



Evolutionary mode of the ostracod, *Velatomorpha altilis*, from the Joggins Fossil Cliffs UNESCO World Heritage Site

MELISSA GREY, ZOE V. FINKEL, PEIR K. PUFAHL AND LACEY M. REID

LETHAIA



Grey, M., Finkel, Z.V., Pufahl, P.K. & Reid, L.M. 2012: Evolutionary mode of the ostracod, *Velatomorpha altilis*, at the Joggins Fossil Cliffs UNESCO World Heritage Site. *Lethaia*, DOI: 10.1111/j.1502-3931.2012.00328.x

The estuarine ostracod *Velatomorpha altilis* was analysed for size and shape changes over a 2–3 million-year interval within a portion of the Joggins Fossil Cliffs World Heritage Site. This represents one of a very few number of studies focused on evolutionary trends within marginal environments and contributes to a growing body of research that attempts to link evolutionary patterns with processes. We measured nearly 400 ostracod specimens and used a quantitative model-based test to assess mode of evolution. Samples of ostracods were also analysed for their stable oxygen and carbon isotopic compositions in an attempt to supplement paleoenvironmental interpretations. Stasis was the strongly supported model for mode of evolution in both size and shape metrics, lending support to previous hypotheses that organisms from fluctuating, and therefore stressed, environments, should exhibit stasis because they are genetically well adapted to environmental change over geological time-scales. Stable isotopic compositions indicate samples were diagenetically altered and thus do not preserve a primary signature of paleoenvironmental conditions. Future work should look to other marginal organisms to test whether stasis is indeed a trend in these types of environments. □ *Carboniferous, estuarine ostracod, environment, evolutionary mode.*

Melissa Grey [curator@jogginsfossilcliffs.net], Joggins Fossil Institute, 100 Main St. Joggins, NS B01 1A0 Canada; Zoe V. Finkel [zfinkel@mta.ca], Environmental Science Program, Mount Allison University, Sackville, NB E4L 1G7 Canada; Peir K. Pufahl [peir.pufahl@acadiau.ca], Department of Earth and Environmental Science, Acadia University, Wolfville, NS B4P 2R6 Canada; Lacey M. Reid [lacey.reid@chem.queensu.ca], Department of Chemistry, Queen's University, Kingston, ON K7L 3N6 Canada; manuscript received on 24/1//2012; manuscript accepted on 17/5/2012.

There are three dominant modes of evolution exhibited within the fossil record: stasis (punctuated equilibrium); directional (gradual) change; and, random walks. The relative importance (= frequency) of each of these modes had been debated until Hunt (2007) published his large-scale statistical study of modes across many lineages (from macro- to micro-fossils and invertebrates to vertebrates) and found that nearly 95% of sequences exhibited either stasis or random change; only 5% represented directional change. Using Hunt's (2006) robust statistical methods for analysing evolutionary mode, it is now possible to begin to explore why one mode should be favoured over another in a consistent manner. In other words, we can now study what factors are responsible for the patterns we see in the fossil record.

Linking evolutionary trends with environment is a common goal for biologists and palaeontologists alike and can increase our understanding of macroevolution in general (e.g. Sheldon 1996; Alroy 1998; Kingsolver & Pfennig 2004; Finkel *et al.* 2005; Hunt & Roy 2006; Hone & Benton 2007; Grey *et al.* 2008; Erwin 2009; Hunt *et al.* 2010). For instance, recent work in the marine realm has suggested that body-size

evolutionary trends are dependent on environmental conditions (Finkel *et al.* 2007; Hunt *et al.* 2010) and that evolutionary patterns in general can be linked with paleoenvironment (Grey *et al.* 2008). In addition, Sheldon's (1996) 'plus ça change' model suggests that organisms in fluctuating environments are more likely to display patterns of stasis, whereas those in stable environments are more likely to exhibit gradual patterns. The majority of evolutionary studies thus far have concentrated on marine, lacustrine, or terrestrial environments (e.g. Erwin & Anstey 1995; Alroy 1998; Finkel *et al.* 2005; Hunt 2007; Novack-Gottshall 2008), whereas few (if any) have considered trends of species living in marginal environments, such as brackish conditions. The present study aims to fill this gap and contribute to a growing body of work that endeavours to relate evolutionary patterns with processes. Specifically, this study documents and interprets evolutionary patterns for body size and shape in the estuarine ostracod *Velatomorpha altilis* (Tibert & Dewey 2006). Body-size evolution for deep-sea ostracods, in particular, has been linked to climate change in a recent study (Hunt *et al.* 2010). However, according to the 'plus ça change' model (Sheldon 1996),

estuarine organisms should experience stasis because they are generalists adapted to living in a fluctuating environment. A secondary focus of this research is to assess whether the stable carbon and oxygen isotopic composition of Carboniferous ostracods from the study site can be used to further evaluate the effects of environmental change on evolution. Such an approach may yield additional information about changes in seawater salinity, temperature and primary productivity that can be linked to observed evolutionary trends.

Study area

The Joggins Fossil Cliffs UNESCO World Heritage Site (Nova Scotia, Canada; Fig. 1) has an unparalleled fossil record of terrestrial life, preserved *in situ*, from the Pennsylvanian (Late Carboniferous Period) (Falcon-Lang *et al.* 2006; Boon & Calder 2007; DiMichele & Falcon-Lang 2011). This record also extends to the aquatic realm, with many species of amphibians, fish, bivalves, crustaceans, agglutinated foraminifera and ostracods preserved primarily within numerous sandstone, calcareous shale and limestone beds. The World Heritage Site extends ca. 15 km and includes units of the Mississippian Mabou Group and the Pennsylvanian Cumberland Group (Fig. 2). The estimated age range for this time period spans from the Brigantian (late Viséan) to the Langsettian (late Bashkirian?) (Utting *et al.* 2010), encompassing almost 15 million years.

On-going research at Joggins since the mid-nineteenth century (see Rygel & Shipley 2005; Falcon-Lang 2006; Grey & Finkel 2011; for reviews) has resulted in many advances in the general geology, paleobiology and paleoenvironmental reconstruction of the Joggins section (e.g. Archer *et al.* 1995; Davies *et al.* 2005; Falcon-Lang *et al.* 2006; Grey *et al.* 2011). Three distinct paleoenvironments are recognized within the Joggins Formation alone: (1) terrestrial

drylands; (2) terrestrial wetlands and (3) coastal plains and seas (Davies & Gibling 2003; Davies *et al.* 2005; Falcon-Lang *et al.* 2006). Whereas the ecosystem reconstructions for the terrestrial environments are robust, the aquatic environment and degree of marine influence has been the subject of continued debate for decades. Recent data, however, suggest that Joggins Formation freshens upwards from predominantly marine conditions at its base; the presence of brachiopods, echinoderm fragments and framboidal pyrite indicate normal marine salinities of ca. 35‰ (Grey *et al.* 2011). At the top of the formation, abundant bivalves with freshwater affinities and thicker, more numerous coal beds indicate a brackish, deltaic environment (Grey *et al.* 2011); trace fossil analysis also supports this interpretation (Dafoe *et al.* 2011 and L. Dafoe, personal communication, 2011). This profound shift in paleoenvironment with time in the Joggins Formation provides an unparalleled opportunity to examine the link between evolutionary patterns and environmental change in estuarine fauna. Less is known about the Boss Point Formation, but we included this in our study as it contains the oldest limestone (and therefore ostracods) in the entire World Heritage Site.

Material and methods

Specimens

Samples from 15 limestone beds through the Joggins Formation were collected from the cliff-face and/or outcrop when exposed at low tide (Fig. 3). An additional sample from the top of the older Boss Point Formation limestone was also collected (refer to Fig. 2). The stratigraphical position of these samples encompasses ca. 2–3 million years. In total, 19 samples from 16 stratigraphical levels representing a total of 393 ostracod specimens were collected (Table 1). Polished thin sections were made for faunal analysis of limestones under transmitted and cathodoluminescence (CL) and are the focus of Grey *et al.* (2011). The study area contains only two species of ostracods: *Velatomorpha altilis* comprises nearly 95% of the specimens, whereas *Carbonita pungens* are uncommon ($\approx 5\%$) (Tibert & Dewey 2006; Grey *et al.* 2011; refer to Fig. 4 for a selection of specimens from four stratigraphical intervals). Limestone samples were crushed using an agate mortar and pestle and were placed in Erlenmeyer flasks with approximately 5 g of Calgon powdered soap in each. Each sample was placed on a heated stir plate, covered and left for 1 week. Samples were then sieved with deionized water using three mesh sizes: 500 μm , 250 μm

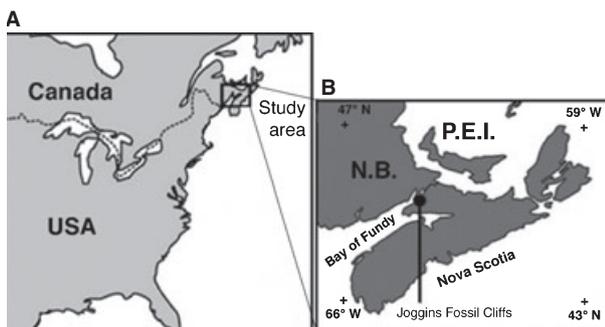


Fig. 1. Location of the 14.7 km Joggins Fossil Cliffs World Heritage Site. A, location in North America. B, location in the Cumberland Basin (Bay of Fundy), Nova Scotia, Canada.

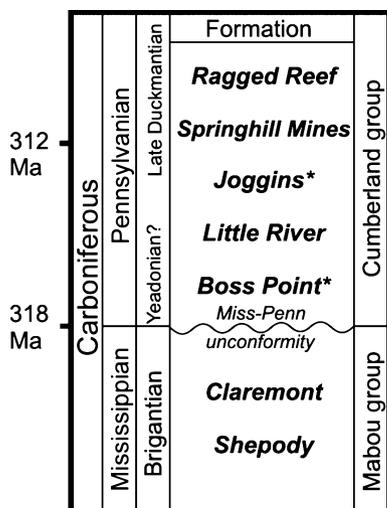


Fig. 2. Stratigraphical column depicting the geological formations and their corresponding age represented in the Joggins Fossil Cliffs UNESCO World Heritage Site according to the IUGS time-scale (altered from Boon & Calder 2007). *Indicates those formations containing limestones sampled for this study.

and 125 μm and the sediments were transferred to petri dishes and left to air dry for 24 hours. Once dry, the samples were placed under a compound microscope to pick the ostracods in each size class; the great majority of carapaces were articulated. The largest size class (500 μm) was used for analyses in an attempt to ensure that only adults were measured. Published taxonomic literature indicates that the average size for adult *V. altilis* is: 927 μm (L); 606 μm (H); 570 μm (W) (Tibert & Dewey 2006). Once picked, the ostracods were mounted with the left valve visible and in the same orientation on standard gridded micro-palaeontological cardboard slides using tragacanth gum as the gluing agent.

Measuring body size and shape

Mounted ostracods from each sample were photographed individually using a digital camera attached to a compound microscope. Digital images of ostracods were calibrated and measured using JMorph, custom software for measuring the size of micro-palaeontological specimens. JMorph generated outline shapes by defining a series of points around the perimeter of the carapace that were used for elliptical Fourier, outline length and shell area analyses. Valve outline and area were used as proxies for body size (e.g. Hunt *et al.* 2010). Valve outlines were used because they have been identified as an important trait to classify Carboniferous non-marine ostracods (Bennett 2008); valve area has also been used in previous studies of marine ostracods (e.g. Hunt *et al.* 2010). The area data were logarithmically transformed prior to analyses (Foote 1991;

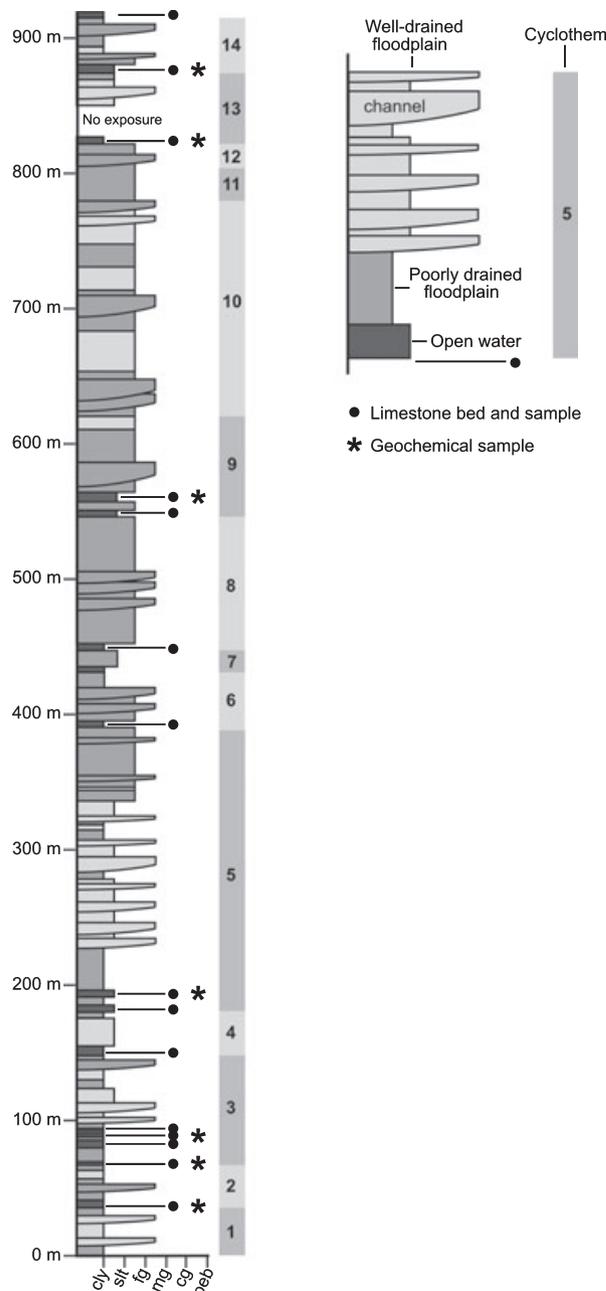


Fig. 3. Stratigraphy of the Joggins Formation illustrating facies associations within cycles and sample locations, including geochemical sample locations. p/y, pyrite; cly, clay; slt, silt; fg, wackestone; mg, packstone; c.g., grainstone and peb., rudstone and boundstone (modified after Grey *et al.* 2011). Sample (for mode and geochemical analysis) from the Boss Point Formation not shown.

Hunt *et al.* 2010) and means and standard deviations were calculated for each sample.

Evolutionary mode

Evolutionary changes in shell shape were considered using elliptical Fourier analyses; this type of outline

Table 1. List of samples collected from the Joggins Fossil Cliffs. Stratigraphical level 1 corresponds to the sample from the Boss Point Formation, whereas levels 2–16 are from the younger Joggins Formation. CV, canonical variate.

Relative stratigraphical level	Total number of specimens	Trait			
		CV1 mean/variance	CV2 mean/variance	Shell area (mm ²) mean \pm variance	Outline length (mm) mean \pm variance
1	30	0.005 \pm 0.0001	0.005 \pm 0.0002	0.6 \pm 0.008	2.89 \pm 0.04
2	10	0.017 \pm 0.0003	-0.006 \pm 0.0002	1.02 \pm 0.14	3.77 \pm 0.5
3	24	0.002 \pm 0.0003	-0.003 \pm 0.0004	0.55 \pm 0.007	2.79 \pm 0.03
4	42	0.005 \pm 0.0003	0.007 \pm 0.0006	0.63 \pm 0.004	2.95 \pm 0.02
5	24	0.001 \pm 0.0004	0.007 \pm 0.0004	0.62 \pm 0.003	2.93 \pm 0.01
6	23	-0.008 \pm 0.0006	-0.009 \pm 0.0003	0.54 \pm 0.004	2.72 \pm 0.02
7	48	-0.01 \pm 0.0004	-0.003 \pm 0.0004	0.67 \pm 0.02	3.02 \pm 0.1
8	18	0.009 \pm 0.0004	-0.002 \pm 0.0003	0.48 \pm 0.002	2.58 \pm 0.01
9	48	-0.003 \pm 0.0006	-0.001 \pm 0.0003	0.58 \pm 0.01	2.83 \pm 0.06
10	20	-0.002 \pm 0.0006	-0.005 \pm 0.0004	0.54 \pm 0.008	2.73 \pm 0.05
11	25	0.01 \pm 0.0003	0.002 \pm 0.0003	0.45 \pm 0.002	2.49 \pm 0.01
12	11	-0.001 \pm 0.0002	0.003 \pm 0.00007	0.49 \pm 0.004	2.64 \pm 0.03
13	24	-0.002 \pm 0.0005	0.001 \pm 0.0006	0.56 \pm 0.02	2.76 \pm 0.11
14	13	-0.004 \pm 0.0004	0.0002 \pm 0.0003	0.44 \pm 0.003	2.48 \pm 0.02
15	24	-0.005 \pm 0.0002	-0.001 \pm 0.0002	0.57 \pm 0.002	2.79 \pm 0.01
16	9	0.005 \pm 0.0001	0.0001 \pm 0.0001	0.58 \pm 0.004	2.84 \pm 0.03

analysis is particularly useful for specimens where there are no landmarks (homologous points) present (Crampton 1995). The Fourier analysis employed the Hangle program (Crampton & Haines 1996) specifically developed for this purpose. The first 12 harmonics were used for the analysis, Fourier coefficients were not standardized and only real numbers (rather than imaginary) were used for subsequent multivariate analyses. A principle component analysis (PCA) was performed using the variance-covariance matrix (Crampton 1995) on the resulting suite of coefficients to condense information from many correlated variables into a few quantities that summarize the variation among individuals; it was used to explore the morphospace of the ostracods and was executed using the program PAST (version 1.38; Hammer *et al.* 2001). A canonical variant analysis (CVA) was used for predictive classification. *A priori* grouping for the CVA was based on stratigraphical level. We utilized a step-wise method for the CVA because it select variables that contribute the most discriminatory power to the model (refer to Cheetham *et al.* 2006). This method is particularly advantageous when a number of characters are measured. Resampling methods help to assess the accuracy of analyses by testing the repeatability of the results; we therefore simulated a jack-knifed approach in SPSS (version 11.0) by selecting the 'leave-one-out classification' option. Shell size was explored through measurements of valve outline length and shell area, calculated from outlines in JMorph.

We explored evolutionary mode using two methods. Biologs, produced by plotting trait values against stratigraphical position, were created as

they help to illustrate temporal morphologic patterns (Reyment 1980; Kelley 1983). The first canonical variate (CV1) from the Fourier analysis was used to explore changes in shell shape, and shell outline length and area were used to explore changes in size. We employed Hunt's (2006) likelihood-based procedure using PaleoTS in the statistical package, R. The test requires the variable mean and variance and total number of specimens for each time interval studied (Table 1); it selects the best fit model of different modes, including: directional, unbiased random walk and stasis. Support for the models was considered with two metrics, Akaike information criterion (AIC_C) and Akaike weights. The model with the lowest AIC_C and highest Akaike weight is the best supported (Hunt 2006).

Geochemical analysis

A subset of eight ostracod samples from the upper Boss Point and throughout the Joggins Formation was analysed for their stable oxygen ($\delta^{18}\text{O}$) and carbon ($\delta^{13}\text{C}$) isotopic compositions (Fig. 3). Because the prismatic micro-structure of these ostracod carapaces is well preserved under both plane-polarized light and cathodoluminescence (Grey *et al.* 2011) their chemistry may further constrain the magnitude of changes in water temperature, salinity and primary productivity through time (e.g. Tibert & Scott 1999; Janz & Venne-mann 2005; Medley *et al.* 2007; Tibert *et al.* 2007; Arp & Mennerich 2008). Ostracods are interpreted to precipitate their carapaces in near isotopic equilibrium with seawater and because they are formed of low-Mg

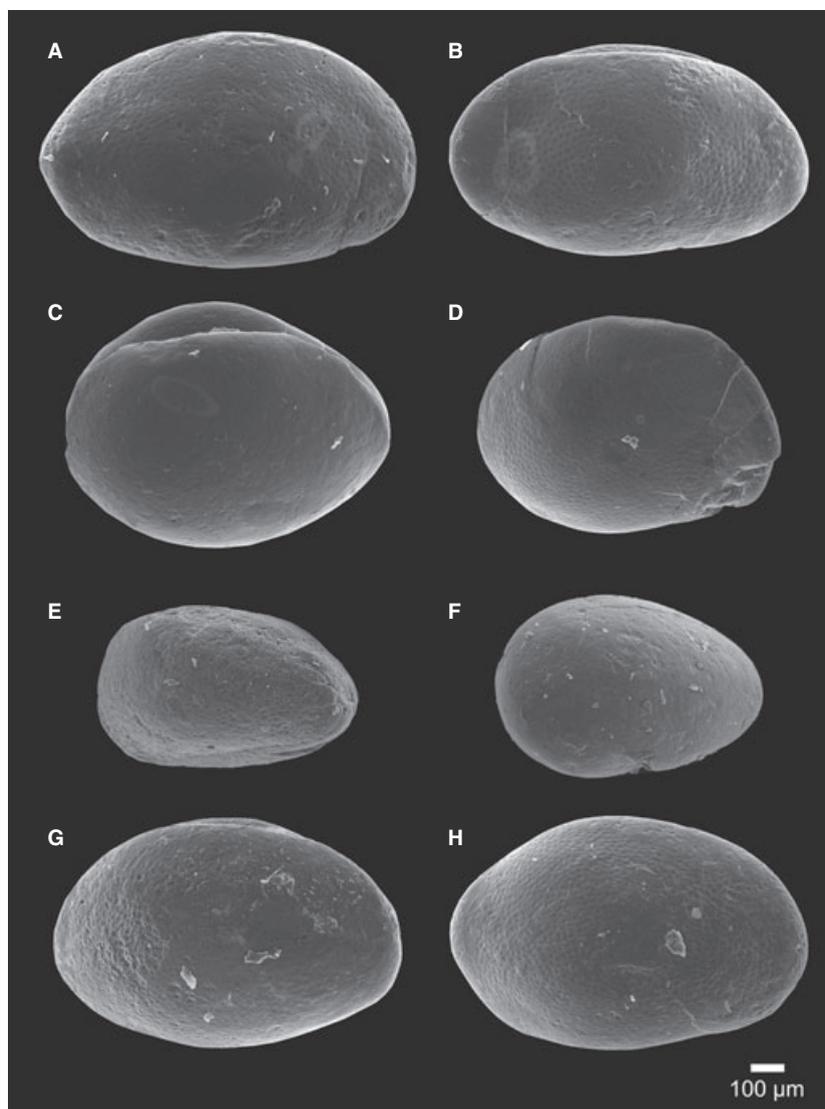


Fig. 4. SEM images of a sample of ostracods from the study site in order of oldest to youngest. A, B, correspond to the limestone sample from the Boss Point Formation. C, D, correspond to cyclothem #3 limestone sample (refer to Fig. 3). E, F, correspond to cyclothem 5; G, H, correspond to cyclothem 13. Specimens housed at the Joggins Fossil Institute, accession number: NSM011GF040.009.

calcite can preserve a robust seawater signature, even during diagenetic alteration (Williams *et al.* 2006; Bennett *et al.* 2011; Decrouy *et al.* 2011).

Each of the eight samples consisted of 5–10 ostracods, analysed at the Queen's Facility for Isotopic Research. Samples were analysed using a Thermo-Finnigan gas bench coupled to a Thermo-Finnigan XP Plus continuous-flow isotope-ratio mass spectrometer by reacting 0.5 mg of powdered carapace with 100% anhydrous phosphoric acid at 72°C. The isotopic composition of four sediment samples was also analysed to place the ostracods in diagenetic context. Sparry calcite cements could not be analysed for such a purpose because none are present. The fractionation factors are those of O'Neal *et al.* (1969) for oxygen and Deines *et al.* (1974) for carbon in the system calcite

and water. Carbon and oxygen isotope results are reported in the usual notation relative to the reference standard of the Peedee belemnite (V-PDB; Craig 1957),

$$\delta = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where R represents the $^{13}\text{C}/^{12}\text{C}$ or $^{18}\text{O}/^{16}\text{O}$. Replicate analyses indicate a reproducibility of $\pm 0.2\text{‰}$ for both.

Results and discussion

Evolutionary mode

Most of the previous work on ostracod evolutionary mode has been from deep marine environments (e.g.

Hunt 2007; Hunt *et al.* 2010), with comparatively very little on those from estuarine/marginal environments. In this study, stasis was the most strongly supported model for all characters measured (outline shape/Fourier, outline length and shell area; Figs. 5A–D, Table 2). That is, for the approximately 2–3 million-year interval studied, there were no significant changes in the shape or size of *V. altilis*. However, it is clear, based on studies from the terrestrial (e.g. Calder *et al.* 2005; Falcon-Lang *et al.* 2006) and aquatic environment (Grey *et al.* 2011), that there are significant environmental changes during this period.

There is a direct correlation between the outline length and shell area (Figs. 5C, D); this is an expected outcome because the shape is also not changing significantly (Figs. 5A, B). It is unknown if the outlier visible in Figures 5C, D ($x = 2$), marking the beginning of the Joggins Formation ($x = 1$ is the sample taken from the older Boss Point Formation), represent a real increase in size at this time period. All data points on Figure 5 are the trait averages of many specimens (refer to Table 1), and the values for all 10 specimens from the beginning of the Joggins Formation are larger than the averages for all other stratigraphical levels. Therefore, it appears that this may represent a true size increase from the Boss Point to Joggins Formation. Regardless of this, the overall mode

statistically reflects stasis, meaning that there is no net change over the entire time period studied.

Our results support Sheldon's (1996) 'plus ça change' model, whereby organisms in fluctuating environments are more likely to exhibit stasis. Brackish/estuarine organisms are generally tolerant to changes in the environment and this may translate into resistance to evolutionary change over geologically 'short' periods such as the time interval studied herein. Future work should focus on other organisms from marginal environments to determine if this is a legitimate trend. A recent study on an 'ecologically flexible' temnospondyl experienced an extreme case of stasis over 35 My (Schoch & Witzmann 2012), and also lends support to the 'plus ça change' model. Although the cause(s) of stasis is still very much debated (Hunt 2007 and references therein), additional studies that can compare evolutionary modes between different ecological strategies (e.g. r-selected vs. K-selected; generalists vs. specialists) and environments (stable vs. unstable; planktonic vs. benthic) should result in an increased understanding of the link between pattern and process of macroevolution.

Geochemical analysis

Ostracods have $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values that range from -12.3 to -9.5‰ and -11.0 to -0.5‰ respectively

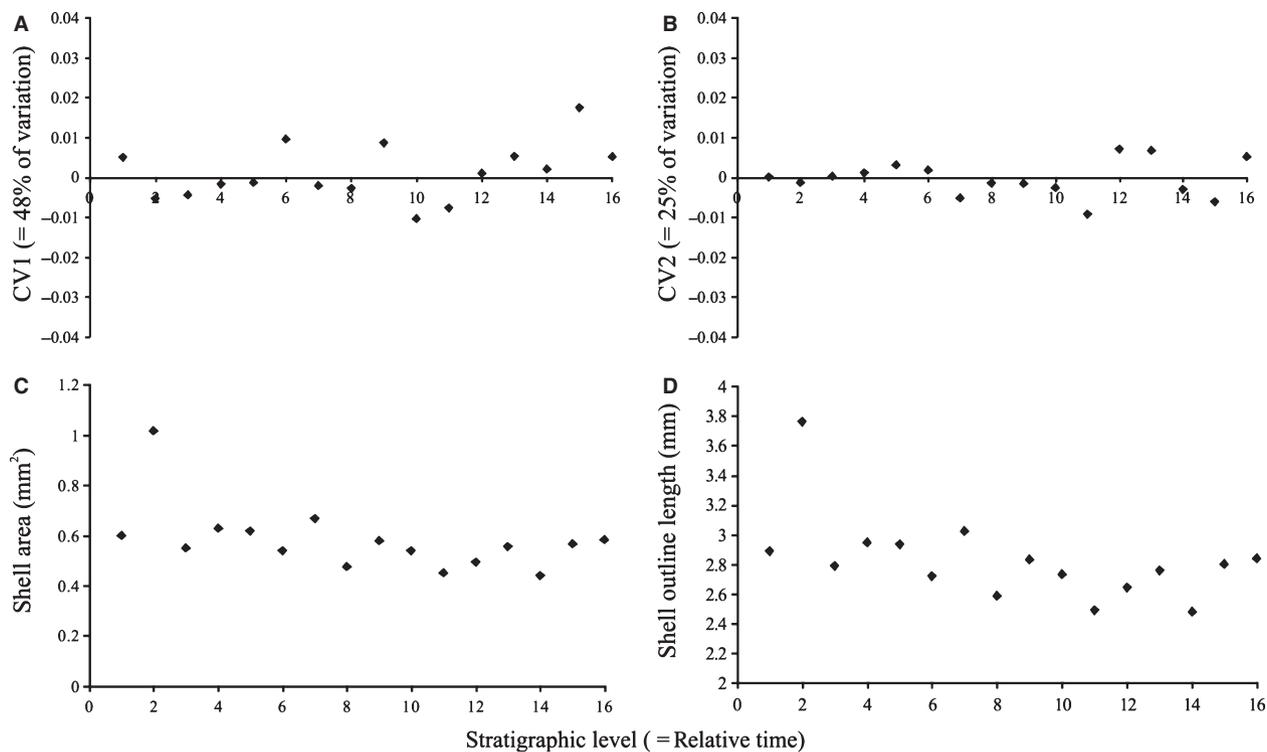


Fig. 5. Biologs (trait means vs. relative time) for A, B, outline shape from Fourier analyses; C, outline length and D, shell area.

Table 2. Evolutionary model-fitting results using Hunt's (2008) joint parameterization method. The best-supported model for each trait is in bold. AIC_C, Akaike information criterion; GRW, generalized random walk (= directional change); URW, unbiased random walk; omega stasis, measure of the total magnitude of evolutionary variation (Hunt 2007).

Trait	Type	AIC _C			Akaike weights			Omega stasis
		GRW	URW	Stasis	GRW	URW	Stasis	
CV1	Fourier	-103	-106	-109	0.03	0.14	0.83	2.6*10 ⁻⁵
CV2	Fourier	-118	-120	-122	0.1	0.29	0.61	6.3*10 ⁻⁶
Outline length	Size	18	15	9.8	0.01	0.67	0.92	0.075
Shell area	Size	-6.3	-9.9	-16	0.009	0.05	0.94	0.0154

(Table 3). The stable oxygen ($\delta^{18}\text{O}$) and carbon ($\delta^{13}\text{C}$) isotopic compositions of ostracods are interpreted to reflect diagenetic alteration and thus cannot be used to augment paleoenvironmental interpretations. When $\delta^{18}\text{O}$ data are compared with values from Upper Carboniferous, open marine brachiopods that are interpreted to be unaltered (~ -3.5 to -0.5‰ ; Brand 1994; Grossman *et al.* 2002), the ostracod values are as much as -11.8‰ lower. The $\delta^{13}\text{C}$ values of Joggins ostracods are as much 17.5‰ lower than interpreted seawater values, which range from 1.0 to 6.5‰ (Brand 1994; Grossman *et al.* 2002). The enclosing carbonate sediments have a similar range of isotopic values (Table 3).

While ostracods have been reported to precipitate their carapaces in near isotopic equilibrium with ambient seawater (e.g. Decrouy *et al.* 2011), when $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values are compared with the higher 'open marine' values it is apparent that the ostracods have been altered during meteoric diagenesis. The low values in ostracods are common in limestones where meteoric waters fix the isotopic composition of shells during alteration, often with no evidence of recrystallization (*cf.* Kyser *et al.* 1998). The ranges of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values in the Joggins ostracods are also consistent with low values from Carboniferous calcretes, a proxy for the chemistry of meteoric water, and other Carboniferous ostracods that have been altered by diagenetic processes (Williams *et al.* 2006; Jutras *et al.* 2007; Bennett *et al.* 2011). Although such low $\delta^{18}\text{O}$ values can be imparted to the shells of organisms living in freshwater or brackish environments, it is unlikely that this is the case in the Joggins study site as the isotopic compositions of ostracods from the basal marine portion of the section are similar to those from freshwater environments at the top. Similarly, if the $\delta^{13}\text{C}$ values recorded this freshening event they should not be so consistently low through the entire formation.

Future geochemical work may include ostracods from other lithologies in the Joggins Formation (and beyond) where there is potentially better preservation. For example, Carboniferous mudstones in the

Table 3. $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values from Upper Carboniferous ostracods and enclosing sediments samples from the Cumberland Group. Data are listed based on sample type and in stratigraphical order from youngest to oldest.

Sample	Description	$\delta^{18}\text{O}$ (‰)	$\delta^{13}\text{C}$ (‰)
JOG-C-25-O	Ostracod	-9.5	-0.5
JOG-C-18-O	Ostracod	-10.4	-8.1
JOG-13-O	Ostracod	-10.8	-11.0
JOG-C-7-O	Ostracod	-10.9	-5.1
JOG-5-O	Ostracod	-12.1	-5.1
JOG-4-O	Ostracod	-10.6	-7.3
JOG-C-1-O	Ostracod	-11.7	-7.9
Boss Pt-O	Ostracod	-9.9	-9.1
JOG-C-23-LS	Limestone	-7.7	-1.1
JOG-C-18-LS	Limestone	-9.0	-2.0
JOG-C-17-LS	Limestone	-10.8	-6.8
JOG-1-LS	Limestone	-10.3	-5.5

Midland Valley of Scotland contained better-preserved ostracods than in the limestones (C.E. Bennett, personal communication, 2012).

Conclusions

While the geochemical analyses revealed that the ostracods studied were altered and could not be used for paleoenvironmental interpretation, the sedimentological data indicate changing environmental conditions through time. Stasis is the strongly supported model for evolution in *V. altilis* at the Joggins site; this result supports Sheldon's (1996) 'plus ça change' model wherein organisms living in variable or stressful environments are more likely to show stasis over other modes of evolution. Whether stasis is a general trend for marginal environments is yet to be determined and would be valuable for future study. While linking evolutionary patterns with processes remains a challenge, small-scale studies such as these are critical because they add to a growing body of work with the goal of increasing our understanding of macroevolution and teasing apart the relative effects of environmental vs. genetic influences on evolution.

Acknowledgements. — All collections were made with a Heritage Research Permit granted by the Province of Nova Scotia (P2009NS02). We thank N. Tibert for extraction protocol; Annas Aziz for aiding in field collecting; Haixin Xu (Acadia Centre for Microstructural Analysis) for SEM usage and P. Lelievre for JMorph development and insightful discussion. Diligent and helpful reviews were provided by Carys E. Bennett and Gene Hunt. This research was made possible by grants from the Natural Sciences and Engineering Research Council of Canada (Post-Doctoral grant to M.G. and Discovery Grants to Z.V.F. and P.K.P.).

References

- Aloy, J. 1998: Cope's rule and the dynamics of body mass evolution in North American mammals. *Science* 280, 731–734.
- Archer, A.W., Calder, J.H., Gibling, M.R., Naylor, R.D., Reid, D.R. & Wightman, W.G. 1995: Invertebrate trace fossils and agglutinated foraminifera as indicators of marine influence within the classic Carboniferous section at Joggins, Nova Scotia, Canada. *Canadian Journal of Earth Sciences* 32, 2027–2039.
- Arp, G. & Mennerich, C. 2008: Ostracod assemblages, palaeoenvironment and cyclicity of Purbeck-type sediments of the Münders Formation (Lower Cretaceous, Hils Syncline, N-Germany). *Palaeogeography, Palaeoclimatology, Palaeoecology* 264, 230–249.
- Bennett, C.E. 2008: A review of the Carboniferous colonisation of non-marine environments by ostracods. *Palaeobiodiversity and Palaeoenvironments* 88, 37–46.
- Bennett, C.E., Williams, M., Leng, M.J., Siveter, D.J., Davies, S.J., Sloane, H.J. & Wilkinson, I.P. 2011: Diagenesis of fossil ostracods: Implications for stable isotope based palaeoenvironmental reconstruction. *Palaeogeography, Paleoclimatology, Palaeoecology* 305, 150–161.
- Boon, J. & Calder, J.H. 2007: Nomination of the Joggins Fossil Cliffs for Inscription on the World Heritage List, United Nations Educational, Scientific and Cultural Organization on-line publication: <http://www.whc.unesco.org/en/list/1285/documents>, 129 pp.
- Brand, U. 1994: Continental hydrology and climatology of the Carboniferous Joggins Formation (Lower Cumberland group) at Joggins, Nova Scotia – evidence from the geochemistry of bivalves. *Palaeogeography, Palaeoclimatology, Palaeoecology* 106, 307–321.
- Calder, J.H., Rygel, M.C., Ryan, R.J., Gibling, M.R., Falcon-Lang, H.J. & Hebert, B.L. 2005: Stratigraphy and sedimentology of early Pennsylvanian red beds at Lower Cove, Nova Scotia, Canada: The Little River Formation with redefinition of the Joggins Formation. *Atlantic Geology* 41, 143–167.
- Cheetham, A.H., Sanner, J., Taylor, P.D. & Ostrovsky, A.N. 2006: Morphological differentiation of avicularia and the proliferation of species in mid-Cretaceous *Wilbertopora* Cheetham, 1954 (Bryozoa: Cheilostomata). *Journal of Palaeontology* 80, 49–71.
- Craig, H. 1957: Isotopic standards for carbon and oxygen and correlation factors for mass-spectrometric analysis of carbon dioxide. *Geochimica et Cosmochimica Acta* 12, 133–149.
- Crampton, J.S. 1995: Elliptic Fourier shape analysis of fossil bivalves: some practical considerations. *Lethaia* 28, 179–186.
- Crampton, J.S. & Haines, A.J. 1996: User's manual for programs HANGLE, HMATCH, and HCURVE for the Fourier shape analysis of two-dimensional outlines. 96/37, 28 pp.
- Dafoe, L.T., Stimson, M. & Gibling, M.R. 2011: One more piece to the puzzle: new developments in the trace fossil record from the Pennsylvanian Joggins Formation. *Abstracts of the Atlantic Geoscience Society 37th Annual Colloquium & Annual General Meeting*.
- Davies, S.J. & Gibling, M.R. 2003: Architecture of coastal and alluvial deposits in an extensional basin: the Carboniferous Joggins Formation of eastern Canada. *Sedimentology* 50, 415–439.
- Davies, S.J., Gibling, M.R., Rygel, M.C., Calder, J.H. & Skiller, D.M. 2005: The Pennsylvanian Joggins Formation of Nova Scotia: Sedimentological log and stratigraphical framework of the historic fossil cliffs. *Atlantic Geology* 41, 115–142.
- Decrouy, L., Vennemann, T.W. & Ariztegui, D. 2011: Controls on ostracod valve geochemistry, Part 1: Variations of environmental parameters in ostracod (micro-)habitats. *Geochimica et Cosmochimica Acta* 75, 7364–7379.
- Deines, P., Langmuir, D. & Harmon, R.S. 1974: Stable carbon isotope ratios and the existence of a gas phase in the evolution of carbonate ground waters. *Geochimica et Cosmochimica Acta* 38, 1147–1164.
- DiMichele, W.A. & Falcon-Lang, H.J. 2011: Fossil forests in growth position (T0 assemblages): origin, taphonomic biases and palaeoecological significance. *Journal of the Geological Society* 168, 585–605.
- Erwin, D.H. 2009: Climate as a driver of evolutionary change. *Current Biology* 19, R575–R583.
- Erwin, D.H. & Anstey, R.L. 1995: Speciation in the Fossil Record. In Erwin, D.H. & Anstey, R.L. (eds): *New Approaches to Speciation in the Fossil Record*, 11–38. Columbia University Press, New York.
- Falcon-Lang, H.J. 2006: A history of research at the Joggins fossil cliffs of Nova Scotia, Canada, the world's finest Pennsylvanian section. *Proceedings of the Geologists Association* 117, 377–392.
- Falcon-Lang, H.J., Benton, M.J., Braddy, S.J. & Davies, S.J. 2006: The Pennsylvanian tropical biome reconstructed from the Joggins Formation of Nova Scotia, Canada. *Journal of the Geological Society* 163, 561–576.
- Finkel, Z.V., Katz, M.E., Wright, J.D., Schofield, O.M.E. & Falkowski, P.G. 2005: Climatically driven macroevolutionary patterns in the size of marine diatoms over the Cenozoic. *Proceedings of the National Academy of Sciences USA* 102, 8927–8932.
- Finkel, Z.V., Sebbio, J., Feist-Burkhardt, S., Irwin, A.J., Katz, M.E., Schofield, O.M.E., Young, J.R. & Falkowski, P.G. 2007: A universal driver of macroevolutionary change in the size of marine phytoplankton over the Cenozoic. *Proceedings of the National Academy of Sciences USA* 104, 20416–20420.
- Foote, M. 1991: Analysis of morphological data. In Gilin-Sky, N.L. & Signor, P.W. (eds): *Analytical Paleobiology*, volume 4, 59–86. The Paleontological Society, University of Tennessee, Knoxville.
- Grey, M. & Finkel, Z.V. 2011: The Joggins Fossil Cliffs UNESCO World Heritage site: a review of recent research. *Atlantic Geology* 47, 185–200.
- Grey, M., Haggart, J.W. & Smith, P.L. 2008: Variation in evolutionary patterns across the geographic range of a Fossil bivalve. *Science* 322, 1238–1241.
- Grey, M., Pufahl, P.K. & Abdul, A.A. 2011: Using multiple environmental proxies to determine degree of marine influence and paleogeographical position of the Joggins Fossil Cliffs UNESCO World Heritage Site. *Palaio* 26, 256–263.
- Grossman, E.L., Bruckschen, P., Mii, H.-S., Chuvashov, B.I., Yancey, T.E. & Veizer, J. 2002: Carboniferous paleoclimate and global change: Isotopic evidence from the Russian Platform. In Chuvashov, B. I. & Amon, E. O. (eds): *Carboniferous stratigraphy and Paleogeography in Eurasia*, 61–71. Institute of Geology and Geochemistry, Russian Academy of Sciences, Urals Branch, Ekaterinburg.
- Hammer, O., Harper, D.A.T. & Ryan, P.D. 2001: PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4, 9.
- Hone, D.W.E. & Benton, M.J. 2007: Cope's Rule in the Pterosauria, and differing perceptions of Cope's Rule at different taxonomic levels. *Journal of Evolutionary Biology* 20, 1164–1170.
- Hunt, G. 2006: Fitting and comparing models of phyletic evolution: random walks and beyond. *Paleobiology* 32, 578–601.
- Hunt, G. 2007: The relative importance of directional change, random walks, and stasis in the evolution of fossil lineages. *Proceedings of the National Academy of Sciences* 104, 18404–18408.
- Hunt, G. 2008: Evolutionary patterns within fossil lineages: model-based assessment of modes, rates, punctuations and process. In Bambach, R.K. & Kelley, P.H. (eds): *From Evolution to Geobiology: Research Questions Driving Paleontology at the Start of a New*

- Century, 117–131. The Paleontological Society, Yale Printing and Publishing Services, New Haven.
- Hunt, G. & Roy, K. 2006: Climate change, body size evolution, and Cope's Rule in deep-sea ostracodes. *Proceedings of the National Academy of Sciences USA* 103, 1347–1352.
- Hunt, G., Wicaksono, S.A., Brown, J.E. & MacLeod, K.G. 2010: Climate-driven body-size trends in the ostracod fauna of the deep Indian Ocean. *Palaeontology* 53, 1255–1268.
- Janz, H. & Vennemann, T.W. 2005: Isotopic composition (O, C, Sr, and Nd) and trace element ratios (Sr/Ca, Mg/Ca) of Miocene marine and brackish ostracods from North Alpine Foreland deposits (Germany and Austria) as indicators for palaeoclimate. *Palaeogeography, Palaeoclimatology, Palaeoecology* 225, 216–247.
- Jutras, P., Utting, J. & McLeod, J. 2007: Link between long-lasting basins and the development of thick massive phreatic calcareous hardpans in the Mississippian Windsor and Percé groups of eastern Canada. *Sedimentary Geology* 201, 75–92.
- Kelley, P.H. 1983: Evolutionary patterns of eight Chesapeake Group molluscs: evidence for the model of Punctuated Equilibrium. *Journal of Paleontology* 57, 581–598.
- Kingsolver, J.G. & Pfennig, D.W. 2004: Individual-level selection as a cause of Cope's Rule of phyletic size increase. *Evolution* 58, 1608–1612.
- Kyser, T., James, N.P. & Bone, Y.B. 1998: Alteration of Cenozoic cool-water carbonates to low-Mg calcite in marine waters, Gambier Embayment, South Australia. *Journal of Sedimentary Research* 68, 947–955.
- Medley, P., Tibert, N.E., Patterson, W.P., Curran, H.A., Greer, L. & Colin, J.-P. 2007: Paleosalinity history of middle Holocene lagoonal and lacustrine deposits in the Enriquillo Valley, Dominican Republic based on pore morphometrics and isotope geochemistry of ostracoda. *Micropaleontology* 53, 1–11.
- Novack-Gottshall, P.M. 2008: Ecosystem-wide body-size trends in Cambrian-Devonian marine invertebrate lineages. *Paleobiology* 34, 210–228.
- O'Neal, J.R., Clayton, R.N. & Mayeda, T.K. 1969: Oxygen isotope fractionation in divalent metal carbonate. *Journal of Chemical Physics* 51, 5547–5558.
- Reyment, R.A. 1980: *Morphometric Methods in Biostratigraphy*, 175 pp. Academic Press, London.
- Rygel, M.C. & Shipley, B.C. 2005: 'Such a section as never was put together before': Logan, Dawson, Lyell and mid-nineteenth century measurements of the Pennsylvanian Joggins Section of Nova Scotia. *Atlantic Geology* 41, 87–102.
- Schoch, R.R. & Witzmann, F. 2012: Cranial morphology of the plagiosaurid *Gerrothorax pulcherrimus* as an extreme example of evolutionary stasis. *Lethaia* 45, 371–385.
- Sheldon, P.R. 1996: Plus ça change - a model for stasis and evolution in different environments. *Palaeogeography, Palaeoclimatology, Palaeoecology* 127, 209–227.
- Tibert, N.E. & Dewey, C.P. 2006: *Velatomorpha*, a new healdioidean ostracode genus from the early Pennsylvanian Joggins Formation, Nova Scotia, Canada. *Micropaleontology* 52, 51–66.
- Tibert, N.E. & Scott, D.B. 1999: Ostracodes and Agglutinated Foraminifera as Indicators of Palaeoenvironmental Change in an Early Carboniferous Brackish Bay, Atlantic Canada. *Palaios* 14, 246–260.
- Tibert, N.E., Patterson, W.P., Diefendorf, A.F., Martini, A. & Stanton, C. 2007: Holocene temperature variability in western Ireland: Evidence from limnic ostracode assemblages and stable isotope values. *Stratigraphy* 4, 1–9.
- Utting, J., Giles, P.S. & Dolby, G. 2010: Palynostratigraphy of Mississippian and Pennsylvanian rocks, Joggins area, Nova Scotia and New Brunswick, Canada. *Palynology* 34, 43–89.
- Williams, M., Leng, M.J., Stephenson, M.H., Andrews, J.E., Wilkinson, I.P., Siveter, D.J., Horne, D.J. & Vannier, J.M.C. 2006: Evidence that Early Carboniferous ostracods colonised coastal flood plain brackish water environments. *Palaeogeography, Palaeoclimatology, Palaeoecology* 230, 299–318.