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

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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 frambooidal 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 (≈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
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 J Morph, custom software for measuring the size of micro-palaeontological specimens. J Morph 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; 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.

<table>
<thead>
<tr>
<th>Relative stratigraphical level</th>
<th>Total number of specimens</th>
<th>Trait</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>CV1 mean/variance</td>
<td>CV2 mean/variance</td>
<td>Shell area (mm²)</td>
<td>Outline length (mm)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>mean ± variance</td>
<td>mean ± variance</td>
</tr>
<tr>
<td>1</td>
<td>30</td>
<td>0.005 ± 0.0001</td>
<td>0.005 ± 0.0002</td>
<td>0.6 ± 0.008</td>
<td>2.89 ± 0.04</td>
</tr>
<tr>
<td>2</td>
<td>10</td>
<td>0.017 ± 0.0003</td>
<td>−0.006 ± 0.0002</td>
<td>1.02 ± 0.14</td>
<td>3.77 ± 0.5</td>
</tr>
<tr>
<td>3</td>
<td>24</td>
<td>0.002 ± 0.0003</td>
<td>−0.003 ± 0.0004</td>
<td>0.55 ± 0.007</td>
<td>2.79 ± 0.03</td>
</tr>
<tr>
<td>4</td>
<td>42</td>
<td>0.005 ± 0.0004</td>
<td>0.007 ± 0.0006</td>
<td>0.63 ± 0.004</td>
<td>2.95 ± 0.02</td>
</tr>
<tr>
<td>5</td>
<td>24</td>
<td>0.001 ± 0.0004</td>
<td>0.007 ± 0.0004</td>
<td>0.62 ± 0.003</td>
<td>2.93 ± 0.01</td>
</tr>
<tr>
<td>6</td>
<td>23</td>
<td>−0.008 ± 0.0006</td>
<td>−0.009 ± 0.0003</td>
<td>0.54 ± 0.004</td>
<td>2.72 ± 0.02</td>
</tr>
<tr>
<td>7</td>
<td>48</td>
<td>−0.01 ± 0.0004</td>
<td>−0.003 ± 0.0004</td>
<td>0.67 ± 0.02</td>
<td>3.02 ± 0.1</td>
</tr>
<tr>
<td>8</td>
<td>18</td>
<td>0.009 ± 0.0004</td>
<td>−0.002 ± 0.0003</td>
<td>0.48 ± 0.002</td>
<td>2.58 ± 0.01</td>
</tr>
<tr>
<td>9</td>
<td>48</td>
<td>−0.003 ± 0.0006</td>
<td>−0.001 ± 0.0003</td>
<td>0.58 ± 0.01</td>
<td>2.83 ± 0.06</td>
</tr>
<tr>
<td>10</td>
<td>20</td>
<td>−0.002 ± 0.0006</td>
<td>−0.005 ± 0.0004</td>
<td>0.54 ± 0.008</td>
<td>2.73 ± 0.05</td>
</tr>
<tr>
<td>11</td>
<td>25</td>
<td>0.01 ± 0.0003</td>
<td>0.002 ± 0.0003</td>
<td>0.45 ± 0.002</td>
<td>2.49 ± 0.01</td>
</tr>
<tr>
<td>12</td>
<td>11</td>
<td>−0.001 ± 0.0002</td>
<td>0.003 ± 0.00007</td>
<td>0.49 ± 0.004</td>
<td>2.64 ± 0.03</td>
</tr>
<tr>
<td>13</td>
<td>24</td>
<td>−0.002 ± 0.0005</td>
<td>0.001 ± 0.0006</td>
<td>0.56 ± 0.02</td>
<td>2.76 ± 0.11</td>
</tr>
<tr>
<td>14</td>
<td>13</td>
<td>−0.004 ± 0.0004</td>
<td>0.0002 ± 0.0003</td>
<td>0.44 ± 0.003</td>
<td>2.48 ± 0.02</td>
</tr>
<tr>
<td>15</td>
<td>24</td>
<td>−0.005 ± 0.0002</td>
<td>−0.001 ± 0.0002</td>
<td>0.57 ± 0.002</td>
<td>2.79 ± 0.01</td>
</tr>
<tr>
<td>16</td>
<td>9</td>
<td>0.005 ± 0.0001</td>
<td>0.0001 ± 0.0001</td>
<td>0.58 ± 0.004</td>
<td>2.84 ± 0.03</td>
</tr>
</tbody>
</table>

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 variate 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<sub>C</sub>) and Akaike weights. The model with the lowest AIC<sub>C</sub> 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 (δ<sup>18</sup>O) and carbon (δ<sup>13</sup>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
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),

$$\delta = \left[ \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] \times 1000$$

where R represents the $^{13}$C/$^{12}$C or $^{18}$O/$^{16}$O. Replicate analyses indicate a reproducibility of ±0.2‰ 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/Fou-rier, 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 $\delta^{18}O$ and $\delta^{13}C$ values that range from $-12.3$ to $-9.5\%o$ and $-11.0$ to $-0.5\%o$, respectively.

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![Fig. 5. Biologs (trait means vs. relative time) for A, B, outline shape from Fourier analyses; C, outline length and D, shell area.](image-url)
(Table 3). The stable oxygen ($\delta^{18}O$) and carbon ($\delta^{13}C$) isotopic compositions of ostracods are interpreted to reflect diagentic alteration and thus cannot be used to augment paleoenvironmental interpretations. When $\delta^{18}O$ data are compared with values from Upper Carboniferous, open marine brachiopods that are interpreted to be unaltered (~3.5 to $-0.5\%_o$; Brand 1994; Grossman et al., 2002), the ostracod values are as much as $-11.8\%_o$ lower. The $\delta^{13}C$ values of Joggins ostracods are as much 17.5$\%_o$ lower than interpreted seawater values, which range from 1.0 to $6.5\%_o$ (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 $\delta^{18}O$ and $\delta^{13}C$ 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 $\delta^{18}O$ and $\delta^{13}C$ values in the Joggins ostracods are also consistent with low values from Carboniferous calcrites, a proxy for the chemistry of meteoric water, and other Carboniferous ostracods that have been altered by diagentic processes (Williams et al., 2006; Jutras et al., 2007; Bennett et al., 2011). Although such low $\delta^{18}O$ 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 $\delta^{13}C$ 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 Midland Valley of Scotland contained better-preserved ostracods than in the limestones (C.E. Bennett, personal communication, 2012).

**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).

<table>
<thead>
<tr>
<th>Trait</th>
<th>Type</th>
<th>GRW</th>
<th>URW</th>
<th>Stasis</th>
<th>Omega stasis</th>
</tr>
</thead>
<tbody>
<tr>
<td>CV1</td>
<td>Fourier</td>
<td>-103</td>
<td>-106</td>
<td>-109</td>
<td>0.03 0.14 0.83 2.6*10^{-5}</td>
</tr>
<tr>
<td>CV2</td>
<td>Fourier</td>
<td>-118</td>
<td>-120</td>
<td>-122</td>
<td>0.1 0.29 0.61 6.3*10^{-6}</td>
</tr>
<tr>
<td>Outline length</td>
<td>Size</td>
<td>18</td>
<td>15</td>
<td>9.8</td>
<td>0.01 0.67 0.92 0.075</td>
</tr>
<tr>
<td>Shell area</td>
<td>Size</td>
<td>-6.3</td>
<td>-9.9</td>
<td>-16</td>
<td>0.009 0.05 0.94 0.0154</td>
</tr>
</tbody>
</table>

**Table 3.** $\delta^{18}O$ and $\delta^{13}C$ 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.

<table>
<thead>
<tr>
<th>Sample</th>
<th>Description</th>
<th>$\delta^{18}O$ ($%_o$)</th>
<th>$\delta^{13}C$ ($%_o$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>JOG-C-25-O</td>
<td>Ostracod</td>
<td>-9.5</td>
<td>-0.5</td>
</tr>
<tr>
<td>JOG-C-18-O</td>
<td>Ostracod</td>
<td>-10.4</td>
<td>-8.1</td>
</tr>
<tr>
<td>JOG-13-O</td>
<td>Ostracod</td>
<td>-10.8</td>
<td>-11.0</td>
</tr>
<tr>
<td>JOG-C-7-O</td>
<td>Ostracod</td>
<td>-10.9</td>
<td>-5.1</td>
</tr>
<tr>
<td>JOG-5-O</td>
<td>Ostracod</td>
<td>-12.1</td>
<td>-5.1</td>
</tr>
<tr>
<td>JOG-4-O</td>
<td>Ostracod</td>
<td>-10.6</td>
<td>-7.3</td>
</tr>
<tr>
<td>JOG-C-1-O</td>
<td>Ostracod</td>
<td>-11.7</td>
<td>-7.9</td>
</tr>
<tr>
<td>Boss Pt-O</td>
<td>Ostracod</td>
<td>-9.9</td>
<td>-9.1</td>
</tr>
<tr>
<td>JOG-C-23-LS</td>
<td>Limestone</td>
<td>-7.7</td>
<td>-1.1</td>
</tr>
<tr>
<td>JOG-C-18-LS</td>
<td>Limestone</td>
<td>-9.0</td>
<td>-2.0</td>
</tr>
<tr>
<td>JOG-C-17-LS</td>
<td>Limestone</td>
<td>-10.8</td>
<td>-6.8</td>
</tr>
<tr>
<td>JOG-1-LS</td>
<td>Limestone</td>
<td>-10.3</td>
<td>-5.5</td>
</tr>
</tbody>
</table>

**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.
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