Canadian Journal of Earth Sciences
Revue canadienne des sciences de la Terre

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Journal:	<i>Canadian Journal of Earth Sciences</i>
Manuscript ID	cjes-2015-0183.R1
Manuscript Type:	Article
Date Submitted by the Author:	08-Dec-2015
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Keyword:	Paleoecology, <i>Pentameroides</i> , Evolution, Laurentia, early Silurian

**Paleolatitudinal morpho-gradient of the early Silurian brachiopod *Pentameroides* in
Laurentia**

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Abstract: *Pentameroides* is a large-shelled pentameride brachiopod, which was widespread throughout Laurentia in the early Silurian (Telychian). Evolving from *Pentamerus* in the early Telychian, it dispersed from its subtropical/high tropical origin to sub-equatorial intracratonic seas by the late Llandovery. In this study large collections of reef-dwelling *Pentameroides septentrionalis* from the Attawapiskat Formation, Akimiski Island, Nunavut and level-bottom-inhabiting *Pentameroides subrectus* from the Fossil Hill Formation, Manitoulin Island, Ontario, and the Jupiter Formation, Anticosti Island, Quebec, were biometrically analyzed for seven external morphological features. Bivariate and ordination analysis (PCA) revealed that *P. septentrionalis* has a more globose, more biconvex shell with a larger ventral umbo than *P. subrectus*. These morphological differences, coupled with their excellent preservation in shallow-water reefal environments, suggest that *P. septentrionalis* was adapted to a relatively low-turbulence, hurricane-free, nutrient stressed environment near the equator ($<10^{\circ}$ S) while *P. subrectus* lived in storm-dominated higher tropical latitudes ($\sim 15\text{--}25^{\circ}$ S). This interpretation is corroborated by the morphology of level-bottom-dwelling *Harpidium* and *Sulcipentamerus* from the paleoequatorial lower Silurian of North Greenland, which exhibit morphological features similar to those of *P. septentrionalis* even though it did not inhabit a reefal environment. PCA analysis reveals that *P. septentrionalis* resembles *P. subrectus* in early ontogeny, suggesting that *P. septentrionalis* evolved from *P. subrectus* as it moved northwards from high tropical to near equatorial settings.

Keywords: Paleoecology, *Pentameroides*, Evolution, Laurentia, early Silurian

Draft

Introduction

Pentameroides Schuchert and Cooper, 1931 is a large-shelled pentameride brachiopod that is commonly found in the lower Silurian (Telychian) carbonate facies of Laurentia and Baltica. In modern North America, well-preserved shells of *Pentameroides* are abundant in the Attawapiskat Formation in the Hudson Bay lowlands of northern Ontario, Manitoba, and Nunavut (Jin et al. 1993), the Hopkinton Dolomite of Iowa (Johnson 1979), the Merriton Formation of the southern Ontario and New York (Kilgour 1963), the Fossil Hill Formation of Manitoulin Island, Ontario (Chiang 1971; Copper 1978), the upper Jupiter Formation of Anticosti Island, Quebec (Jin and Copper 2000), and the Samuelsen Høj and Hauge Bjerger formations of North Greenland (Rasmussen 2009; Fig. 1). The occurrence of *Pentameroides* in deep-water basinal facies is known from the upper Whittaker Formation (uppermost Telychian–basal Sheinwoodian) of Mackenzie Mountains, although this may have been in debris flow deposits derived from shallower carbonate shelf settings (Jin and Chatterton 1997).

Pentameroides evolved from *Pentamerus* Sowerby, 1831 during the early–middle Telychian. The mode of this speciation event has been debated, with some considering it a case of phyletic gradualism (Johnson 1979; Johnson and Colville 1982), whereas others suggest a pattern of punctuated equilibrium (Glasser 2002). In any case, *Pentameroides* existed alongside *Pentamerus* during the middle and late Telychian, showing that the origin of *Pentameroides* was indeed a case of cladogenesis (Glasser 2002). From the southern margin of Laurentia *Pentameroides* spread northwards to occupy subequatorial intracratonic basins by the latest Llandovery, with the genus comprising of at least three species: *Pentameroides subrectus* Hall and Clarke, 1893, *Pentameroides costellata* Chiang, 1971, and *Pentameroides septentrionalis* Whiteaves, 1904.

This study is based on two species of *Pentameroides*, *Pentameroides subrectus* found throughout the higher paleolatitudinal American mid-continent (Johnson 1979), Michigan (Chiang 1971), and Anticosti basins (Jin and Copper 2000), and *Pentameroides septentrionalis* (see Jin and Copper 1986), in the sub-equatorial Hudson Bay and Moose River basins (Jin et al. 1993). In addition to living at different latitudes, the two species inhabited two different shallow marine environments. *P. subrectus* is found in storm-dominated, level-bottom environment whereas *P. septentrionalis* inhabited hurricane-free coral-stromatoporoid reefal settings (Jin et al. 1993). *P. costellata* is not included because it is a rare species and very few well-preserved shells are available for biometric study. In relation to Zeigler's (1965) classic level-bottom brachiopod community zones (see also Ziegler et al. 1968; Boucot 1975), *Pentameroides* is thought to be similar to *Pentamerus* (Chiang 1971; Johnson 1979); inhabiting a moderate water depth (BA 3) equivalent to a mid-shelf environment between the *Eocoelia* and *Stricklandia* community zones. This zoned community structure, however, cannot be applied directly to reefal settings due to high substrate heterogeneity and more complex paleoecological and paleocommunity structures (Jin 2003).

Gradients in paleolatitudes and depositional environments appear to manifest in differing morphological and taphonomic characters between localities and species of *Pentameroides*. *P. septentrionalis* exhibits excellent preservation, with large, complete, and very thin-walled hollow shells (their anterior parts being as thin as an egg shell) found commonly in apparently shallow-water, coral-stromatoporoid reefs. This is in contrast to the micrite-infilled and broken shells of *P. subrectus* from higher latitude environments. In this study, specimens of *P. septentrionalis* from Akimiski Island, Nunavut, and *P. subrectus* from Manitoulin Island, Ontario, and Anticosti Island, Quebec (Fig. 2) were biometrically measured and statistically analyzed in order to

identify any significant morphological differences between the species and to determine what environmental factors, if any, affected the evolution of the genus.

Geological settings

Attawapiskat Formation, Akimiski Island, Hudson Bay Basin

The middle–upper Telychian Attawapiskat Formation is predominantly a succession of reefal carbonates in the Hudson Bay and Moose River basins (Sanford 1987; Suchy and Stearn 1993). The reefs are primarily built by corals and stromatoporoids and are associated with an unusually rich and diverse benthic shelly fauna dominated by brachiopods, but also including common trilobites, bivalves, gastropods, cephalopods, and ostracods (Jin et al. 1993). The reefs show 8–10 m of vertical relief in known surface exposures (Suchy 1992), but the entire formation encircles the Hudson Bay Basin and is up to 200 m thick in some locations (Sanford 1987; Suchy and Stearn 1993). During the Llandovery, the northern margin of the Hudson Bay Basin was situated over the equator (Torsvik and Cocks 2013), and the Attawapiskat Formation in the southern part of the Hudson Bay Basin and the Moose River Basin was accumulated in a sub-equatorial paleogeographic setting. This formation is found in outcrop on Akimiski Island, James Bay, Nunavut as well as along the Attawapiskat, Ekwan, and Severn rivers in northern Ontario. Stratigraphically, the Attawapiskat Formation is interfingered and underlain by the commonly restricted shallow-water carbonates of the Ekwan River Formation (Lavoie et al. 2014), and overlain by the evaporate-dominated Kenogami River Formation (Sanford 1987; Lavoie et al. 2014). The Attawapiskat and Ekwan River formations possess similar diagenetic qualities including the precipitation of nonferroan micrite and peloids (see Eggie et al. 2014). The overlying evaporites suggest that the Attawapiskat reefs mark the end of an early Silurian open

marine Hudson Bay Platform and correlate with the late Telychian global regression (Haq and Schutter 2008).

The fringing and barrier coral-stromatoporoid reef complexes of the Attawapiskat Formation represent the complete recovery of the reef ecosystem after the end Ordovician mass extinction. These reefs also mark the initial stage of shelly faunal diversification associated with metazoan reefs (Chow and Stearn 1988), in addition to the moderately diverse shelly fauna of the upper Aeronian East Point reefs (Menier Formation) of Anticosti Island (Copper and Jin 2015). The Attawapiskat brachiopod faunas show excellent preservation, high alpha- and beta-diversity in the reef and inter-reef settings, and can be divided into eight associations (Jin 2002): the *Lissatrypa* association, the *Septatrypa* association, the *Septatrypa-Pentameroides* association, the *Gypidula* association, the *Gotatrypa* association, the *Trimerella* association, the *Eocoelia* association, and the *Pentameroides* association. Among these recognized brachiopod-dominated associations, several are characterized by a dominant or common component of the large-shelled *Pentameroides septentrionalis*. Trilobites are the only other group in the Attawapiskat Formation to have received focussed taxonomic (Norford 1981) and taphonomic (Westrop and Rudkin 1999) attention. Four distinctive associations have been recorded, but three of these primarily reflect post-mortem sorting processes of individual sclerites rather than original community composition. Each of the three taphonomic associations is known to occur with or adjacent to abundant large-shelled *P. septentrionalis*. The fourth trilobite association, comprising numerous small intact exoskeletons of several different taxa, probably represents sheltered in situ preservation of reef cavity- or crevasse-dwelling (coelobiontic) juveniles and adults.

Fossil Hill Formation, Manitoulin Island, Ontario

The Fossil Hill Formation of Manitoulin Island, partly correlative to the Merriton Formation in the Niagara Falls region (Brunton et al. 2009), is early–middle Telychian in age, approximately 30–40 m thick (Copper 1978), and consists of thin to medium bedded, grey, richly fossiliferous dolostones, with common chertified intervals (Chiang 1971, Copper 1978). It overlies the thin, dolomitized and ripple-marked Mindemoya Formation and is disconformably overlain by the greyish-green, argillaceous dolomicrite to wackestone Rockway Formation from Manitoulin Island to Niagara Falls (Brunton et al. 2009).

On Manitoulin Island the formation is separated into three unnamed units. The lower unit contains condensed beds with abundant *Pentamerus*. The middle unit consists of less fossiliferous lime mudstone–wackestone (Brunton et al. 2009), but may have patches of large favositid coral and stromatoporoid biostromes (Copper 1978; Johnson 1981). The upper unit is characterized by dolomudstone and dolowackestone with abundant chert and pentameride communities. *Pentamerus* from the lower Fossil Hill is replaced here by the very abundant *Pentameroides* community in which *P. subrectus* dominates up to 95% of the community (Copper 1978). This formation was likely deposited in a storm-dominated carbonate environment ~15° south of paleoequator. This is suggested by the thin lenses of pentameride shell coquina found throughout the formation (Copper 1978). In addition, the shells of *P. subrectus* from this formation show generally poor preservation and are often broken, disarticulated, and infilled by micritic mud.

Jupiter Formation, Anticosti Island, Quebec

The Jupiter Formation is a thick succession of upper Aeronian–middle Telychian carbonates (Jin and Copper 2015) bounded by the East Point Member reefs of the Menier Formation below and the reefal and crinoidal grainstones of the Chicotte Formation above

(Brunton and Copper 1994; Copper and Jin 2012, 2015). The Jupiter Formation, as revised by Copper and Jin (2015), is divided into four members: the Richardson, Cybele, Ferrum, and Pavillon members. The lower three members comprise mainly micritic mudstone and calcareous shale, in which the pentameride brachiopods are represented mainly by stricklandiids. The Pavillon Member is composed of grey argillaceous micrite, wackestones, packstones, grainstones, blueish-green shale, and contains abundant shell beds (Copper and Long 1990). Brachiopods are very common in this member with abundant atrypides, athyrides, and pentamerides (Jin and Copper 2000). The top few meters of the member record the transition from *Pentamerus oblongus* to *Pentameroides subrectus* (Jin and Copper 2000; Glasser 2002).

The Jupiter Formation accumulated in the higher tropics of the early Silurian, marked by frequent storm deposits (Copper and Jin 2012, 2015). Even in the mid- to outer-shelf BA3 to BA4 settings, the *Pentamerus* and stricklandiid shells are often reworked, disarticulated, or truncated, and infilled by very fine micritic matrix (Jin 2008). This is true also for *Pentameroides* as shells in the upper Pavillon Member range from well preserved in micritic mudstone to broken and disarticulated shell packstones. It is important to note, however, that *P. subrectus* does not occur in the overlying Chicotte reefs and crinoid grainstone facies (Jin and Copper 2000), showing that this species could not inhabit the very shallow subtidal environment in the high paleotropics, unlike its slightly younger, subequatorial relative, *P. septentrionalis*, in the Attawapiskat reefs.

Materials and methods

Well-preserved specimens of *P. septentrionalis* (Fig. 3; Repository information: Royal Ontario Museum (Invertebrate Palaeontology) Toronto, ON) were selected for biometric analysis from five collections (samples AK2, AK5, AK6, and AK8) in the Attawapiskat Formation along

the north shore of Akimiski Island, Nunavut. Each of the five collections contributed 59, 53, 52, 53, and 105 specimens respectively, making up a total of 322 specimens. These shells are often found in life position, associated with large framework-building tabulate corals and stromatoporoids of the reef. Disarticulation is relatively rare and most shells are found intact and often hollow with only a thin layer of isopachous calcitic cement lining the interior (Fig 4: A, B). Well-preserved shells representing a complete ontogenetic sequence of this species can be observed, from very small (<10 mm) juvenile to very large (>65 mm) forms. The large mature shells from this formation often show asymmetrical and distorted shapes as a consequence of growing in tightly crowded clusters. These clusters generally occur in depressions within the reef between the large favositid corals where young shells could grow before being compressed and deformed by other surrounding shells (Jin 2002).

Specimens of *P. subrectus* from the Fossil Hill Formation of Manitoulin Island, Ontario (Fig. 5) were also selected for measurement in this study. Although the samples are dominated by incomplete shells, well-preserved whole shells from two collections (M25 and M26) were selected for analysis. These two subsets consisted of 39 and 36 specimens respectively, amounting to a total of 75 specimens. One small collection containing six specimens of *P. subrectus* from the Jupiter Formation of Anticosti Island, Quebec was also used for this study. The shells from these localities are more poorly preserved than those from Akimiski Island and are often broken, deformed (particularly in the transverse plane), and filled by a fine grained micritic matrix (Fig 4: C, D). This poorer preservation results in the relatively small size of the Manitoulin and Anticosti collections compared to the Akimiski Island collection.

A total of 403 specimens were measured using a pair of electronic calipers for the following characteristics: total shell length, ventral umbonal height, length from the dorsal apex

to the ventral umbo, the total shell width, the total shell thickness, the thickness of the ventral valve, and the thickness of the dorsal valve (Fig. 6). Three morphology indices were also developed and utilized in the statistical comparison between the two species. The indices are as follows:

T/W: Thickness/width, proxy for globosity — a higher value means a more globose shell;

U/L: Ventral umbonal height/ length, proxy for the size of the ventral umbo compared to the total shell — higher values indicate a large umbo and larger umbonal shell proportion;

Td/Tv: Dorsal valve thickness/Ventral valve thickness, proxy for biconvexity — higher values indicate a more convex shell.

The dataset derived from the measurements was analyzed statistically using the PAST Software Package v 3.08 (Hammer et al. 2001; Hammer and Harper 2006.) in several linear regression comparisons between the different collections and species. Principal components analysis (PCA) was also performed to create a scatter plot to detect possible ordination or trends of morphological changes.

Results

Statistical analyses of the biometric measurements revealed several morphological trends among the collections of *P. septentrionalis* and *P. subrectus*. All slopes from linear regressions of the discovered trends as well as their associated standard errors are shown together in Table 1A. Based on these values, t-tests were performed on the slopes for each comparison to determine if the results are statistically significant. It was found that the differences in slopes represent statistically different results at a 95% confidence interval in all cases (Table 1B).

Shell size and globosity

The shells of *P. septentrionalis* tend to be much larger and more globose (total shell width compared to total shell thickness) than those of *P. subrectus* (Table 2). Maximum widths and thicknesses of the three groups clearly show the size differences between *P. septentrionalis* (maximum width = 68.1 mm, thickness = 46.8 mm), *P. subrectus* of Manitoulin Island (max. width = 45.0 mm; thickness = 33.8 mm), and *P. subrectus* of Anticosti Island (max. width = 48.0 mm; thickness = 20.7 mm). The two species also show a clear difference in the linear regression comparison of these features (slope of *P. septentrionalis* = 0.58; slope of *P. subrectus* = 0.41; Fig. 7).

Ventral umbonal height compared to total shell length

The ventral umbones of *P. septentrionalis* are generally high, with an average umbonal height of 7.6 mm (max = 20.0 mm). This character contrasts with the smaller umbones of *P. subrectus* from Manitoulin Island (average = 6.0 mm, max. = 11.4 mm) and Anticosti Island (average = 4.6 mm, max. = 6.6 mm). When compared to the total shell length, the ventral umbones of *P. septentrionalis* take up a larger proportion of the shell than the umbones of *P. subrectus* (Table 3). This trend is shown graphically in Figure 8 with *P. septentrionalis* having a slope of 0.25 and *P. subrectus* having a slope of 0.14.

Dorsal valve thickness vs. ventral valve thickness (depth)

A third morphological difference lies in the ratio between the thicknesses (depth) of the two valves between the species. The average dorsal to ventral valve depth ratio is 0.76 for *P. septentrionalis*, compared to 0.68 for *P. subrectus*. This difference is less pronounced than the

other relationships but is still significantly different (Table 1B) in the linear regressions (Fig. 9). The slope of the regression of *P. septentrionalis* is 0.67 while the slope of *P. subrectus* is 0.52.

Principal components analysis (PCA)

PCA yielded a distinct grouping pattern based on 403 specimens and 7 biometric variables (see Methods). Due to the large number of well-preserved *P. septentrionalis* samples, including juvenile shells, the ontogenetic variation of *P. septentrionalis* can be seen in its widespread data points. In this analysis Component 1 accounted for ~77% of the variance with Component 2 accounting for ~11% of the total variance within the sample. This suggests that the PCA yielded distinct principal components, which are statistically representative of the variation observed between the two *Pentameroides* species. Three groups were identifiable in the PCA plot (Fig. 10); Group A represents very small juvenile shells of *P. septentrionalis* as well as an outlying small specimen of *P. subrectus* from Manitoulin Island, Group B contains the majority of *P. subrectus* from both localities and the mid-sized specimens of *P. septentrionalis*, and Group C consists of the large to giant sized specimens of *P. septentrionalis* and large outlying specimens of *P. subrectus*.

Discussions

Morphology and implications for paleoecology and evolution

The large samples of well-preserved *P. septentrionalis* shells made it possible to examine a fairly complete ontogenetic sequence using multivariate analysis. In the PCA plot (Fig. 10), Groups A and B show that juvenile specimens of this species cluster closely with the majority of the adult specimens of *P. subrectus* before diverging into their derived adult morphology in Group C. It appears that *P. subrectus* maintains its lenticular morphology, only increasing in

size, throughout ontogeny (Fig. 5), whereas *P. septentrionalis* diverges into its more globular and biconvex adult morphology in late ontogeny (Figs. 7, 8, 9). The ontogenetic transformation of *P. septentrionalis* shell morphology is so drastic that the equibiconvex shells in early ontogeny were originally classified in a separate genus and species, *Meristina expansa* Whiteaves, 1904 before being revised (see Jin and Copper 1986). The similarities in early ontogeny between *P. subrectus* and *P. septentrionalis*, combined with the first appearance datum (FAD) (*P. subrectus* in the middle Telychian; *P. septentrionalis* in the late Telychian) strongly suggest that *P. septentrionalis* evolved from *P. subrectus* during the middle to late Telychian as the genus migrated from higher to mid-tropics to equatorial settings.

The adult morphology of *P. septentrionalis* (Fig. 3 A-E) likely evolved as a mechanism to improve energy efficiency in the shallow water reefal environment it inhabited. The globular shell shape and increased convexity would allow for the organism to house larger lophophores and therefore improve feeding and respiratory efficiency. The large ventral umbones of the adult specimens reflect a change in life position throughout ontogeny. Like most pentamerides, *Pentameroides* did not have a functioning pedicle to anchor itself to the substrate. They instead maintained their posterior-down life position by crowding and thickening the shell walls of their posteriors (Ziegler 1966). The large reef-dwelling *P. septentrionalis* expanded on this life strategy by enlarging their ventral valves and umbones and changed from an erect or sub-erect life position in early ontogeny to a recumbent orientation in late ontogeny. This enabled the growth of a deeper and largely immobile ventral valve to accommodate larger lophophores (projected from a relatively small dorsal valve, to which the lophophores are attached) to improve feeding/respiratory efficiency. It would also reduce metabolic energy output, requiring only the small and thin dorsal valve to be mobilized for opening and closing the

shell. This type of life position and morphology also occurs in the level-bottom-dwelling *Sulcipentamerus* and *Harpidium* of the paleoequatorial lower Silurian Washington Land Group of North Greenland (Fig. 1; Jin et al. 2009). In these taxa the morphology is more extreme than in *P. septentrionalis* as the ventral valve has deepened into a horn like structure with the dorsal valve sitting atop as a 'lid' (Fig. 11). It is important to note that these taxa inhabited a level-bottom environment while *P. septentrionalis* inhabited a reefal environment, indicating that this morphology was independent of ecological guild types.

It should also be noted that the North Greenland pentamerides evolved into this derived morphology in the level-bottom ecosystem, but *P. subrectus*, which also inhabited level-bottom environments, retained its vertical life position like *Pentamerus* (Jin 2008). As shown in the PCA plot (Fig. 10), *P. subrectus* maintains a lenticular, nearly equibiconvex shell shape throughout ontogeny while *P. septentrionalis* become globular and more ventribiconvex in gerontic forms. A possible explanation is that high frequency of severe storms in the mid- to higher paleotropics (such as the Michigan and Anticosti basins) prevented *P. subrectus* from evolving a recumbent life position because a relatively deep, immobile ventral valve in such a position would be susceptible to smothering by mud during storms. A shell vertically oriented on the substrate would be much more efficient for shedding storm-deposited mud when the two valves are open. A high energy environment would provide sufficient oxygenation and nutrient supply so that the selection pressure for larger lophophores would be much reduced for *P. subrectus* compared to *P. septentrionalis*.

Taphonomy and paleoenvironmental interpretations

The differences in morphology and taphonomy between the two species of *Pentameroides* are closely related to relative storm frequency in the environments that they

inhabited. It has been shown by Jin et al. (2013) that, in the Ordovician and Silurian, Laurentia featured a hurricane-free zone approximately 10° north and south of the equator, similar to that of the modern near-equatorial tropics. Paleogeographically, the Michigan and Anticosti Basins were 15–25° south while the Hudson Bay region was within 10° of the equator (Fig. 1; Torsvik and Cocks 2013). This suggests that the Attawapiskat coral-stromatoporoid reefal environments experienced very few severe storms which allowed *P. septentrionalis* to evolve a larger, globular shell, with a proportionally larger and deeper recumbent ventral valve, resulting in a recumbent living position in gerontic forms (Fig. 10 Group C).

This interpretation finds support in the taphonomic characters of *P. septentrionalis* in the Attawapiskat Formation, especially the common preservation of larger, thin-walled, hollow shells in a shallow water reefal setting (Fig. 4 A, B). This type of preservation could not have occurred in an environment subjected to frequent, hurricane-grade storms. The shells of *P. subrectus* from the higher tropics, however, do signify a storm-dominated environment as they are often broken, disarticulated, deformed, and infilled with micritic matrix (Fig. 4 C, D). These taphonomic features are even more significant when depth of water is taken into account. The level-bottom *P. subrectus* dominated communities likely inhabited a mid to outer shelf (BA 3/BA 4) depth and were subjected to powerful storms while the much shallower Attawapiskat reefal settings experienced insignificant storm damage (Fig. 12). These taphonomic differences indicate that storm frequency and therefore paleolatitudinal position were major factors influencing the derivation of *P. septentrionalis* from *P. subrectus*.

Conclusions

1. Principal component analysis shows that *Pentameroides septentrionalis* resembles *P. subrectus* at early growth stage but diverges in morphology during late ontogeny, indicating that *Pentameroides septentrionalis* evolved from *P. subrectus*.
2. Morphological characteristics of *P. septentrionalis* (increased globosity and convexity, larger ventral valve and umbo) are adaptations to increase energy efficiency living in a hurricane-free, but nutrient-stressed environment. This change in morphology is maximized in the *Harpidium* and *Sulcipentamerus* shells of paleoequatorial North Greenland.
3. A change from vertical (*P. subrectus*) to recumbent (*P. septentrionalis*) life position was related to reduced need for mud-shedding in a depositional setting that lacked hurricane grade storms.
4. Excellent preservation of large, egg-thin shells of *P. septentrionalis* in the shallow-water reefal facies of the Attawapiskat Formation indicates a hurricane free near-equatorial paleoenvironment, whereas poorly preserved shell of *P. subrectus* from Manitoulin and Anticosti islands suggest high tropical storm-dominated environments.

Acknowledgements

Paul Copper kindly made available his collection of *Pentameroides* from Manitoulin Island for this study. The Nunavut government facilitated this research project by permitting fossil collection on Akimiski Island. Funding for this study was provided by the Natural Science and Engineering Research Council of Canada (Jin), The Royal Ontario Museum, and the National Geographic Society (Grant No. 7300-02 to Rudkin). This paper is a contribution to IGCP Project 591: The Lower to Middle Paleozoic Revolution.

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Table 1. A) List of slope and standard error values for each of the morphological character linear regression comparisons. **B)** Statistical t-Tests for each comparison.

A)				
Morphology Comparison	Slopes		Standard Errors	
	<i>P. septentrionalis</i>	<i>P. subrectus</i>	<i>P. septentrionalis</i>	<i>P. subrectus</i>
Shell Thickness v. Shell Width	0.58348	0.41369	0.023744	0.047881
Umbonal Height v. Shell Length	0.24953	0.14285	0.012661	0.014602
Dorsal Thickness v. Ventral Thickness	0.67324	0.51835	0.026515	0.065183

B)				
t-Test (0.95 confidence)	t- value	d.f.	p- value	Conclusion
Shell Thickness v. Shell Width	3.17691103	399	0.00160433	Statistically different
Umbonal Height v. Shell Length	5.51983974	399	6.00E-08	Statistically different
Dorsal Thickness v. Ventral Thickness	2.20109516	399	0.02830133	Statistically different

Table 2. Maximum and minimum values (mm) of total shell length, total shell width, and total shell thickness for the three collections.

	Maximum Length	Minimum Length	Maximum Width	Minimum Width	Maximum Thickness	Minimum Thickness
<i>P. septentrionalis</i>	66.4	7.7	68.1	6.9	46.8	5.2
<i>P. subrectus</i> - Manitoulin Island	64.5	13.6	45.0	12.5	33.8	8.6
<i>P. subrectus</i> - Anticosti Island	N/A (broken shell)	27.1	48.0	27.3	20.7	13.8

Table 3. Maximum, minimum, and average ventral umbo lengths (mm) and average proportion of ventral umbo to total shell length for the three collections.

	Maximum Ventral Umbo Length	Minimum Ventral Umbo Length	Average Ventral Umbo Length	Average Proportion of Total Shell Length
<i>P. septentrionalis</i>	20.0	1.0	7.6	19.8%
<i>P. subrectus</i> - Manitoulin Island	11.4	2.3	6.0	18.4%
<i>P. subrectus</i> - Anticosti Island	6.6	2.8	4.6	12.4%

Figure Captions

Fig. 1. Map of Laurentia, Baltica, and Avalonia in the late Telychian (430 Ma). Thickened lines indicate boundaries of the paleoplates. Squares denote locations of *Pentameroides subrectus*: 1. Jupiter Formation, Anticosti Island, Quebec; 2. Merriton Formation, Southern Ontario and New York; 3. Fossil Hill Formation, Manitoulin Island, Ontario; 4. Hopkinton Dolomite, Iowa. Circles indicate locations of *Pentameroides septentrionalis*; 5. Attawapiskat Formation, Hudson Bay and Moose River Basins; 6, 7, 8. Samuelsen Høj and Hauge Bjerger formations, North Greenland. Star denotes location of *Harpidium* and *Sulcipentamerus* Washington Land Group, North Greenland. Based on Torsvik and Cocks's (2013) paleogeography.

Fig. 2. Map of modern eastern Canada showing study areas.

Fig. 3. *Pentameroides septentrionalis*, Attawapiskat Formation, Akimiski Island, Nunavut. A-E: Specimen ROM 63693 late ontogeny, dorsal, ventral, lateral, posterior, and anterior views. F-J: Specimen ROM 63694 early ontogeny, dorsal, ventral, lateral, posterior, and anterior views. K-O: Specimen ROM 63695 transitioning morphology, dorsal, ventral, lateral, posterior, and anterior views. Scale bars are 1 cm.

Fig. 4. Differing taphonomies of *P. septentrionalis* (A/B) and *P. subrectus* (C/D). Note the egg-thin shell and isopachous cement filling in A/B and the broken and infilled shell of C/D. Scale bars are 1 cm. Arrows mark the interiors of the shells. Specimen A: ROM 63696, Specimen B: ROM 63697, Specimen C/D: A1395.

Fig. 5. *Pentameroides subrectus*, Fossil Hill Formation, Manitoulin Island, Ontario. A-E: Specimen M25-2 dorsal, ventral, lateral, posterior, and anterior views. F-J: Specimen M25-43 dorsal, ventral, lateral, posterior, and anterior views. Scale bars are 1 cm.

Fig. 6. External morphological characters measured in this study.

567 Fig. 7. Plot comparing globosity (total shell width vs total shell thickness) of *P. septentrionalis*
568 and *P. subrectus*.

569 Fig. 8. Plot comparing ventral umbo length to total shell length of *P. septentrionalis* and *P.*
570 *subrectus*.

571 Fig. 9. Plot comparing biconvexity (dorsal valve thickness vs ventral valve thickness) of *P.*
572 *septentrionalis* and *P. subrectus*.

573 Fig. 10. PCA plot showing distribution of the three collections. Group A: juvenile *P.*
574 *septentrionalis* and outlying small *P. subrectus* from Manitoulin Island; Group B: mid- sized *P.*
575 *septentrionalis* and adult *P. subrectus*; Group C: large sized *P. septentrionalis* and outlying large
576 *P. subrectus* from Manitoulin Island.

577 Fig. 11. The interpreted life positions of: *P. subrectus* in high tropical level-bottom environments
578 (A/A1), *P. septentrionalis* in low tropical reefal environments (B/B1), and *Harpidium* and
579 *Sulcipientamerus* in equatorial level-bottom environments (C/C1). Note the transition in life
580 position from vertical (*P. subrectus*) to recumbent (*P. septentrionalis* and
581 *Harpidium/Sulcipientamerus*) as latitude decreases.

582 Fig. 12. Comparison between environments of low tropical reef environment and high tropical
583 storm-dominated level-bottom communities. Differences in water depth habitation and
584 taphonomy are shown in the reconstructed shell beds.

585

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A) Low Tropical Hudson Bay Region

B) High Tropical Michigan/Anticosti Basins

Fig. 12. Comparison between environments of low tropical reef environment and high tropical storm dominated level-bottom communities. Differences in water depth habitation and taphonomy are shown in the reconstructed shell beds.