glassia* ? sp. 2, *Johnsonatrypa imbricata*, *Mesopholidostrophia lamellosa*, *M. salopiensis granti*, *Opikella* sp., *Parmorthina havliceki*, *Plectatrypa rongi*, *Salopina robitaillensis*, *S. gama*, *S.?* sp., indet. athyridid sp. These brachiopods can be vagrant members of any community. It is difficult to trace community origin for any of them. The second group include the following species: *Barrandina* sp., *Caryogyps chattertoni*, *Merista* sp., *Morinorhynchus crispus*, *Pseudoprotathyris ? modzalevskayae*, *Resserella canalis celtica*, *P. variabilis*, *Rhynchotreta americaniformis*, *Spirigerina copperi*, *Streptis glomerata*. Most of them have wide environmental tolerance and are known from BA 3 to BA 5 communities. There is inadequate information to assign them to one community or another.

As illustrated in Table 2, the B-H fauna contains a mixture of communities ranging from a rough-water, platform BA 3 position to a quiet-water, off platform BA 5 position. These communities tell a story of a warm Early Silurian sea. Reef communities dominated the shelf platform while diversified small brachiopods colonized the muddy basin in abundance. Debris flows, probably induced by storms or earthquakes, swept through the assorted communities and brought them all together in the final burial site.

### Paleobiogeography

The B-H fauna belongs to the warm water North Silurian Realm. The North Silurian Realm has been subdivided into two regions containing at least five provinces (Boucot 1985, 1990; Boucot – Blodgett, in press; Wang et al. 1984; Rong Jia-yu et al. 1995). A comparative study

of the fauna with the coeval faunas of the North Silurian Realm provides a direct test of the current subdivision scheme. These subdivisions are as the follows:

- North Atlantic Region
  - North American Province
  - European Province
- Uralian-Cordilleran Region
  - Sino-Australian Province
  - Mongolo-Okhotsk Province
  - “Remainder of the Region”

Few brachiopod collections are as accurately dated as the B-H fauna. For practical purposes all fauna of Wenlockian age are treated as coeval. The following 13 coeval faunas are compiled from published sources. In areas lacking sufficient age data the extracted fauna may include Llandoveryan or Ludlovian genera. Below is a brief description of each selected fauna. Only the main references are given for each fauna.

The British fauna includes all brachiopods from Wenlockian strata of Great Britain and Ireland (Cocks 1978; Bassett 1970, 1972, 1974, 1977; Ratcliffe 1999).

The Bohemian fauna includes all brachiopods from Wenlockian strata of Bohemia (Havlíček 1967, 1977, 1980; Havlíček – Štorch 1999).

The Baltic fauna includes all brachiopods from Wenlockian strata of the eastern Baltics of the former USSR, Gotland, Norway, and Podolia (Baarli et al. 1999; Bassett – Cocks 1974; Musteikis – Paskevicius 1999; Gritsenko et al., 1999).

The Acadian fauna includes all brachiopods from Late Llandoveryan (C5) to Wenlockian strata (possibly including some Ludlovian occurrences) of the coastal area extending from Nova Scotia and New Brunswick, to south-eastern Maine (Boucot et al. 1966; Harper 1973).

The North American fauna includes all brachiopods from Wenlockian strata of the Mid-Continent (Amsden 1968, 1978; Boucot 1999; Brett 1999; Witzke – Johnson 1999).

The Eastern Great Basin fauna includes all brachiopods from Wenlockian strata of the Eastern Great Basin,

Table 2 Community framework of the Baillie Hamilton fauna.

Benthic Assemblage	Turbulent Condition	Normal Current Activity	Quiet Condition
1			
2			
3	<i>Trimerella</i> Community	<i>Janius</i> Community	<i>Spirinella</i> Community
	<i>Liljevallia</i> -Stromatoporoid Community <i>Rhipidium</i> Community <i>Vosmivestum-Conchidium</i> Community	<i>Severella-Spondylopyxis</i> Community	
4		<i>Skenidioides</i> Community	<i>Gracianella</i> Community
5			<i>Dicoelosia-Epitomyonia</i> Community

southern California and New Mexico (Boucot et al. 1988; Sheehan 1976, 1982).

The Uralian fauna includes all brachiopods from Wenlockian strata of the east-central Urals (Sapelnikov 1972; Sapelnikov et al. 1999).

The Iranian fauna includes brachiopods from Wenlockian strata of northern Iran (Cocks 1979).

The Tuvan-Mongolian fauna includes all brachiopods from Wenlockian strata of the Altai and Mongolia (Rozman 1999; Vladimirskaia – Kulkov 1999).

The Chinese fauna includes brachiopods from the Upper Llandoveryan to Ludlovian strata primarily of South China (Wang et al. 1984).

The Australian fauna includes brachiopods from Wenlockian strata of Australia (Strusz 1982, 1985; Strusz – Garratt 1999).

The Mackenzie fauna includes brachiopods from Wenlockian strata of the Mackenzie Mountains (Lenz 1977, 1999).

The Nevada fauna includes brachiopods from Wenlockian part of the Roberts Mountains Formation (Johnson et al. 1976).

The generic assignment of some species is updated here in the attempt to obtain a more or less standardized database. For example, species assigned to *Vagranella* in both the Mackenzie and Nevada faunas are assigned to *Vosmiverstum* because they both have a short medium septum. The type species of *Vagranella* lacks a medium septum. The *Leangella* of those two faunas is assignable to Amsden's subgenus *Opikella* based on its parvicostellate ornament. *?Fardenia* of the Mackenzie fauna has a well developed pseudodeltidium and it should be assigned to *Morinorhynchus*. The *Anastrophia* of the Altai is clearly assignable to the subgenus *Grayina*.

The Affinity Index (AI) of Savage et al. (1979) is used here to measure the taxonomic similarities of the B-H fauna to coeval faunas. The index is derived from the formula:

$$AI = \{(C - C^{cosom}) / (N1 - N1^{cosom})\} \times 100$$

Where C is the number of genera common to the two samples being compared,  $C^{cosom}$ , the number of cosmopolitan genera common to the two samples, N1, the number of genera in the smaller sample,  $N1^{cosom}$  the number of cosmopolitan genera in the smaller sample. Table 3 lists the resulting AI values of the B-H fauna calculated against each of the 13 coeval faunas. The AI calculation is based on data excluding any questionably identified genera in any fauna, although including genera with questionable identification does not change any result significantly. The appendix provides the data for the AI calculation.

As expected, the B-H fauna has its closest relationship with the Mackenzie and Nevada faunas. The three faunas were derived from similar host rocks and are characterized by BA 4–5 communities. Variable amounts of shallow-water community elements are present in each fauna as a result of downslope mixing. Each of the faunas actually represents a segment of a continuous faunal belt that rimmed the western margin of the North Amer-

ican continent. The host rock units, i.e. the Cape Phillips Formation in the Arctic Canada, the Whittaker-Road River transition in the Mackenzie Mountain, and the Roberts Mountains in Nevada, signify a unique environment of the Cordilleran sea during the Silurian. The environment is characterized by a carbonate platform with a steep offshore slope as indicated by frequent debris flows. The slope then leads into a vast graptolitic basin. The brachiopod communities that colonized the steep slopes had few endemic genera. *Spondylopyxis* is so far only found in Nevada and Baillie Hamilton Island. *Dicoelospirifer* and *Johnsonatrypa* may also be endemic. However, both genera are only represented by a handful of specimens in the large B-H collection. Therefore, their absence elsewhere may be an artifact of sampling. Finally, the Cordilleran *Dicoelosia* species such as *D. parvifrons* and *D. bailliehamiltonensis* can be distinguished from the extra-Cordilleran *D. biloba* group. Further study may show that the two species groups have distinctive biogeographical distribution.

The comparison with the Uralian faunas is complicated by environmental factors. BA 4–5 communities are absent from the Urals and China, resulting in depressed AI values. The fact the BA 3 communities are underrepresented in the Cordilleran faunas further compounds the problem. The Iranian fauna is represented by a small sample collected from a single locality. The fauna can be assigned to the BA 4–5 *Dicoelosia-Skenidioides* Community with *Xerxespirifer* as a noticeably endemic genus. Because of its small sample size the resulting AI value is questionable.

The Tuvan-Mongolian fauna is characterized by the highly endemic *Tuvaella* Community. It shares a zero AI value with the B-H fauna. The fauna has long been recognized as a separate biogeographical unit. Rong et al. (1995) summarized the various names given to the biogeographical unit. They proposed to recognize the area with the unique *Tuvaella* fauna as the Mongolo-Okhotsk Province.

The Australian fauna includes both shallow and deep-water communities. However, pentamerids are unusually sparse in the faunal list. Limestone with abundant pentamerids are present in New South Wales, but have not been studied (Boucot, personal communication). The incompleteness of the fauna probably has a negative effect on the AI value.

The Chinese fauna lumps together faunas of Llandoveryan to Ludlovian age. Until the Wenlockian fauna is isolated from the rest, the current AI is unreliable. On the basis of the Ludlovian-Pridolian *Retziella* Fauna, Rong et al. (1995) defined the Sino-Australian Province as a new subdivision of the Uralian-Cordilleran Region. They suggested that elements of the *Retziella* fauna may occur in the Wenlock in the same area. The current study certainly does not contradict the Sino-Australian subdivision.

Despite the environmental disparity, the Uralian faunas in general show higher AI values with the B-H fauna

than the North American and the European faunas do. The free faunal exchange between the Cordilleran and Uralian is illustrated by their abundant subrianiids, eospiriferids with a striate cardinal process, as well as such characteristic genera as *Gracianella* and *Epitomyonia*.

The high taxonomic similarity shared by the B-H fauna and the Eastern Great Basin fauna is assumed to be a result of boundary mixing. The latter is a platform fauna situated on the boundary that divided the North American fauna from the Cordilleran fauna. In this boundary area, brachiopods typical of the North America Region, such as *Apopentamerus*, *Microcardinalia*, and *Rhipidium*, coexisted with the Uralian-Cordilleran genera *Vosmivestum* and *Cymbidium*. A mixed boundary fauna is characteristic of a gradational faunal barrier most likely produced by gradual changes in environment such as climatic gradients.

The North American fauna from the Mid-Continent has a noticeably low AI value with the B-H fauna. Similarly, the European faunas show distant relationships with the B-H fauna. Both the North American and European faunas are well studied and include a complete spectrum of communities ranging from BA 2 to 5. The low AI values are not affected by any environmental factors. It reflects a true biogeographical distinction.

To summarize, the B-H fauna is a part of the Cordilleran megafauna characterized by its deep-water slope dwelling communities. The faunal exchange between the Cordillera and the Urals was not hindered, in spite of largely different habitats of the two regions. Reproductive communication is indicated by shared brachiopods of the two regions. The Mongolian fauna was very distinct from the Cordilleran fauna. The zero AI value supports the existence of the Mongolo-Okhotsk Province. The presence of the Sino-Australian Province is not contradicted by this study. Faunal exchange between the Uralian-Cordilleran and the North American or the European faunas was restricted, as indicated by the consis-

tently low AI values. The presence of a mixed boundary fauna in the Eastern Great Basin suggests an environmental gradient, such as a climatic gradient, that may have served as a faunal barrier. The analysis supports Boucot's Silurian biogeographic divisions. Among various models of Silurian global reconstructions, the Pangaea proposed by Boucot – Gray (1979) provides the best fit for the results of this study. In the Pangaea model, faunas of the Uralian-Cordilleran Region are connected by equatorial currents. A faunal barrier associated with a climatic gradient is implied, where the North Atlantic Region is sandwiched between the low latitude Uralian-Cordilleran Region and the high latitude Malvinokaffric Realm.

## Conclusion

The B-H fauna contains a mixture of shelf and off-shelf communities. These communities occupied a number of environments ranging from the carbonate shelf, into a muddy slope, and finally grading into a graptolitic basin. The *Dicoelosia-Epitomyonia* Community is a characteristic deep-water community of the Wenlockian Cordilleran sea. The Cordilleran fauna is considered to belong to the Uralian-Cordilleran Region, although the environmental disparity between Uralian and Cordilleran seas make it difficult to compare the faunas from the two areas. The existence of a mixed fauna between the Cordilleran fauna and the North American fauna suggests a gradual environmental barrier separated the two biogeographical units.

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Table 3 The Affinity Index of the Baillie Hamilton fauna with 13 coeval faunas.

Coeval Fauna	C-C <sup>esom</sup>	N1-N1 <sup>esom</sup>	AI
Baillie Hamilton	32	32	100
Mackenzie	8	18	44
Nevada	7	15	47
Eastern Great Basin	9	23	39
Iran	2	10	20
Urals	4	20	20
China	5	32	16
Australia	2	17	12
Tuvan-Mongolia	0	25	0
North America	4	32	13
Great Britain	2	32	6
Bohemia	3	32	9
Baltic	3	32	9
Acadia	0	23	0

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GENERA	1. Baillie Hamilton	2. Mackenzie	3. Nevada	4. Eastern Great Basin	5. Urals	6. China	7. Australia	8. Tuvan-Mongolia	9. North America	10. Great Britain	11. Bohemia	12. Baltic	13. Acadia	14. Iran
<i>"Ancillotoechia"</i>	+	+	+											
<i>"Camarotoechia"</i>														
<i>"Costristricklandia"</i>														
<i>"Cymbidium"</i>			+											
<i>"Cymostrophia"</i>														
<i>"Dolerorthis"</i>														
<i>"Leptostrophia"</i>				+										
<i>"Schuchertella"</i>			+											
<i>Acromeristina</i>								+						
<i>Acutilineolus</i>									+					
<i>Aegiria</i>	+			+	+	+				+	+			
<i>Aegiromena</i>						+					+			
<i>Agarhyncha</i>														
<i>Alaskospira</i>						+								
<i>Ambonorthella</i>										+				
<i>Amphistrophia</i>		+							+	+	+	+	+	
<i>Amphistrophiella</i>								+						
<i>Amsdenina</i>	+	+		+					+					
<i>Anabaria</i>					+									
<i>Anastrophia</i>			+					+	+	+	+	+	+	
<i>Ancillotoechia</i>		+		+				+	+	+	+			
<i>Antirhynchonella</i>	+			+					+	+	+			
<i>Apopentamerus</i>								+						
<i>Araspirifer</i>										+				
<i>Aratoechia</i>										+				
<i>Arctomeristina</i>								+						
<i>Arcualla</i>	+	+	+	+										
<i>Ascanigypa</i>										+				
<i>Atrypa</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Atrypina</i>			+	+	+	+	+	+	+	+	+	+	+	
<i>Atrypinopsis</i>		+		+										
<i>Atrypoidea</i>		+	+	+										
<i>Atrypopsis</i>				+	+									
<i>Aulacatrypa</i>										+				
<i>Australina</i>						+	+							
<i>Barrandina</i>	+			+										
<i>Bleshidium</i>										+				
<i>Boucotides</i>									+	+				
<i>Boucotinskia</i>									+	+				
<i>Brachymimulus</i>									+	+				
<i>Brachyprion</i>				+				+	+	+	+	+	+	
<i>Bracteoleptaena</i>										+				
<i>Brevilamnulella</i>						+								
<i>Brooksina</i>				+										
<i>Bucegia</i>										+				
<i>Callipentamerus</i>								+						
<i>Camerella</i>								+						
<i>Capelliniella</i>				+										
<i>Caryogyps</i>	+													
<i>Cinerorthis</i>										+				
<i>Cingulodermis</i>										+				
<i>Cliftonia</i>	+													
<i>Clorinda</i>	+			+				+			+		+	
<i>Coelospira</i>			+	+	+									
<i>Conchidium</i>	+	+	+	+							+			
<i>Coolinia</i>			+					+	+	+	+	+	+	
<i>Cordatomyonia</i>									+					
<i>Costistricklandia</i>										+				
<i>Craniops</i>								+	+	+	+			
<i>Cryptatrypa</i>				+						+				

GENERA	1. Baillie Hamilton	2. Mackenzie	3. Nevada	4. Eastern Great Basin	5. Urals	6. China	7. Australia	8. Tuvan-Mongolia	9. North America	10. Great Britain	11. Bohemia	12. Baltic	13. Acadia	14. Iran
<i>Cymbidium</i>	+	+	+											
<i>Cyphomena</i>														
<i>Cyrtia</i>	+	+	+	+	+		+	+	+	+	+	+	+	
<i>Dalejina</i>	+	+		+				+	+	+	+	+	+	
<i>Decoropugnax</i>		+												
<i>Delthyris</i>						+					+			
<i>Desquamatia</i>											+			
<i>Diabolirhynchia</i>								+						
<i>Dicamaropsis</i>									+					
<i>Dicoelosia</i>	+	+	+	+		+		+	+	+	+	+	+	+
<i>Dicoelospirifer</i>	+													
<i>Dictyonella</i>								+	+	+				
<i>Dinobolus</i>								+						
<i>Dnestrina</i>									+					
<i>Dolerorthis</i>			+			+		+	+	+	+	+	+	
<i>Dubaria</i>		+												
<i>Dubioleptina</i>										+				
<i>Elegesta</i>								+						
<i>Endospirifer</i>							+							
<i>Eocoelia</i>									+	+	+	+		
<i>Eokarpinskia</i>						+								
<i>Eomegastrophia</i>				+										
<i>Eopholidostrophia</i>								+						
<i>Eoplectodonta</i>		+	+	+				+	+	+	+	+	+	
<i>Eoreticularia</i>						+	+							
<i>Eoschizophoria</i>								+						
<i>Eospinatrypa</i>		+	+						+	+				
<i>Eospirifer</i>	+	+		+	+			+	+	+	+	+	+	
<i>Eospirigerina</i>								+						
<i>Epelidoaegiria</i>														
<i>Epitomyonia</i>	+	+	+											+
<i>Eridorthis</i>									+					
<i>Estonirhynchia</i>										+				
<i>Fardenia</i>														+
<i>Fascizetina</i>	+													
<i>Ferganella</i>				+	+	+		+			+	+		
<i>Flabellitesia</i>	+			+				+						
<i>Gelidorthina</i>											+			
<i>Giraldibella</i>											+			
<i>Glassia</i>		+								+	+			
<i>Glassina</i>										+	+			
<i>Glyptorthis</i>										+	+	+	+	
<i>Gotatrypa</i>						+					+			
<i>Gracianella</i>	+	+	+			+								
<i>Grayina</i>	+										+			
<i>Gunnarella</i>											+			
<i>Gypidula</i>			+	+	+	+		+	+	+	+	+	+	
<i>Harpidium</i>						+	+							
<i>Hedeina</i>	+							+		+				
<i>Hesperorthis</i>										+	+	+	+	
<i>Heterorthisella</i>														+
<i>Hircinisca</i>						+		+		+				
<i>Hirnantia</i>	+													
<i>Holcospirifer</i>										+				
<i>Hollardina</i>											+			
<i>Homeospira</i>			+						+	+	+			
<i>Homoospirella</i>										+				
<i>Hostimena</i>											+			
<i>Howellella</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Hyattidina</i>										+	+			



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GENERA	1. Baillie Hamilton	2. Mackenzie	3. Nevada	4. Eastern Great Basin	5. Urals	6. China	7. Australia	8. Tuvan-Mongolia	9. North America	10. Great Britain	11. Bohemia	12. Baltic	13. Acadia	14. Iran
<i>Idiorthis</i>														+
<i>Indaclor</i>														
<i>Isorthis</i>	+													
<i>Isovella</i>														
<i>Janius</i>	+	+	+	+	+									
<i>Johnsoniatrypa</i>	+													
<i>Jolvia</i>														
<i>Jonesea</i>	+	+												
<i>Katastrophomena</i>														
<i>Kirkidium</i>														
<i>Kozlowskiellina</i>		+												
<i>Leangella</i>														
<i>Lenatoechia</i>														
<i>Lepidoleptaena</i>														
<i>Leptaena</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Leptaenisca</i>														
<i>Leptaenoidea</i>														
<i>Leptagonia</i>														
<i>Leptostrophia</i>														
<i>Leptostrophiella</i>														
<i>Leveneia</i>														
<i>Liljevallia</i>	+													
<i>Limbatrypa</i>														
<i>Lingula</i>														
<i>Linguopugnoides</i>														
<i>Linoporella</i>														
<i>Linostrophomena</i>														
<i>Liocoelia</i>														
<i>Lioleptaena</i>														
<i>Lissatrypa</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Lissatrypella</i>														
<i>Lissidium</i>	+													
<i>Lissocoelina</i>	+													
<i>Machaeraria</i>														
<i>Macroleura</i>														
<i>Maoristrophia</i>														
<i>Marklandella</i>														
<i>Mclearnites</i>														
<i>Mclearnitesella</i>														
<i>Megaspinochonetes</i>														
<i>Megastrophia</i>														
<i>Meifodia</i>														
<i>Mendacella</i>														
<i>Merciella</i>														
<i>Merista</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Meristina</i>														
<i>Mesodowiella</i>														
<i>Mesodouvillina</i>														
<i>Mesoleptostrophia</i>														
<i>Mesolissostrophia</i>														
<i>Mesopholidostrophia</i>	+													
<i>Metathyrisina</i>														
<i>Mezounia</i>														
<i>Microcardinalia</i>														
<i>Microsphaeridiorhynchus</i>														
<i>Mitchellella</i>														
<i>Molongia</i>														
<i>Mongolirhynchia</i>														
<i>Mongolostrophia</i>														
<i>Mongolotoechia</i>														
<i>Morinorhynchus</i>	+	+												
<i>Myriospirifer</i>														
<i>Nalivkinia</i>														
<i>Nanospira</i>														
<i>Nikiforovaena</i>														
<i>Niorhynchus</i>														
<i>Nucleospira</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Oglupes</i>														
<i>Onniella</i>														
<i>Onychotreta</i>														
<i>Opikella</i>	+	+	+											
<i>Orthostrophella</i>														
<i>Oxoplecia</i>														
<i>Paranisopleurella</i>	+													
<i>Pararhipidium</i>														
<i>Parastrophina</i>														
<i>Parastrophinella</i>														
<i>Parmorthina</i>	+													
<i>Pembrostrophia</i>														
<i>Pentameroides</i>														
<i>Pentamerus</i>														
<i>Pentlandella</i>														
<i>Pentlandina</i>	+													
<i>Pholidostrophia</i>														
<i>Pinguella</i>														
<i>Pinguispirifer</i>														
<i>Placocliftonia</i>														
<i>Placotriplezia</i>														
<i>Plagiorhynchia</i>	+	+												
<i>Platystrophia</i>														
<i>Plectatrypa</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Plectodonta</i>														
<i>Plectotreta</i>														
<i>Pleurocornu</i>														
<i>Plicidium</i>														
<i>Plicocyrtia</i>	+	+												
<i>Plicoplasia</i>	+													
<i>Plicostricklandia</i>														
<i>Plicostropheodonta</i>														
<i>Procarinatina</i>														
<i>Proreticularia</i>														
<i>Protathyris</i>														
<i>Proteorthis</i>														
<i>Protochonetes</i>														
<i>Protocortezorthis</i>														
<i>Protomegastrophia</i>														
<i>Protozeuga</i>														
<i>Pseudocamarotoechia</i>														
<i>Pseudomeristina</i>														
<i>Pseudoprotathyris</i>														
<i>Pseudomendacella</i>	+													
<i>Ptychopleurella</i>	+	+	+											
<i>Qianomena</i>														
<i>Quasistrophonella</i>														
<i>Ravozetina</i>														
<i>Resserella</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Reticulariopsis</i>														
<i>Reticulatrype</i>	+	+												
<i>Retziella</i>														
<i>Reveroides</i>	+													

N. Zhang: Paleocology and paleobiogeography of Wenlockian (Silurian) brachiopods of the Cape Phillips Formation from Baillie Hamilton Island, Arctic Canada

GENERA	1. Baillie Hamilton	2. Mackenzie	3. Nevada	4. Eastern Great Basin	5. Urals	6. China	7. Australia	8. Tuvan-Mongolia	9. North America	10. Great Britain	11. Bohemia	12. Baltic	13. Acadia	14. Iran
<i>Rhipidium</i>				+	+				+	+				
<i>Rhynchospirina</i>														+
<i>Rhynchotreta</i>	+	+	+	+	+				+	+	+			
<i>Rostricellula</i>							+							+
<i>Rufispirifer</i>										+				
<i>Salopina</i>	+	+	+	+					+	+	+	+	+	+
<i>Salopinella</i>														
<i>Savageina</i>														+
<i>Scammomena</i>										+				
<i>Schizonema</i>										+	+			
<i>Schizotreta</i>								+						
<i>Septatrypa</i>										+	+			
<i>Severella</i>	+													
<i>Shagamella</i>														+
<i>Sibirispira</i>						+								
<i>Sieberella</i>														+
<i>Skenidioides</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Sphaerirhynchia</i>								+	+	+	+	+		
<i>Spinatrypa</i>													+	
<i>Spinatrypina</i>													+	
<i>Spinella</i>									+					
<i>Spinochonetes</i>														
<i>Spirigerina</i>	+	+	+	+	+	+	+	+	+	+				
<i>Spirinella</i>	+	+	+	+	+	+								
<i>Spondylobolus</i>										+				
<i>Spondylopyxis</i>	+													
<i>Spondylostrophia</i>		+												
<i>Spurispirifer</i>	+									+				
<i>Stegerhynchops</i>											+			
<i>Stegerhynchus</i>	+	+	+	+					+	+	+	+	+	+
<i>Stegorhynchella</i>								+						
<i>Stenorhynchia</i>											+			
<i>Streptis</i>	+	+								+	+	+		
<i>Stricklandia</i>											+			
<i>Strispirifer</i>							+	+	+	+	+	+	+	

GENERA	1. Baillie Hamilton	2. Mackenzie	3. Nevada	4. Eastern Great Basin	5. Urals	6. China	7. Australia	8. Tuvan-Mongolia	9. North America	10. Great Britain	11. Bohemia	12. Baltic	13. Acadia	14. Iran
<i>Stropheodonta</i>														
<i>Strophochonetes</i>														
<i>Strophonella</i>							+							+
<i>Strophonellites</i>								+	+	+	+			
<i>Strophoprion</i>								+	+	+	+	+		
<i>Sulcatina</i>								+						
<i>Supertrilobus</i>								+						
<i>Tannuspirifer</i>											+			
<i>Tastaria</i>														
<i>Tectatrypa</i>														
<i>Tenellodermis</i>														
<i>Terazkia</i>													+	
<i>Thebesia</i>	+												+	
<i>Trematospira</i>														
<i>Trigonirhynchia</i>														
<i>Trimerella</i>	+	+												
<i>Triplesia</i>														
<i>Tufoleptina</i>														
<i>Tuvaella</i>														
<i>Tuvaerhynchus</i>														
<i>Tyersella</i>														
<i>Vadum</i>														
<i>Valdaria</i>														
<i>Virgiana</i>														
<i>Virginiaata</i>														
<i>Visbyella</i>	+													
<i>Vosmiverstum</i>	+	+	+	+	+									
<i>Wangyuia</i>	+													
<i>Whitfieldella</i>														
<i>Xerxespirifer</i>														
<i>Xinanospirifer</i>														
<i>Ygera</i>														
<i>Ygerodiscus</i>														
<i>Zygatrypa</i>	+													
<i>Zygospiraella</i>														

### Paleoekologie a paleobiogeografie wenlockých (silur) brachiopodů souvrství Cape Phillips z ostrova Baillie Hamilton v arktické Kanadě

Fauna z ostrova Baillie Hamilton obsahuje směsici mělkovodních a hlubokovodních brachiopodů v uloženinách turbiditního charakteru. Využitím kritérií, jakými jsou tafonomie, četnost výskytu a model složení společenstev byly ve sběrech rozeznány prvky celkem deseti bentických společenstev. Tato společenstva reprezentují severní zakončení faunistického pruhu kordilérské oblasti wenlockého stáří. Fauna z ostrova Baillie Hamilton náleží do uralo-kordilérské provincie. Vysoký index podobnosti se stejně starou faunou východní části Velké pánve (Great Basin) naznačuje, že mezi uralo-kordilérskou provincií a severoamerickou provincií existoval postupný gradient v charakteru marinního prostředí.