Exploring Evolutionary Patterns and Processes

A Case Study Using the Mesozoic Bivalve Buchia

by

Melissa Grey

M.Sc., The University of Guelph, 2001 B.Sc.(hon.), Acadia University, 1999

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

in

The Faculty of Graduate Studies

(Geological Sciences)

THE UNIVERSITY OF BRITISH COLUMBIA

(Vancouver)

February, 2009

© Melissa Grey 2009

Abstract

The fossil record is the only direct source of data for studying modes (patterns) and rates of morphological change over geologic time periods. Determining modes is critical for understanding macroevolutionary processes, but just how modes can vary within a taxon, and why, have hitherto been largely understudied. To address this, I examined patterns of morphological change in the shell of the Mesozoic marine bivalve genus *Buchia* over its geographic and temporal range. *Buchia* was chosen as a test subject because it is abundant, well-preserved across a variety of facies, and is widely distributed across the Northern Hemisphere where the likelihood of multiple lineages is low. While the focus of this thesis is on evolutionary patterns, it is also necessary to address issues of taxonomy and geographical variation, making this research applicable to a wide-variety of fields.

Previous to this study there was no protocol for measuring buchiid valves, nor was the genus studied in a quantitative manner. Throughout this research I used ten morphological characters to describe shell shape and size. Multivariate methods (principle component and canonical variate analyses) were employed to discriminate between species of *Buchia* and examine how morphological characters change through time and space within the genus. Evolutionary patterns were delineated using two well-established programs that discriminate between multiple modes of evolution. Overall, nearly 2000 specimens from eight geographical locations around the world were studied for this thesis.

I found the genus *Buchia* was a useful tool for evolutionary studies as it can be studied quantitatively in space and time. Specifically I have found that buchiid species can be delineated using morphometrics; the genus is restricted to the Northern Hemisphere; while the environment significantly affects morphology, there is no evidence of a latitudinal gradient; diversity and disparity within *Buchia* are not correlated; most evolutionary modes conformed to random walks or stasis; and modes and rates vary across the geographical range of the genus. Overall, I have found that the environment plays an important role in shaping both morphology and modes.

Table of Contents

| A | bstra | ${f ct}$ |
|---------------|--------|---|
| Tε | able c | of Contents |
| \mathbf{Li} | st of | Tables vi |
| \mathbf{Li} | st of | Figures |
| A | cknov | wledgements |
| D | edica | tion |
| \mathbf{St} | atem | ent of Co-Authorship |
| 1 | Intr | $\mathbf{roduction}$ |
| | 1.1 | Introductory Statement |
| | 1.2 | Background Information |
| | | 1.2.1 Biodiversity and Species Concepts |
| | | 1.2.2 Methodologies and Tools for Delineating Morphospecies 3 |
| | | 1.2.3 The Formation of Species |
| | | 1.2.4 Diversity and Disparity Estimates |
| | 1.3 | Research Statement |
| | 1.4 | Previous Work |
| | | 1.4.1 Buchiids |
| | | 1.4.2 Patterns in Space (Biogeography) 8 |
| | | 1.4.3 Patterns in Time (Modes and Rates) |
| | | 1.4.4 Patterns in Time and Space |
| | 1.5 | Purpose and Summary of Objectives |
| | 1.6 | Presentation |
| | 1.7 | Tables |
| | 1.8 | Figures |
| | 1.9 | References |
| | | |

| 2 | Spe Buo | cies Discrimination and Evolutionary Mode of <i>Buchia</i> (Bivalvia: chiidae) from Upper Jurassic to Lower Cretaceous Strata of |
|----------|--------------|---|
| | Gra | ssy Island, British Columbia, Canada |
| | 2.1 | Introduction |
| | 2.2 | Material and Methods |
| | | 2.2.1 Material $\ldots \ldots 24$ |
| | | 2.2.2 Morphometric Measurements |
| | | 2.2.3 Taxonomic Analyses |
| | | 2.2.4 Evolutionary Mode |
| | | 2.2.5 Correlation Between Lithology and Morphology 29 |
| | 2.3 | Results and Discussion |
| | | 2.3.1 Taxonomic Analyses |
| | | 2.3.2 Evolutionary Mode |
| | | 2.3.3 Correlation Between Lithology and Morphology |
| | 2.4 | Conclusions |
| | 2.5 | Tables |
| | 2.6 | Figures |
| | 2.7 | References |
| 3 | A N Car | New Species of <i>Buchia</i> (Bivalvia: Buchiidae) from British Columbia nada, with an Analysis of Buchiid Bipolarity |
| | 3.1 | Introduction |
| | 3.2 | Material |
| | 3.3 | Methods |
| | | 3.3.1 Morphometric Measurements |
| | | 3.3.2 Taxonomic Analyses |
| | 3.4 | Results and Discussion |
| | 3.5 | Systematic Paleontology |
| | 3.6 | Conclusion |
| | 3.7 | Tables 65 |
| | 3.8 | Figures |
| | 3.9 | References |
| 4 | Ма | mbalagical Variability in Time and Space, on Evenuela of Dat |
| 4 | ton | Within Duchiid Divelves (Divelvis, Duchiides) |
| | | Is within Buchind Divalves (Divalvia, Buchindae) |
| | 4.1 19 | Matorial 90 |
| | '±.∠ ∕ ? | Conoral Mathada |
| | ч.9 ДД | Coographical Variation of Shall Shape |
| | 4.4 | $\begin{array}{c} \text{Geographical variation of other shape} \dots \dots \dots \dots \dots \dots \dots \dots \dots $ |
| | | $\mathbf{G}_{\mathbf{G}}$ |

| | | 4.4.2 Results and Discussion |
|---|----------|--|
| | 4.5 | Latitudinal Gradient |
| | | 4.5.1 Methods and Results $\ldots \ldots $ 85 |
| | | $4.5.2 \text{Discussion} \dots \dots \dots \dots \dots \dots \dots \dots \dots $ |
| | 4.6 | Disparity and Diversity over Space and Time |
| | | $4.6.1 \text{Methods} \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots $ |
| | | 4.6.2 Results and Discussion |
| | 4.7 | Summary and Conclusions |
| | 4.8 | Tables 91 |
| | 4.9 | Figures |
| | 4.10 | References |
| _ | . | |
| 5 | Vari | ation in Evolutionary Patterns Across the Geographic Range |
| | of a | Fossil Bivalve |
| | 5.1 | Summary of Research (Article as Published in Science) |
| | 5.2 | Supporting Online Material |
| | | 5.2.1 Materials and Methods $\ldots \ldots \ldots$ |
| | | 5.2.2 Morphometric Measurements |
| | | 5.2.3 Morphological Change |
| | 5.3 | Tables |
| | 5.4 | Figures |
| | 5.5 | References |
| 0 | C | 1.40 |
| 0 | Con | $\begin{array}{c} \text{clusion} & \dots & $ |
| | 6.1 | Summary of Results |
| | 6.2 | Significance of Research and its Limitations |
| | 6.3 | Future Research |
| | 6.4 | References |

List of Tables

| 1.1 | Agents of selection as adapted from Allmon and Ross (1990) | 14 |
|-----------------------------------|---|----------|
| 2.1 | Variable means used to characterize shell morphology for each species of <i>Buchia</i> | 35 |
| 2.2 | Correlation of all morphological variables on the first two principal components. Variables are defined in Figure 2.3. | 36 |
| 2.32.4 | Classification summary for specimens from the Grassy Island section, contrasting the original with the cross-validated (based on a simu- lated jackknifed approach) results. Numbers in parentheses represent the percentage of correctly classified individuals. 68% of the original grouped cases were classified correctly according to Jeletzky's qual- itative assessments; 66% of the cross-validated grouped cases were correctly classified. $1 = B$. cf. blanfordiana; $2 = B$. okensis; $3 = B$. uncitoides; $4 = B$. tolmatschowi; $5 = B$. pacifica | 37 |
| | a Bonferroni correction. | 38 |
| 3.1 | Summary of collections used in analyses. All buchiid specimens are from the Southern Hemisphere, with the exception of B . cf. blan- fordiana. NIGP = Nanjing Institute of Geology and Palaeontology; | |
| 3.2 | GSC = Geological Survey of Canada; BAS = British Antarctic Survey. Correlation of all morphological variables on the first two principal components for the analysis on linear and angular measurements on buchiid left valves. Variables are defined in Figure 3.3 | 65 66 |
| | | |

| 3.3 | Classification summary (based on a jackknifing) for linear and angu- lar measurements of left valves of Northern and Southern Hemisphere material. Numbers in parentheses represent the percentage of classi- fied correctly individuals. Overall, 86% of cases were correctly clas- sified. $1 =$ Southern Hemisphere (<i>B. blanfordiana</i> and other related taxa); $2 =$ Northern Hemisphere (<i>B. cf. blanfordiana</i>) | 6 |
|-----|---|----|
| 3.4 | Classification summary (based on a jackknifing) for Fourier analysis on left valves of Northern and Southern Hemisphere buchiid mate- rial. Numbers in parentheses represent the percentage of correctly classified individuals. 81.4% of cases were correctly classified. $1 =$ Southern Hemisphere (<i>B. blanfordiana</i> and other related taxa); $2 =$ Northern Hemisphere (<i>B. cf. blanfordiana</i>) 6 | 57 |
| 4.1 | Summary of collections used in analyses. AU = Auckland University; BAS = British Antarctic Survey; UC = University of Copenhagen (Geological Museum of Denmark and Geological Institute); GNS = Institute of Geological and Nuclear Sciences (NZ); GSC = Geolog- ical Survey of Canada; NIGP = Nanjing Institute of Geology and Palaeontology; VSEGEI = All Russian Geological Research Institute. 9 | 1 |
| 4.2 | Correlation of all morphological variables on the first two principal components for all five principal component analyses performed in this study. $1-3 = B$. okensis, B. volgensis and B. unschensis, re- spectively, across their geographic ranges; $4 =$ all three species using location as the grouping variable; and $5 =$ all data from all loca- tions (used for latitudinal gradient analysis). Variables are defined in | |
| 4.3 | Figure 4.1 | 2 |
| 5.1 | Modes and rates for all geographical locations studied for the primary $(CV1)$ | 5 |
| 5.2 | Summary of the collections used in analyses. GSC = Geological Survey of Canada (Ottawa, Vancouver); NIGP = Nanjing Institute of Geology and Palaeontology; UC = University of Copenhagen (Geological Museum of Denmark and Geological Institute); VSEGEI = All Russian Geological Research Institute (St. Petersburg). B.C. = | J |
| | British Columbia. | 6 |

| 5.3 | Maximum-likelihood results for the Canadian Arctic: GRW repre- |
|-----|--|
| | sents a generalized random walk (= directional) and URW is an un- |
| | biased random walk (= random walk). Of the three models, the one |
| | with the lowest AIC_{C} and highest Akaike weight is the most appro- |
| | priate fit for the data (in bold). The number of stratigraphic intervals |
| | and the average number of individuals measured per interval for each |
| | section is found in Table 5.2 |
| 5.4 | Maximum-likelihood results for Grassy Island, British Columbia 127 |
| 5.5 | Maximum-likelihood results for Taseko Lakes, British Columbia 128 |
| 5.6 | Maximum-likelihood results for China |
| 5.7 | Maximum-likelihood results for Greenland |
| 5.8 | Maximum-likelihood results for Russia |

List of Figures

| 1.1 | Location map of buchiid fauna worldwide (adapted from Li and Grant- Mackie 1988). | 15 |
|-----|---|----------|
| 1.2 | Shape trends on the left value of the genus <i>Buchia</i> : curvoid; obliquoid; orthoid; inversoid, respectively (adapted from Zakharov 1987) | 15 |
| 2.1 | Location map of the stratigraphic section on Grassy Island, off the west coast of Vancouver Island, British Columbia (NTS map-area 92E/14) | 39 |
| 2.2 | Stratigraphic column of the Jurassic-Cretaceous succession exposed at Grassy Island, with key <i>Buchia</i> species photographs and valve shape information found within each zone. Bed-by-bed fossil collec- tions were made throughout the entire section at Grassy Island and were identified initially by J.A. Jeletzky. Details of the stratigraphic | |
| 2.3 | distribution of fossil collections are presented in Grey <i>et al.</i> (2007). Features used to characterize shell morphology in buchiid bivalves: 1, dorsalmost point (umbo) on hinge margin; 2, posteriormost point; 3, ventralmost point; 4, anteriormost point; 5, intersection of lines measuring maximum valve length and valve width; 6, point directly beneath highest point on left valve; 7, highest point on left valve. Morphological variables measured: ventral angle of crest-line* (I); dorsal angle of crest-line (J); dorsal length (Ld; 1-5); ventral length (Lv; 5-3); anterior width (Wa; 4-5); posterior width (Wp; 5-2); dor- sal distance to highest point on valve (Dd; 1-6); ventral distance to highest point on valve (Dv; 6-3); inflation (In; 6-7) and delta (Δ ; av- erage distance between concentric rings). *The "crest-line" is defined as the imaginary line joining the highest points of the left valve of | 40 |
| 2.4 | Buchia (Pavlow 1907) and has been recognized as a taxonomically valuable feature (Jeletzky 1966) | 41 42 |
| | | |

| 2.5 | PCA results showing clear separation in the morphospace for <i>B. paci</i> - | |
|------|---|----|
| | fica and B. cf. blanfordiana. | 43 |
| 2.6 | Results from the CVA for all of Jeletzky's assigned species from | |
| | Grassy Island, British Columbia. Axes CV1 and CV2 represent 69% | |
| | and 18.5% respectively of the character variation within the section. | |
| | CV1 represents crest-line variation (angles J and I on Fig. 3) and | |
| | CV2 represents shell inflation ("In" on Fig. 3) | 44 |
| 2.7 | CVA results showing clear separation of <i>B. pacifica</i> and <i>B. cf. blan</i> - | |
| | fordiana | 45 |
| 2.8 | PCA results from the Fourier analysis, illustrating overlap in the | |
| | morphospace for all of Jeletzky's assigned species from Grassy Island, | |
| | British Columbia. Axes PC1 and PC2 represent 45% and 25% respec- | |
| | tively of the character variation within the section. Fourier analyses | |
| | captured much less of the morphological variation in buchiid shells | |
| | than analyses using angles and linear measurements | 46 |
| 2.9 | PCA results from the Fourier analysis showing separation in the mor- | |
| | phospace for <i>B. pacifica</i> and <i>B.</i> cf. <i>blanfordiana</i> | 47 |
| 2.10 | Biolog created by plotting the canonical variate means (centroids) | |
| | for the first canonical variate (CV1) against stratigraphic position. | |
| | Outlines on the right are plots of the average shape of the shells as | |
| | they relate to the morphospace | 48 |
| 2.11 | Hurst estimate analysis of the evolutionary pattern described by the | |
| | stratophenetic series, with h values $\gg 0.5$ indicating increasing direc- | |
| | tionality and a gradualistic evolutionary mode | 49 |
| 2.12 | PCA results using lithology as the grouping variable from the section | |
| | at Grassy Island, British Columbia. Axes PC1 and PC2 represent | |
| | 70% and $15.4%$ respectively of the variation within the section. While | |
| | there is a clear separation in the morphospace at the disconformity | |
| | between the mudstones of the lower part of the section (Kapoose | |
| | Formation) and the coarser-grained lithofacies in the upper part of the | |
| | section (One Tree Formation), shell morphology does not appear to | |
| | be highly related to lithofacies, taken as a proxy for paleoenvironment. | 50 |
| 2.13 | PCA results, with only the group means plotted, using lithology | |
| | as the grouping variable from the section at Grassy Island, British | |
| | Columbia. Axes PC1 and PC2 represent 70% and 15.4% respectively | |
| | of the variation within the section. There is no obvious trend in mean | |
| | shape from coarse to fine facies | 51 |

| 3.1 | Location map of buchiid faunas worldwide (adapted from Li and Grant-Mackie, 1988). Not pictured: Alexander Island, western Antarc- | |
|-----|---|----|
| | tica. Circles indicate the occurances of the genus <i>Buchia</i> , while squares indicate the genus <i>Australobuchia</i> | 68 |
| 3.2 | Representative suite of specimens used for analysis: Figs 1-9. <i>Buchia columbiana</i> n. sp., all from Grassy Island, BC, GSC Locality 18366. 1-3, holotype, GSC 34955. 1, left valve. 2, right valve. 3, side-view. | |
| 3.3 | view. 7-9, paratype, GSC 34950. 4, left valve. 5, light valve. 6, side-view. 7-9, paratype, GSC 34957. 7, left valve. 8, right valve. 9, side-view. Figs 10-12. <i>B. blanfordiana</i> from Muktinath, Nepal, GSC collections. 10, left valve. 11, right valve. 12, side-view. Figs 13-15. <i>B. spitiensis</i> from Jarlemai Siltstone Formation, NW Australia, GSC plaster cast. 13, left valve. 14, right valve. 15, side-view. Figs 16-18. <i>M. malayomaorica</i> from Kawhia Harbour, New Zealand. 16, left valve. 17, right valve. 18, side-view. Figs 19-21. <i>B. plicata</i> from Mangoli Quarry, New Zealand, GSC plaster cast. 19, left valve. 20, right valve. 21, side-view. | 69 |
| 0.0 | 1, dorsalmost point (umbo) on hinge margin; 2, posteriormost point; 3, ventralmost point; 4, anteriormost point; 5, intersection of lines measuring maximum valve length and valve width; 6, point directly beneath highest point on left valve; 7, highest point on left valve. Morphological variables measured: ventral angle of crest-line* (I); dorsal angle of crest-line (J); dorsal length (Ld; 1-5); ventral length (Lv; 5-3); anterior width (Wa; 4-5); posterior width (Wp; 5-2); dor- sal distance to highest point on valve (Dd; 1-6); ventral distance to highest point on valve (Dv; 6-3); inflation (In; 6-7) and delta (Δ ; av- erage distance between concentric rings). *The "crest-line" is defined as the imaginary line joining the highest points of the left valve of | |
| 3.4 | as the imaginary line joining the highest points of the left valve of <i>Buchia</i> (Pavlow 1907) and has been recognized as a taxonomically valuable feature (Jeletzky 1966) | 70 |
| | component axis | 71 |

| 3.5 | PCA results from the Fourier analysis using the left valve show over- lap in the morphospace between <i>B</i> . cf. <i>blanfordiana</i> and <i>B</i> . <i>blanfor- diana</i> . Representative specimen images of <i>B</i> . <i>plicata</i> (left), <i>B</i> . <i>blan- fordiana</i> (middle), and <i>B</i> . cf. <i>blanfordiana</i> (right) are overlaid. Inset: | - |
|-----|--|----|
| 3.6 | % of variation explained by each principal component axis | 72 |
| 3.7 | Histograms of the canonical variate from the discriminant analy- sis between Northern Hemisphere ($B.$ cf. blanfordiana) and South- ern Hemisphere ($B.$ blanfordiana and related species) material using Fourier analyses on the left valves of buchiid specimens: histograms of the canonical variate indicate a significant difference between the two | 73 |
| 4.1 | Features used to characterize shell morphology in buchiid bivalves: 1, dorsalmost point (umbo) on hinge margin; 2, posteriormost point; 3, ventralmost point; 4, anteriormost point; 5, intersection of lines measuring maximum valve length and valve width; 6, point directly beneath highest point on left valve; 7, highest point on left valve. Morphological variables measured: ventral angle of crest-line* (I); dorsal angle of crest-line (J); dorsal length (Ld; 1-5); ventral length (Lv; 5-3); anterior width (Wa; 4-5); posterior width (Wp; 5-2); dor- sal distance to highest point on valve (Dd; 1-6); ventral distance to highest point on valve (Dv; 6-3); and inflation (In; 6-7). *The "crest- line" is defined as the imaginary line joining the highest points of the left valve of <i>Buchia</i> (Pavlow 1907) and has been recognized as a | |
| 4.2 | taxonomically valuable feature (Jeletzky 1966) Buchiid geographical range (white/grey circles and squares); circles indicate <i>Buchia</i> (Northern Hemisphere buchiids) locations, while squares indicate locations of <i>Australobuchia</i> (Southern Hemisphere buchiids) (modified after Li and Grant-Mackie, 1988). Grey enclosures indicate locations of material used in this study. Not pictured: Alexander Is- | 94 |
| 4.3 | land, western Antarctica | 95 |
| | priori grouping variable. | 96 |

xii

| 4.4 | Scatterplot from the canonical variate analysis (CVA) for <i>B. okensis</i> where location is the <i>a priori</i> grouping variable. 94% of specimens were correctly classified according to their geographic location; this |
|------|---|
| | indicates that most specimens differ enough in morphology between locations that they can be categorized to their geographical origin |
| | CV1 was a function of primarily posterior width (Wp, Figure 4.1) |
| 4.5 | and CV2 was a function of primarily anterior width (Wa, Figure 4.1). 97 Scatterplot from the PCA for $B.$ volgensis, using location as the a |
| 4.6 | priori grouping variable, showing overlap in the morphospace. \dots 98 Scatterplot from the CVA for <i>B</i> valuencies 75% of specimens were |
| 4.0 | correctly classified according to their geographic location. CV1 was a function of primarily inflation (In, Figure 4.1) and CV2 was a function |
| | of primarily ventral angle of crest-line (angle I, Figure 4.1) 99 |
| 4.7 | Scatterplot from the PCA for <i>B. unschensis</i> , using location as the |
| | <i>a priori</i> grouping variable, showing considerable overlap in the mor- |
| 4.8 | Scatterplot from the CVA for <i>B. unschensis.</i> 53% of specimens were |
| | correctly classified according to their geographic location. CV1 was a |
| | function of primarily inflation (In, Figure 4.1) and CV2 was a function |
| 49 | of primarily dorsal angle of crest-line (angle 1, Figure 4.1) 101 Scatterplot from the PCA of data from three species (<i>B</i> volgensis <i>B</i> |
| 1.0 | unschensis and B. okensis) that are found in some or all of the follow- |
| | ing six locations: Arctic, China, Grassy Island, Greenland, Russia, |
| 4 10 | and Taseko Lakes. Species was used as the <i>a priori</i> grouping variable. 102 |
| 4.10 | Scatterplot from the UVA of data from three species (<i>B. volgensis</i> , <i>B. unschensis</i> and <i>B. okensis</i>) that are found in some or all of the |
| | six locations, using species as the <i>a priori</i> grouping variable. 75% of |
| | specimens were correctly classified according to their species designa- |
| | tion. CV1 was primarily a function of ventral length (Lv, Figure 4.1) |
| 1 11 | and CV2 was primarily a function of inflation (In, Figure 4.1) 103 Scatterplot from the CVA of data from three spacies (B valuencie |
| 7.11 | B. unschensis and B. okensis) that are found in some or all of the |
| | six locations, using location as the <i>a priori</i> grouping variable. 71% of |
| | specimens were correctly classified according to their geographic lo- |
| | (Wp, Figure 4.1) and CV2 was primarily a function of antorior width (Wp, Figure |
| | 4.1). \ldots |
| 4.12 | The first principal component (using location as the grouping vari- |
| | able) versus paleolatitude (y = $-0.01x + 0.41$, R ² = 0.16) 105 |

| 4.13 | The primary canonical variate (using location as the grouping variable) versus paleolatitude ($y = -0.02x + 0.80$, $R^2 = 0.68$). CV1 was primarily a function of ventral length (Lv, Figure 4.1) and CV2 was primarily a function of posterior width (Wp Figure 4.1) | 106 |
|------|---|------------|
| 4.14 | Diversity versus disparity and their corresponding error bars (the calculations for these are described in the text) over the geograph- ical range of buchids used in this study. There is not a significant | 107 |
| 4.15 | correlation between the two metrics | 107 |
| 4.16 | Discordance and concordance between diversity and disparity through the temporal range of buchids (the calculations for error bars are described in the text). | 109 |
| 5.1 | Locations of collection material used in this study (grey circles) across the geographic range of the genus <i>Buchia</i> (grey and white circles), modified from Li and Grant-Mackie (1988). Squares represent the newly-recognized and closely related genus <i>Australobuchia</i> (Grey <i>et</i> | 100 |
| 5.2 | al. 2008b; Hikuroa and Grant-Mackie 2006) | 130 131 |
| 5.3 | Features used to characterize shell morphology in buchild bivalves: 1, dorsalmost point (umbo) on hinge margin; 2, posteriormost point; 3, ventralmost point; 4, anteriormost point; 5, intersection of lines measuring maximum valve length and valve width; 6, point directly beneath highest point on left valve; 7, highest point on left valve. Morphological variables measured: ventral angle of crest-line* (I); dorsal angle of crest-line (J); dorsal length (Ld; 1-5); ventral length (Lv; 5-3); anterior width (Wa; 4-5); posterior width (Wp; 5-2); dor- sal distance to highest point on valve (Dd; 1-6); ventral distance to highest point on valve (Dv; 6-3); inflation (In; 6-7) and delta (Δ ; av- erage distance between concentric rings). *The "crest-line" is defined as the imaginary line joining the highest points of the left valve of Buchia (Pavlow 1907) and has been recognized as a taxonomically | |
| | valuable feature (Jeletzky 1966) | 132 |

| 5.4 | Morphological change in the primary canonical axis (CV1) over rel- | |
|-----|---|----|
| | ative time for each of the six locations studied: A) Canadian Arctic; | |
| | B) Grassy Island, Canada; C) Taseko Lakes, Canada; D) eastern | |
| | Heilongjiang Province, China; E) East Greenland; and F) Far East | |
| | Russia (S. Primorye). CV1 represents the linear combination of vari- | |
| | ables that best separates between stratigraphic intervals (i.e. shows | |
| | the most change) | 34 |
| 5.5 | Hurst estimate analysis for buchiids from the stratigraphic sections | |
| | at: A) Canadian Arctic; B) Grassy Island, Canada; C) Taseko Lakes, | |
| | Canada; and D) East Greenland. A weakly directional evolutionary | |
| | mode is interpreted for Grassy Island (average $h = 0.7$, average P = | |
| | 0.4); stasis is interpreted for Greenland (average $h = 0.14$, average | |
| | P = 0.99; and the Arctic (average $h = 0.2$, average $P = 0.91$) and | |
| | Taseko Lakes (average $h = 0.33$, average $P = 0.85$) show random walks. | 35 |
| 5.6 | Evolutionary rate (delta, Δ) histograms for the multivariate analysis | |
| | of buchiid morphology for the stratigraphic sections at: A) the Cana- | |
| | dian Arctic; B) Grassy Island, Canada; C) Taseko Lakes, Canada; | |
| | D) eastern Heilongjiang Province, China; E) East Greenland; and F) | |
| | Far East Russia (S. Primorye). Hatched patterns represent stabilizing | |
| | selection and black represents genetic drift | 36 |

Acknowledgements

I am a very lucky person to have so many wonderful and supportive people in my life. I firstly have to express my sincerest thanks to my advisors, Jim Haggart and Paul Smith, who supported me every step of the way. Their interest and enthusiasm, generous funding, and advice have made them an absolute pleasure to work with. Jim, in particular, got me started on this adventure and for that I will always be most thankful.

Thanks to Stuart Sutherland for his input as a member of my committee and for keeping up my humour.

My lab-mates Andrew Caruthers, Emily Hopkin, Louise Longridge, and Farshad Shirohammad offered much advice, laughter, and interesting conversation. Thankyou for being such fun!

A very special thanks to: T. Bogdanova, E. Kalacheva, and I. Sey (All-Russian Geological Institute (VSEGEI)); A. Crame (British Antarctic Survey); J.S. Crampton (Geological and Nuclear Sciences of New Zealand); J. Dougherty (Geological Survey of Canada); J. Grant-Mackie, D. Hikuroa, and N. Hudson (Auckland University); D.A.T. Harper and J. Rassmussen (Geological Museum, Copenhagen); P. Alsen and F. Surlyk (Geological Institute, Copenhagen); and J. Sha (Nanjing Institute of Geology and Palaeontology) for use of their collections and gracious hospitality; to P.G. Lelièvre for creating the MatLab morphometrics programs (MorphLab 1.0); and to G. Hunt and P. Roopnarine for their help and use of their program codes for analysing mode.

My husband (Peter Lelièvre), parents (Pam and Don Grey), family (Linda Sweet and Pearl Wolsh), and dearest friends (Holly Bourne, Arlene Doucette, Thomas Egli, Sarah Foster, Keith Patterson, Marc Raymond, Julie Scott-Ashe, and Jody Weir) have all been incredibly supportive. My sincere thanks for being there through the best and worst times - what would I have done without you? Thanks also to my dog, Noah, for providing endless amounts of cuddles and entertainment.

Financial support was provided by Paul Smith, the Department of Earth and Ocean Sciences, and a Graduate Fellowship from NSERC.

Dedication

To my husband Peter, my partner in every way, who provided insight, elbow grease (who else would spend their weekend helping me format my thesis?!), love, and encouragement.

Statement of Co-Authorship

This thesis results from the work and leadership of Melissa Grey. Melissa is principally responsible for performing the research and data analysis and virtually all manuscript content. This research produced co-authored papers with J.W. Haggart and P.L. Smith who provided advisory roles including the discussion of techniques, collections, data analysis, and conclusions. They also had editorial roles.

Chapter 1

Introduction

1.1 Introductory Statement

Studies of evolutionary patterns are essential to our understanding of the processes involved in organismal diversification (speciation) over geologic time. Speciation, the formation of new biological species, and macroevolutionary patterns in general, comprise the least understood major features of evolution. However, a comprehensive understanding of speciation is of critical importance as it is a principal factor in the maintenance of biodiversity, a key aspect of conservation biology. Currently, biodiversity is a particularly important topic as many are declaring that the world has entered into a biodiversity crisis (e.g. Wilson 1993; Lawton and May 1995; Pimm *et al.* 1995; Thomas *et al.* 2004a; Thomas *et al.* 2004b), heralded by some as the "sixth mass extinction" (e.g. Leakey and Lewin 1995). Fortunately, the fossil record offers a two dimensional perspective for evolutionary studies because patterns can be explored in both space and time. Buchiid bivalves, of the Late Jurassic to Early Cretaceous, provide a powerful and, to date, unique tool for the study of evolutionary patterns in the fossil record.

1.2 Background Information

1.2.1 Biodiversity and Species Concepts

Biodiversity is often measured in terms of species numbers. Species are the most basic unit of the biological taxonomic hierarchy and their definition is the subject of continued debate. While many different species concepts have been proposed, at least three are widely accepted: the biological, phylogenetic, and morphospecies concepts. While these and other species concepts differ from each other, there are some fundamental points that are common to them all: species are groups of interbreeding populations; species are a fundamental unit of evolution; and groups of species evolve independently of each other.

The biological species concept is commonly used by biologists and is the legal definition employed by the Endangered Species Act and Species at Risk Act, each representing the flagship biodiversity legislation in the United States and Canada, respectively. The critical point in the biological species concept is reproductive isolation; this is useful because it confirms lack of gene flow, but it is often hard to assess in living biological populations, and even more so in fossil populations.

The phylogenetic or evolutionary species concept focuses on monophyletic groups, those that contain all the known descendants of a single common ancestor. In this species concept, species are the smallest diagnosable unit within the monophyletic group and are identified by interpreting the phylogeny (evolutionary relationships) of closely related populations; therefore, any population forming an isolated branch of the main phylogenetic stem is considered a distinct species. The distinguishing factor between different species is a "species-specific trait" that may be as trivial as a slight, although statistically significant, site substitution in DNA. Among many arguments against using the phylogenetic species concept, one key factor is that phylogenies are often difficult to construct, for both recent and fossil populations.

Paleontologists specifically rely on the morphospecies concept, where species are defined by morphological differences. When rigorous tests of reproductive isolation or well-estimated phylogenies are lacking (as is often the case), contemporary biologists also employ this concept. The central feature of this concept is that morphological differences represent genetic differences; an advantage of the concept is that it can be widely and easily applied - but used inappropriately, however, it can be biologically meaningless! The best study exemplifying this species concept in the fossil record is the work undertaken on bryozoans by Jackson and Cheetham (1990, 1994), who showed that morphospecies are indeed genetically different from each other. This also holds true for other organisms as well, for example, gastropods (Michaux 1989), corals (Budd and Johnson 1996), and Foraminifera (Huber *et al.* 1997).

1.2.2 Methodologies and Tools for Delineating Morphospecies

A common method of applying the morphological species concept is through phenetic discrimination. This is often based on multiple morphological characters, where groups that occupy a single morphospace (separation from other groups based on numerous morphological traits) are considered unique species. Landmark-based techniques utilize homologous (sharing a common ancestor) points for comparisons and are statistically more powerful than traditional techniques using linear and angular measurements or Fourier (outline) analysis, but all have been applied successfully and extensively (see Budd and Potts 1994; Crampton 1995; and Kowalewski *et al.* 1997 for respective examples of each procedure). Buchiid fossils lack homologous points and therefore preclude the use of landmark-based methods.

The primary statistics used for traditional methods of phenetic discrimination are principal component analysis (PCA) and discriminant or canonical variate analysis (DA or CVA). PCA is a technique that summarizes the variation among individuals by condensing information from many correlated variables into a few quantities. CVA produces an ordination of the data in two dimensions that best reflects the Mahalanobis distances (a measure of distance between two points in multivariate space) among the means of all variables (i.e. group centroids) and is used for predictive classification. Fourier (outline shape) analyses are ideal for organisms such as *Buchia* bivalves because these fossil types lack homologous points on their shells. Outline shape is also a key morphological character that, in most bivalves, reflects both phylogenetic history and function and life habit (Crampton 1995). Fourier coefficients can be standardized for size based on shell area, allowing analyses to be based solely on shape changes. PCAs and CVAs can then be performed on the resulting suite of Fourier coefficients.

1.2.3 The Formation of Species

Species form through isolation (physical or otherwise) by reducing or eliminating gene flow. Once gene flow has been diminished, the primary evolutionary forces that allow species divergence to occur are genetic drift, natural selection, and mutation.

Genetic drift is the random fixation and loss of alleles and is most pronounced in small populations. Speciation as a result of drift has been controversial and some evidence suggesting the minimal effect of drift has been presented by Grant and Grant (1996), who showed that, while over the last 150 years there have been hundreds (if not more) of small populations introduced to new habitats due to human activity, few, if any, of these studies have demonstrated dramatic changes in genotypes due to drift.

Natural selection acts on individuals rather than populations and requires that certain (not random) variants in a population do better than others. The variants that do better will survive to reproduce and transfer their specific traits, or genes, to the next generation. Since evolution is a response to selection, it can only occur when traits have a genetic basis. Selection therefore produces adaptations in the form of a trait or suite of traits that allow its possessor to succeed in the face of one or more agents of selection. Agents of selection are, in essence, potential controls on evolution and include abiotic, biotic, intrinsic, and extrinsic factors (Table 1.1).

There is significant debate about the importance of natural selection as an evolutionary force; Gould and Eldredge (1993), for instance, stated that selection alone could not be responsible for the large-scale changes observed in the fossil record. A common measure for expressing the strength of selection is obtained by calculating the multivariate selection gradient (where the gradient is a vector of partial regression coefficients) from a multiple regression, with the various traits as the independent variables and relative fitness as the dependent variable (Lande and Arnold 1983). It is important to use multivariate methods for determining which traits in a correlated group are the focus of direct selection, as phenotypic correlations among traits are very common and natural selection acts on many characters simultaneously (Lande and Arnold 1983). Selection has often been measured in biological studies (see Endler 1986; Kingsolver *et al.* 2001; and Hereford *et al.* 2004 for reviews) and ranges from small to relatively large values (ranging from -1 to 1, with an overall median of 0.16), but it is rare that it can be measured for fossils (but see Pachut and Anstey 2004 and Grey *et al.* 2006 for examples). Recent neontological work has found that natural selection has often been underestimated and can actually be quite strong (Hereford *et al.* 2004).

Mutation is the final major evolutionary force and is a source of new genetic makeup (in the form of new alleles and genes). A mutation is specifically an alteration of DNA (genotype) that may or may not produce an expression in an organism's phenotype. It is the ultimate source of genetic variation and therefore provides the raw material for evolution; but mutation itself is not a powerful evolutionary force - only when combined with drift or selection, can mutation be strong.

1.2.4 Diversity and Disparity Estimates

While only approximately 1.7 million species have been identified and named (Heywood and Watson 1995), current estimates for the global diversity of living species ranges from 10 to 100 million (Pimm *et al.* 1995; Stork 1996). By comparison with current diversity estimates, there are only approximately 250,000 named fossil species (Raup 1976). This is likely to be a gross underestimate of actual numbers, however, because only a very small number of species are likely to ever become fossilized. In paleontology, values of taxonomic diversity (calculated as numbers of species) are often supplemented with those of disparity (morphological diversity), leading to an improved understanding of the processes of diversification and extinction. The relationship between the two metrics can also yield useful information about evolutionary mechanisms and these have been studied over geographical ranges (Moyne and Neige 2007), during periods of known extinctions (e.g. Villier and Korn 2004), during faunal invasions (Navarro *et al.* 2005), and over the temporal range of a taxon (e.g. blastoids: Foote 1991; crinoids: Foote 1999; angiosperms: Lupia 1999; cuttlefish: Neige 2003). Disparity can be calculated by a variety of methods, but among the most common is to use the sum of variances of scores on the first three principal components from a principal component analysis (Villier and Eble 2004).

A variety of approaches for estimating current extinction rates suggest that extinctions today are occurring at a rate of 100 to 1000 times the normal, or background, extinction rate and that in the coming centuries the Earth will experience a mass extinction on the same scale as those documented in the fossil record (Smith *et al.* 1983a, b). Contributions from evolutionary biology and paleontology to conservation include: the identification of species; producing phylogenies that can help inform decisions about conservation priorities (e.g. higher priority to phylogenetically distinct taxa); identifying biodiversity "hotspots"; using the fossil record as a baseline for diversity and trends (i.e. before human activity); and finally, using the fossil record to document long periods of evolutionary patterns in order to infer processes.

1.3 Research Statement

Identifying controls on the tempo and mode of evolution should provide important insights into patterns and processes of speciation, and of evolution in general (Simpson 1944). Research deciphering evolutionary patterns in the fossil record requires a strict protocol that is not often met by most studies: fine-scale resolution; sampling from sections distributed over the geographic range of the taxa; and biometric capture of morphology are all minimal requirements for studies of temporal patterns (Erwin and Anstey 1995). Erwin and Anstey (1995) call for new work on tempo and mode of speciation as a function of different environments, life history strategies, geographic settings, and geological times. The research presented in this thesis represents such a contribution.

This thesis contains three broad themes that are widely applicable to the fields of evolution, conservation, and biostratigraphy:

- 1. how morphology varies across geographic range;
- 2. how patterns of evolution vary over the geographic range of a genus; and
- 3. inferring influences on evolution from observed patterns.

The temporal resolution of buchild bivalves makes them an ideal candidate for the study of evolutionary patterns as they are geographically widespread in Upper Jurassic and Lower Cretaceous rocks and are found in abundance within short, successive stratigraphic intervals. *Buchia* has previously been studied primarily for stratigraphic correlation and, until recently, there have been few studies addressing their evolutionary development and history.

1.4 Previous Work

1.4.1 Buchiids

The family Buchiidae, now placed in the superfamily Monotoidea (Begg and Campbell 1985), was distributed widely in marine environments on most continents (Figure 1.1) from the Late Triassic to the Early Cretaceous. The genus *Buchia*, the last known representative of the family, is known only from the Late Oxfordian (Late Jurassic) to Hauterivian (Early Cretaceous) (Zakharov 1981). Buchiids were epifaunal, attached filter feeders that formed reef-like structures in some locations (Zakharov 1981). The genus *Buchia* is among the most biostratigraphically important bivalve genera of the Cretaceous (Kauffman 1973) and has traditionally been used to provide zonal indices for intervals of the Upper Jurassic to the Lower Cretaceous in the Northern Hemisphere (Jeletzky 1965; Surlyk and Zakharov 1982; Zakharov 1987; Sey and Kalacheva 1999; and others). *Buchia* species are biochronologically valuable because they are abundant in a variety of facies, geographically widely distributed, characterized by a high rate of evolution, and readily determined taxonomically by focusing on morphological characteristics such as shell sculpture and shape, beak incurvature, and shape of the bysuss ear (Jeletzky 1965).

While structures such as the bysuss ear and parts of the right ligamental plate can change considerably over geologic time, these rarely preserved features cannot be measured and, therefore, cannot be used for statistical analyses. More easily recognizable are the changes in the beak orientation and overall shape of the shell. The four primary buchiid shape trends exhibited through time are inversoid (late Jurassic), orthoid (early Berriasian), obliquoid (late Berriasian), and curvoid (early Valanginian) (Figure 1.2) (Zakharov 1981, 1987). Based on evolutionary trends, Jeletzky (1965) proposed new fossil zones for the western Canadian Cordillera, British Columbia. These "Buchia zones" are still in use today and include the B. cf. blanfordiana, B. okensis, B. uncitoides, B. tolmatschowi and B. pacifica zones (Jeletzky 1965).

Despite their use in biostratigraphy, there have been few quantitative studies on buchild bivalves (but see Crampton 1994) and even standard measurement parameters for the valves have not been established. The morphological evolution of buchilds has rarely been considered and has never been previously studied using quantitative measures.

1.4.2 Patterns in Space (Biogeography)

The study of geographical variation is crucial as there is a growing body of evidence showing that it is a primary determinant of biodiversity gradients (Allen and Gillooly 2006) - a timely topic as many scientists believe that the world has entered into a biodiversity crisis (e.g. Pimm *et al.* 1995). Geographical variation has been the subject of numerous paleontological and biological investigations and this research has addressed: intraspecific versus environmental variation (e.g. Crampton 1996; Stempien *et al.* 2002; Stempien and Kowalewski 2004); disparity (morphological diversity) estimates (e.g. Foote 1991, 1993; Villier and Korn 2004); comparisons of taxonomic diversity and disparity (e.g. Moyne and Neige 2007); and paleoenvironmental reconstruction potential (e.g. Aguirre *et al.* 2006). Few studies, however, have considered the variation of a genus over its geographic range (but see Courville and Cronier 2005, and Crampton and Gale 2005). This area of research can provide evidence of how morphological patterns vary both spatially and temporally. How the genus, and the species therein, are affected by geography is also of critical importance to its usefulness in biostratigraphy.

According to Crame (1993), members of the family Buchiidae represent the most conspicuous example of Late Jurassic bipolarity (high latitude distribution). Bipolar genera may have existed through the greater part of Late Jurassic-Early Cretaceous time due to global climatic zonation and, ultimately, tectonic events, such as the final break-up of the supercontinent Pangaea (Crame 1993). Debate has continued regarding whether *Buchia senso stricto* had a bipolar distribution - standard doctrine has assumed that the genus is found in both the Northern and Southern Hemispheres, although some workers have suggested that it is restricted to the Northern Hemisphere and that closely related, but apparently different genera (e.g. *Australobuchia*; *Malayomaorica*) are found in the Southern Hemisphere (Jeletzky 1963; Zakharov 1981, 1987). Research in this thesis specifically addresses this debate.

1.4.3 Patterns in Time (Modes and Rates)

One of the fundamental steps towards obtaining a deeper understanding of evolutionary processes is to first decipher patterns of evolutionary tempo and mode (Simpson 1944). The quantification of tempo and classification of mode of evolution in the fossil record has improved over the past six decades, but many important questions remain. At a basic level, the relative frequencies of various modes of evolution have not been fully addressed (see Erwin and Anstey 1995; Jackson and Cheetham 1999; and Benton and Pearson 2001 for reviews) and this is primarily because of the wide-ranging variation in methodologies used for determining evolutionary mode (e.g. Bookstein 1987, 1988; Hannisdal 2007; Hunt 2006; Lynch 1990; Roopnarine 2001 and others). Other issues, such as what factors determine mode, how mode and rate relate to each other, and the relative importance of natural selection on evolution, are far from being resolved.

In recent reviews of the literature, many have begun to look for patterns of mode. For instance, research has revealed that planktonic organisms are more likely to exhibit patterns of gradualism, whereas benchic organisms exhibit patterns of stasis and punctuations (e.g. Benton and Pearson 2001; Hunt 2007). This pattern fits in well with Sheldon's (1996) "plus ca change" model, where he relates mode with environment: organisms in fluctuating environments are more likely to display patterns of stasis whereas those in stable environments are more likely to exhibit gradual patterns. Hunt (2007) reanalyzed many fossil lineages in light of his newly developed method for determining mode and found that only 5% of cases supported directional evolution, whereas 95% supported (nearly equally) stasis or random walks. This finding does not negate the importance of natural selection, but it does indicate that selection only acts over geologically short periods of time. The prominence of random walks also does not necessarily support random genetic drift as the primary evolutionary force; rather, it could indicate adaptive optima that meander over time and under a variety of conditions. As Hunt (2007) indicates, linking pattern with process is still controversial because evolutionary mode can be consistent with a variety of microevolutionary circumstances, but this type of research is useful nevertheless.

1.4.4 Patterns in Time and Space

To my knowledge, there have been no studies of evolutionary mode over the geographic range of a taxon.

1.5 Purpose and Summary of Objectives

The purpose of this research is to use the genus *Buchia* as a test subject for understanding patterns of evolution and speciation, or, more specifically, to study the variation of evolutionary tempos and modes within the genus over its geographical range. Once patterns are deciphered, processes can then be inferred. This work should also have important implications for our understanding of *Buchia* itself and its use for biostratigraphic purposes. Specific objectives are to:

- 1. Develop a standard protocol for measuring buchild bivalves, similar to those existing for other biostratigraphically important groups, such as inoceramids;
- 2. Evaluate the current taxonomy and biostratigraphy of *Buchia* in the Northeast Pacific subprovince. My hypothesis is that if traditional measures (i.e. angular and linear measurements) of valves can distinguish between buchiid species in the Northeast Pacific subprovince, then morphometrics should be a useful tool for assessing the taxonomy of the genus *Buchia* worldwide;
- 3. Assess buchiid bipolarity through a comparative study with Southern Hemisphere *B. blanfordiana* and Northern Hemisphere *B.* cf. *blanfordiana*. My hypothesis is that if populations are not distinct between hemispheres, then *Buchia* is a bipolar genus. The alternative hypothesis is that if populations are distinct, then *Buchia* is not a bipolar genus and Northern and Southern Hemisphere buchiids should thus be differentiated taxonomically;
- 4. Assess biogeographic variation of *Buchia* morphology in order to determine what affects morphological variation. My hypothesis is that if the amount of biogeographical variation is large, then this indicates the importance of

geography, and presumably the environment, on morphology. If this is the case, this may have a profound effect on the value of the genus *Buchia* for biostratigraphic purposes. If biogeographic variation is small, then individual species should be easily recognizable over their range and will have a negligible effect on biostratigraphy;

- 5. Compare disparity and diversity over time and space. My hypothesis is that diversity and disparity metrics will not be correlated, as found in previous studies with other taxa, but will both decline at the end of the genus' extinction; and
- 6. Determine and compare evolutionary patterns of *Buchia* species over their geographic range in order to understand what influences tempo and mode of evolution. My hypothesis is that if modes and rates are different between locations, this indicates an environmental control on evolution. Alternatively, if modes and rates are similar, this indicates a genetic control.

1.6 Presentation

The body of this thesis consists of four chapters (Chapters 2-5) and each chapter represents a self-contained research article: Chapters 2 and 3 are published, Chapter 4 is in review, and Chapter 5 has been preliminarily accepted (see the footnotes at the start of each chapter for publication information). The chapters are arranged in the order the research was conducted - for instance, before analysing modes of evolution across the geographic range of the genus, it was necessary to first establish a protocol for the measurement of the valves and the statistical methods used throughout the entire study. While the manuscript-based approach to writing a dissertation is advantageous in that it results in rapid dissemination of results to the scientific community, some redundancy within the text, figures, and tables contained between chapters is inevitable.

Chapter 2 describes research involving the biometrics of *Buchia* bivalves and its application to species identification. It also aims to quantitatively identify the mode

of evolution within the section studied.

Chapter 3 explores the proposed bipolarity of the genus *Buchia* by studying populations of buchiids from the Northern and Southern Hemispheres.

Chapter 4 is a study on the morphological variability of buchiids in space and time, including potential latitudinal gradients, and compares the metrics of diversity and disparity. Material is from eight locations from the Northern and Southern Hemispheres.

Chapter 5 is a comprehensive study of evolutionary patterns of Buchia from six locations across the Northern Hemisphere.

1.7 Tables

| | Extrinsic | Intrinsic |
|---------|-------------------|------------------------------|
| | (= environmental) | (= genetics $)$ |
| Biotic | Predators | Adaptations |
| | Competition | Constraints |
| Abiotic | Climate | Surface-volume relationships |
| | Mass extinctions | Calcite growth |
| | Substrate | |
| | Sea level | |

Table 1.1: Agents of selection as adapted from Allmon and Ross (1990).

1.8 Figures



Figure 1.1: Location map of buchiid fauna worldwide (adapted from Li and Grant-Mackie 1988).



Figure 1.2: Shape trends on the left valve of the genus *Buchia*: curvoid; obliquoid; orthoid; inversoid, respectively (adapted from Zakharov 1987).

1.9 References

AGUIRRE, M. L., PEREZ, S. I. and SIRCH, Y. N. 2006. Morphological variability of *Brachidontes* Swainson (Bivalvia, Mytilidae) in the marine Quaternary of Argentina (SW Atlantic). Palaeogeography, Palaeoclimatology, Palaeoecology, 239, 100-125.

ALLEN, A. P. and GILLOOLY, J. F. 2006. Assessing latitudinal gradients in speciation rates and biodiversity at the global scale. Ecology Letters, 9, 947-954.

ALLMON, W. D. and ROSS, R. M. 1990. Specifying Causal Factors in Evolution: The Paleontological Contribution, 1-17. *In* R. M. Ross and W. D. Allmon (eds.), Causes of Evolution: a Paleontological Perspective. The University of Chicago Press, Chicago.

BEGG, J. G. and CAMPBELL, H. J. 1985. *Etalia*, a new Middle Triassic (Anisian) bivalve from New Zealand, and its relationship with other pteriomorphs. New Zealand Journal of Geology and Geophysics, 28, 725-741.

BENTON, M. J. and PEARSON, P. N. 2001. Speciation in the fossil record. Trends in Ecology and Evolution, 16, 405-411.

BOOKSTEIN, F. L. 1987. Random walk and the existence of evolutionary rates. Paleobiology, 13, 446-464.

–. 1988. Random walk and the biometrics of morphological characters. Evolutionary Biology, 9, 369-398.

BUDD, A. F. and JOHNSON, K. G. 1996. Recognizing species of late Cenozoic *Scleractinia* and their evolutionary patterns. Paleontological Society Paper, 1, 59-79.

– and POTTS, D. C. 1994. Recognizing morphospecies in colonial reef corals: I. Landmark-based methods. Paleobiology, 20, 484-505.

COURVILLE, P. and CRONIER, C. 2005. Diversity or disparity in the Jurassic (Upper Callovian) genus *Kosmoceras* (Ammonitina): a morphometric approach. Journal of Paleontology, 79, 944-953.

CRAME, J. A. 1993. Bipolar molluscs and their evolutionary implications. Journal of Biogeography, 20, 145-161.

CRAMPTON, J. S. 1994. Shape analysis of pterioid bivalves, its utility in high reso-

lution biostratigraphic studies, 4th International Congress on Jurassic Stratigraphy and Geology, 16.

-. 1995. Elliptic Fourier shape analysis of fossil bivalves: some practical considerations. Lethaia, 28, 179-186.

-. 1996. Biometric analysis, systematics and evolution of Albian *Actinoceramus* (Cretaceous Bivalvia, Inoceramidae). Monograph of the Institute of Geological and Nuclear Sciences, 15, 1-80.

– and GALE, A. S. 2005. A plastic boomerang: speciation and intraspecific evolution in the Cretaceous bivalve *Actinoceramus*. Paleobiology, 31, 559-577.

ENDLER, J. A. 1986. Natural Selection in the Wild. Princeton University Press, Princeton, NJ.

ERWIN, D. H. and ANSTEY, R. L. 1995. Speciation in the Fossil Record, 11-38. *In* D. H. Erwin and R. L. Anstey (eds.), New Approaches to Speciation in the Fossil Record. Columbia University Press, New York.

FOOTE, M. 1991. Morphological and taxonomic diversity in a clade's history: the blastoid record and stochastic simulations. Contributions from the Museum of Paleontology, 28, 101-140.

-. 1993. Discordance and concordance between morphological and taxonomic diversity. Paleobiology, 19, 185-204.

-. 1999. Morphological diversity in the evolutionary radiation of Paleozoic and post-Paleozoic crinoids. Paleobiology, 25 (suppl. to No. 2), 1-115.

GOULD, S. J. and ELDREDGE, N. 1993. Punctuated equilibrium comes of age. Nature, 366, 223-227.

GRANT, P. R. and GRANT, B. R. 1996. Speciation and hybridization in island birds. Philosophical Transactions of the Royal Society of London, Series B, 351, 765-772.

GREY, M., BOULDING, E. G. and BROOKFIELD, M. E. 2006. Estimating multivariate selection gradients in the fossil record: a naticid gastropod case study. Paleobiology, 32, 100-108.

HANNISDAL, B. 2007. Inferring phenotypic evolution in the fossil record by Bayesian inversion. Paleobiology, 33, 98-115.

HEREFORD, J., HANSEN, T. F. and HOULE, D. 2004. Comparing strengths of directional selection: how strong is strong? Evolution, 58, 2133-2143.

HEYWOOD, V. H. and WATSON, R. T. 1995. Global Diversity Assessment. Cambridge University Press, Cambridge.

HUBER, B. T., BIJIMA, J. and K., D. 1997. Cryptic speciation in the living foraminifer *Globigerinella siphonifera* (d'Orbigny). Paleobiology, 23, 33-62.

HUNT, G. 2006. Fitting and comparing models of phyletic evolution: random walks and beyond. Paleobiology, 32, 578-601.

-. 2007. The relative importance of directional change, random walks, and stasis in the evolution of fossil lineages. Proceedings of the National Academy of Science, USA, 104, 18404-18408.

JACKSON, J. B. C. and CHEETHAM, A. H. 1990. Evolutionary significance of morphospecies: a test with cheilostome Bryozoa. Science, 248, 579-583.

-. 1994. Phylogeny reconstruction and the tempo of speciation in cheilostome Bryozoa. Paleobiology, 20, 407-423.

-. 1999. Tempo and mode of speciation in the sea. Trends in Ecology and Evolution, 14, 72-77.

JELETZKY, J. A. 1963. *Malayomaorica* gen. nov. (Family Aviculopectinidae) from the Indo-Pacific Upper Jurassic; with comments on related forms. Palaeontology, 6, 148-160.

–. 1965. Late Upper Jurassic and Early Lower Cretaceous fossil zones of the Canadian western Cordillera, British Columbia. Geological Survey of Canada Bulletin, 103.

KAUFFMAN, E. G. 1973. Cretaceous Bivalvia, 353-384. In A. Hallam (ed.), Atlas of Palaeobiogeography. Elsevier Scientific Publishing Co., New York.

KINGSOLVER, J. G., HOEKSTRA, H. E., HOEKSTRA, J. M., BERRIGAN, D., VIGNIERI, S. N., HILL, C. E., HOANG, A., GIBERT, P. and BEERLI, P. 2001. The strength of phenotypic selection in natural populations. The American Naturalist, 157, 245-261.

KOWALEWSKI, M., DYRESON, E., MARCOT, J. D., VARGAS, J. A., FLESSA, K. W. and HALLMAN, D. P. 1997. Phenetic discrimination of biometric simpletons:
paleobiological implications of morphospecies in the lingulide brachiopod *Glottidia*. Paleobiology, 23, 444-469.

LANDE, R. and ARNOLD, S. J. 1983. The measurement of selection on correlated characters. Evolution, 37, 1210-1226.

LAWTON, J. H. and MAY, R. M. 1995. Extinction rates. Oxford University Press, Oxford.

LEAKEY, R. E. and LEWIN, R. 1995. The sixth extinction: patterns of life and the future of humankind. Doubleday, New York.

LI, X. and GRANT-MACKIE, J. A. 1988. Upper Jurassic and Lower Cretaceous *Buchia* (Bivalvia) from southern Tibet, and some wider considerations. Alcheringa, 12, 249-268.

LUPIA, R. 1999. Discordant morphological disparity and taxonomic diversity during the Cretaceous angiosperm radiation: North American pollen record. Paleobiology, 25, 1-28.

LYNCH, M. 1990. The rate of morphological evolution in mammals from the standpoint of the neutral expectation. The American Naturalist, 136, 727-741.

MICHAUX, B. 1989. Morphological variation of species through time. Biological Journal of the Linnaean Society, 38, 238-255.

MOYNE, S. and NEIGE, P. 2007. The space-time relationship of taxonomic diversity and morphological disparity in the Middle Jurassic ammonite radiation. Palaeo-geography, Palaeoclimatology, Palaeoecology, 248, 82-95.

NAVARRO, N., NEIGE, P. and MARCHAND, D. 2005. Faunal invasions as a source of morphological constraints and innovations? The diversification of the early Cardioceratidae (Ammonoidea; Middle Jurassic). Paleobiology, 31.

NEIGE, P. 2003. Spatial patterns of disparity and diversity of the Recent cuttlefishes (Cephalopoda) across the Old World. Journal of Biogeography, 30, 1125-1137.

PACHUT, J. and ANSTEY, R. L. 2004. Rates of evolution and selection intensity in species transitions within the Ordovician Bryozoan genus *Peronopora*. Geological Society of America Abstracts with Programs, 424.

PIMM, S. L., RUSSELL, G. J., GITTLEMAN, J. L. and BROOKS, T. M. 1995. The future of biodiversity. Science, 269, 347-350. RAUP, D. M. 1976. Species diversity in the Phanerozoic: a tabulation. Paleobiology, 2, 279-288.

ROOPNARINE, P. D. 2001. The description and classification of evolutionary mode: a computational approach. Paleobiology, 27, 446-465.

SEY, I. I. and KALACHEVA, E. D. 1999. Lower Berriasian of Southern Primorye (Far East Russia) and the problem of Boreal-Tethyan correlation. Palaeogeography, Palaeoclimatology, Palaeoecology, 150, 49-63.

SHELDON, P. R. 1996. Plus ça change - a model for stasis and evolution in different environments. Palaeogeography, Palaeoclimatology, Palaeoecology, 127, 209-227.

SIMPSON, G. G. 1944. Tempo and Mode in Evolution.

SMITH, F. D. M., MAY, R. M., PELLEW, R., JOHNSON, T. H. and WALTER, K. S. 1993a. Estimating extinction rates. Nature, 364, 494-496.

-. 1993b. How much do we know about the current extinction rate? Trends in Ecology and Evolution, 8, 375-378.

STEMPIEN, J. A. 2002. Spatial and environmental dimensions of shelly morphospaces: geometric morphometrics of the mactrid bivalve *Mulinia*, Geological Society of America, Abstracts with Programs.

– and KOWALEWSKI, M. 2004. Quantifying geographic variability of a lineage: the geometric morphospace of *Mulina*. Geological Society of America Abstracts with Programs, 133-134.

STORK, N. E. 1996. Measuring global biodiversity and its decline, 41-68. In M. L. Reaka-Kudla, D. E. Wilson and E. O. Wilson (eds.), Biodiversity II. National Academy Press, Washington DC.

SURLYK, F. and ZAKHAROV, V. A. 1982. Buchiid bivalves from the Upper Jurassic and Lower Cretaceous of East Greenland. Palaeontology, 25, 727-753.

THOMAS, C. D., CAMERON, A., GREEN, R. E., BAKKENES, M., BEAU-MONT, L. J., COLLINGHAM, Y. C., ERASMUS, B. F. N., DE SIQUEIRA, M. F., GRAINGER, A., HANNAH, L., HUGHES, L., HUNTLEY, B., A.S., V. J., G.F., M., MILES, L., ORTEGA-HUERTA, M. A., PETERSON, A. T., PHILLIPS, O. L. and WILLIAMS, S. E. 2004a. Extinction risk from climate change. Nature, 427, 145-148. THOMAS, J. A., TELFER, M. G., ROY, D. B., PRESTON, C. D., GREENWOOD, J. J. D., ASHER, J., FOX, R., CLARKE, R. T. and LAWTON, J. H. 2004b. Comparative losses of British butterflies, birds, and plants and the global extinction crisis. Science, 303, 1879-1881.

VILLIER, L. and EBLE, G. J. 2004. Assessing the robustness of disparity estimates: the impact of morphometric scheme, temporal scale, and taxonomic level in spatangoid echinoids. Paleobiology, 30, 652-665.

– and KORN, D. 2004. Morphological disparity of ammonoids and the mark of Permian mass extinctions. Science, 306, 264-266.

WILSON, E. O. 1993. The Diversity of Life. Harvard University Press, Cambridge.

ZAKHAROV, V. A. 1981. Buchiidae and biostratigraphy of the Boreal Upper Jurassic and Neocomian. Trudy Institut Geologii Geofiziki, 458, 1-270 [In Russian].

-. 1987. The Bivalve *Buchia* and the Jurassic-Cretaceous boundary in the Boreal Province. Cretaceous Research, 8, 141-153.

Chapter 2

Species Discrimination and Evolutionary Mode of *Buchia* (Bivalvia: Buchiidae) from Upper Jurassic to Lower Cretaceous Strata of Grassy Island, British Columbia, Canada¹

2.1 Introduction

The genus *Buchia* Rouillier 1845 is among the most biostratigraphically important cosmopolitan genera of the later Mesozoic (Kauffman 1973) and has been used traditionally to correlate Upper Jurassic to Lower Cretaceous strata of the Northern Hemisphere. Species of *Buchia* are biostratigraphically valuable because they are abundant in a variety of facies, widely distributed geographically, characterized by a high rate of evolutionary turnover, and readily determined taxonomically by focusing on morphological characteristics such as shell sculpture and shape, beak incurvature, and shape of the bysuss ear (Jeletzky 1965). Assessing evolutionary trends within

¹A version of this chapter has been published: GREY, M., HAGGART, J. W. and SMITH, P. L. 2008. Species discrimination and evolutionary mode of *Buchia* (Bivalvia: Buchiidae) from Upper Jurassic - Lower Cretaceous strata of Grassy Island, British Columbia, Canada. Palaeontology, 51, 583-595.

the genus, Jeletzky (1965) proposed a succession of biostratigraphic zones utilizing species of *Buchia* for the western Canadian Cordillera, British Columbia. These established *Buchia* zones are widely utilized today in geological correlation and include the *B.* cf. *blanfordiana* Jeletzky 1965, *B. okensis* Pavlow 1907, *B. uncitoides* Pavlow 1907, *B. tolmatschowi* Sokolov 1908 and *B. pacifica* Jeletzky 1965 zones (Jeletzky 1965).

Morphological features such as the bysuss ear and parts of the right ligamental plate change considerably in buchiids over geologic time, yet these features are rarely preserved and are difficult to describe morphometrically (Jeletzky 1965, 1966), therefore, it is critical to be able to identify specimens even when these features are not available (which is often the case). More easily recognizable are changes in the beak orientation and overall shape of the shell (i.e. retrocrescent, infracrescent and straight forms), and these are the features we focus on for this paper.

Despite being biochronologically valuable, disagreements in the designation of buchild species within the genus are common. Imlay (1959) was the first to suggest that the genus had been subdivided into a biostratigraphically unrealistic number of species on the basis of small differences in shell shape, size and ornamentation. Imlay (1959) also noted that many of the previously recognized species grade into each other within a single population and he attempted to take into account biological and environmental factors affecting the variability of the shell morphology. In contrast, Jeletzky (1965) disagreed with Imlay's amalgamation of species and followed the nomenclature originally proposed by Crickmay (1925, 1930) and others (Pavlow 1907; Sokolov 1908) who not only split buchiids into many more species, but also named several variants. These variants include: B. okensis var. subokensis Pavlow 1907, var. canadiana Crickmay 1930, and var. elliptica Pavlow 1907; B. uncitoides var. catamorpha Crickmay 1930, var. spasskensoides Crickmay 1930, and var. acutistriata Crickmay 1930; and B. tolmatschowi var. americana Sokolov 1908. These examples illustrate the need for objective, statistical testing for species discrimination in this fossil taxon.

Today, over 30 species are assigned to the genus *Buchia* (Zakharov 1981) and the reliability of species designations has never been verified using the now common

practice of morphometrics. Despite their importance for biostratigraphy, there have been few, if any, quantitative studies of buchild bivalves (but see Crampton 1994) and even standard measurement parameters for the valves have not been established.

The purpose of this study is two-fold. First, we develop a protocol for the systematic description of *Buchia* shell morphology using multivariate morphometrics and employ this to examine species designations. The biostratigraphic value of the *Buchia* succession is contingent on the ease of taxonomic differentiation of the various species in the lineage and this should be rigorously verified through quantitative study. Second, we assess the evolutionary mode of *Buchia*, based on a large number of populations from a single stratigraphic section, with a consideration of whether ecophenotypic variation is an important influence on morphology.

2.2 Material and Methods

2.2.1 Material

Buchiid material used in this study, mostly consisting of casts and internal moulds of shells, comes from collections of the Geological Survey of Canada (GSC) held in Ottawa, Ontario, and Vancouver, British Columbia, Canada. The collections were originally made by J.A. Jeletzky in the 1940s to 1960s during several visits to Grassy Island, off the west coast of Vancouver Island, British Columbia (Figure 2.1). The Grassy Island section spans the Tithonian (Upper Jurassic) to Lower Valanginian (Lower Cretaceous) and includes the upper part of the Upper Jurassic Kapoose Formation of Muller *et al.* (1981) and the lower part of the Lower Cretaceous One Tree Formation of Bancroft (1937) and Jeletzky (1950, 1965) (Figure 2.2). The Kapoose Formation (Tithonian) consists of mudstone and shale beds with abundant calcareous concretions and common sandstone interbeds, whereas the One Tree Formation (Berriasian-Valanginian) consists primarily of medium- to coarse-grained sandstone beds with interbeds of siltstone and sandy shale (Grey *et al.* 2007). On the basis of missing faunal zones, a disconformity spanning the uppermost Tithonian is inferred to separate the two formations (Jeletzky 1965). These missing zones include: *B. piochii* f. typ. Gabb 1864, *B. fischeriana* d'Orbigny 1845 and *B. terebratuloides* s. lato Lahusen 1888. Both formations are assigned to the Middle Jurassic-Lower Cretaceous Kyuquot Group (Muller *et al.* 1981) and are interpreted as a shallow-marine shelf assemblage characterized by extensive storm deposits.

Jeletzky collected bed-by-bed through the Grassy Island section, and the resultant collections provide a large number of stratigraphically well-constrained populations of buchiid specimens and associated other molluscs. Collections are represented by 113 different stratigraphic levels, each representing a single bed. Beds range in thickness from 0.06 to 24 m, with a mean bed thickness of 1.95 m. Jeletzky made a fossil collection from each bed and each collection includes dozens to hundreds of individual buchiid specimens. Each collection thus provides a representative overview of buchiid species present during a single 'short' time interval.

Fifteen different species and variants of *Buchia* have been documented by Jeletzky in the Grassy Island section, but the principal taxa include *B.* cf. *blanfordiana*, *B. okensis*, *B. uncitoides*, *B. tolmatschowi* and *B. pacifica*. Shape trends in the left valves can be easily recognized within the section: *B.* cf. *blanfordiana* are retrocrescent (sickle-shaped; Newell and Boyd 1970); *B. okensis* are retrocrescent to straight; and *B. uncitoides*, *B. tolmatschowi* and *B. pacifica* are straight to infracrescent (Figure 2.2). For a detailed summary of the Grassy Island section, refer to Grey *et al.* (2007).

Using the Jeletzky collections, we measured a total of 765 shells selected from 113 successive stratigraphic levels within the section. Shells range in length from 10 to 70 mm. In addition, we assigned collections to a lithofacies (calcareous mudstone, mudstone, sandstone, shale and siltstone) based on an examination of the matrix, as well as Jeletzky's descriptive comments and our personal field observations.

2.2.2 Morphometric Measurements

The exterior and side views for all unbroken left valves from each stratigraphic level were photographed in the same orientation using a Nikon D70 digital camera. We used the left valve for consistency and also because it exhibits greater morphological variance, similar to inoceramids (Crampton 1996). Images were saved to computer files and measured with a custom-designed morphometrics program (MorphLab 1.0).

To describe shell shape, we used ten morphometric variables that include angular and linear measurements and one calculation of the average distance between commarginal (or quasi-marginal; Ubukata 2005) ribs (Figure 2.3; the variable means for each species are given in Table 2.1). These ribs are not necessarily related to growth lines and several mechanisms have been proposed for their formation, including oscillation in regulatory systems (Hammer 2000). Of particular note is the variable termed the 'crest-line': this is defined as the imaginary line (corresponding to the maximum growth vector) joining the highest points of the left value of Buchia (Pavlow 1907) and has been recognized as a taxonomically valuable feature (Jeletzky 1966). We assessed the taxonomic significance of these morphometric variables, allowing us to establish a statistical protocol for the discrimination of Buchia species. Such variables should be mutually independent (Schatz 2001) and should contribute to the overall discrimination of species. We explore the extent to which this is the case in the taxonomic analyses presented below. Outline shapes, defined as a series of points around the perimeter of the shell, were also generated by the MorphLab 1.0 program and were used for Fourier analyses.

2.2.3 Taxonomic Analyses

We utilized phenetic discrimination of linear and angular measurements (Kowalewski *et al.* 1997) and outline shape (Fourier analyses: Crampton 1996; Haines and Crampton 2000) to define the *Buchia* morphospace and determine morphospecies. Linear and angular variables of buchiids were log-transformed prior to analyses (Kowalewski *et al.* 1997). Landmark-based statistical methods, although more pow-

erful, could not be employed in our study because of a lack of homologous points on the *Buchia* shell. Despite this limitation, phenetic discrimination using traditional morphometric techniques has proven useful in providing taxonomic resolution even for morphologically simple fossils (e.g. lingulide brachiopods; Kowalewski *et al.* 1997) and sister species (e.g. arcid bivalves; Marko and Jackson 2001).

Phenetic discrimination included a combination of principal component analyses (PCA) and a step-wise canonical variate analysis (CVA). PCA is a technique that condenses information from many correlated variables into a few quantities that summarize the variation among individuals; it was used to explore the *Buchia* morphospace and was executed using the correlation matrix with the program PAST (version 1.38; Hammer *et al.* 2001).

The CVA was used to determine which variables discriminate between groups of previously identified species and also for predictive classification. A priori grouping for the canonical variate analysis was based on Jeletzky's taxonomic identifications (Grey *et al.* 2007). We utilized a step-wise method for the CVA because it selects variables that contribute the most discriminatory power to the model (refer to Cheetham *et al.* 2006); this method is advantageous when there are a number of characters measured. Re-sampling methods help to assess the accuracy of analyses by testing the repeatability of the results; we therefore simulated a jackknifed approach in SPSS (version 11.0) by selecting the 'leave-one-out classification' option. For comparison, we ran ten step-wise discriminant analyses (DA) on all species pairs and applied a Bonferroni correction for multiple tests. Discriminant analyses are similar to CVAs, but are used when comparing only two groups.

Species were recognized statistically if the PCA showed distinctive morphospaces and/or the CVA/DAs indicated a reasonably high discriminatory power (i.e. a high percentage of individuals that correctly matched Jeletzky's taxonomic identifications). A low percentage of individuals that match Jeletzky's classification indicate that either species assessments based on visual examination may be inaccurate, or that our statistical tests may be missing important taxonomic information. In order to explore the effect of ontogenetic variation, we also performed analyses by size class (based on valve length: 1-3 cm [= juvenile]; 3-5 cm [=immature]; and 5-7 cm

[= mature]).

Outline shape can be a valuable morphological character, making Fourier analyses ideal for morphometric studies, especially for bivalves lacking homologous points on their shells (Crampton 1995; Crampton and Maxwell 2000). Analyses were run in Hangle (Crampton and Haines 1996) and Htree (Crampton and Haines, unpublished). Fourier coefficients were standardized for size based on shell area; therefore, the analysis is based solely on shape changes. A PCA and CVA were performed on the resulting suite of Fourier coefficients in the same manner as outlined above, with the exception that the PCA was based on the variance-covariance matrix (Crampton 1995).

2.2.4 Evolutionary Mode

We explored evolutionary mode using two methods. A biolog, produced by plotting the first canonical variate (CV1) values against stratigraphic position, was created as it helps to illustrate temporal morphologic patterns (Kelley 1983; Reyment 1980). We employed Roopnarine's (2001) random walk model for a stratophenetic series as a quantitative method for exploring evolutionary mode. Tests of evolutionary mode in a stratophenetic series require use of the random walk model as the null hypothesis because random walks can display characteristics indicative of directional evolutionary trends (Roopnarine 2001). Roopnarine's (2001) method calculates the Hurst estimate (h) of a series and is based on the Hurst exponent (H) - a measure of its persistent, or anti-persistent, deviation from any overall trend; see Roopnarine (2001) and Roopnarine et al. (1999) for further details. The Hurst exponent is estimated by regressing all log-transformed pair-wise differences of morphological values against the relevant log-transformed intervals of relative or absolute time (Roopnarine 2001). Morphological values in this case are the averaged primary canonical variate (CV1) values for each stratigraphic level calculated from the morphometric analysis as described earlier. We utilized the random walk program, Enigma-2.4 for Linux (Roopnarine 2001), to assess evolutionary mode within the Grassy Island section. Hurst estimate values can range from 0 to 1; high values (i.e. h > 0.9) indicate

strong directional change, while low values can indicate stasis (h < 0.2) or random walks (0.25 < h < 0.55) (Roopnarine 2001). P values indicate the probability of a random walk - low P values (P < 0.5) mean there is a small probability the pattern was generated by a random process, while high P values (P = 0.9) indicate random walks (Roopnarine 2001).

2.2.5 Correlation Between Lithology and Morphology

We performed a principal component analysis with lithology as the grouping variable to assess the correlation between changes in shell morphology and lithology (a proxy for paleoenvironment). If the data group by lithology, then morphological variation is dependent on environmental conditions, suggesting that ecophenotypic variation is an important factor controlling morphology. This is a coarse study of ecophenotypy as we are only assessing how it relates to substrate changes and we do not take into account biological factors (e.g. predation pressure, population density), nor do we include a comprehensive facies analysis.

2.3 Results and Discussion

2.3.1 Taxonomic Analyses

The primary principal component axis (PC1= 70% of variation) was a function of the linear measurements and delta, whereas PC2 (15.4% of variation) was represented by the crest-line angles (Table 2.2). The principal component analysis shows considerable overlap in the morphospace between previously designated species (Figure 2.4), with the exception of the two end members (*B. pacifica* and *B. cf. blanfor-diana*) (Figure 2.5). A large degree of morphological variation from the inferred mode of life (crowding) of these taxa was expected and may mean that a reasonably large sample (e.g. 10-30 specimens) is required for confident assignment to species. A similar conclusion was reached by Kelly (1990) for buchilds in Europe.

Approximately two-thirds of the specimens were classified correctly according to Jeletzky's idenfications, and all four canonical variate functions are significant, but only the first two have been plotted as they account for most of the variation (87.5%; Figure 2.6-2.7; Table 2.3). All variables were used in the step-wise canonical variate analysis, but the primary canonical variate (CV1) is largely a function of the crest-line angles. CV2 is primarily a function of inflation. The very large within-sample variances contribute to reduced discrimination.

Results that were divided by size class (not figured) showed similar separation between *Buchia* species as the results with all size classes, indicating that differences are not based on ontogenetic stage (proxied as length; refer to Crampton and Maxwell (2000)).

Discriminant analyses between all species pairs revealed a much higher percentage of correctly classified specimens, ranging from 77% to 99% (Table 2.4), indicating morphological differences between all previously identified species. Therefore, Jeletzky's visual assessment of species is statistically supported. This result also demonstrates that, depending on the species pair, different morphological variables are important for discrimination (Table 2.4). Therefore, while results from the CVA indicate that the angles of the crest line and inflation have the most discriminatory power, step-wise DAs between species pairs demonstrate the variables with the most discriminatory power can differ. We therefore recommend that all ten morphological variables be measured and utilized in subsequent taxonomic analyses of the genus *Buchia*.

These results, taken together, show that the morphology of *Buchia* species is highly variable and that different species of buchiids will be difficult to recognize in small sample sizes (e.g. <10 specimens). This observation is corroborated by taxonomic identification of buchiid collections using non-statistical techniques. Crampton (1996) found similar results for an Albian inoceramid (*Actinoceramus*) and suggested that, despite morphological overlap between species, they could be classified as taxonomically distinct with an examination of sufficiently large sample sizes. This issue has ramifications for the usefulness of the *Buchia* zones constructed by Jeletzky (1965) and may be a more pervasive problem throughout the genus. Similar mor-

phological analyses of other *Buchia* zones in other geographic regions are required to fully assess the implications for taxonomic differentiation within the genus.

This research is not intended to replace traditional methods of identifying buchiids, only to enhance it. When available, hinge information, right valve morphology and more detailed observations of shell ornamentation are important factors involved in identification. We show that even when these features are not preserved it is still possible to discriminate between species with large enough sample sizes. Our results also suggest that some, perhaps most, species variants may not hold a great deal of taxonomic value. We encourage the use of multivariate morphometrics, in association with details of the hinge, etc., in such analyses because visual assessments are more subject to interpretation than are those obtained through quantitative methods.

Fourier analyses yielded results that were also suitable for discrimination of *Buchia* species (Figure 2.8). PC1 and PC2 captured a total of 70% of the variation and 63% of the specimens were classified correctly with the CVA. The results are similar to the phenetic discrimination with the linear and angular measurements in that there is no clear separation in the morphospace (Figure 2.8), except between *B. pacifica* and *B.* cf. *blanfordiana* (Figure 2.9).

2.3.2 Evolutionary Mode

The biolog (Figure 2.10) created for all individuals of *Buchia* on the discriminant axis that best separated the previously assigned species (CV1) shows a gradual shift from *B*. cf. *blanfordiana* to *B. pacifica*, where differences are based predominantly on angles of the crest-line. We qualitatively classify this as a gradualistic trend because the change is consistent and directional through time and the two end members separate well from each other.

The result from the Hurst estimate analysis, using the primary canonical variate as a measure of overall morphological change, exhibits significant gradual directionality throughout the entire interval of time. This is documented by the trajectory's high Hurst estimate values (h) and relatively low probabilities (P) of being generated by a random process (Figure 2.11). The null hypothesis that the series represents a random walk is therefore rejected, supporting the qualitative conclusion that the trend is gradualistic. The mid-section of the biolog looks like an episode of stasis (Figure 2.10), but this is not supported by the Hurst estimate analysis. Cases of stasis would have very low h values (h \ll 0.5) and high P values (Roopnarine 2001). We explain the apparent large jump in morphology between the *B*. cf. *blanfordiana* and *B. okensis* zones as related to the disconformity in the section (Figure 2.2; Jeletzky 1965), rather than a punctuated change.

As far as the authors are aware, this is the first study to apply Roopnarine's (2001) random walk test to macrofossils. Future research will ascertain whether the gradualistic evolutionary pattern is common within the buchiid lineage by comparing modes from a variety of geographic settings. Some members of the closely related family Inoceramidae also display gradual evolutionary modes (e.g. Crampton 1996; Crampton and Gale 2005) and other Mesozoic bivalves display non-branching gradualism (Fortey 1988) and gradualism and stasis (Geary 1987).

2.3.3 Correlation Between Lithology and Morphology

The PCA with linear/angular measurements using lithology as the grouping variable shows no clear groupings (Figure 2.12), nor does there appear to be a trend in mean shape from coarse to fine facies (Figure 2.13). The notable exception is the separation between mudstone and all other lithofacies, including calcareous mudstone, sandstone, shale and siltstone (Figure 2.12-2.13). This break occurs at the disconformity observed in the Grassy Island section (refer to Figure 2.2). Otherwise, it appears that *Buchia* morphology does not correlate with lithology and that substrate-related ecophenotypic variation may not be an important influence on morphology on a large scale. However, this relationship needs to be assessed further to include a more comprehensive facies analysis and also to examine other sections from different regions of British Columbia (BC). For example, if evolutionary patterns are similar between different terranes in BC, this provides better evidence that ecophenotypy is not a significant factor on morphological change. We also believe that ecophenotypic change is more important to consider when assessing patterns on smaller time scales. This research encompasses approximately ten million years and surely any morphological change over this amount of time is due to evolutionary (genotypic) rather than phenotypic changes.

2.4 Conclusions

Results from the multivariate techniques employed in our study have important implications for the taxonomy of the genus *Buchia* and its usefulness for biostratigraphy. This research is also particularly useful for investigation into evolutionary patterns over time because: it includes abundant material from closely spaced stratigraphic intervals that provides fine-scale temporal resolution; morphological change through time within the genus is captured using a standard suite of biometrics; and ecophenotypic variation on shell morphology is considered.

In conclusion, we have found the following.

- 1. Phenetic discrimination using both outline shapes and angular and linear measurements appear equally useful for buchiid species discrimination.
- 2. Existing *Buchia* species concepts in the western Canadian Cordillera are supported through the use of multivariate morphometrics, despite significant overlap in *Buchia* morphospace. This overlap means that moderate to large sample sizes are required for biostratigraphic studies, especially when other taxonomically important features (including those of the hinge, right-valve and ornament) are not preserved.
- 3. Species variants as described by Crickmay (1925, 1930) and Jeletzky (1965) may not be taxonomically valid.
- 4. Overall, the angles of the crest-line and inflation are the most important discriminatory variables for differentiating species of *Buchia*. However, dis-

crimination works best when comparing species pairs rather than groups and primary discriminatory variables change depending on the species pair.

- 5. Morphological change exhibited by Grassy Island *Buchia* from the Late Jurassic to Early Cretaceous is gradualistic.
- 6. Preliminary analysis suggests that morphological change within *Buchia* does not appear to be a function of ecophenotypic variation, but this hypothesis requires further assessment.

| Tables |
|--------|
| Ŋ |
| 2 |

| | | Morpł | nologic | al vari | ables | | | | | |
|---------------------|---------|---------|---------|---------|-------|------|------|------|-------|-------|
| Species | Angle J | Angle I | Ld | Lv | Wa | Wp | Dd | Dv | \ln | Delta |
| $B. \ pacifica$ | -5.19 | 11.60 | 2.16 | 1.38 | 1.20 | 1.07 | 1.42 | 2.13 | 1.27 | 0.22 |
| $B.\ tolmatschowi$ | -13.10 | 13.10 | 2.51 | 1.64 | 1.35 | 1.14 | 1.85 | 2.45 | 1.46 | 0.24 |
| B. uncitoides | -2.53 | 3.17 | 1.78 | 1.09 | 0.99 | 0.80 | 1.07 | 1.88 | 0.81 | 0.16 |
| $B. \ okensis$ | 0.65 | -0.52 | 1.91 | 0.93 | 1.16 | 0.96 | 1.16 | 2.11 | 0.97 | 0.19 |
| B. cf. blanfordiana | 14.80 | -12.90 | 1.59 | 1.18 | 0.93 | 0.71 | 0.92 | 1.71 | 0.81 | 0.13 |

Table 2.1: Variable means used to characterize shell morphology for each species of Buchia.

| Variable | PC1 | PC2 |
|---------------------------------|-------|-------|
| Dorsal angle of crest-line (J) | -0.33 | 0.86 |
| Ventral angle of crest-line (I) | 0.42 | -0.82 |
| Dorsal length (Ld; $1-5$) | 0.95 | 0.13 |
| Ventral length (Lv; $5-3$) | 0.95 | 0.04 |
| Anterior width (Wa; 4-5) | 0.92 | 0.22 |
| Posterior width (Wp; $5-2$) | 0.90 | 0.08 |
| Dorsal distance (Dd; 1-6) | 0.93 | -0.05 |
| Ventral distance $(Dv; 6-3)$ | 0.91 | 0.23 |
| Inflation (In; $6-7$) | 0.93 | 0.05 |
| Delta | 0.84 | -0.02 |

Table 2.2: Correlation of all morphological variables on the first two principal components. Variables are defined in Figure 2.3.

| | | I | Predicted Group Membership | | | | | |
|-----------|---------|--------|----------------------------|--------|---------|--------|-----|--|
| | Species | 1 | 2 | 3 | 4 | 5 | | |
| Original | 1 | 81 | 11 | 2 | 0 | 1 | 95 | |
| | | (85%) | (12%) | (2.1%) | (0.0%) | 1.1% | | |
| | 2 | 2 | 103 | 42 | 1 | 2 | 150 | |
| | | (1.3%) | (69%) | (28%) | (0.70%) | (1.3%) | | |
| | 3 | 6 | 67 | 222 | 17) | 17 | 329 | |
| | | (1.8%) | (20%) | (68%) | (5.2%) | (5.2%) | | |
| | 4 | 0 | 1 | 6 | 47 | 6 | 60 | |
| | | (0.0%) | (1.7%) | (10%) | (78%) | (10%) | | |
| | 5 | 3 | 5 | 17 | 40 | 66 | 131 | |
| | | (2.3%) | (3.8%) | (13%) | (31%) | (50%) | | |
| Cross- | 1 | 80 | 11 | 3 | 0 | 1 | 95 | |
| validated | | (84%) | (12%) | (3.2%) | (0.0%) | (1.1%) | | |
| | 2 | 2 | 100 | 44 | 1 | 2 | 150 | |
| | | (1.3%) | (67%) | (29%) | (0.70%) | (2.0%) | | |
| | 3 | 6 | 68 | 218 | 19 | 18 | 329 | |
| | | (1.8%) | (21%) | (66%) | (5.8%) | (5.5%) | 329 | |
| | 4 | 0 | 1 | 6 | 44 | 9 | 60 | |
| | | (0.0%) | (1.7%) | (10%) | (73%) | (15%) | 60 | |
| | 5 | 3 | 5 | 17 | 42 | 64 | 131 | |
| | | (2.3%) | (3.8%) | (13%) | (32%) | (49%) | | |

Table 2.3: Classification summary for specimens from the Grassy Island section, contrasting the original with the cross-validated (based on a simulated jackknifed approach) results. Numbers in parentheses represent the percentage of correctly classified individuals. 68% of the original grouped cases were classified correctly according to Jeletzky's qualitative assessments; 66% of the cross-validated grouped cases were correctly classified. 1 = B. cf. blanfordiana; 2 = B. okensis; 3 = B. uncitoides; 4 = B. tolmatschowi; 5 = B. pacifica.

| Species pair | Percent | Wilks' λ | P-value | Sample | Characters |
|---------------------|---------|------------------|-------------|--------|--------------------------|
| | correct | | | Size | |
| B. pacifica | 78 | 0.637 | 0.000^{*} | 191 | Dd, J, In, Δ |
| B. tolmatschowi | (77) | | | | |
| B. pacifica | 91 | 0.435 | 0.000^{*} | 465 | In, I, Dd, Lv, |
| B. uncitoides | (90) | | | | Wa, Ld, Dv, J |
| B. pacifica | 94 | 0.329 | 0.000^{*} | 281 | I, In, Ld, Wa, Dv |
| B. okensis | (94) | | | | |
| B. pacifica | 97.3 | 0.208 | 0.000^{*} | 226 | I, J, Wp |
| B. cf. blanfordiana | (97) | | | | |
| B. tolmatschowi | 93 | 0.450 | 0.000^{*} | 389 | In, Lv, J, Wp, |
| B. uncitoides | (92) | | | | Dv |
| B. tolmatschowi | 99 | 0.228 | 0.000^{*} | 210 | I, J, Dd, Lv, Wa |
| B. okensis | (98) | | | | Dv |
| B. tolmatschowi | 99 | 0.137 | 0.000^{*} | 155 | I, J, Lv |
| B. cf. blanfordiana | (99) | | | | |
| B. uncitoides | 75 | 0.745 | 0.000^{*} | 479 | I, J, Wa, Wp, Δ , |
| B. okensis | (74) | | | | In, Ld |
| B. uncitoides | 95 | 0.404 | 0.000* | 424 | J, I |
| B. cf. blanfordiana | (95) | | | | |
| B. okensis | 96 | 0.279 | 0.000* | 245 | I, J, Δ , Wa, In |
| B. cf. blanfordiana | (94) | | | | |

*significant after Bonferroni correction for ten tests ($\alpha = 0.05/10$)

Table 2.4: Classification summary for ten discriminant analyses using species as *a priori* groupings for specimens from the Grassy Island section. Numbers in parentheses represent the percentage correctly classified after cross-validation (based a simulated jackknifed approach across specimens). The last column indicates which characters, in order of most to least importance, were picked by the step-wise DA for discrimination between the two species. Refer to Figure 2.3 for an explanation of character abbreviations. All tests are significant after a Bonferroni correction.

2.6 Figures



Figure 2.1: Location map of the stratigraphic section on Grassy Island, off the west coast of Vancouver Island, British Columbia (NTS map-area 92E/14).



Figure 2.2: Stratigraphic column of the Jurassic-Cretaceous succession exposed at Grassy Island, with key *Buchia* species photographs and valve shape information found within each zone. Bed-by-bed fossil collections were made throughout the entire section at Grassy Island and were identified initially by J.A. Jeletzky. Details of the stratigraphic distribution of fossil collections are presented in Grey *et al.* (2007).



Figure 2.3: Features used to characterize shell morphology in buchild bivalves: 1, dorsalmost point (umbo) on hinge margin; 2, posteriormost point; 3, ventralmost point; 4, anteriormost point; 5, intersection of lines measuring maximum valve length and valve width; 6, point directly beneath highest point on left valve; 7, highest point on left valve. Morphological variables measured: ventral angle of crest-line* (I); dorsal angle of crest-line (J); dorsal length (Ld; 1-5); ventral length (Lv; 5-3); anterior width (Wa; 4-5); posterior width (Wp; 5-2); dorsal distance to highest point on valve (Dd; 1-6); ventral distance to highest point on valve (Dv; 6-3); inflation (In; 6-7) and delta (Δ ; average distance between concentric rings). *The "crest-line" is defined as the imaginary line joining the highest points of the left valve of *Buchia* (Pavlow 1907) and has been recognized as a taxonomically valuable feature (Jeletzky 1966).



Figure 2.4: PCA results show overlap in *Buchia* morphospace for all species based on visual assessments by Jeletzky from Grassy Island, British Columbia. Axes PC1 and PC2 represent 70% and 15.4% respectively of the character variation within the section.



Figure 2.5: PCA results showing clear separation in the morphospace for B. pacifica and B. cf. blanfordiana.



Figure 2.6: Results from the CVA for all of Jeletzky's assigned species from Grassy Island, British Columbia. Axes CV1 and CV2 represent 69% and 18.5% respectively of the character variation within the section. CV1 represents crest-line variation (angles J and I on Fig. 3) and CV2 represents shell inflation ("In" on Fig. 3).



Figure 2.7: CVA results showing clear separation of B. pacifica and B. cf. blanfordiana.



Figure 2.8: PCA results from the Fourier analysis, illustrating overlap in the morphospace for all of Jeletzky's assigned species from Grassy Island, British Columbia. Axes PC1 and PC2 represent 45% and 25% respectively of the character variation within the section. Fourier analyses captured much less of the morphological variation in buchiid shells than analyses using angles and linear measurements.



Figure 2.9: PCA results from the Fourier analysis showing separation in the morphospace for *B. pacifica* and *B.* cf. *blanfordiana*.



Figure 2.10: Biolog created by plotting the canonical variate means (centroids) for the first canonical variate (CV1) against stratigraphic position. Outlines on the right are plots of the average shape of the shells as they relate to the morphospace.



Figure 2.11: Hurst estimate analysis of the evolutionary pattern described by the stratophenetic series, with h values $\gg 0.5$ indicating increasing directionality and a gradualistic evolutionary mode.



Figure 2.12: PCA results using lithology as the grouping variable from the section at Grassy Island, British Columbia. Axes PC1 and PC2 represent 70% and 15.4% respectively of the variation within the section. While there is a clear separation in the morphospace at the disconformity between the mudstones of the lower part of the section (Kapoose Formation) and the coarser-grained lithofacies in the upper part of the section (One Tree Formation), shell morphology does not appear to be highly related to lithofacies, taken as a proxy for paleoenvironment.



2.6. Figures

Figure 2.13: PCA results, with only the group means plotted, using lithology as the grouping variable from the section at Grassy Island, British Columbia. Axes PC1 and PC2 represent 70% and 15.4% respectively of the variation within the section. There is no obvious trend in mean shape from coarse to fine facies.

2.7 References

BANCROFT, M. F. 1937. Gold-bearing deposits on the west coast of Vancouver Island between Esperanza Inlet and Alberni Canal. Geological Survey of Canada, Memoir, 204, 34 pp.

CHEETHAM, A. H., SANNER, J., TAYLOR, P. D. and OSTROVSKY, A. N. 2006. Morphological differentiation of *Avicularia* and the proliferation of species in mid-Cretaceous *Wilbertopora* Cheetham, 1954 (Bryozoa: *Cheilostomata*). Journal of Paleontology, 80, 49-71.

CRAMPTON, J. S. 1994. Shape analysis of pterioid bivalves, its utility in high resolution biostratigraphic studies. 4th International Congress on Jurassic Stratigraphy and Geology; Abstracts: 16.

–. 1995. Elliptic Fourier shape analysis of fossil bivalves: some practical considerations. Lethaia, 28, 179-186.

-. 1996. Biometric analysis, systematics and evolution of Albian *Actinoceramus* (Cretaceous Bivalvia, Inoceramidae). Monograph of the Institute of Geological and Nuclear Sciences [New Zealand], 15, 1-80.

– and GALE, A. S. 2005. A plastic boomerang: speciation and intraspecific evolution in the Cretaceous bivalve *Actinoceramus*. Paleobiology, 31, 559-577.

– and 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.

– and MAXWELL, P. A. 2000. Size: all it's shaped up to be? Evolution of shape through the lifespan of the Cenozoic bivalve *Spissatella* (Crassatellidae), 399-423. *In* HARPER, E. M., TAYLOR, J. D., CRAME, J. A. (eds.). The Evolutionary Biology of the Bivalvia. Volume 177. Geological Society, Special Publications, London, 494 pp.

CRICKMAY, C. H. 1925. The geology and paleontology of the Harrison Lake district, British Columbia, together with a review of the Jurassic faunas and stratigraphy of western North America. Stanford University, Stanford, California, 88 pp.

-. 1930. Fossils from Harrison Lake area, British Columbia. Geological Survey of Canada Bulletin, 63, 33-60.

FORTEY, R. A. 1988. Seeing is believing: gradualism and punctuated equilibria in

the fossil record. Scientific Progress, 72, 1-19.

GABB, W. M. 1864. Description of the Cretaceous fossils. California Geological Survey, Palaeontology, 1, 57-243.

GEARY, D. H. 1987. Evolutionary tempo and mode in a sequence of the Upper Cretaceous bivalve Pleurocardia. Paleobiology, 16, 140-151.

GREY, M., HAGGART, J. W. and JELETZKY, J. A. 2007. Uppermost Jurassic (Portlandian) to lowermost Cretaceous (Valanginian) section at Grassy Island, west coast of Vancouver Island, British Columbia. Geological Survey of Canada Openfile, 5666.

HAINES, A. J. and CRAMPTON, J. S. 2000. Improvements to the method of Fourier shape analysis as applied in morphometric studies. Palaeontology, 43, 765-783.

HAMMER, O. 2000. A theory for the formation of commarginal ribs in mollusc shells by regulative oscillation. Journal of Molluscan Studies, 66, 383-391.

-, HARPER, D. A. T. and RYAN, P. D. 2001. PAST: Paleontological statistics software package for education and data analysis. Palaeontologia Electronica, 4, 9 pp.

IMLAY, R. W. 1959. Succession and speciation of the pelecypod Aucella. U.S. Geological Survey, Professional Paper, 314-G, 155-169, pls. 16-19.

JELETZKY, J. A. 1950. Stratigraphy of the west coast of Vancouver Island between Kyuquot Sound and Esperanza Inlet, British Columbia. Geological Survey of Canada, Paper, 50-37, 51 pp.

-. 1965. Late Upper Jurassic and early Lower Cretaceous fossil zones of the Canadian western Cordillera, British Columbia. Geological Survey of Canada, Bulletin, 103, 70 pp.

-. 1966. Upper Volgian (latest Jurassic) Ammonites and Buchias of Arctic Canada.
Geological Survey of Canada, Bulletin, 128, 51 pp., 8 pls.

KAUFFMAN, E. G. 1973. Cretaceous Bivalvia, 353-384. In HALLAM, A. (ed.). Atlas of Palaeobiogeography. Elsevier Scientific Publishing Co., New York, 531 pp.

KELLEY, P. H. 1983. Evolutionary patterns of eight Chesapeake Group molluscs: evidence for the model of Punctuated Equilibria. Journal of Paleontology, 57, 581-

598.

KELLY, S. R. A. 1990. Biostratigraphy of the bivalve *Buchia* in the Late Jurassic and Early Cretaceous sediments of Europe, 129-151. *In* MENNER, V. V. (ed.). The Jurassic-Cretaceous Boundary. Trudy Instituta Geologiya i Geofizika Siberia Otdelenie, 699. Nauka, Moscow. 192 pp, 8 pls. [In Russian].

KOWALEWSKI, M., DYRESON, E., MARCOT, J. D., VARGAS, J. A., FLESSA, K. W. and HALLMAN, D. P. 1997. Phenetic discrimination of biometric simpletons: paleobiological implications of morphospecies in the lingulide brachiopod Glottidia. Paleobiology, 23, 444-469.

LAHUSEN, I. 1888. Uber die russischen Aucellen. Mmoires du Comit Gologique, 8, 45 pgs.

MARKO, P. B. and JACKSON, J. B. C. 2001. Patterns of morphological diversity among and within arcid bivalve species pairs separated by the Isthmus of Panama. Journal of Paleontology, 75, 590-606.

MULLER, J. E., CAMERON, B. E. B. and NORTHCOTE, K. E. 1981. Geology and mineral deposits of Nootka Sound map-area, Vancouver Island, British Columbia. Geological Survey of Canada, Paper, 80-16, 53 pp.

NEWELL, N. D. and BOYD, D. W. 1970. Oyster-like Permian Bivalvia. Bulletin of the American Museum of Natural History, 143, 221-281.

D'ORBIGNY, A. 1845. Mollusques. In Gologie de la Russie d'Europe et des Montagnes de l'Oural. Systme Jurassique. Volume 2. J. Murray & Bertrand, Londres-Paris: 419-512.

PAVLOW, A. P. 1907. Enchanement des aucelles et aucellines du crtac Russe. Nouveaux Memoir de la Socit Imperiale Naturalistes de Moscou, 5, 455-570.

REYMENT, R. A. 1980. Morphometric Methods in Biostratigraphy. Academic Press, London, 175 pp.

ROOPNARINE, P. D. 2001. The description and classification of evolutionary mode: a computational approach. Paleobiology, 27, 446-465.

–, BYARS, G. and FITZGERALD, P. 1999. An agenetic evolution, stratophenetic patterns, and random walk models. Paleobiology, 25, 41-57.

ROUILLIER, C. 1845. Explication de la coupe gologique des environs de Moscou.
Bulletin de la Socit Impriale des Naturalistes de Moscou, 19, 359-467.

SCHATZ, W. 2001. Taxonomic significance of biometric characters and the consequences for classification and biostratigraphy, exemplified through moussoneliform daonellas (*Daonella*, Bivalvia; Triassic). Palontologische Zeitschrift, 75, 51-70.

SOKOLOV, D. N. 1908. Ueber Aucellen aus dem Norden und Osten von Siberien. Mmoires de l'Acadmie Impriale des Sciences de St. Ptersbourg, ser. 8, 21, 18 pp.

UBUKATA, T. 2005. Theoretical morphology of bivalve shell sculptures. Paleobiology, 31, 643-655.

ZAKHAROV, V. A. 1981. Buchiidae and biostratigraphy of the Boreal Upper Jurassic and Neocomian. Trudy Institut Geologii Geofiziki, 458, 1-270 [In Russian].

Chapter 3

A New Species of *Buchia* (Bivalvia: Buchiidae) from British Columbia, Canada, with an Analysis of Buchiid Bipolarity²

3.1 Introduction

The bivalve *Buchia* Rouillier 1845 is a biostratigraphically important genus (Kauffman 1973) that ranges from the late Oxfordian (Late Jurassic) to Hauterivian (Early Cretaceous) (Zakharov 1981) and has traditionally been used to correlate strata in the Northern Hemisphere. The genus belongs to the family Buchiidae Cox 1953 whose members represent a prominent example of Late Jurassic bipolarity (Figure 3.1), a common disjunct biogeographic distribution pattern (Crame 1993). Taxa distributed only at high latitudes in both hemispheres are referred to as bipolar, or antitropical, and are known from the Early Jurassic to Recent (Crame 1986, 1992). Bipolar families, and perhaps even genera, may have existed through the greater part of Late Jurassic-Early Cretaceous time due to global climatic zonation and, ultimately, tectonic events, such as the continental break-up of Pangaea (Crame 1993).

²A version of this chapter has been published: GREY, M., HAGGART, J. W. and SMITH, P. L. 2008. A new species of Buchia (Bivalvia: Buchiidae) from British Columbia, Canada, with an analysis of buchiid bipolarity. Journal of Paleontology, 82, 391-397.

3.1. Introduction

The evolutionary centre of the genus *Buchia* is presumed to be in the circumboreal realm (Zakharov 1987), and Li and Grant-Mackie (1988) hypothesized that Northern and Southern Hemisphere buchiids are congeneric and that migration occurred between them. *Buchia* may have migrated southwards from the Boreal region to its southernmost extent by way of three possible oceanic routes: western, central, or eastern (Li and Grant-Mackie 1988). These routes are similar to hypothesized gene flow between modern bipolar populations of foraminifers (Darling *et al.* 2000). An alternative to the migration hypothesis is that northern and southern populations evolved independently and are morphologically similar due to convergent evolution (Crame 1986). *Buchia* appeared at similar times in both hemispheres (Li and Grant-Mackie 1988, fig. 14), suggesting that they could either migrate and establish themselves in new environments quickly, or that they evolved independently.

Debate is ongoing about whether *Buchia senso stricto* was established in the Southern Hemisphere during the Late Jurassic; some workers believe the genus was restricted to the Northern Hemisphere and that closely related, but apparently different genera (e.g. *Australobuchia* Zakharov 1981 and *Malayomaorica* Jeletzky 1963), existed contemporaneously in the Southern Hemisphere (Jeletzky 1963; Zakharov 1981, 1987; Crame 1993). Others believe that morphological differences are too minor to merit separate taxonomic classification (e.g. Li and Grant-Mackie 1988; Sha and Fürsich 1994). Sha and Fürsich (1994) in particular noted that buchiid species had a high potential to travel long distances within a single generation because of their planktotrophic larvae. They postulated that buchiids could reach a global distribution over several generations, but never flourished in tropical areas because of their preference for cool water temperatures (Sha and Fürsich 1994).

Members of the family Buchiidae are important index fossils, especially around the Jurassic-Cretaceous boundary, because of their relative ease of identification, regular stratigraphic distribution and their high preservation potential (Jeletzky 1965; Li and Grant-Mackie 1988; Sha and Fürsich 1994). Several buchiid zones have been established and correlated with standard ammonite zonations (e.g. Jeletzky 1965; Surlyk and Zakharov 1982). Jeletzky (1965) erected a succession of *Buchia* zones for the Upper Jurassic-Lower Cretaceous rocks of British Columbia and described

Tithonian-aged (i.e. ca. late Middle Volgian; Zakharov 1987; Zakharov *et al.* 1997) Buchia cf. blanfordiana shells, suggesting that they were similar to *B. blanfordiana* Stoliczka 1866 and *B. subpallasi* Krumbeck 1934 of the Indo-Pacific, and *B. plicata* Zittel 1870 of New Zealand. Jeletzky (1984) further suggested that *B. cf. blanfordiana* had a restricted geographical range in the North Pacific Province, indicative of an endemic, and was presumably a phylogenetic dead-end offshoot of the *B. mosquensis* Buch 1844 species group, a suggestion originally proposed by Konovalov (1977). However, this proposition was not supported quantitatively and, to the authors' knowledge, it has never been investigated further.

The purpose of this research is to explore the bipolarity of the genus *Buchia* by quantitatively comparing buchiid collections from each hemisphere. If populations from different hemispheres fall within different morphospaces, and are easily discriminated, this supports retention of the Southern Hemisphere genera *Australobuchia* and *Malayomaorica* as distinct from *Buchia sensu stricto*. We also assess whether *B*. cf. *blanfordiana* is sufficiently distinct from *Buchia blanfordiana* to warrant designation as a new species.

3.2 Material

We compared *B.* cf. *blanfordiana* material from the North Pacific Province (Grassy Island section, Grey *et al.* 2007) with material from the Southern Hemisphere, including *B. blanfordiana*, *B. plicata*, *B. spitiensis* Holdhaus 1913 and *Malayomaorica malayomaorica* Krumbeck 1923 (Figure 3.2). Refer to Table 3.1 for collection information and a summary of buchild species used for this study.

3.3 Methods

3.3.1 Morphometric Measurements

We photographed the exterior and side views for all unbroken left and right valves using a Nikon D70 digital camera. Images were saved as JPEGs and measured with a custom-designed morphometrics program written in MatLab (Buchia_gui). Buchia_gui is available to interested users upon request to the primary author.

We measured ten morphometric variables that had been used successfully in a previous study for taxonomic discrimination in buchiids (see Grey *et al.* 2008) on a total of 107 shells. Morphometric variables included angular and linear measurements and one calculation of the average distance between concentric commarginal ribs (Figure 3.3). Outline shapes, defined as a series of points around the perimeter of the shell, were also created in the Buchia_gui program and were used for Fourier analyses.

3.3.2 Taxonomic Analyses

Disagreements in the designation of *Buchia* species are common and it has only been recently that multivariate morphometrics have been applied to assess the reliability of these designations (refer to Grey *et al.* 2008). We performed phenetic discrimination separately on left and right valves of all shells with linear and angular measurements. Phenetic discrimination using traditional morphometric techniques has proven useful in providing taxonomic resolution even for morphologically simple fossils (e.g. lingulide brachiopods; Kowalewski *et al.* 1997) and sister species (e.g. arcid bivalves; Marko and Jackson 2001). All variables were log-transformed prior to analyses in order to ensure normality of variables while maintaining allometries (Kowalewski *et al.* 1997).

Phenetic discrimination included a combination of principal component analyses (PCA) and step-wise discriminant analyses (DA). PCA is a technique that condenses

information from many correlated variables into a few quantities that summarize the variation among individuals; it was used to compare the morphospace between Northern and Southern Hemisphere buchiids and was executed using the program PAST (version 1.38; Hammer *et al.* 2001). The DA was used to determine which variables discriminate between the two groups of previously identified species and also for predictive classification. We executed the DAs using the program SPSS (version 11.0) and based *a priori* grouping on geographical location (i.e. Northern or Southern Hemisphere). We utilized a step-wise method for the DAs because it selects variables that contribute the most discriminatory power to the model (refer to Cheetham *et al.* 2006). This method is advantageous when there are a number of characters measured. Re-sampling methods help to assess the accuracy of analyses by testing the repeatability of the results; we therefore simulated a jackknife procedure in SPSS (version 11.0) by selecting the 'leave-one-out classification' option.

We performed Fourier analyses because outline shape can be a valuable morphological character for many bivalves (Crampton and Maxwell 2000). Analyses were run in HANGLE, HMATCH, and HCURVE (Crampton and Haines 1996) on left and right valves separately and we followed procedures outlined by Crampton (1995) and Crampton and Maxwell (2000). A PCA and DA were performed on the resulting suite of Fourier coefficients in the same manner as outlined above, with the exception that the PCA was based on the variance-covariance matrix, rather than the correlation matrix (Crampton 1995).

If the PCAs for both the linear/angular measurements and the Fourier analyses show distinctive morphospaces, and the groups are statistically significant using discriminant analyses, this supports the hypothesis that Southern Hemisphere material may belong to another genus and that the genus *Buchia* is not truly bipolar. It is also evidence that *B*. cf. *blanfordiana* should be considered taxonomically distinct.

3.4 Results and Discussion

For all analyses, right and left valves gave similar results; we therefore provide only left valve results.

The PCA showed considerable overlap in the morphospace for both the linear/angular measurements and the Fourier analyses (Figs. 3.4-3.5). A large degree of morphological variation was expected because a previous study (Grey *et al.* 2008) indicated that the morphology of *Buchia* species is highly variable, possibly due to their mode of life (crowding). PC1 and PC2 for the linear and angular measurements accounted for 80% of the variation (Figure 3.4). PC1 was represented by the size variables (lengths, widths and shell inflation) whereas PC2 was represented by shape variables (angles of the crest-line) (Table 3.2). The best separation of specimens occurred along PC1, indicating size differences between species from each hemisphere (Figure 3.4); those specimens from each hemisphere that overlapped were therefore similar in size. PC1 and PC2 from the Fourier analysis only captured 45% of the variation (Figure 3.5) and required a larger number of PC axes to explain the variation (Figure 3.5, inset), but only the first two are shown because this is where the best separation between hemispheres occurs.

Discriminant analyses had high percentages of correctly classified specimens, ranging from 86% for the linear/angular measurements to 81.4% for the Fourier analysis (Tables 3.3-3.4), and both DAs were significant (linear/angular measurements: Wilks' lambda = 0.469; p < 0.001; Fourier analysis: Wilks' lambda = 0.479; p < 0.001). Histograms along the discriminant axis also showed a clear separation between northern and southern forms (Figs. 3.6-3.7). Differences for the analysis using linear/angular measurements were primarily based on the dorsal and ventral distance and the ventral length (refer to Figure 3.3), indicating dissimilarities in shell proportions. Southern Hemisphere taxa had longer ventral length values than the northern *B*. cf. *blanfordiana*, while the dorsal and ventral distances signify differences on the highest point of the shells between Northern and Southern Hemisphere species. Fourier analyses also indicate that there are significant differences in the outline shape of taxa from each hemisphere. Taking the previous statements into account, misclassified specimens were generally similar in size and shell proportions (and therefore indistinguishable using multivariate morphometrics) and, in some cases, poorly preserved.

Our comparisons of valves from Late Jurassic buchiid species of the Southern and Northern Hemispheres indicate that they are morphologically distinct and warrant separate taxonomic status. This supports Crame's (1990) and Hikuroa and Grant-Mackie's (2008) findings that important morphological differences exist between Northern and Southern Hemisphere buchiids. It also supports Zakharov's (1981) creation (and its subsequent acceptance by Hikuroa and Grant-Mackie (2008)) of the genus Australobuchia for the Southern Hemisphere. Our data illustrate that B. cf. blanfordiana Jeletzky 1965 should be formally renamed, as originally hypothesized by Jeletzky (1984), and we accordingly rename this taxon below as Buchia columbiana n. sp. Our findings also require that the B. cf. blanfordiana Zone of Jeletzky (1965) in the Canadian western Cordillera be renamed the Buchia columbiana Zone.

3.5 Systematic Paleontology

All measured and figured specimens documented herein are deposited in the Type Collection of the Geological Survey of Canada (GSC), Vancouver annex.

Class BIVALVIA Linn 1758 Subclass PTERIOMORPHIA Beurlen 1944 Order PTERIOIDA Newell 1965 Suborder PTERIINA Newell 1965 Superfamily PECTINACEA Rafinesque 1815 Family BUCHIIDAE Cox 1953 Genus *BUCHIA* Rouillier 1845

TYPE SPECIES: *Avicula mosquensis* Buch 1844 from the Lower to Middle Volgian of the Moscow region (Sha and Fürsich 1994).

Buchia columbiana new species

Figs. 3.2.1-3.2.3

B. cf. blanfordiana JELETZKY 1965, p. 18, pl. II, figs. 2-4, 6-7; pl. III, figs. 4-8.

DIAGNOSIS: Small- to medium-sized and pronouncedly inequivalve shell. Overall shape right-handed-incurved. Left valve thick. Right valve flat to gently convex. Beak long and tightly coiled. Shell sculpture varies, but commarginal ribs are generally distinct and coarse to fine.

DESCRIPTION: A pronouncedly inequivalve, medium-sized form. Anterior margin broadly rounded and posterior margin concave near the umbo, turning convex toward the ventral margin. Shell longer than wide. Location of greatest inflation just off the centre of the shell, closer to the dorsal margin.

Left valve right-handedly incurved, thick and arched in the anterior-posterior aspect. Triangular beak is long and coiled toward the anterior margin. Right valve flat to gently convex, with a near-circular to slightly oblong outline. Beak slightly rounded to pointed and oriented straight on the dorsal margin. Beak much lower than on left valve.

Shell sculpture varies. Commarginal ribs usually distinct and either closely-spaced with fine ribbing or widely-spaced with coarse ribbing. Byssus ear is spoon-shaped and shallow (rarely observed).

ETYMOLOGY: After British Columbia, the province where the specimens were collected.

HOLOTYPE: GSC number 34955, GSC Locality 18366 (Figs. 3.2.1-3.2.3) from the upper Upper Jurassic *B.* cf. *blanfordiana* Zone (now named *Buchia columbiana* Zone), Kapoose Formation (Muller *et al.* 1981), Grassy Island section, Nootka Sound map area, Vancouver Island.

PARATYPES: GSC numbers 34956 and 34957, respectively, all from GSC Locality 18366 (Figs. 3.2.4-3.2.9 and Table 3.1) from the upper Upper Jurassic *B.* cf. *blan*-

fordiana Zone (now named Buchia columbiana Zone), Kapoose Formation (Muller et al. 1981), Grassy Island section (Grey et al. 2007), Nootka Sound map area.

OCCURRENCE: Lower Tithonian beds of the North Pacific Province: western British Columbia and northwest Washington State; known uncommonly in northern California, the Richardson Mountains of Yukon Territory, and questionably in northeastern British Columbia.

DISCUSSION: Jeletzky (1965) recognized *B.* cf. blanfordiana (now Buchia columbiana n. sp.) as morphologically distinct from other Northern Hemisphere forms and thought it similar to *B. blanfordiana* of the Southern Hemisphere. Buchia columbiana n. sp. also differs from Southern Hemisphere forms such as *B. blanfordiana*, *B. plicata* and *B. spitiensis*. Shell incurvature is similar to other Jurassic forms, but there are significant differences in shell proportions. Buchia columbiana has a proportionally longer ventral length (Lv, Figure 3.3) and the highest point on the shell occurs more dorsally on southern forms. The outline shapes of the right and left valves are also dissimilar between northern and southern forms, especially near the umbo region of the right valve: southern forms have a deep groove on the anterior-dorsal part of the shell (Figure 3.2).

3.6 Conclusion

Based on morphometrics, we have recognized that buchiid taxa from the Northern and Southern Hemispheres are morphologically different and should be classified as such. While we have found that the genus *Buchia* is not essentially bipolar, the family Buchiidae certainly is. Continued and detailed studies on buchiids, especially phylogenetic analyses, throughout their geographic and stratigraphic ranges should help to assess how closely related northern and southern buchiids are and when they diverged.

| Species | Collection | Age | Locality | $N_{0.*}$ | Reference |
|-------------------------------|--------------|----------------|---------------------------|-----------|-------------------|
| | location | | | | |
| B. blanfordiana | NIGP | Tithonian | Southern Xizang, Tibet | 2 | Shi-Xuan 1999 |
| B. sp. ex gr. blanfordiana | GSC | Tithonian | Muktinath, Nepal | | 1 |
| B. cf. blanfordiana | GSC | Tithonian | Grassy Island, BC | 65 | Grey et al. 2007 |
| B. extensa | NIGP | Tithonian | Southern Xizang, Tibet | 2 | Shi-Xuan 1999 |
| B. plicata | GSC (cast) | L. Tithonian | Waikato Heads, NZ | 4 | Jeletzky 1965 |
| $B. \ plicata,$ | BAS | Tithonian | Himalia Ridge | 28 | Crame and Howlett |
| $B. \ spitiensis,$ | | | Formation of Alexander | | 1988; Butterworth |
| B. blanfordiana | | | Island, Antarctica | | $et \ al. \ 1988$ |
| $B. \ spitiensis$ | GSC (cast) | Tithonian | Jarlemai Siltstone | 2 | 1 |
| | | | Formation of Dampier | | |
| | | | Downs, NW Australia | | |
| B. spitiensis | NIGP | Tithonian | Southern Xizang, Tibet | 2 | Shi-Xuan 1999 |
| M. malayomaorica | GSC | early- to mid- | Kawhia Harbour, | 1 | Jeletzky 1963 |
| | | Kimmeridgian | New Zealand | | |
| *Number of individu | als studied. | | | | |

Table 3.1: Summary of collections used in analyses. All buchiid specimens are from the Southern Hemisphere, with the exception of B, cf. blanfordiana. NIGP = Nanjing Institute of Geology and Palaeontology; GSC = Geological Survey of Canada; BAS = British Antarctic Survey.

3.7. Tables

65

3.7 Tables

| Variable | PC1 | PC2 |
|---------------------------------|-------|-------|
| Dorsal angle of crest-line (J) | -0.02 | -0.77 |
| Ventral angle of crest-line (I) | 0.03 | 0.45 |
| Dorsal length (Ld; $1-5$) | 0.34 | -0.04 |
| Ventral length (Lv; $5-3$) | 0.40 | 0.14 |
| Anterior width (Wa; 4-5) | 0.39 | -0.35 |
| Posterior width (Wp; $5-2$) | 0.38 | 0.08 |
| Dorsal distance (Dd; 1-6) | 0.39 | 0.20 |
| Ventral distance $(Dv; 6-3)$ | 0.41 | -0.09 |
| Inflation (In; 6-7) | 0.34 | -0.01 |

Table 3.2: Correlation of all morphological variables on the first two principal components for the analysis on linear and angular measurements on buchiid left valves. Variables are defined in Figure 3.3

| | Predic | cted Group Membership | |
|---------|--------|-----------------------|----|
| Species | 1 | 2 | Ν |
| 1 | 19 | 9 | 28 |
| | (68) | (32.1) | |
| 2 | 8 | 87 | 95 |
| | (8.4) | (91.6) | |

Table 3.3: Classification summary (based on a jackknifing) for linear and angular measurements of left valves of Northern and Southern Hemisphere material. Numbers in parentheses represent the percentage of classified correctly individuals. Overall, 86% of cases were correctly classified. 1 = Southern Hemisphere (*B. blanfordiana* and other related taxa); 2 = Northern Hemisphere (*B. cf. blanfordiana*).

| | Predi | cted Group Membership | |
|---------|-------|-----------------------|----|
| Species | 1 | 2 | Ν |
| 1 | 57 | 8 | 65 |
| | (88) | (12) | |
| 2 | 11 | 26 | 37 |
| | (30) | (70.3) | |

Table 3.4: Classification summary (based on a jackknifing) for Fourier analysis on left valves of Northern and Southern Hemisphere buchiid material. Numbers in parentheses represent the percentage of correctly classified individuals. 81.4% of cases were correctly classified. 1 = Southern Hemisphere (*B. blanfordiana* and other related taxa); 2 = Northern Hemisphere (*B. cf. blanfordiana*).

3.8 Figures



Figure 3.1: Location map of buchiid faunas worldwide (adapted from Li and Grant-Mackie, 1988). Not pictured: Alexander Island, western Antarctica. Circles indicate the occurances of the genus *Buchia*, while squares indicate the genus *Australobuchia*.



Figure 3.2: Representative suite of specimens used for analysis: Figs 1-9. Buchia columbiana n. sp., all from Grassy Island, BC, GSC Locality 18366. 1-3, holotype, GSC 34955. 1, left valve. 2, right valve. 3, side-view. 4-6, paratype, GSC 34956. 4, left valve. 5, right valve. 6, side-view. 7-9, paratype, GSC 34957. 7, left valve. 8, right valve. 9, side-view. Figs 10-12. B. blanfordiana from Muktinath, Nepal, GSC collections. 10, left valve. 11, right valve. 12, side-view. Figs 13-15. B. spitiensis from Jarlemai Siltstone Formation, NW Australia, GSC plaster cast. 13, left valve. 14, right valve. 15, side-view. Figs 16-18. M. malayomaorica from Kawhia Harbour, New Zealand. 16, left valve. 17, right valve. 18, side-view. Figs 19-21. B. plicata from Mangoli Quarry, New Zealand, GSC plaster cast. 19, left valve. 20, right valve. 21, side-view.



Figure 3.3: Features used to characterize shell morphology in buchiid bivalves: 1, dorsalmost point (umbo) on hinge margin; 2, posteriormost point; 3, ventralmost point; 4, anteriormost point; 5, intersection of lines measuring maximum valve length and valve width; 6, point directly beneath highest point on left valve; 7, highest point on left valve. Morphological variables measured: ventral angle of crest-line* (I); dorsal angle of crest-line (J); dorsal length (Ld; 1-5); ventral length (Lv; 5-3); anterior width (Wa; 4-5); posterior width (Wp; 5-2); dorsal distance to highest point on valve (Dd; 1-6); ventral distance to highest point on valve (Dv; 6-3); inflation (In; 6-7) and delta (Δ ; average distance between concentric rings). *The "crest-line" is defined as the imaginary line joining the highest points of the left valve of *Buchia* (Pavlow 1907) and has been recognized as a taxonomically valuable feature (Jeletzky 1966).



Figure 3.4: PCA results using linear and angular measurements on the left valve show overlap in the morphospace between Northern Hemisphere (B. cf. blanfordiana) and Southern Hemisphere (B. blanfordiana and related species) buchiids. Representative specimen images (scaled) of B. cf. blanfordiana (left), B. blanfordiana (middle), and B. plicata (right) are overlaid. Inset: % of variation explained by each principal component axis.



Figure 3.5: PCA results from the Fourier analysis using the left valve show overlap in the morphospace between B. cf. blanfordiana and B. blanfordiana. Representative specimen images of B. plicata (left), B. blanfordiana (middle), and B. cf. blanfordiana (right) are overlaid. Inset: % of variation explained by each principal component axis.



Figure 3.6: Histograms of the canonical variate (a combination of Lv, Dd and Dv) from the discriminant analysis between Northern Hemisphere (B. cf. blanfordiana) and Southern Hemisphere (B. blanfordiana and related species) buchid material using linear and angular measurements on the left valve indicate a significant difference between the two.



Figure 3.7: Histograms of the canonical variate from the discriminant analysis between Northern Hemisphere (B. cf. blanfordiana) and Southern Hemisphere (B. blanfordiana and related species) material using Fourier analyses on the left valves of buchiid specimens: histograms of the canonical variate indicate a significant difference between the two.

3.9 References

BEURLEN, K. 1944. Beitrge zur Stammesgeschichte der Muscheln. Mnchen Akademie Sitzungsberichte, 11, 113-131.

BUCH, L. V. 1844. Ueber einige neue Versteinerungen aus Moskau. Neues Jahrbuch fr Mineralogie, Geologie und Palaeontologie, 1844, 536-539.

BUTTERWORTH, P. J., CRAME, J. A., HOWLETT, P. J. and MACDONALD, D. I. M. 1988. Lithostratigraphy of Upper Jurassic - Lower Cretaceous strata of eastern Alexander Island, Antarctica. Cretaceous Research, 9, 249-264.

CHEETHAM, A. H., SANNER, J., TAYLOR, P. D. and OSTROVSKY, A. N. 2006. Morphological differentiation of *Avicularia* and the proliferation of species in Mid-Cretaceous *Wilbertopora* Cheetham, 1954 (Bryozoa: Cheilostomata). Journal of Paleontology, 80, 49-71.

COX, L. R. 1953. Lower Cretaceous Gastropoda, Lamellibranchia and Annelida from Alexander Island (Falkland Islands Dependencies). Scientific Reports of the British Antarctic Survey, 4, 14 pp.

CRAME, J. A. 1986. Late Mesozoic bipolar bivalve faunas. Geological Magazine, 123, 611-618.

-. 1990. Buchiid bivalves from the Jurassic-Cretaceous boundary in Antarctica, 151-161. In V. V. Menner (ed.), Granitsa yury i mela.Volume 699. Trudy Instituta Geologiya i Geofizika Siberia Otdelenie, Nauka, Moscow.

-. 1992. Evolutionary history of the polar regions. Historical Biology, 6, 37-60.

-. 1993. Bipolar molluscs and their evolutionary implications. Journal of Biogeography, 20, 145-161.

– and HOWLETT, P. J. 1988. Late Jurassic and Early Cretaceous biostratigraphy of the Fossil Bluff Formation, Alexander Island. British Antarctic Survey Bulletin, 78, 1-35.

– and KELLEY, S. R. A. 1995. Composition and distribution of the inoceramid bivalve genus *Anopaea*. Palaeontology, 38, 87-103.

CRAMPTON, J. S. and 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.

– and MAXWELL, P. A. 2000. Size: all it's shaped up to be? Evolution of shape through the lifespan of the Cenozoic bivalve *Spissatella* (Crassatellidae), 399-423. *In* E. M. Harper, J.D. Taylor, J.A. Crame (ed.), The Evolutionary Biology of the Bivalvia.Volume 177. Geological Society, Special Publications, London.

DARLING, K. F., WADE, C. M., STEWART, I. A., KROON, D., DINGLE, R. and BROWN, A. J. L. 2000. Molecular evidence for genetic mixing of Arctic and Antarctic subpolar populations of planktonic foraminifers. Nature, 405, 43-47.

GREY, M., HAGGART, J. W. and JELETZKY, J. A. 2007. Uppermost Jurassic (Portlandian) to lowermost Cretaceous (Valanginian) section at Grassy Island, west coast of Vancouver Island, British Columbia. Geological Survey of Canada Openfile, 5666.

-, HAGGART, J. W. and SMITH, P. L. 2008. Species discrimination and evolutionary mode of Buchia (Bivalvia: Buchiidae) from Upper Jurassic–Lower Cretaceous strata of Grassy Island, British Columbia, Canada. Palaeontology, 51, 583-595.

HAMMER, O. 2000. A theory for the formation of commarginal ribs in mollusc shells by regulative oscillation. Journal of Molluscan Studies, 66, 383-391.

HIKUROA, D. and GRANT-MACKIE, J. A. 2000. Late Jurassic Buchiids. Geological Society of New Zealand Miscellaneous Publication, 108A, 68.

-. 2008. New species of Late Jurassic *Australobuchia* (Bivalvia) from the Murihiku Terrane, Port Waikato - Kawhia region, New Zealand. Alchergina, 32, 1-26.

HOLDHAUS, K. 1913. The fauna of the Spiti shales (Lamellibranchiata and Gastropoda). Paleontologica Indica, 4, 397-456.

JELETZKY, J. A. 1963. *Malayomaorica* gen. nov. (Family Aviculopectinidae) from the Indo-Pacific Upper Jurassic; with comments on related forms. Palaeontology, 6, 148-160.

–. 1965. Late Upper Jurassic and Early Lower Cretaceous fossil zones of the Canadian western Cordillera, British Columbia. Geological Survey of Canada Bulletin, 103.

 –. 1966. Upper Volgian (Latest Jurassic) Ammonites and Buchias of Arctic Canada. Geological Survey of Canada Bulletin, 128.

-. 1984. Jurassic-Cretaceous boundary beds of Western and Arctic Canada and the problem of Tithonian-Berriasian stages in the Boreal Realm, 175-255. In G.

E. G. Westermann (ed.), Jurassic-Cretaceous Biochronology and Paleogeography of North America.Volume 27. Geological Association of Canada Special Paper.

KAUFFMAN, E. G. 1973. Cretaceous Bivalvia, 353-384. In A. Hallam (ed.), Atlas of Palaeobiogeography. Elsevier Scientific Publishing Co., New York.

KONOVALOV, V. P. 1977. The genus *Buchia* in the Pacific realm., 139-154. *In* Vladivostock (ed.), Evolution of the Pacific biota.

KOWALEWSKI, M., DYRESON, E., MARCOT, J. D., VARGAS, J. A., FLESSA, K. W. and HALLMAN, D. P. 1997. Phenetic discrimination of biometric simpletons: paleobiological implications of morphospecies in the lingulide brachiopod *Glottidia*. Paleobiology, 23, 444-469.

KRUMBECK, L. 1923. Zur Kenntnis des Juras der Inseln Timor sowie des Aucellen-Horizontes von Seran und Bura. Palontologie von Timor, 12, 1-120.

KRUMBECK, L. 1934. Die Aucellen von Misol. Neues Jahrbuch. Beilage-Band, 71 (Abt. B), 422-469.

LI, X. and GRANT-MACKIE, J. A. 1988. Upper Jurassic and Lower Cretaceous *Buchia* (Bivalvia) from southern Tibet, and some wider considerations. Alcheringa, 12, 249-268.

LINNE, C. 1758. Systema Naturae per Regna Naturae. Laurentius Salvius, Stockholm, 824 pp.

NEWELL, N. D. 1965. Classification of the Bivalvia. American Museum Novitates, 2206, 1-25.

PAVLOW, A. P. 1907. Enchainement des aucelles et aucellines du cretace Russe. Nouveaux Memoir de Societe Imperiale Naturalle de Moscou, 5, 455-570.

RAFINESQUE, C. S. 1815. Analyse de la nature tableau de l'Univers et des corps organizes. Author, Palermo224.

ROUILLIER, C. 1845. Explication de la coupe gologique des environs de Moscou. Bulletin de la Socit Impriale des Naturalistes de Moscou, 19, 359-467.

SHA, J. and FÜRSICH, F. T. 1994. Bivalve faunas of eastern Heilongjiang, northeastern China. II. The Late Jurassic and Early Cretaceous buchiid fauna. Beringeria, 12, 3-93.

SHI-XUAN, W. 1999. Cretaceous bivalve biogeography in Qinghai-Xizang Plateau.

Acta Palaeontologica Sinica, 38, 1-31.

STOLICZKA, F. 1866. The Fossil Cephalopoda of the Cretaceous Rocks of Southern India (Ammonitidae). Memoirs of the Geological Survey of India, Palaeontologia Indica, 3, 155-216.

SURLYK, F. and ZAKHAROV, V. A. 1982. Buchiid bivalves from the Upper Jurassic and Lower Cretaceous of East Greenland. Palaeontology, 25, 727-753.

ZAKHAROV, V. A. 1987. The Bivalve *Buchia* and the Jurassic-Cretaceous Boundary in the Boreal Province. Cretaceous Research, 8, 141-153.

-, SURLYK, F. and DALLAND, A. 1981. Upper Jurassic -Lower Cretaceous *Buchia* from Andoy, northern Norway. Norsk Geologisk Tidsskrift, 61, 261-269.

ZITTEL, K. A. V. 1870. Die Fauna der ltern Cephalopoden-fhrenden Tithonbildungen. Palaeontographica, Cassel, 1, 119-310.

Chapter 4

Morphological Variability in Time and Space: an Example of Patterns Within Buchiid Bivalves (Bivalvia, Buchiidae)

4.1 Introduction

Geographical variation can result from adaptation to local environments and/or genetic drift and is an important factor when considering the nature of species and how they evolve. Every population of a species differs in some way from all others and the degree to which they differ varies; species between populations can range from being nearly identical (interspecific variability is minimal) to having a distinctness almost at the species level (interspecific variability is large) (Mayr 1963).

The study of geographical variation has been the topic of many paleontological and biological investigations, with research involving intraspecific versus environmental variation (e.g. Crampton 1996; Stempien *et al.* 2002; Stempien and Kowalewski 2004); disparity (morphological diversity) estimates (e.g. Foote 1993; Villier and Korn 2004; Neige *et al.* 1997, 2001); comparisons of taxonomic diversity and disparity (e.g. Moyne and Neige 2007); and paleoenvironmental reconstruction potential (e.g. Aguirre *et al.* 2006). However, few studies have looked at the variation of a genus over its range (but see Courville and Cronier 2005, and Crampton and

Gale 2005) and this avenue of research can provide evidence of how morphological patterns vary both spatially and temporally. The study of geographical variation is critical as there is a growing body of evidence showing that it is a primary determinant of biodiversity gradients (Allen and Gillooly 2006) - a timely topic as many scientists believe that the world has entered into a modern biodiversity crisis (Pimm *et al.* 1995).

Buchiid bivalves, and in particular the genus *Buchia* Rouillier 1845 (Late Oxfordian-Hauterivian), are well-known for their biostratigraphic utility (e.g. Jeletzky 1965; Kauffman 1973); they are also useful, however, for the study of evolutionary patterns (e.g. Grey *et al.* 2008) and geographic variation. Buchiids are abundant and often well-preserved in a variety of facies, widely distributed geographically, and readily determined taxonomically through the use of morphometric analyses, despite a large amount of interspecific variability (Grey *et al.* 2008). Traditional morphometric techniques have shown that, while the most important discriminatory variables for differentiating species of *Buchia* are the angles of the crest-line and inflation (see Figure 4.1), variables can and do change depending on the species that are being compared; it is therefore important to retain and utilize all previously defined variables for analyses (Grey *et al.* 2008).

In this study we examine morphological variability of buchiids over their geographic and temporal range by: 1) quantifying geographic variation within the genus and identifying its role on morphology; 2) determining potential latitudinal gradients; and 3) comparing disparity and diversity over time and space.

4.2 Material

We undertook statistical comparisons of eight geographically widely separated and roughly co-eval collections of buchiids from the Oxfordian (Late Jurassic) to Hauterivian (Early Cretaceous). The examined material is from: Antarctica (Alexander Island); Arctic Canada (Ellesmere Island); China (Eastern Heilongjiang); East Greenland (Jameson Land and Wollaston Forland); Far East Russia (Southern Primorye and Far North); Grassy Island and Taseko Lakes, British Columbia, Canada (these are located on the Wrangellia and Cadwallader terranes, respectively); and New Zealand (North Island, Murihiku Terrane) (refer to Table 4.1 and Figure 4.2). The bulk of this material was obtained from institutional collections and represents stratigraphically constrained series.

The number of specimens ranged from 28 to 765 for each collection, with a total of 1855 specimens measured (Table 4.1). Out of the approximately 40 species within the genus *Buchia* (and the related Southern Hemisphere genus *Australobuchia* Za-kharov 1981), we have 30 represented in our study. Thus we have a nearly complete view of taxonomic diversity because most other species not represented here are endemic to areas that we did not include in this study. We have also included specimens of *Praebuchia* Zakharov 1981 (of Oxfordian age, Late Jurassic) as this genus is considered to be the direct ancestor of *Buchia* (Zakharov 1987).

Paleolatitudes for each study location were estimated and were, for the most part, taken from Crame (2002) whereas others (i.e. Ellesmere Island and terranes in British Columbia) were estimated based on current research (Torsvik *et al.* 2001 and Stamatakos *et al.* 2001; Carter and Haggart 2006; Schrder-Adams and Haggart 2006; Smith 2006, respectively).

Buchiids are found in a variety of facies (from shallow, inner shelf to deeper-water facies), representing different paleoenvironments (e.g. Sha and Fursich 2004). Bivalves are well known to vary morphologically across a wide-range of habitats and have thus been important for paleoenvironmental reconstruction (e.g. Aguirre *et al.* 2006), but previous studies (e.g. Grey *et al.* 2008) with the genus *Buchia* from the Grassy Island section in British Columbia (Canada) have shown that local ecophenotypic effects on morphology are minimal. For instance, morphology was not notably affected by facies-type (Grey *et al.* 2008). What is not known is whether buchiid morphology can be affected by larger environmental variations, which is why it is important to study morphological change over the genus' geographic range (representing a variety of paleolatitudes and environmental conditions, Table 4.1).

Taxonomic validity of Buchia species using multivariate morphometrics has been

undertaken for the section at Grassy Island, British Columbia (Grey *et al.* 2008) and preliminary work has also been carried out for the other localities used for this study. Results for all the localities are similar to those from Grassy Island: while there is considerable interspecific variability within previously recognized species, all are deemed statistically valid based on the morphological characters we measured. We therefore accept all the previously designated species as such for the purposes of this research.

4.3 General Methods

The exterior and side views for all unbroken left valves from each geographical area were photographed using a Nikon D70 digital camera. We used the left valve for consistency and also because it exhibits greater morphological variance. Images measured with a custom-designed morphometrics program created in MatLab (MorphLab 1.0, available from the authors).

Nine morphometric variables were used to describe shell shape; these include angular and linear measurements that have been used previously (Grey *et al.* 2008) to describe morphology between species of *Buchia* (Figure 4.1). Linear and angular variables of buchiids were standardized using log-transformations prior to analyses (Kowalewski *et al.* 1997). We applied multivariate morphometrics using phenetic discrimination of linear and angular measurements to define the buchiid morphospace. Phenetic discrimination included a combination of principal component analyses (PCA) and step-wise canonical variate analyses (CVA). PCAs, executed using the program PAST (version 1.38, Hammer *et al.* 2001), were used to explore the morphospace of buchiids and CVAs, executed using SPSS (version 11.0), were used for predictive classification (high percentages indicate that specimens were correctly classified to their *a priori* groups based on morphological characteristics). *A priori* groupings for both analyses were based either on geographical location or taxonomic group (= species). We utilized a step-wise method for the CVA because it selects variables that contribute the most discriminatory power to the model (refer to Cheetham *et al.* 2006) and this method is advantageous when there are a number of characters measured. We also simulated a jackknifed approach in SPSS (version 11.0) by selecting the 'leave-one-out classification' option.

4.4 Geographical Variation of Shell Shape

4.4.1 Methods

A variety of morphometric analyses were performed in order to determine the effect of geography on buchiid morphology. We applied the above methods to investigate geographic variability within a single species that was found in at least three locations, using location as the *a priori* grouping variable. Separate analyses were therefore performed for each of *B. volgensis*, *B. unschensis*, and *B. okensis*. We also grouped data from the three species and performed another analysis using species as the *a priori* grouping variable; this was to determine if PCAs and CVAs discriminate between species (i.e. species used as the grouping variable) better than, or as well as, geography (i.e. location used as the grouping variable). Geography is an important factor influencing morphology if the data cluster by location and if the percentages of correctly classified specimens are high (or as high as when species is the grouping variable).

4.4.2 Results and Discussion

Results indicate that geographic variation plays an important role in buchiid morphology (Figs. 3-7). There is variable separation between locations in the morphospace (Figs. 3-5, see Table 4.2 for principal component loadings for all tests) and the percentage of correct classification according to location ranges from 53% (*B. unschensis*) to 94% (*B. okensis*) (Table 4.3). Higher classification rates indicate large interspecific variability across the geographic range of that species; therefore, *B. okensis* is more variable than *B. unschensis* across its geographic range.

The fairly large number of correctly classified specimens according to location for B. volgensis and B. okensis means that there are morphological differences between populations of the same species that can be attributed to geography. The morphological characters that best distinguish between locations (i.e. CV1 and CV2) vary according to the species analysed (Table 4.3). For instance, B. okensis is primarily distinguished by width across its geographical range, while B. volgensis and B. unschensis are distinguished by angles of the crest-line and inflation (Table 4.3).

A PCA for all three species (species used as the grouping variable) showed considerable overlap in the morphospace (Figure 4.9), but a moderately high classification rate of 75% was obtained from the CVA (Figure 4.10). Comparatively, a CVA of data from the three species above that are found in some or all of the six locations, using location as the *a priori* grouping variable, gave a classification rate of 71% (Figure 4.11). These similar rates of classification indicate that there is nearly as much variation between geographical locations as there is between species.

Overall, results indicate that geographic variation is an important factor influencing morphology of buchiids. These results are comparable to those of Stempien and Kowalewski (2004), who found the geographic morphospace of the bivalve *Mulinia* varied significantly and that the amount of variation between geographic regions was similar to the amount of intraspecific variation between two species. Crampton (1996), on the other hand, found geographic variation was negligible compared to intraspecific variation for the bivalve *Actinoceramus* - species differences outweighed those between geographical locations, suggesting that genetics are more important for morphological variation than are environmental differences. Our results suggest that geographical (a rough proxy for environmental) differences can have a similar role on morphology as genetics, and also raise important issues of taxonomy: how morphologically different do two populations from different locations need to be before they are considered separate species? For the case of *B. okensis* in particular, it may be prudent to assign species variant names.

4.5 Latitudinal Gradient

4.5.1 Methods and Results

Latitudinal gradients with respect to morphology and speciation are well documented in the fossil record (see Crame 2002 and Aguirre *et al.* 2006 for examples). An example of a gradient commonly found between populations, both fossil and Recent, is termed Bergmann's size rule, whereby there is a positive relationship between latitude and size of organisms of the same species. This has been found in organisms from fossil ostracodes (Hunt and Roy 2006) to modern birds (Ashton 2002). Latitudinal gradients have also been observed in Devonian and Carboniferous brachiopod shell ornamentation that may have resulted from differential predation (Dietl and Kelley 2001).

We explored whether gradients existed for buchiids over the range of paleolatitudes sampled in this study (from 75°S to 66°N) by performing a PCA using all data for all locations studied. We plotted the primary principal component (PC1; see Table 4.2 for loadings), which accounted for 67% of the variation, against paleolatitude (Figure 4.12). A Pearson correlation and regression analysis indicate that there is not a significant relationship between latitude and morphology (r= -0.29, p= 0.5; $R^2=0.16$, p= 0.32). This is also the case for PC2 versus paleolatitude (not figured; r= -0.19, p= 0.65; $R^2=0.12$, p= 0.54). Next, we plotted the primary canonical variate (CV1), representing the combination of variables (mainly a function of ventral length) that best separates locations and accounts for the most variation (53%), against paleolatitude (Figure 4.13). We found a fairly high regression coefficient ($R^2=0.68$, p= 0.01), but the Pearson correlation is not significant (r= -0.38; p= 0.35).

4.5.2 Discussion

Our results suggest that a gradient may exist for buchiids along CV1 and it is possible that with additional data points from more regions (especially those from lower latitudes, i.e. Tibet and Indonesia) one may be found. It is also important to note that the latitude of Eastern Heilongjiang in China is not known and we have instead used its current latitude for approximation (the paleolatitude may consequently be off by 10-20°). Most of the paleolatitudes, however, are well-supported in the literature (Crame 2002: East Greenland, Far East Russia, New Zealand, and Antarctica) and evidence suggests that Ellesmere Island (Canadian Arctic) and the two terranes (Wrangellia and Cadwallader) in British Columbia, Canada were in their current latitudes in the Jurassic (Torsvik *et al.* 2001 and Stamatakos *et al.* 2001; Carter and Haggart 2006; Schrder-Adams and Haggart 2006; Smith 2006, respectively).

The previous analyses included geographic-temporal data (i.e. time is not held constant) and we therefore explored the effect of time on latitudinal gradients. PC1 and CV1 were plotted against paleolatitude (not shown) for each time period, or age, in the buchiid lineage: Oxfordian, Kimmeridgian, Tithonian, Berriasian, Valanginian, and Hauterivian. We did not find evidence of a gradient in any case. Overall our results indicate that, while morphology differs according to geographic region, there is currently no evidence for a trend in those differences along a latitudinal gradient.

In our study of gradients we included all data from all locations, giving a general view of buchiid morphology by latitude, but future studies should focus on individual species of *Buchia* and/or *Australobuchia* over their range to add to our understanding of gradients within the two genera.

4.6 Disparity and Diversity over Space and Time

4.6.1 Methods

Calculations of taxonomic diversity are often supplemented with those of disparity (morphological diversity), leading to an improved understanding of the processes of diversification and extinction. The relationship between the two metrics also can yield useful information about evolutionary mechanisms. Disparity and diversity have been studied over geographical ranges (Moyne and Neige 2007), during periods of known extinctions (e.g. Villier and Korn 2004), during faunal invasions (Navarro *et al.* 2005), and over the range of a taxon (e.g. angiosperms: Lupia 1999; cuttlefish: Neige 2003; echinoids: Villier and Elbe 2004).

Diversity measures were obtained by species counts and the corresponding error bars were calculated as $\pm \sqrt{D}$, where D is the number of species (Moyne and Neige 2007). We calculated disparity using the sum of variances of scores on the first three principal components from the PCA in the above section. The sum of variances method is particularly useful for this study because it is relatively insensitive to sample size (Movne and Neige 2007). The first three axes account for more than 88% of the variation and, as outlined in Villier and Elbe (2004), adding more axes would not affect patterns because the axes are less influential on disparity and would add approximately the same amount of disparity to any group. Following the methods of Villier and Elbe (2004) to reduce the artificial weighting of variables and emphasize the main sources of variance, we scaled principle component scores by multiplying them by the square root of the eigenvalue. All disparity estimates were bootstrapped (500 replicates), where the mean value of the bootstrap distribution was used as the disparity estimate for the sample and standard deviations from that were also calculated (Villier and Elbe 2004). The bootstrap was performed using MatLab.

Moyne and Neige (2007) studied diversity and disparity signals over the geographic range of Middle Jurassic ammonites and found that three biodiversity crises during this time had left different paleogeographical signatures. We therefore calculated disparity and diversity values for each geographical location and time period. Latitudinal and temporal trends were considered by employing Spearman's correlation analyses (Villier and Elbe 2004).

4.6.2 Results and Discussion

Disparity over the eight geographical locations ranges from 19 to 60 and diversity ranges from 3 to 19 (Figure 4.14). Higher values of disparity indicate greater mor-

phological diversity; therefore, buchilds from the Arctic, China and Greenland have the most wide-ranging morphologies (with overlapping standard deviations), while the localities from two different terranes in British Columbia (Grassy Island and Taseko Lakes) have more constrained morphologies (Figure 4.14). Although the method we used to calculate disparity is relatively insensitive to sample size, results from China and the Arctic should still be viewed with caution because they represent the locations with some of the smallest sample sizes (future work will need to include more specimens to confirm this result). In addition, we performed identical analyses for disparity within a single species, B. okensis (this was the species found in the most locations: Grassy Island and Taseko Lakes, B.C., Russia and Greenland), over its entire geographical range and found similar results in that Grassy Island and Taseko Lakes have the lowest disparity values (23 and 24, respectively); Russia and Greenland have much larger disparities (40 and 60, respectively). We did not find a clear relationship between diversity and disparity (Figure 4.14) and this finding supports others' work that taxonomic diversity is a poor predictor of morphological diversity (disparity) (e.g. Foote 1993; Neige 2003).

Latitudinal trends are not apparent in either disparity (Spearman's Rho = -0.60; p = 0.21) or diversity (Spearman's Rho = -0.26; p = 0.62) (Figure 4.15) for our spatiotemporal data. As in the above section, we explored the effect of time by performing the same analysis, but only for the Tithonian (this is the only time in which all localities are represented). The results are similar: there is no latitudinal trend for either disparity (Spearman's Rho = -0.48; p = 0.91) or diversity (Spearman's Rho = 0.49; p = 0.91) and there is no relationship between diversity and disparity (not figured).

There is discordance between disparity and diversity through much of the genus' time range (Figure 4.16). However, as *Buchia* heads towards extinction in the Hauterivian, both disparity and diversity decline, and disparity reaches an ultimate low (Figure 4.16), perhaps suggesting in this case that the extinction was selective of morphology. This pattern has also been documented by other groups, such as the Cambrian blastoids (Foote 1992). Villier and Korn (2004) also found that, over 30 million years, disparity for Paleozoic ammonoids declined and reached a minimum

just before the Permian mass extinction.

Discordances have often been attributed to biases such as taxonomic, temporal, or the choice of morphological characters measured, but there is increasing evidence that discordances are real events that are due to phenomena such as biodiversity crises (e.g. Moyne and Neige 2007). Our results are similar to those found for Old World cuttlefishes (Neige 2003), where there were no latitudinal gradients found and no linear relationship between diversity and disparity (i.e. disparity is not predicted by the number of species).

Our sample numbers for the locations used in this study varied between 28 and 765; in order to ensure that this did not affect our measures of diversity and disparity, we determined that sample number was not correlated to either metric using both a regression analysis (disparity: $R^2 = 0.47$, p=0.06; diversity: $R^2 = 0.01$, p=0.93) and a Pearson correlation (disparity: r = -0.5, p=0.21; diversity: r = 0.48, p=0.23). Hence, our results appear not to be influenced by sample size.

Disparity and diversity are often positively correlated during the beginning of a radiation (Foote 1993), but our results do not show this trend: we found that disparity was high and diversity low at the initial diversification of buchiids in the Late Oxfordian (Figure 4.16). Our results may be confounded here because the only data we have for this time period includes ten specimens of *Praebuchia* (proposed ancestors to the genus *Buchia*) from two localities (seven are from Indonesia and are in Auckland University's collection, New Zealand; three others are from East Greenland). Further study will require additional data from early species of *Buchia* (such as stratigraphically lower occurrences of *B. concentrica* in the Boreal Realm) during this time period to test if our results for the Oxfordian are accurate.

4.7 Summary and Conclusions

This research adds to a growing body of work on patterns of geographical variation and is the first to do so for the genus *Buchia*. Our research highlights three key points:

- 1. Geography is a significant variable affecting morphology, perhaps nearly as important as the morphological effects of speciation.
- 2. While geography can have an important influence on morphology, we found no evidence to support a correlation between geography (paleolatitude) and morphology (shell shape), disparity (morphological diversity), or diversity (number of species).
- 3. Disparity and diversity are not always correlated, however both metrics decreased as the genus became closer to extinction, a pattern that has been documented for a variety of other taxa.
| Locality | Paleo- | Depositional | Age Range | No. | No. | Primary |
|---|-----------------|--------------------------|----------------------------------|------------------|----------------------------|--------------------|
| (collection location) | latitude | environment | | $loc.^{\dagger}$ | $\mathrm{spp.}^{\ddagger}$ | reference |
| Alexander Island, | $15^{\circ}S$ | $\operatorname{Shallow}$ | Tithonian | 28 | က | Butterworth et al. |
| Antarctica (BAS) | | | | | | 1988, Crame and |
| | | | | | | Howlett 1988 |
| Ellesmere Island, | $81^{\circ}N$ | Shallow | Middle Tithonian - | 39 | ъ | Jeletzky 1966 |
| Canadian Arctic (GSC) | | | Berriasian | | | |
| Eastern Heilongjiang, | 46- | Deep | Middle Tithonian - | 59 | 9 | Sha et al. 2003 |
| China [*] (NIGP) | $48^{\circ}N$ | | mid-Valanginian | | | |
| Jameson Land and | $49.5^{\circ}N$ | Deep with | Late Oxfordian - | 206 | 14 | Surlyk and |
| Wollaston Forland, | | some shallow | Late Valanginian | | | Zakharov 1982, |
| East Greenland (UC) | | deposits | | | | Alsen 2006 |
| Far East Russia | $71^{\circ}N$ | Shallow | Kimmeridgian - | 301 | 19 | Sey and Kalacheva |
| (VSEGEI) | | | mid-Valanginian | | | 1993, 1999 |
| Wrangellia Terrane, | $49^{\circ}N$ | Shallow | Late Tithonian - | 765 | ъ | Grey et al. 2007 |
| Grassy Island, B.C. [*] (GSC) | | | Valanginian | | | |
| Murihiku Terrane, | $65^{\circ}S$ | Deep | Late Oxfordian - | 193 | 4 | Hikuroa and Grant- |
| New Zealand (AU, GNS) | | | Middle Tithonian | | | Mackie 2008 |
| Cadwallader Terrane, | $51^{\circ}N$ | Shallow | Late Tithonian - | 246 | 11 | Jeletzky and |
| Taseko Lakes, B.C. [*] (GSC) | | | Hauterivian | | | Tipper 1968 |
| *The paleolatitudes for these | locations | are approximate | ed as there is no curre | ent con | sensus d | on their placement |
| during this time period. $^{\dagger}Nu$ | mber of in | dividuals studie | d per location. [‡] Num | ber of s | species. | |
| | | | | | | |

Table 4.1: Summary of collections used in analyses. AU = Auckland University; BAS = British Antarctic Survey; UC = University of Copenhagen (Geological Museum of Denmark and Geological Institute); GNS = Institute of Geological and Nuclear Sciences (NZ); GSC = Geological Survey of Canada; NIGP = Nanjing Institute of Geology and Palaeontology; VSEGEI = All Russian Geological Research Institute.

4.8. Tables

4.8 Tables

| Variable | PC1 | PC2 | Variable | PC1 | PC2 |
|-----------------|----------|-----------|------------------|----------|-----------|
| Dorsal angle of | 1) 0.15 | 1) 0.70 | Ventral angle of | 1) -0.18 | 1) -0.67 |
| crest-line (J) | 2) 0.00 | 2) -0.70 | crest-line (I) | 2) 0.01 | 2) 0.70 |
| | 3) -0.70 | 3) -0.68 | | 3) 0.70 | 3) 0.71 |
| | 4) 0.14 | 4) 0.68 | | 4) -0.10 | 4) -0.71 |
| | 5) -0.01 | 5) 0.70 | | 5) 0.02 | 5) - 0.69 |
| Dorsal length | 1) 0.37 | 1) -0.11 | Ventral length | 1) 0.37 | 1) -0.08 |
| (Ld; 1-5) | 2) 0.37 | 2) 0.04 | (Lv; 5-3) | 2) 0.38 | 2) -0.03 |
| | 3) 0.04 | 3) 0.08 | | 3) -0.03 | 3) 0.01 |
| | 4) 0.39 | 4) -0.09 | | 4) 0.39 | 4) -0.04 |
| | 5) 0.39 | 5) - 0.01 | | 5) 0.37 | 5) 0.07 |
| Anterior width | 1) 0.37 | 1) -0.05 | Posterior width | 1) 0.37 | 1) -0.15 |
| (Wa; 4-5) | 2) 0.38 | 2) 0.00 | (Wp; 5-2) | 2) 0.37 | 2) 0.03 |
| | 3) 0.00 | 3) 0.00 | | 3) 0.04 | 3) -0.00 |
| | 4) 0.38 | 4) -0.02 | | 4) 0.32 | 4) -0.08 |
| | 5) 0.38 | 5) 0.09 | | 5) 0.37 | 5) - 0.05 |
| Dorsal distance | 1) 0.37 | 1) -0.05 | Ventral distance | 1) 0.37 | 1) -0.12 |
| (Dd; 1-6) | 2) 0.39 | 2) 0.02 | (Dv; 6-3) | 2) 0.39 | 2) -0.04 |
| | 3) 0.02 | 3) -0.02 | | 3) -0.04 | 3) 0.09 |
| | 4) 0.38 | 4) -0.03 | | 4) 0.37 | 4) -0.07 |
| | 5) 0.38 | 5) -0.05 | | 5) 0.38 | 5) 0.08 |
| Inflation | 1) 0.36 | 1) -0.05 | | | |
| (In; 6-7) | 2) 0.37 | 2) -0.04 | | | |
| | 3) -0.04 | 3) 0.14 | | | |
| | 4) 0.37 | 4) -0.11 | | | |
| | 5) 0.37 | 5) - 0.07 | | | |

Table 4.2: Correlation of all morphological variables on the first two principal components for all five principal component analyses performed in this study. 1-3 = B. *okensis*, *B. volgensis* and *B. unschensis*, respectively, across their geographic ranges; 4 = all three species using location as the grouping variable; and 5 = all data from all locations (used for latitudinal gradient analysis). Variables are defined in Figure 4.1.

| | Locations | PC1 | PC2 | CV1 | CV2 | CV1 | CV2 | Classi- |
|------|--------------------|------|-----|------|------|------------|----------------|-------------|
| | (grouping | (%) | (%) | (%) | (%) | | | fication |
| | variable) | | | | | | | rate $(\%)$ |
| | Grassy Island | 64 | 17 | 85.6 | 13.5 | Posterior | Anterior | 94 |
| | Greenland, Russia, | | | | | width (Wp) | width (Wa) | |
| | Taseko Lakes | | | | | | | |
| is | China, | 74.3 | 18 | 93 | 7 | Inflation | Ventral | 75 |
| | Greenland, | | | | | (In) | angle of the | |
| | Russia | | | | | | crest-line (J) | |
| isis | Arctic, China, | 73 | 21 | 70.2 | 16.1 | Inflation | Dorsal | 53 |
| | Greenland, | | | | | (In) | angle of the | |
| | Russia | | | | | | crest-line (I) | |

| centage of variation attributed to each axis in the principal component (PC) and canonical variate | the morphological variable associated with the first two canonical variate axes, and classification | ses performed for each species. |
|--|---|---------------------------------|
| able 4.3: Percentage of v | UV) analyses, the morph | tes for analyses perform |

4.8. Tables

4.9 Figures



Figure 4.1: Features used to characterize shell morphology in buchiid bivalves: 1, dorsalmost point (umbo) on hinge margin; 2, posteriormost point; 3, ventralmost point; 4, anteriormost point; 5, intersection of lines measuring maximum valve length and valve width; 6, point directly beneath highest point on left valve; 7, highest point on left valve. Morphological variables measured: ventral angle of crest-line* (I); dorsal angle of crest-line (J); dorsal length (Ld; 1-5); ventral length (Lv; 5-3); anterior width (Wa; 4-5); posterior width (Wp; 5-2); dorsal distance to highest point on valve (Dd; 1-6); ventral distance to highest point on valve (Dv; 6-3); and inflation (In; 6-7). *The "crest-line" is defined as the imaginary line joining the highest points of the left valve of *Buchia* (Pavlow 1907) and has been recognized as a taxonomically valuable feature (Jeletzky 1966).



Figure 4.2: Buchiid geographical range (white/grey circles and squares); circles indicate *Buchia* (Northern Hemisphere buchiids) locations, while squares indicate locations of *Australobuchia* (Southern Hemisphere buchiids) (modified after Li and Grant-Mackie, 1988). Grey enclosures indicate locations of material used in this study. Not pictured: Alexander Island, western Antarctica.



Figure 4.3: Scatterplot from the principal component analysis (PCA) showing overlap in the morphospace for B. okensis using location as the *a priori* grouping variable.



Figure 4.4: Scatterplot from the canonical variate analysis (CVA) for *B. okensis* where location is the *a priori* grouping variable. 94% of specimens were correctly classified according to their geographic location; this indicates that most specimens differ enough in morphology between locations that they can be categorized to their geographical origin. CV1 was a function of primarily posterior width (Wp, Figure 4.1) and CV2 was a function of primarily anterior width (Wa, Figure 4.1).



Figure 4.5: Scatterplot from the PCA for *B. volgensis*, using location as the *a priori* grouping variable, showing overlap in the morphospace.



Figure 4.6: Scatterplot from the CVA for *B. volgensis.* 75% of specimens were correctly classified according to their geographic location. CV1 was a function of primarily inflation (In, Figure 4.1) and CV2 was a function of primarily ventral angle of crest-line (angle I, Figure 4.1).



Figure 4.7: Scatterplot from the PCA for *B. unschensis*, using location as the *a priori* grouping variable, showing considerable overlap in the morphospace.



Figure 4.8: Scatterplot from the CVA for *B. unschensis.* 53% of specimens were correctly classified according to their geographic location. CV1 was a function of primarily inflation (In, Figure 4.1) and CV2 was a function of primarily dorsal angle of crest-line (angle I, Figure 4.1).



Figure 4.9: Scatterplot from the PCA of data from three species (*B. volgensis*, *B. unschensis* and *B. okensis*) that are found in some or all of the following six locations: Arctic, China, Grassy Island, Greenland, Russia, and Taseko Lakes. Species was used as the *a priori* grouping variable.



Figure 4.10: Scatterplot from the CVA of data from three species (*B. volgensis*, *B. unschensis* and *B. okensis*) that are found in some or all of the six locations, using species as the *a priori* grouping variable. 75% of specimens were correctly classified according to their species designation. CV1 was primarily a function of ventral length (Lv, Figure 4.1) and CV2 was primarily a function of inflation (In, Figure 4.1).



Figure 4.11: Scatterplot from the CVA of data from three species (*B. volgensis*, *B. unschensis* and *B. okensis*) that are found in some or all of the six locations, using location as the *a priori* grouping variable. 71% of specimens were correctly classified according to their geographic location. CV1 was primarily a function of posterior width (Wp, Figure 4.1) and CV2 was primarily a function of anterior width (Wa, Figure 4.1).



Figure 4.12: The first principal component (using location as the grouping variable) versus paleolatitude (y = -0.01x + 0.41, R² = 0.16).



Figure 4.13: The primary canonical variate (using location as the grouping variable) versus paleolatitude (y = -0.02x + 0.80, $R^2 = 0.68$). CV1 was primarily a function of ventral length (Lv, Figure 4.1) and CV2 was primarily a function of posterior width (Wp, Figure 4.1).



Figure 4.14: Diversity versus disparity and their corresponding error bars (the calculations for these are described in the text) over the geographical range of buchiids used in this study. There is not a significant correlation between the two metrics.



Figure 4.15: Disparity and diversity versus paleolatitude (disparity: y = -0.13x + 44, $R^2 = 0.18$; diversity: y = 0.05x + 7.4, $R^2 = 0.24$).



Figure 4.16: Discordance and concordance between diversity and disparity through the temporal range of buchiids (the calculations for error bars are described in the text).

4.10 References

AGUIRRE, M. L., PEREZ, S. I. and SIRCH, Y. N. 2006. Morphological variability of *Brachidontes* Swainson (Bivalvia, Mytilidae) in the marine Quaternary of Argentina (SW Atlantic). Palaeogeography, Palaeoclimatology, Palaeoecology, 239, 100-125.

ALLEN, A. P. and GILLOOLY, J. F. 2006. Assessing latitudinal gradients in speciation rates and biodiversity at the global scale. Ecology Letters, 9, 947-954.

ALSEN, P. 2006. The Early Cretaceous (Late Ryazanian - Early Hauterivian) ammonite fauna of North-East Greenland: taxonomy, biostratigraphy, and biogeography. Fossils and Strata, 53, 229.

ASHTON, K.G. 2002. Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. Global Ecology and Biogeography, 11, 505-524.

BUTTERWORTH, P. J., CRAME, J. A., HOWLETT, P. J. and MACDONALD, D. I. M. 1988. Lithostratigraphy of Upper Jurassic - Lower Cretaceous strata of eastern Alexander Island, Antarctica. Cretaceous Research, 9, 249-264.

CARTER, E.S., HAGGART, J.W. 2006. Radiolarian biogeography of the Pacific region indicates a mid- to high-latitude ($> 30^{\circ}C$) position for the Insular superterrane since the late Early Jurassic, 109-132. *In* J.W. Haggart, R.J. Enkin, J.W.H. Monger (Eds.), Paleogeography of the North American Cordillera: Evidence For and Against Large-Scale Displacements. Geological Association of Canada, Special Paper 46.

CHEETHAM, A. H., SANNER, J., TAYLOR, P. D. and OSTROVSKY, A. N. 2006. Morphological differentiation of Avicularia and the proliferation of species in Mid-Cretaceous *Wilbertopora* Cheetham, 1954 (Bryozoa: Cheilostomata). Journal of Paleontology, 80, 49-71.

COURVILLE, P. and CRONIER, C. 2005. Diversity or disparity in the Jurassic (Upper Callovian) genus *Kosmoceras* (Ammonitina): A morphometric approach. Journal of Paleontology, 79, 944-953.

CRAME, J. A. 2002. Evolution of taxonomic diversity gradients in the marine realm: a comparison of Late Jurassic and Recent bivalve faunas. Paleobiology, 28, 184-207.

– and HOWLETT, P. J. 1988. Late Jurassic and Early Cretaceous biostratigraphy

of the Fossil Bluff Formation, Alexander Island. British Antarctic Survey Bulletin, 78, 1-35.

CRAMPTON, J. S. 1996. Biometric analysis, systematics and evolution of Albian *Actinoceramus* (Cretaceous Bivalvia, Inoceramidae). Monograph of the Institute of Geological and Nuclear Sciences, 15, 1-80.

– and GALE, A. S. 2005. A plastic boomerang: speciation and intraspecific evolution in the Cretaceous bivalve Actinoceramus. Paleobiology, 31, 559-577.

DIETL, G.P. AND P.H. KELLEY. 2001. Mid-Paleozoic latitudinal predation gradient: distribution of brachiopod ornamentation reflects shifting Carboniferous climate. Geology, 29, 111-114.

FOOTE, M. 1992. Paleozoic record of morphological diversity in blastozoan echinoderms. Proceedings of the National Academy of Sciences, USA, 89, 7325-7329.

-. 1993. Discordance and concordance between morphological and taxonomic diversity. Paleobiology, 19, 185-204.

GREY, M., HAGGART, J. W. and JELETZKY, J. A. 2007. Uppermost Jurassic (Portlandian) to lowermost Cretaceous (Valanginian) section at Grassy Island, west coast of Vancouver Island, British Columbia. Geological Survey of Canada Openfile, 5666.

-, HAGGART, J. W. and SMITH, P. L. 2008. Species discrimination and evolutionary mode of *Buchia* (Bivalvia: Buchiidae) from Upper Jurassic to Lower Cretaceous strata of Grassy Island, British Columbia, Canada. Palaeontology, 51, 583-595.

HAMMER, O., HARPER, D. A. T. and RYAN, P. D. 2001. PAST: Paleontological statistics software package for education and data analysis. Palaeontologia Electronica, 4, 9.

HIKUROA, D. and GRANT-MACKIE, J. A. 2008. New species of Late Jurassic *Australobuchia* (Bivalvia) from the Murihiku Terrane, Port Waikato - Kawhia region, New Zealand. Alchergina, 32. 1-26.

JELETZKY, J. A. 1965. Late Upper Jurassic and Early Lower Cretaceous Fossil Zones of the Canadian Western Cordillera, British Columbia. Geological Survey of Canada Bulletin, 103.

 -. 1966. Upper Volgian (Latest Jurassic) Ammonites and Buchias of Arctic Canada. Geological Survey of Canada Bulletin, 128. – and TIPPER, H. W. 1968. Upper Jurassic and Cretaceous Rocks of Taseko Lakes Map-Area and their Bearing on the Geological History of Southwestern British Columbia. Geological Survey of Canada Paper, 67-54, 218p.

KAUFFMAN, E. G. 1973. Cretaceous Bivalvia, 353-384. In A. Hallam (ed.), Atlas of Palaeobiogeography. Elsevier Scientific Publishing Co., New York.

KOWALEWSKI, M., DYRESON, E., MARCOT, J. D., VARGAS, J. A., FLESSA, K. W. and HALLMAN, D. P. 1997. Phenetic discrimination of biometric simpletons: paleobiological implications of morphospecies in the lingulide brachiopod *Glottidia*. Paleobiology, 23, 444-469.

LI, X. and GRANT-MACKIE, J. A. 1988. Upper Jurassic and Lower Cretaceous *Buchia* (Bivalvia) from southern Tibet, and some wider considerations. Alcheringa, 12, 249-268.

LUPIA, R. 1999. Discordant morphological disparity and taxonomic diversity during the Cretaceous angiosperm radiation: North American pollen record. Paleobiology, 25, 1-28.

MAYR, E. 1963. Animal species and evolution. Harvard University Press, Cambridge, 797 pp.

MOYNE, S. and NEIGE, P. 2007. The space-time relationship of taxonomic diversity and morphological disparity in the Middle Jurassic ammonite radiation. Palaeo-geography, Palaeoclimatology, Palaeoecology, 248, 82-95.

NAVARRO, N., NEIGE, P. and MARCHAND, D. 2005. Faunal invasions as a source of morphological constraints and innovations? The diversification of the early Cardioceratidae (Ammonoidea; Middle Jurassic). Paleobiology, 31, 98-116.

NEIGE, P. 2003. Spatial patterns of disparity and diversity of the Recent cuttlefishes (Cephalopoda) across the Old World. Journal of Biogeography, 30, 1125-1137.

NEIGE, P., MARCHAND, D. and BONNOT. A. 1997. Ammonoid morphological signal versus sea-level changes. Geological Magazine, 134, 261-264.

–, ELMI, S. and RULLEAU, L. 2001. Existe-t-il une crise au passage Lias - Dogger chez les ammonites? Approche morphomtrique par quantification da la disparit morphologique. Bulletin de la Socit Gologique de France, 172, 257-264.

PAVLOW, A. P. 1907. Enchanement des aucelles et aucellines du crtac Russe. Nouveaux Memoir de la Socit Imperiale Naturalistes de Moscou, 5, 455-570. PIMM, S.L., RUSSELL, G.J., GITTLEMAN, J.L., BROOKS, T.M. 1995. The future of biodiversity. Science, 269, 347-350.

ROUILLIER, C. 1845. Explication de la coupe gologique des environs de Moscou. Bulletin de la Socit Impriale des Naturalistes de Moscou, 19, 359-467.

SCHRDER-ADAMS, C.J., HAGGART, J.W. 2006. Biogeography of Foraminifera in tectonic reconstructions: limitations and constraints on the paleogeographic position of Wrangellia, 95-108. *In* J.W. Haggart, R.J. Enkin, J.W.H. Monger (Eds.), Paleogeography of the North American Cordillera: Evidence For and Against Large-Scale Displacements. Geological Association of Canada, Special Paper 46.

SEY, I.I., KALACHEVA, E.D. 1993. Buchiids and zonal stratigraphy of the Upper Jurassic deposits of the northern Far East of Russia. Geology and Geophysics, 34, 46-60 (in Russian).

 1999. Lower Berriasian of Southern Primorye (Far East Russia) and the problem of Boreal-Tethyan correlation. Palaeogeography, Palaeoclimatology, Palaeoecology, 150, 49-63.

SHA, J., MATSUKAWA, M., CAI, H., JIANG, B., ITO, M., HE, C. and GU, Z. 2003. The Upper Jurassic-Lower Cretaceous of eastern Heilongjiang, northeast China: stratigraphy and regional basin history. Cretaceous Research, 24, 715-728.

- and FURSICH, F. T. 1994. Bivalve faunas of eastern Heilongjiang, northeastern China. II. The Late Jurassic and Early Cretaceous buchiid fauna. Beringeria, 12, 3-93.

SMITH, P.L. 2006. Paleobiogeography and Early Jurassic Molluscs in the context of terrane displacements in western Canada, 81-94. *In* J.W. Haggart, R.J. Enkin, J.W.H. Monger (Eds.), Paleogeography of the North American Cordillera: Evidence For and Against Large-Scale Displacements. Geological Association of Canada, Special Paper 46.

STAMATAKOS, J. A., TROP, J. M. and RIDGWAY, K. D. 2001. Late Cretaceous paleogeography of Wrangellia: Paleomagnetism of the MacColl Ridge Formation, southern Alaska, revisited. Geology, 29, 947-950.

STEMPIEN, J. A. 2002. Spatial and environmental dimensions of shelly morphospaces: geometric morphometrics of the mactrid bivalve *Mulinia*, Geological Society of America Abstracts with Programs.

– and KOWALEWSKI, M. 2004. Quantifying geographic variability of a lineage:

the geometric morphospace of *Mulinia*, Geological Society of America Abstracts with Programs, 133-134.

SURLYK, F. and ZAKHAROV, V. A. 1982. Buchiid bivalves from the Upper Jurassic and Lower Cretaceous of East Greenland. Palaeontology, 25, 727-753.

TORSVIK, T.H., VAN DER VOO, R., MEERT, J.G., MOSAR, J., WALDER-HAUG, H.J. 2001. Reconstructions of the continents around the North Atlantic at about the 60th parallel. Earth and Planetary Science Letters, 187, 55-69.

VILLIER, L. and EBLE, G. J. 2004. Assessing the robustness of disparity estimates: the impact of morphometric scheme, temporal scale, and taxonomic level in spatangoid echinoids. Paleobiology, 30, 652-665.

– and KORN, D. 2004. Morphological Disparity of Ammonoids and the Mark of Permian Mass Extinctions. Science, 306, 264-266.

ZAKHAROV, V. A. 1979. The evolution of buchiids (Bivalvia) in the Pacific, 14th Pacific Science Congress Abstracts 1 (Stratigraphy and Paleobiogeography of the Pacific Ring's Pre-Cambrian and Phanerozoic), 93-95.

-. 1981. Buchiidae and biostratigraphy of the Boreal Upper Jurassic and Neocomian. Trudy Institut Geologii Geofiziki, 458, 1-270 (in Russian).

-. 1987. The Bivalve *Buchia* and the Jurassic-Cretaceous Boundary in the Boreal Province. Cretaceous Research, 8, 141-153.

Chapter 5

Variation in Evolutionary Patterns Across the Geographic Range of a Fossil Bivalve³

5.1 Summary of Research (Article as Published in Science)

Documenting patterns of morphological change (modes) and the speed at which they occur (rates) are fundamental to our understanding of macroevolutionary processes over geologic time. The fossil record has provided examples of three principal modes of evolution, namely: random walks; directional change (gradualism); and stasis, which is often interrupted by punctuated change. The ability to quantify rates and classify modes of evolution in the fossil record has improved over the past several decades with the advent of quantitative model-based tests (e.g. Lynch 1990; Roopnarine 2001; Hunt 2006; Hannisdal 2007). However, what remains virtually unknown is whether modes and rates of evolution vary within a taxon, but this is difficult to assess because it requires large samples spanning both the geographic and temporal range of the taxon. *Buchia*, a marine bivalve distantly related to mussels, meets these requirements. The genus existed for approximately 25 million

³A version of this chapter has been published: GREY, M., HAGGART, J. W. and SMITH, P. L. 2008. Patterns across the geographic range of a fossil bivalve. Science, 322, 1238-1242. To preserve the original format of the manuscript this chapter contains two sections: the first contains the text that appears as a Report in Science; the second contains materials, methods, and other more detailed information that appears as "Supporting Online Material" on Science Online.

years, arising during the early Late Jurassic and becoming extinct in the Early Cretaceous (Jeletzky 1965), and includes numerous species that lived in a variety of sedimentary environments across the Northern Hemisphere (Figures 5.1, 5.2). Most *Buchia* species are widely distributed and their dispersal was geologically instantaneous; the genus is thus particularly useful for the study of evolutionary patterns. These features also contribute to the value and importance of *Buchia* species as time-diagnostic index fossils for biostratigraphic correlations in the Northern Hemisphere (e.g. Jeletzky 1965; Surlyk and Zakharov 1982; Sey and Kalacheva 1999; Sha *et al.* 2003).

Of the three principal modes of evolution, random walks are non-directional over time, oscillating around a mean morphology (Hunt 2006). A random-walk pattern does not imply that the role of evolutionary processes, such as natural selection, is negligible for a particular taxon, only that sustained directionality or stasis is not observed (Hunt 2006). When observed in the fossil record, directional changes usually imply that evolution is gradual (Hunt 2006). Punctuations can also be directional but because they take place over geologically rapid time periods (e.g. thousands to a few millions of years), they are less likely to be preserved in the fossil record (but see Jackson and Cheetham (1999) for some examples of punctuations). There is no widely accepted definition of stasis, although it is often described as representing either a constrained change (Roopnarine 2001) or no net change (Sheets and Mitchell 2001). A recent survey of over one hundred fossil sequences comprising a variety of taxa, all analyzed using the same method for determining mode, has shown that directional evolution is rare and/or brief and most fossil lineages exhibit evolutionary patterns that conform to random walks or stasis (Hunt 2007). What remains unclear, however, is whether evolutionary patterns differ within the history and geographic range of a taxon. To examine this, we studied evolutionary modes and rates over much of Buchia's temporal and geographic range. Below, after a brief description of the material used and measurements taken, we present our research on mode and then proceed to our research on rates.

Fossil material used for this study was obtained from previously published and temporally well-resolved stratigraphic sections (refer to section 5.2). We observed morphological change in the shape and size of buchiid shells over time by measuring six traits, defined by linear and angular measurements (Figure 5.3), on more than 1500 shells whose relative geologic ages were known. The traits measured have been used in other buchiid studies to differentiate between species (Grey *et al.* 2008a). Fossil specimens were taken from previously collected and published material from six locations, including: the Canadian Arctic; Grassy Island and Taseko Lakes, British Columbia, Canada; eastern Heilongjiang Province, China; East Greenland; and Southern Primorye, Far East Russia (refer to section 5.2). Study locations are essentially coeval (Figure 5.2), represent a reflective sample of the geographical range of *Buchia* (paleolatitudes ranged from 47 - 81°N; Table 5.1, Figure 5.1), and span much of the genus's temporal range (Figure 5.2), within which a number of ancestordescendant relationships have been proposed (Jeletzky 1965; refer to section 5.2). The locations also represent a variety of marine depositional environments, from shallow water, inner-shelf settings to deep water deposits (Table 5.1, Table 5.2).

The data used to determine mode of evolution include the six individual morphological traits and the primary and secondary canonical variates from canonical variate analysis (CVA). CVA determines which variables discriminate between groups of previously identified specimens and is also used for predictive classification. A priori grouping for the CVA was based on the stratigraphy (a proxy for time) of each specimen; this allowed for changes in morphology to be tracked through relative time (e.g. a specimen found in a higher part of the geologic section is geologically "younger" than one found in the lower part of the section). Canonical variates (e.g. CV1 and CV2) are a linear combination of the measured traits and represent the most important variables for morphological distinction of buchiid specimens through time (i.e. they are the traits which exhibit the most change) (Figure 5.4, Table 5.1). We explored evolutionary mode using two quantitative methods: the program Enigma 2.4 (Roopnarine 2001; refer to section 5.2) uses a random walk model for a stratophenetic series and the program PaleoTS (Hunt 2006; refer to section 5.2) uses a likelihood-based procedure that chooses among models of different modes. The random walk method calculates Hurst estimates (h) and P values. Hurst estimates range from 0 to 1, where high values of h (i.e. h > 0.9) indicate strong directional change, while low values can indicate stasis (h < 0.2) or random

walks (0.25 < h < 0.55) (Roopnarine 2001; refer to section 5.2). P values indicate the probability of a random walk: low P values (P < 0.5) suggest that there is a small probability the pattern was generated by a random process, while high P values (P = 0.9) indicate random walks or stasis (Roopnarine 2001; refer to section 5.2). The likelihood-based procedure chooses the best fit of the data among three models: directional, unbiased random walk, and stasis. Support for the models was assessed 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; refer to section 5.2). Results in Figure 5.4 and Table 5.1 illustrate the need for using quantitative versus qualitative classification of evolutionary mode because visual inspection of data plots cannot always distinguish the patterns that can be delineated using model-based tests (Roopnarine 2001 and Fig.1A-C of Hunt 2006).

Results from both mode tests were equivalent and show that the mode of evolution varied between locations (Table 5.1 and Tables 5.3-5.8). For the six locations studied, we found that stasis occurs more often in deeper-water environments and random walks occur more often at the highest paleolatitudes (Table 5.1). For ease of display, we only provide results from both mode tests for the primary canonical variable [CV1, from the canonical variate analysis] (Table 5.1) and results for the other morphological traits are shown from the likelihood-based tests (Table 5.3-5.8). For CV1, five of the six locations show either stasis or random walks, with only one identified case of directionality (Table 5.1). Hurst estimates (Figure 5.5A-D) indicate weak directionality for Grassy Island (h = 0.7, P = 0.4) (Figure 5.5B), stasis for Greenland (average h = 0.14, average P = 0.99) (Figure 5.5D), and random walks for both the Arctic (average h = 0.2, average P = 0.91) (Figure 5.5A) and Taseko Lakes (average h = 0.33, average P = 0.85) (Figure 5.5C) locations. The likelihood tests supported all of these findings (Tables 5.3-5.5, 5.7). The mode for the localities in China and Russia could not be assessed reliably with Hurst estimates due to low numbers of stratigraphic intervals (Roopnarine 2001; Table 5.2); however, the number of samples was not an issue for the likelihood-based test, which supports stasis and random modes, respectively (Tables 5.6, 5.8). All other traits studied, including the secondary canonical variable (CV2) and the six individual traits, show similar results in their distribution of modes. Out of 42 mode tests using the likelihoodbased procedure, only 5% were directional while 43% conformed to stasis and 52% to random walks (Tables 5.3-5.8). These frequencies are similar to a recent survey that examined a variety of macro- and microfossil lineages and traits (Hunt 2007).

Research addressing the distribution and variability of evolutionary rates during a species' existence is critical for exploring the relationship between mode and rate (Roopnarine 2003). There are a variety of metrics used to calculate rates. The common darwin metric has an inverse relationship with time (Gingerich 1983), meaning that neontological studies will inherently have higher rates because they sample a much shorter period of time (e.g. Reznick *et al.* 1997). We used a method based on trait variances and generation time (time needed to complete one generation) to minimize any dependence on absolute time scales (Lynch 1990). Rates less than 1×10^{-4} represent stabilizing selection; those less than 5×10^{-2} represent genetic drift; and rates greater than 5×10^{-2} are indicative of directional selection (Lynch 1990).

The average rates for all geographical locations range from 8.8×10^{-7} to 1.8×10^{-5} (Table 5.1). All rates for all locations range from 9×10^{-9} to 1.2×10^{-2} and most are in the realm of stabilizing selection, while some suggest the occurrence of genetic drift (Figure 5.6A-F). There are no examples of rates above 5×10^{-2} and therefore directional selection was not detected. The same method applied to fossil stickleback fish found that, despite other types of evidence supporting directional selection in the lineage, selection did not apparently affect the observed morphological changes, suggesting that this method is biased against finding evidence for directional change (Bell *et al.* 2006). For fossils, the number of generations between successive samples is generally so high that the amount of morphological change would have to be unrealistically high for directional selection to be detected with current methods.

To summarize, our research compared trends for the same taxon in different geographical locations and identified a possible environmental influence on evolutionary modes and rates. We found the two current quantitative methods used for delineating evolutionary mode provide equivalent results but that the likelihood-based test can be more useful when comparing sequences with fewer time (= stratigraphic) intervals. Our analysis demonstrates that, for the same suite of characters over similar time periods, all three modes of evolution (directional, random, and stasis) are found within the genus *Buchia* throughout its geographic range, indicating that there is an environmental component to mode. More specifically, we found that there may be a relationship between mode and paleolatitude, as random evolutionary trajectories were all found at the highest paleolatitudes (Table 5.1), but this must be confirmed by studying buchiids at a wider range of paleolatitudes. Our results also suggest that, in *Buchia*, stasis occurs more frequently in deep-water marine environments.

5.2 Supporting Online Material

5.2.1 Materials and Methods

Buchiid specimens used in this study, mostly representing internal casts of shells, were obtained from previously collected and published material from six geographic locations, including: the Canadian Arctic Archipelago (Jeletzky 1966); Grassy Island (Grey *et al.* 2007) and Taseko Lakes (Jeletzky and Tipper 1968; Umhoefer *et al.* 2002), British Columbia, Canada; eastern Heilongjiang Province, China (Sha *et al.* 2003); East Greenland (Surlyk and Zakharov 1982; Alsen 2006); and Southern Primorye, Far East Russia (Sey and Kalacheva 1993; Sey and Kalacheva 1999) (Table 5.2, Figure 5.1). Stratigraphic successions sampled in all locations are assumed to be approximately coeval, ranging in age from Kimmeridgian (Late Jurassic) to Hauterivian (Early Cretaceous), and provide a reasonable sample of the total geographic range of the genus (Figure 5.1). Zonal indicator species of *Buchia* found in each location, and their time ranges, are listed in Figure 5.2. Strata at each location represent shallow- to deep-water marine environments, based on information from the primary references (Table 5.1, Table 5.2).

A recent study (Bocxlaer *et al.* 2008) has reminded us of the importance of stratigraphic control and phylogenetic relationships when assessing evolutionary mode. This work reanalyzed a classic case of punctuated equilibrium in Turkana Basin molluscs and found that the hypothesized "punctuations" were actually biological invasions; the original phylogenetic conclusions were thus incorrect (Bocxlaer *et al.* 2008). While a quantitative phylogenetic study has not formally been undertaken for the genus, *Buchia* is a well-studied widespread group and is arguably the most important fossil group for correlation of Upper Jurassic-Lower Cretaceous strata of the Northern Hemisphere (e.g. Jeletzky 1965; Sha and Fürsich 1994; Sey and Kalacheva 1999). Species within the genus are recognized to be widespread and directly comparable across the genus' geographic range, showing no evidence of lineage replacement. Moreover, based on larval shell analysis, it is apparent that buchiids had planktotrophic larvae (Sha and Fürsich 1994), allowing them to disperse over wide geographic ranges in geologically short time frames. Available evidence suggests that development of multiple lineages in the genus would have been highly unlikely.

5.2.2 Morphometric Measurements

The exterior and side views for all unbroken left valves from each stratigraphic level were photographed with a Nikon D70 digital camera. Images were saved to computer files and measured with a custom-made morphometrics program in MatLab (MorphLab 1.0). The left valve was selected for consistency and because it possesses greater morphologic variance. We measured a total of 1535 shells from the six study locations, ranging in sample size from 42 to 747 individuals (Table 5.2). Each of the specimens was from a known stratigraphic interval and the number of stratigraphic intervals and specimens measured therein for each section varied (Table 5.2), but this should not affect the results for mode. The mean morphology within an interval was used for mode analyses and intervals with only one specimen were not included. To describe shell shape and size, we utilized six morphometric variables that included angular and linear measurements, and one calculation of the average distance between concentric rings (Figure 5.3; Grey et al. 2008a). Variables were log-transformed prior to analyses to correct for potential unequal variation between variables measured in different units (i.e. linear and angular measurements) (Kowalewski et al. 1997).

5.2.3 Morphological Change

Mode

Changes in morphology over time (approximated by the stratigraphic interval) were tracked through the study sections using the six individual variables measured (as described above) and also the primary and secondary variates from step-wise canonical variate analyses (CVA). The CVAs were performed for each geographic location and used the same six variables as above. Step-wise CVA was utilized because, when a number of characters are measured, it selects the variables that contribute the most discriminatory power to the model (Cheetham *et al.* 2006). A priori grouping for the CVAs was based on stratigraphic order of the samples. CV1 was represented by a variety of traits, the most common being the angles of the crest-line, and represented between 33-67% of the variation for all analyses within each geographical location studied (Table 5.1).

Modes of evolution, falling within one of three categories (random walk, directional change, or stasis), were explored using a random walk model for a stratophenetic series (using the program Enigma 2.4, designed specifically for stratophenetic series where the data are incomplete and time-averaged, (Roopnarine 2001)) and a likelihood-based procedure to choose among models of mode (using the program PaleoTS in the statistical package R (Hunt 2006)). The random walk model calculates the Hurst estimate (h) of a series and is a measure of its persistent or anti-persistent deviation from any overall trend (Roopnarine 2001). The Hurst estimate is calculated by performing a log-transformed regression of pairwise differences of morphological values against intervals of relative or absolute time (Roopnarine 2001). Morphological values in our analysis are either the six univariate or primary canonical variate (CV1) values for each stratigraphic level (an approximation of geologic time), calculated from the canonical variate analysis described previously. Hurst estimates range from 0 to 1 and are a measure of the rate at which the variance of a time series increases with increasing temporal scale. The rejection of a random-walk model, based on h and P estimates, supports the hypothesis that the observed change is a result of directional or stabilizing selection (Roopnarine 2001).

Data required for the likelihood-based analysis consist of the number of individuals measured, trait mean, trait variance, and the relative or absolute time for each stratigraphic/time interval (Hunt 2006). Support for the models was based on two metrics. The bias-corrected Akaike Information Criterion (AIC_C) and Akaike weights were used to estimate the probability that each mode model is the best of the three considered; these were calculated with the package paleoTS (Hunt 2006). For ease of display, we show only the results for the likelihood-based tests for individual traits and the multivariate trait, CV2 (secondary discriminant variable) (Table 5.3-5.8). Note that our samples from Arctic Canada have few individuals per sample - this may affect results for the mode tests in that a random walk may be preferentially picked over other modes, but this does not affect our overall conclusions.

Rate

There are a variety of metrics used to calculate rates, such as darwins, haldanes, and others. The darwin has an inverse relationship with time (Gingerich 1993), meaning that neontological studies will inherently have higher rates because they take place over much shorter periods of time. We estimated rates using a method that was developed on the basis of variances and generation time, making it less obviously dependent on absolute time scales (Lynch 1990). Using this method, rates were calculated from successive samples in units of variance:

$$\Delta = \text{VarB}(\ln z) [\text{t Varw}(\ln z)]$$

where $VarB(\ln z)$ and $Varw(\ln z)$ are the observed between- and within-sample components of the phenotypic variance for log-transformed measures, z is the phenotypic value, and t is the number of generations between successive samples (Lynch 1990). In this case, z represents the linear combination of variables on the primary discriminant axis (CV1) and this metric, as well as the haldane, is appropriate to use for calculation with multivariate data (Hendry and Kinnison 1999). We have assumed a generation time of two years on the basis of extant mussels (*Mytilus edulis*) - probably the closest living relative of *Buchia* as they are both in the Order Pteriomorphia), resulting in at least 50,000 generations between consecutive samples but this number rises significantly in those locations where temporal resolution is coarser (including the data from Russia and China where the estimate for number of generations between samples rises to over 100,000). Rates of neutral mutation that are less than 1×10^{-4} represent stabilizing selection; those that are less than 5×10^{-2} represent genetic drift; and rates that are greater than 5×10^{-2} are indicative of directional selection (Lynch 1988). These rate estimates have been used for vertebrates but may also be pertinent for invertebrates as neutral mutation rates for invertebrates and vertebrates are invariant (Gillooly *et al.* 2005). We found that most rates fall with in the expected range for stabilizing selection (hatched), while few fall within genetic drift (black) and none in directional selection (Figure 5.6A-F).

| CV1 Components [‡] | Dorsal angle, Ventral angle (57%) | Dorsal angle, Ventral angle (67%) | Dorsal angle, Ventral angle (60%) | Length (34%) | Dorsal angle (33%) | Height, Length (40%) | sensus on their placement Hurst estimates (refer to section 5.2) for canonical |
|--|--------------------------------------|--------------------------------------|--------------------------------------|-----------------------------------|---|---|---|
| Average rate $(\times 10^{-5})$ | 1.8 | 2.2 | 7.3 | 3.6 | 1.8 | 0.088 | urrent cons ssed with F d (refer to s |
| Mode from Hurst estimate and maximum likelihood tests | random walk | weakly directional | random walk | stasis† | stasis | random walk [†] | imated as there is no c dities could not be asse of traits measured an |
| Depositional marine environment (from primary reference, Table 5.2) | Shallow | Shallow | Shallow | Deep | Deep, with some shallow-water deposits | Shallow | hese locations are approx [†] The mode for these loca gure 5.3 for a description |
| Paleo- latitude (°N) | 81 | 49* | 51* | 47* | 49.5 | 71 | tudes for t ae period. Refer to Fi ure. |
| Location | Arctic Canada | Grassy Island, B.C. | Taseko Lakes, B.C. | Eastern Heilongjiang, China | East Greenland | Southern Primorye, Far East Russia | *The paleolati during this tim section 5.2). ‡ variate proced |

Table 5.1: Modes and rates for all geographical locations studied for the primary canonical variate (CV1).

125

5.3 Tables

| | | | | | 1 | | 1 | | 1 | | | | | | | 1 |
|-------------------|----------|--------------------|------------------------------|--------------------|--------------------|--------------|---------------------------|-----------------------------|--------------------|-----------------|---------------------------|--------------------|-------------------------|------------------------|-----------|------------------------------|
| Primary reference | | Jeletzky 1966 | | | Grey et al. 2007 | | Jeletzky and Tipper 1968; | Umhoefer <i>et al.</i> 2002 | Sha et al. 2003 | | Surlyk and Zakharov 1982; | Alsen 2006 | Sey and Kalacheva 1993; | Sey and Kalacheva 1999 | | aber of individuals measured |
| $N_{0.*}$ | | 42 | (35, 1.5) | | 747 | (100, 8) | 246 | (82, 4.3) | 59 | (12, 5.4) | 165 | (34, 4.9) | 246 | (12, 30) | | verage nun |
| Collection | location | GSC | | | GSC | | GSC | | NIGP | | UC | | VSEGEI | | | c intervals, a |
| Age range | | Middle Tithonian - | Berriasian | | Late Tithonian - | Valanginian | Late Tithonian - | Hauterivian | Middle Tithonian - | mid-Valanginian | Kimmeridgian - | Hauterivian | Kimmeridgian - | mid-Valanginian | | umber of stratigraphic |
| Locality | | Canadian Arctic | $\operatorname{Archipelago}$ | (Ellesmere Island) | Grassy Island, | B.C., Canada | Taseko Lakes, | B.C., Canada | China (Eastern | Heilongjiang) | East Greenland | (Alexander Island) | Far East Russia | (North and South | Primorye) | *Number studied (n |

per interval).

Table 5.2: Summary of the collections used in analyses. GSC = Geological Survey of Canada (Ottawa, Vancouver); NIGP = Nanjing Institute of Geology and Palaeontology; UC = University of Copenhagen (Geological Museum of Denmark and Geological Institute); VSEGEI = All Russian Geological Research Institute (St. Petersburg). B.C. = British Columbia.
| | | | AICC | | Akaike weights | | | |
|---------------------|--------------|------|-------|--------|----------------|------|--------|--|
| Trait | Type | GRW | URŴ | Stasis | GRW | URW | Stasis | |
| CV1 | multivariate | 30.8 | 20.0 | 29.0 | 0.005 | 0.98 | 0.01 | |
| CV2 | multivariate | 33.5 | 21.6 | 32.3 | 0.003 | 0.99 | 0.01 | |
| Total length | size | 27.7 | 16.4 | 26.7 | 0.003 | 0.99 | 0.006 | |
| Total width | size | 26.5 | 14.9 | 24.5 | 0.003 | 0.99 | 0.008 | |
| Height | size | 20.4 | 8.74 | 17.7 | 0.003 | 0.99 | 0.01 | |
| Dorsal angle shape | | 46.4 | 34.8 | 43.4 | 0.003 | 0.98 | 0.01 | |
| Ventral angle shape | | 43 | 31.4 | 41.5 | 0.003 | 0.99 | 0.006 | |
| Delta | number | 6.34 | -5.45 | 3.8 | 0.003 | 0.99 | 0.009 | |

Table 5.3: Maximum-likelihood results for the Canadian Arctic: GRW represents a generalized random walk (= directional) and URW is an unbiased random walk (= random walk). Of the three models, the one with the lowest AIC_C and highest Akaike weight is the most appropriate fit for the data (in bold). The number of stratigraphic intervals and the average number of individuals measured per interval for each section is found in Table 5.2.

| | | | AICC | Akaike weights | | | |
|---------------------|-------------------|--------|--------------------|----------------|-------|------|--------|
| Trait | Type | GRW | URŴ | Stasis | GRW | URW | Stasis |
| CV1 | multivariate | 202.1 | 202.1 204.1 | | 0.73 | 0.27 | 0* |
| CV2 | multivariate | 205.1 | 203.0 | 255.4 | 0.26 | 0.74 | 0* |
| Total length | Total length size | | 188.5 | 182.9 | 0.02 | 0.06 | 0.92 |
| Total width | size | -34.2 | -33.7 | 162.9 | 0.56 | 0.44 | 0* |
| Height size | | -94.2 | -94.8 | 72.8 | 0.42 | 0.58 | 0* |
| Dorsal angle | shape | 590.7 | 588.6 | 671.0 | 0.26 | 0.73 | 0* |
| Ventral angle shape | | 543.8 | 522.3 | 680.9 | 0.32 | 0.68 | 0* |
| Delta number | | -155.6 | -160.2 | -151.3 | 0.001 | 0.99 | 0.009 |

*Values below 1×10^{-4} are shown as 0.

Table 5.4: Maximum-likelihood results for Grassy Island, British Columbia.

| | | | AICC | | Akaike weights | | | | | |
|---------------------|------------------|--------|--------|--------|----------------|------|--------|--|--|--|
| Trait | Type | GRW | URW | Stasis | GRW | URW | Stasis | | | |
| CV1 | CV1 multivariate | | | 213.1 | 0.28 | 0.72 | 0* | | | |
| CV2 | CV2 multivariate | | | 185.1 | 0.02 | 0.91 | | | | |
| Total length size | | 176.2 | 174.1 | 169.8 | 0.04 | 0.10 | 0.86 | | | |
| Total width | size | 135.2 | 133.1 | 131.53 | 0.1 | 0.29 | 0.62 | | | |
| Height | size | 31.5 | 29.4 | 65.3 | 0.26 | 0.74 | 0* | | | |
| Dorsal angle | shape | 372.0 | 370.1 | 428.9 | 0.28 | 0.72 | 0.12 | | | |
| Ventral angle shape | | 346.0 | 344.0 | 428.9 | 0.28 | 0.72 | 0* | | | |
| Delta number | | -132.9 | -135.0 | -157.0 | 0* | 0* | 0.99 | | | |
| | | | | | | | | | | |

*Values below 1×10^{-4} are shown as 0.

Table 5.5: Maximum-likelihood results for Taseko Lakes, British Columbia.

| | | | AICC | | Akaike weights | | | |
|---------------|--------------|-------|------------------|------------------|----------------|------|--------|--|
| Trait | Type | GRW | URW | Stasis | GRW | URW | Stasis | |
| CV1 | multivariate | 36.7 | 35.5 | 35.5 30.7 | | 0.17 | 0.79 | |
| CV2 | multivariate | 41.6 | 28.2 32.0 | | 0.006 | 0.03 | 0.96 | |
| Total length | size | 31.2 | 28 27.2 | | 0.07 | 0.38 | 0.55 | |
| Total width | size | 29.8 | 26.5 | 25.5 | 0.07 | 0.35 | 0.58 | |
| Height | size | 11.9 | 8.45 | 6.6 | 0.05 | 0.27 | 0.68 | |
| Dorsal angle | shape | 70.2 | 66.4 | 62.6 | 0.02 | 0.12 | 0.86 | |
| Ventral angle | shape | 70.2 | 66.4 | 62.5 | 0.02 | 0.12 | 0.86 | |
| Delta | number | -12.3 | -5.6 | -17.8 | 0.05 | 0.24 | 0.72 | |

Table 5.6: Maximum-likelihood results for China.

| | | AICC | | Akaike weights | | | | | | |
|---------------------|---|-------|-------|----------------|--------|--------|--------|--|--|--|
| Trait | Type | GRW | URW | Stasis | GRW | URW | Stasis | | | |
| CV1 | multivariate | 98.6 | 96.3 | 88.5 | 0.01 | 0.02 | 0.97 | | | |
| CV2 | multivariate | 83.6 | 81.0 | 56.9 | 0* | 0* | 0.99 | | | |
| Total length | otal length size 108 10 | | | 94 | 0.001 | 0.002 | 0.99 | | | |
| Total width | size | 92.3 | 90.6 | 78.9 | 0.001 | 0.003 | 0.99 | | | |
| Height | size | 36.5 | 34.8 | 23.7 | 0.001 | 0.004 | 0.99 | | | |
| Dorsal angle | shape | 226.4 | 224.4 | 217.3 | 0.01 | 0.03 | 0.99 | | | |
| Ventral angle shape | | 189.7 | 187.8 | 179.6 | 0.00 | 0.02 | 0.98 | | | |
| Delta numbe | | -76.6 | -79.1 | -94.8 | 0.0001 | 0.0004 | 0.99 | | | |
| *Values balow | *Values below 1×10^{-4} are shown as 0 | | | | | | | | | |

*Values below 1×10^{-4} are shown as 0.

Table 5.7: Maximum-likelihood results for Greenland.

| | AIC _C | | | Akaike weights | | | |
|---------------------|------------------|------------------|-------------------------|----------------|------|------|--------|
| Trait | Type | GRW | URW | Stasis | GRW | URW | Stasis |
| CV1 | multivariate | 37.1 | 34.2 | 37.4 | 0.17 | 0.69 | 0.14 |
| CV2 | multivariate | 27.5 | 23.9 | 26.3 | 0.11 | 0.68 | 0.21 |
| Total length | size | 28.1 24.7 | | 28.2 | 0.13 | 0.74 | 0.13 |
| Total width | size | 22.9 | 19.3 | 21.9 | 0.12 | 0.69 | 0.19 |
| Height | size | 1.15 | 0.045 | 11.2 | 0.36 | 0.63 | 0.002 |
| Dorsal angle | shape | 57.1 | 53.3 | 51.3 | 0.04 | 0.25 | 0.71 |
| Ventral angle shape | | 44.9 | 41.2 | 38.4 | 0.03 | 0.17 | 0.79 |
| Delta | number | -16.4 | 16.4 -20.1 -22.9 | | 0.03 | 0.19 | 0.79 |

Table 5.8: Maximum-likelihood results for Russia.

5.4 Figures



Figure 5.1: Locations of collection material used in this study (grey circles) across the geographic range of the genus *Buchia* (grey and white circles), modified from Li and Grant-Mackie (1988). Squares represent the newly-recognized and closely related genus *Australobuchia* (Grey *et al.* 2008b; Hikuroa and Grant-Mackie 2006).

| Se | | Ď | N/ - | 1 | 2 | 3 | 4 | 5 | | 6 | | | |
|----------|-------------|---|-----------------------|----------------------------|----------------------------|---------------|------------------------|-------|-------------------------|-------|--------------------------------|--|------------|
| Serie | 5 | | Ma (± 2σ) | Grassy Island, B.C. | Taseko Lakes, B.C. | Arctic Canada | East Greenland | н | Eastern leilongjiang | l | ⁻ ar East Russia | | |
| | Hauterivian | | 136.4 ± 2.0 | | | | crassicollis | | | | | | |
| taceous | ginian | n | | | crassicollis | | | | | | | | |
| wer Crei | Valan | _ | 140.2 <u>± 3.0</u> | pacifica | keyserlingi pacifica | | keyserlingi inflata | | pacifica | | pacifica | | eyserlingi |
| Lo | iasian | р | | tolmatschowi uncitoides | tolmatschowi uncitoides | volgensis | volgensis | | | nsis | uncitoides | | |
| | Berri | _ | 145 5 | okensis | okensis | | okensis | | | volge | okensis | | |
| | | | ± 4.0 | | | | unschensis - | ana | unschensis | - | unschensis | | |
| | | ⊃ | | | fischeriana | unschensis | terebratuloides | cheri | | fis | scheriana | | |
| | | | | | | fischeriana | lis | | | | | | |
| | nian | Σ | | columbiana | columbiana | | | | | rı | ussiensis | | |
| assic | Titho | | | | piochii | piochii | | | | | piochii | | |
| r Jura | | | | | mosquensis | | | | | | rugosa | | |
| Jppe | | | 150.8 ± 4.0 | | | | | | | m | osquensis | | |
| | ridgian | D | | | | | | | | | nuistriata | | |
| | Kimme | _ | 155.7 ± 4.0 | | concentrica | | | | | со | ncentrica | | |

Figure 5.2: Zonal succession of key *Buchia* species for each geographical location studied. Absolute ages after Gradstein *et al.* (2004); ages are for the base of each stage; absolute ages have not been established for substage boundaries. Suggested non-contemporaneity of some fossil zones reflects uncertainty in stratigraphic correlations between regions. Empty cells reflect absence of fossiliferous strata. B.C. = British Columbia.



Figure 5.3: Features used to characterize shell morphology in buchiid bivalves: 1, dorsalmost point (umbo) on hinge margin; 2, posteriormost point; 3, ventralmost point; 4, anteriormost point; 5, intersection of lines measuring maximum valve length and valve width; 6, point directly beneath highest point on left valve; 7, highest point on left valve. Morphological variables measured: ventral angle of crest-line* (I); dorsal angle of crest-line (J); dorsal length (Ld; 1-5); ventral length (Lv; 5-3); anterior width (Wa; 4-5); posterior width (Wp; 5-2); dorsal distance to highest point on valve (Dd; 1-6); ventral distance to highest point on valve (Dv; 6-3); inflation (In; 6-7) and delta (Δ ; average distance between concentric rings). *The "crest-line" is defined as the imaginary line joining the highest points of the left valve of *Buchia* (Pavlow 1907) and has been recognized as a taxonomically valuable feature (Jeletzky 1966).



133

Figure 5.4: Morphological change in the primary canonical axis (CV1) over relative time for each of the six locations studied: A) Canadian Arctic; B) Grassy Island, Canada; C) Taseko Lakes, Canada; D) eastern Heilongjiang Province, China; E) East Greenland; and F) Far East Russia (S. Primorye). CV1 represents the linear combination of variables that best separates between stratigraphic intervals (i.e. shows the most change).



Figure 5.5: Hurst estimate analysis for buchiids from the stratigraphic sections at: A) Canadian Arctic; B) Grassy Island, Canada; C) Taseko Lakes, Canada; and D) East Greenland. A weakly directional evolutionary mode is interpreted for Grassy Island (average h = 0.7, average P = 0.4); stasis is interpreted for Greenland (average h = 0.14, average P = 0.99); and the Arctic (average h = 0.2, average P = 0.91) and Taseko Lakes (average h = 0.33, average P = 0.85) show random walks.



Figure 5.6: Evolutionary rate (delta, Δ) histograms for the multivariate analysis of buchiid morphology for the stratigraphic sections at: A) the Canadian Arctic; B) Grassy Island, Canada; C) Taseko Lakes, Canada; D) eastern Heilongjiang Province, China; E) East Greenland; and F) Far East Russia (S. Primorye). Hatched patterns represent stabilizing selection and black represents genetic drift.

5.5 References

ALSEN, P. 2006. The Early Cretaceous (Late Ryazanian - Early Hauterivian) ammonite fauna of North-East Greenland: Taxonomy, biostratigraphy, and biogeography. Fossils and Strata, 53, 1-229.

BELL, M. A., TRAVIS, M. P. and BLOUW, D. M. 2006. Inferring natural selection in a fossil threespine stickleback. Paleobiology, 58, 814-824.

BENTON, M. J. and PEARSON, P. N. 2001. Speciation in the fossil record. Trends in Ecology and Evolution, 16, 405-411.

BOOKSTEIN, F. L. 1987. Random walk and the existence of evolutionary rates. Paleobiology, 13, 446-464.

CHEETHAM, A. H., JACKSON, J. B. C. and HAYEK, L. C. 1993. Quantitative genetics of bryozoan phenotypic evolution. I. Rate tests for random change versus selection in differentiation of living species. Evolution, 47, 1526-1538.

-, SANNER, J., TAYLOR, P. D. and OSTROVSKY, A. N. 2006. Morphological differentiation of Avicularia and the proliferation of species in Mid-Cretaceous *Wilbertopora* Cheetham, 1954 (Bryozoa: Cheilostomata). Journal of Paleontology, 80, 49-71.

ENDLER, J. A. 1986. Natural Selection in the Wild. Princeton University Press, Princeton, NJ.

ERWIN, D. H. and ANSTEY, R. L. 1995. Speciation in the Fossil Record, 11-38. *In* D. H. Erwin and R. L. Anstey (eds.), New Approaches to Speciation in the Fossil Record. Columbia University Press, New York.

GILLOOLY, J. F., ALLEN, A. P., WEST, G. B. and J.H., B. 2005. The rate of DNA evolution: Effects of body size and temperature on the molecular clock. Proceedings of the National Academy of Science, USA, 102, 140-145.

GINGERICH, P. D. 1983. Rates of evolution: effects of time and temporal scaling. Science, 222, 159-161.

-. 1993. Quantification and comparison of evolutionary rates. American Journal of Science, 293A, 453-478.

GRADSTEIN, F. M., OGG, J. G., SMITH, A. G., AGTERBERG, F. P., BLEEKER, W., COOPER, R. A., DAVYDOV, V., GIBBARD, P., HINNOV, L., HOUSE,

M. R., LOURENS, L., LUTERBACHER, H.-P., MCARTHUR, J., MELCHIN, M. J., ROBB, L., SHERGOLD, J., VILLENEUVE, M., WARDLAW, B. R., ALI, J., BRINKHUIS, H., HILGEN, F. J., HOOKER, J., HOWARTH, R. J., KNOLL, A. H., LASKAR, J. MONECHI, S. PLUMB, K. A., POWELL, J., RAFFI, I., RHL, U., SANFILIPPO, A., SCHMITZ, B., SHACKLETON, N. J., SHIELDS, G. A., STRAUSS, H., KOLFSCHOTEN, J., VAN DAM, VEIZER, T. VAN, J., WILSON, D. 2004. A geologic time scale. Cambridge University Press, Cambridge, U.K., 384 p.

GREY, M., BOULDING, E. G. and BROOKFIELD, M. E. 2006. Estimating multivariate selection gradients in the fossil record: a naticid gastropod case study. Paleobiology, 32, 100-108.

-, HAGGART, J. W. and JELETZKY, J. A. 2007. Uppermost Jurassic (Portlandian) to lowermost Cretaceous (Valanginian) section at Grassy Island, west coast of Vancouver Island, British Columbia. Geological Survey of Canada Open-file, 5666.

-, HAGGART, J. W. and SMITH, P. L. 2008a. Species discrimination and evolutionary mode of *Buchia* (Bivalvia: Buchiidae) from Upper Jurassic - Lower Cretaceous strata of Grassy Island, British Columbia, Canada. Palaeontology, 51, 583-595.

-. 2008b. A new species of *Buchia* (Bivalvia: Buchiidae) from British Columbia, Canada, with an analysis of buchiid bipolarity. Journal of Paleontology.

HANNISDAL, B. 2007. Inferring phenotypic evolution in the fossil record by Bayesian inversion. Paleobiology, 33, 98-115.

HENDRY, A. P. and KINNISON, M. T. 1999. Perspective: the pace of modern life: measuring rates of contemporary microevolution. Evolution, 53, 1637-1653.

HEREFORD, J., HANSEN, T. F. and HOULE, D. 2004. Comparing strengths of directional selection: how strong is strong? Evolution, 58, 2133-2143.

HIKUROA, D. and GRANT-MACKIE, J. A. 2006. New species of Late Jurassic Australobuchia (Bivalvia) from the Murihiku Terrane, Port Waikato - Kawhia region, New Zealand. Alchergina.

HUNT, G. 2006. Fitting and comparing models of phyletic evolution: random walks and beyond. Paleobiology, 32, 578-601.

-. 2007. The relative importance of directional change, random walks, and stasis in the evolution of fossil lineages. Proceedings of the National Academy of Science,

USA, 104, 18404-18408.

JACKSON, J. B. C. and CHEETHAM, A. H. 1999. Tempo and mode of speciation in the sea. Trends in Ecology and Evolution, 14, 72-77.

JELETZKY, J. A. 1965. Late Upper Jurassic and Early Lower Cretaceous fossil zones of the Canadian western Cordillera, British Columbia. Geological Survey of Canada Bulletin, 103.

-. 1966. Upper Volgian (Latest Jurassic) Ammonites and *Buchias* of Arctic Canada. Geological Survey of Canada Bulletin, 128.

-. and TIPPER, H. W. 1968. Upper Jurassic and Cretaceous Rocks of Taseko Lakes Map-Area and their Bearing on the Geological History of Southwestern British Columbia. Geological Survey of Canada Paper, 67-54, 218p.

KAUFFMAN, E. G. 1973. Cretaceous Bivavlia, 353-384. In A. Hallam (ed.), Atlas of Palaeobiogeography. Elsevier Scientific Publishing Co., New York.

KINGSOLVER, J. G., HOEKSTRA, H. E., HOEKSTRA, J. M., BERRIGAN, D., VIGNIERI, S. N., HILL, C. E., HOANG, A., GIBERT, P. and BEERLI, P. 2001. The strength of phenotypic selection in natural populations. The American Naturalist, 157, 245-261.

KOWALEWSKI, M., DYRESON, E., MARCOT, J. D., VARGAS, J. A., FLESSA, K. W. and HALLMAN, D. P. 1997. Phenetic discrimination of biometric simpletons: paleobiological implications of morphospecies in the lingulide brachiopod *Glottidia*. Paleobiology, 23, 444-469.

LI, X. and GRANT-MACKIE, J. A. 1988. Upper Jurassic and Lower Cretaceous *Buchia* (Bivalvia) from southern Tibet, and some wider considerations. Alcheringa, 12, 249-268.

LYNCH, M. 1988. The rate of polygenic mutation. Genetical Research, 51, 137-148.

-. 1990. The rate of morphological evolution in mammals from the standpoint of the neutral expectation. The American Naturalist, 136, 727-741.

PACHUT, J. and ANSTEY, R. L. 2004. Rates of evolution and selection intensity in species transitions within the Ordovician Bryozoan genus *Peronopora*, Geological Society of America Abstracts with Programs. Geological Society of America Abstracts with Programs, 424. PAVLOW, A. P. 1907. Enchanement des aucelles et aucellines du crtac Russe. Nouveaux Memoir de la Socit Imperiale Naturalistes de Moscou, 5, 455-570.

REZNICK, D. N., SHAW, F. H., RODD, H. and SHAW, R. G. 1997. Evaluation of the Rate of Evolution in Natural Populations of Guppies (*Poecilia reticulata*). Science, 275, 1934-1937.

ROOPNARINE, P. D. 2001. The description and classification of evolutionary mode: a computational approach. Paleobiology, 27, 446-465.

-. 2003. Analysis of Rates of Morphologic Evolution. Annual Review of Ecology, Evolution and Systematics, 34, 605-632.

-, BYARS, G. and FITZGERALD, P. 1999. Anagenetic evolution, stratophenetic patterns, and random walk models. Paleobiology, 25, 41-57.

SEY, I. I. and KALACHEVA, E. D. 1993. Buchiids and zonal stratigraphy of the Upper Jurassic deposits of the Northern Far East of Russia [In Russian]. Geology and Geophysics, 8, 46-58.

– and KALACHEVA, E. D. 1999. Lower Berriasian of Southern Primorye (Far East Russia) and the problem of Boreal-Tethyan correlation. Palaeogeography, Palaeo-climatology, Palaeoecology, 150, 49-63.

SHA, J., MATSUKAWA, M., CAI, H., JIANG, B., ITO, M., HE, C. and GU, Z. 2003. The Upper Jurassic-Lower Cretaceous of eastern Heilongjiang, northeast China: stratigraphy and regional basin history. Cretaceous Research, 24, 715-728.

SHEETS, H. D. and MITCHELL, C. E. 2001. Why the null matters: statistical tests, random walks and evolution. Genetica, 112-113, 105-125.

SHELDON, P. R. 1996. Plus ça change - a model for stasis and evolution in different environments. Palaeogeography, Palaeoclimatology, Palaeoecology, 127, 209-227.

SURLYK, F. and ZAKHAROV, V. A. 1982. Buchiid bivalves from the Upper Jurassic and Lower Cretaceous of East Greenland. Palaeontology, 25, 727-753.

UMHOEFER, P. J., SCHIARIZZA, P. and ROBINSON, M. 2002. Relay Mountain Group, Tyaughton-Methow basin, southwest British Columbia: a major Middle Jurassic to Early Cretaceous terrane overlap assemblage. Canadian Journal of Earth Sciences, 39, 1143-1167.

VAN BOCXLAER, B., VAN DAMME, D. and FEIBEL, C. S. 2008. Gradual ver-

sus punctuated equilibrium in the Turkana Basin molluscs: evolutionary events or biological invasions? Evolution, 62, 511-520.

Chapter 6

Conclusion

6.1 Summary of Results

This thesis represents a body of research that has investigated spatial, temporal and evolutionary patterns within the late Mesozoic bivalve genus *Buchia* and it contains three broad themes. I have explored:

- 1. How morphology varies across the geographic range of a genus;
- 2. How patterns of evolution vary over the geographic range of a genus; and
- 3. From patterns, I have inferred what influences evolution.

Overall, my research has revealed that geography, and therefore the environment, appears to play a critical role in defining morphological and evolutionary patterns. Specifically, I have found the following:

- 1. At least some previously designated buchiid species can be delineated using morphometrics (Grey *et al.* 2008a).
- 2. The genus *Buchia sensu stricto* is restricted to the Northern Hemisphere (and is therefore not an example of a bipolar genus (Grey *et al.* 2008b)).
- 3. Based on morphometric analysis and comparisons, a new buchiid species in the North Pacific region was recognized (Grey *et al.* 2008b).

- 4. Geography (and therefore environment) affects morphology significantly but that there is no evidence of a latitudinal gradient in morphological features studied (Grey *et al. in prep*).
- 5. Diversity and disparity within *Buchia* are not correlated but both declined just prior to the extinction of the genus (Grey *et al. in prep*).
- 6. The two quantitative methods used to describe evolutionary mode appear to be in agreement with each other (Grey *et al.* 2008c).
- 7. Most modes conformed to random walks or stasis. This was an expected result as sustained directional selection (e.g. over 10 million years) would be unusual (Grey *et al.* 2008c).
- 8. Modes and rates vary across the geographical range of the genus, an indication that they are controlled, at least in part, by environment (Grey *et al.* 2008c).

6.2 Significance of Research and its Limitations

This research has both specific and broad significance. Results that are specifically important to the study of buchiids fall into three categories: 1) biostratigraphic, 2) phylogenetic, and 3) biogeographic. I have found that the morphology of species within the genus *Buchia* is highly variable over its geographic range and this means that buchiid species may be difficult to recognize in small sample sizes. This result can have a large impact on the effectiveness of *Buchia* for biostratigraphy. However, I have also found that species can be identifiable quantitatively with an examination of sufficiently large sample sizes. Therefore, any biostratigraphic study with *Buchia* should contain a reasonable number of specimens (e.g. at least 10 samples per stratigraphic layer, Chapter 2 and Grey *et al.* 2008a). The phylogeny of *Buchia* has never been studied previously; including the morphological characters that I have defined in this thesis should be useful in future phylogenetic research. Finally, I have found that *Buchia* is not a bipolar genus and is restricted to the

Northern Hemisphere. This has been a long-standing debate but my conclusion is also supported by another recent study (Hikuroa and Grant-Mackie 2008).

More broadly, this research has its primary significance in the area of evolutionary theory but it may also have implications for conservation. As we begin to understand more about how evolution, and speciation in particular, we can begin to apply this knowledge to the current biodiversity crisis. The most important result from this body of research is recognition that the environment has important effects on morphology (in fact, environmental effects may be as important as speciation on morphology because I have found that the amount of variation between geographic regions is comparable to the amount of intraspecific variation between two species) and on patterns of evolution (evolutionary modes and rates changed depending on geographical location).

The major conclusions resulting from this research should be viewed as a startingpoint rather than an end-point. It is important to recognize that, especially for Chapter 5, migration rather than evolution may play a role in defining patterns and shifts in morphospace. In paleontology we are limited to the amounts and types of data we can collect. Nevertheless, fossils remain the only physical evidence of life in the past and can offer much in terms of helping to advance the science of evolution.

Those thoughts considered, studies such as these remain critical to our understanding of evolutionary patterns (and, ultimately, processes) but until now have not been undertaken. This is primarily because, until recently, quantitative methods for distinguishing mode were not available. Now, well-tested and easy to use programs are freely available. In the past, cutting-edge evolutionary research with fossils dealt largely with determining the relative importance of punctuated equilibrium versus gradualism. Since the onset of new quantitative methods for determining mode (e.g. Roopnarine 2001 and Hunt 2006), we are able to expand our research more broadly to address questions such as: 1) what is the relative importance of natural selection in the fossil record?; 2) now that three primary modes have been determined (punctuated/static, gradual, random), what causes one mode to occur over the others in a lineage?; 3) why do random and static patterns appear to be more common in the fossil record (see Hunt 2007)? I have focussed my research on the second question and have found that the environment appears to play an important role but there are still many more questions and avenues to explore.

6.3 Future Research

This research is the first attempt to compare trends for the same taxon in different locations, representing diverse paleoenvironmental conditions (i.e. varying latitudes and depositional environments). The most significant insight resulting from this study is the conclusion that the environment is an important factor in defining the morphology and evolutionary patterns of a genus. However, the mechanics of this relationship remain only hypothetical and many questions should now be posed. For instance, is it the abiotic or biotic environment that is the most critical? Does this pattern also exist for other, closely related bivalves, other marine benthics, and other organisms with varied modes of life (e.g. macro- versus microfossils and benthic versus pelagic organisms)? In light of these questions, future research will require:

- 1. A study of closely related genera across their geographical ranges, such as the Southern Hemisphere buchiids *Australobuchia* and inoceramids, to assess whether they also exhibit similar patterns;
- 2. Studies with other marine benchics and other organisms with different modes of life. Eventually, it would be ideal to be able to compare patterns across a diverse range of organisms; and
- 3. A study to assess how mode is correlated with the environment for instance, how physical factors (such as paleolatitude and depositional environment) versus biological factors (such as predation, competition, and invasion) affect mode. Some of this may be accomplished with additional buchiid localities, to expand the current understanding of geographic and evolutionary variation within the group.

A general point to remember is that it is important that future fossil collections be made with these types of studies in mind, so that researchers can use them for evolutionary research. In particular, collections should include as many specimens as possible from a single bed (= stratigraphic layer) and different collections should be made from as many stratigraphic levels within a section as possible. J.A. Jeletzky recognized the importance of this approach in the 1940s and beyond when he collected material for the Geological Survey of Canada.

While continued development and improvement of methods to quantify modes and rates is essential, it is now possible to start using previously described and published methods (especially for mode) for many types of organisms (from macro- to microfossils) in order to begin answering some of the most pertinent questions about evolutionary patterns and processes.

6.4 References

GREY, M., HAGGART, J. W. and SMITH, P. L. 2008a. Species discrimination and evolutionary mode of *Buchia* (Bivalvia: Buchiidae) from Upper Jurassic-Lower Cretaceous strata of Grassy Island, British Columbia, Canada. Palaeontology, 51, 583-595.

-. 2008b. A new species of *Buchia* (Bivalvia: Buchiidae) from British Columbia, Canada, with an analysis of buchiid bipolarity. Journal of Paleontology, 82, 422-428.

-. 2008c. A geographic comparison of evolutionary modes and rates in the bivalve *Buchia* (Bivalvia: Buchiidae). Science.

-. In *prep.* Morphological variability in time and space: an example of patterns with buchiid bivalves (Bivalvia, Buchiidae). Palaeontology.

HIKUROA, D. and GRANT-MACKIE, J. A. 2008. New species of Late Jurassic *Australobuchia* (Bivalvia) from the Murihiku Terrane, Port Waikato - Kawhia region, New Zealand. Alchergina, 32, 1-26.

HUNT, G. 2006. Fitting and comparing models of phyletic evolution: random walks and beyond. Paleobiology, 32, 578-601.

-. 2007. The relative importance of directional change, random walks, and stasis in the evolution of fossil lineages. Proceedings of the National Academy of Science, USA, 104, 18404-18408.

ROOPNARINE, P. D. 2001. The description and classification of evolutionary mode: a computational approach. Paleobiology, 27, 446-465.