

Chapter 2

Evolutionary Change: A Case Study of Extinct Brachiopod Species

Abstract Brachiopods serve as great tools for quantifying evolution of early life. In this study, morphological characters were quantified for 1,100 individual specimens of a single atrypid species from the Middle Devonian Traverse Group of Michigan using geometric morphometric methods. Seven landmark measurements were taken on dorsal valve, ventral valve, and anterior and posterior regions. Specimens were partitioned by their occurrence in four stratigraphic horizons (Bell Shale, Ferron Point, Genshaw Formation, and Norway Point) from the Traverse Group of northeastern Michigan outcrop. Multivariate statistical analyses were performed to test patterns and processes of morphological shape change of species over 6 million year interval of time. Maximum-likelihood method was used to determine the evolutionary rate and mode in morphological divergence in this species over time. If punctuated equilibrium model holds true for brachiopods, then one would expect no significant differences between samples of the species *Pseudoatrypa cf. lineata* from successive stratigraphic units of the 6 million year Middle Devonian Traverse Group over time. Multivariate analysis shows significant shape differences between different time horizons ($p \leq 0.01$) with considerable overlap in morphology excepting abrupt deviation in morphology in the uppermost occurrence. Maximum-likelihood tests further confirm near stasis to near random divergence mode of evolution with slow to moderate rates of evolution for this species lineage. In contrast, if the species evolved in a gradual, directional manner, then one would expect samples close together in time to be more similar to one another than those more separated in time. Euclidean based cluster analysis shows samples closely spaced in time are more similar than those that are widely separated in time. While these results appear to partially support the gradualistic model hypothesis, morphological trend from principal component scores shows substantial morphological overlap among the three lower successions (Bell Shale, Ferron Point, and Genshaw Formation) with some deviation from the uppermost succession (Norway Point) suggesting major influence of stasis and punctuation. Thus, while stasis may have been predominant, evident from stable morphologies observed in the lower strata, anagenetic evolution may also have played an important role as evident from the abrupt change observed within this species later in time. Thus, slow to moderate rates of evolution in this species lineage with stable morphologies in the lower three strata supports stasis, but abrupt

change in the uppermost strata supports gradual anagenetic evolution within the species later in time. Overall, the morphometric data for the *P. cf. lineata* species lineage are consistent with the stratigraphic succession of Traverse Group.

2.1 Introduction

The mode and rate of morphological change in evolutionary fossil and extant species lineages over geologic time has been a hotly debated topic in paleontology and biology over the last three decades. Phyletic gradualism model proposed by several researchers (Simpson 1953; Mayr 1963) and punctuated equilibrium model proposed by others (Eldredge and Gould 1972; Gould and Eldredge 1977; Stanley 1979) have largely attributed to the prevalence of stasis in species over long periods of time. While stasis has been tested in taxa from Middle Devonian Hamilton group, no one has studied the Traverse Group taxa for testing morphological patterns.

The relative importance of stasis has been studied for many fossil lineages. Shape traits like bivalve convexity studied for Neogene *Chesapecten nefrens* for over 4 million year have yielded results in support for stasis (Hunt 2007). Gingerich (2001) illustrates stasis for longer time scales in Cenozoic mammals by considering the shape of a heuristic time-form evolutionary lattice. Roopnarine (2001) originally interpreted the Mio-Pliocene foraminifers *Globorotalia plesiotumida-tumida* as the punctuated anagenetic transformation of *Globorotalia plesiotumida* to *G. tumida* but using the iterative method of subseries of an original stratophenetic series (by measuring the presence of deviations from statistical randomness as the lineage evolves), he interpreted this as “constrained stasis”. Polly (2001) used the Brownian motion model of evolution for reconstructing ancestral nodes versus observed nodes in a fully resolved phylogeny of fossil carnivorans and found that change is constrained in molar areas over longer time intervals. He found that there is change of the sort that one would expect by random selection (Brownian motion) when patterns are measured on a small scale, but that at a very broad scale, (e.g., all mammals) the amount of change was less than if one extrapolated the small scale change to the large scale, suggesting that there is constraint on divergence.

Work of this sort has also been done specifically on brachiopods. Previous workers (Lieberman et al. 1995) tested the morphological variability of the common brachiopod species lineages from size measurements on the pedicle valves of 401 *Mediospirifer audaculus* and 614 *Athyris spiriferoides* from successive stratigraphic horizons in the Hamilton Group (5 million year) of New York. They found morphological overlap within these species between the lowermost and uppermost strata with some variations in the intervening samples of the Hamilton Group. Goldman and Mitchell (1990) tested the internal morphology of three brachiopod species of the Hamilton Group of western New York from size measurements and found only one species of Late Givetian age showed some species

level change. Isaacson and Perry (1977) have not found any significant change in *Tropidoleptus carinatus* of the Givetian age Hamilton Group from the lowest to its highest occurrence, spanning some 40 million year and further, Eldredge tested the same fauna using morphometrics and found almost no significant morphological change in this unit (Brett and Baird 1995). Overall, a majority of Hamilton brachiopod species lineages represent stasis in most cases while some minor evolutionary changes have been recorded in some cases. Unidirectional evolution over geological time intervals is highly unlikely and evolutionary reversals are common (Sheldon 1996).

Not all workers agree that stasis is common within species (Gingerich 1976, 1985; Sheldon 1987; Geary 1995; Webber and Hunda 2007; Geary et al. 2010). Two studies that have most prominently challenged stasis are Gingerich's (1976) work on fossil mammals from the Bighorn Basin of the western United States and Sheldon's (1987) (Fig. 3.6) work on Ordovician trilobites from Wales. Sheldon (1987) reported evidence of phyletic gradualism based on a study of eight lineages of 15,000 Ordovician trilobites from central Wales over a 3 million year interval. He believed that subdividing a species lineage into subspecies often gives a false impression of punctuation and stasis. In another study of Cenozoic gastropod species lineages from Pannonian Basin system, Geary (1995) has emphasized the importance of gradual change in evolutionary paleontological studies. Webber and Hunda (2007) using geometric morphometrics found that certain aspects of the morphological shape of the Upper Ordovician trilobite *Flexicalymene granulosa* change with varying paleoenvironmental conditions during the deposition of Kope and lower Fairview Formations spanning over a 2 million year interval.

This study tests hypothesis of stasis in conjunction with morphological patterns observed both in a gradualistic and punctuated equilibrium framework. In this study, morphological shape change pattern over time is assessed in *Pseudoatrypa cf. lineata* species lineage from the Givetian 6 million year Traverse Group strata. This brachiopod species *Pseudoatrypa cf. lineata* (Webster 1921), was subjected to geometric morphometric and multivariate statistical analyses to examine mode and rate of morphological shape evolution. This species was sampled from the three lower strata of the Middle Devonian Traverse Group of Eastern North America and one upper strata near the top of the Traverse Group. Whether they are present in almost all of the stratigraphic units of the Traverse Group or not, remains unknown. However, plentiful of this species is recognized from the Bell Shale, Ferron Point, Genshaw Formation, and Norway Point stratigraphic units from Alpena and Presque Isle counties of the northeastern outcrop of Michigan.

The Traverse fauna, and the strata of the Traverse Group, have been the subject of many detailed stratigraphic and paleoenvironmental studies (e.g., Ehlers and Kesling 1970; Kesling et al. 1974; Wylie and Huntoon 2003), and these studies allow fossil specimens collected from the Traverse Group to be placed in a paleoenvironment setting. This intensely studied geological system of the Traverse Group presents a good opportunity to study the relationship between

morphological change and environment over time in an individual species lineage *Pseudoatrypa cf. lineata*. For this species, the amount of morphological change through time was determined within shale lithologic settings (nearshore environment), to characterize morphological changes in a more confined paleoenvironmental setting over extended stratigraphic intervals. Whether morphological shape change corresponds with water depth data of Wylie and Huntoon (2003) or not, is also tested in this study.

2.1.1 Hypotheses

(1) If this species *P. cf. lineata* evolved according to the punctuated equilibrium model, in which morphological change occurs predominantly at speciation, thus, remaining static in most of its life, then we would expect no significant differences between samples of the species from successive stratigraphic units of 6 million year Middle Devonian Traverse Group over time; (2) If the species evolved in a gradual, directional manner, then we would expect samples close together in time to be more similar to one another than those more separated in time. Besides, one would also expect directional selection to be acting on this species.

2.2 Geological Background

The geologic setting used to test the proposed hypotheses in the *P. cf. lineata* species lineage is the Traverse Group, a package of rocks from Michigan State, that spans roughly 6.5 million year of the Middle Devonian and Lower Upper Devonian. Their appearance in North America seems to have been driven by the post-Eifelian augmentation of the Acadian orogeny (Wylie and Huntoon 2003). The Traverse Group and its fauna are associated with the influx of siliciclastic sedimentation from this Orogeny (Brett 1986; Cooper et al. 1942; Ettensohn 1985; Ehlers and Kesling 1970; Wylie and Huntoon 2003).

The richly fossiliferous strata from the 6 million year (380.0–374.0 million year) Middle Devonian Traverse Group rocks (Wylie and Huntoon 2003) of the northeastern outcrop of Michigan from Alpena and Presque Isle counties are used for this study. Among the 11 Traverse Group formations ((from base upward): Bell Shale, Rockport Quarry Limestone, Ferron Point Formation, Genshaw Formation, Newton Creek Limestone, Alpena Limestone, Four Mile Dam Formation, Norway Point Formation, Potter Farm Formation, Thunder Bay Limestone, and Squaw Bay Limestone), four of the formations are included in this study for collecting *P. cf. lineata* samples. The study interval for this investigation, which includes the stratigraphic ranges in the northeastern Michigan—Bell Shale, Ferron Point, Genshaw Formation, and Norway Point, was deposited approximately 380 million years ago and represents more than 6.0 million years duration. The Givetian age Traverse

Group is equivalent to the Hamilton Group of New York (Ehlers and Kesling 1970). Thus, this case study will represent a comparative analysis of brachiopod morphological shape change patterns after Lieberman et al. 1995.

These strata comprise a nearly 565-ft. thick succession of sedimentary rocks, primarily shales, claystones, and limestones, which were deposited in predominantly supratidal to nearshore marine settings (Ehlers and Kesling 1970; Wylie and Huntoon 2003). The Bell Shale, about 68 feet in thickness, consists of a basal crinoid rich lag and shales, which were deposited with water depth ranging from 82 to 147 ft. The Ferron Point, about 42 ft. in thickness, consists of soft shales and limestones, deposited with water depth approximately 131 ft. The Genshaw Formation, 116.5 ft. in thickness, consists of soft shales and argillaceous limestones, with water depth ranging from 82 to 131 ft. Norway Point Formation, 45 ft. in thickness, consists of abundant shales and claystones, with limestones, deposited at approximately, 6.5-ft. water depth (Wylie and Huntoon 2003). The formations chosen for data collection in this study are dominated by shales (Wylie and Huntoon 2003) and thus for this study, sampling restricted to shale beds in the four formations allows morphological analysis in a more or less stable environmental setting. Our data were collected from thinly bedded shales of Bell Shale, Ferron Point, Lower Genshaw, and Norway Point formations.

Samples used in morphological shape study are from the Michigan Museum of Paleontology Collections. Some of the samples come from the collections of Alex Bartholomew from State University of New York that have now been deposited at the Indiana University Paleontology Collections.

2.3 Materials and Methods

Samples for this study were collected from Bell Shale, Ferron Point, Genshaw, and Norway Point stratigraphic intervals of the Middle Devonian Traverse Group (6 million year) from the northeastern outcrop of Michigan from Alpena and Presque Isle counties. First, atrypid samples were qualitatively examined and identified based on external morphological characteristics. 1,124 specimens of *P. cf. lineata* was used from a total of four different shale beds at six localities of four above-mentioned strata (Bell Shale = 131; Ferron Point = 330; Genshaw = 506; Norway Point = 157) in Michigan. Samples used in morphological shape study are from the Michigan Museum of Paleontology Collections. Some of the collections of Alex Bartholomew from State University of New York have also been used for this study which are now deposited at the Indiana University Paleontology Collections.

For this study, material has been confined to shale lithology representing supratidal to nearshore environments from 0 to 50 m water depth which may have been interrupted by occasional storms. Overall, these habitats represent low energy conditions interrupted by occasionally very high energy conditions, with normal ranges of marine salinity, oxygen, and temperature. Consequently, the sampled

brachiopods to be analyzed will be less subject to taphonomic distortion through transport or mechanical destruction, while still retaining sufficient diversity and abundance to provide representative samples. However, depending upon the frequency of storm events and the turbidity of the water column from influx of siliciclastic sedimentation from the Taghanic Onlap, the faunas in these settings can be influenced by a variety of environmental parameters like light intensity variations, sedimentation rate, dissolved oxygen concentration, salinity, and temperature variations.

Pseudoatrypa cf. lineata (Brachiopoda) makes an ideal candidate for quantitatively analyzing the morphological shape evolution after controlling for the environmental setting. This species displays a suitable amount of morphological complexity for geometric morphometrics as landmarks selected on various points of the shell help fully describe the shell's morphology. Besides, this species ranges through some of the Traverse group formations (Bell Shale, Ferron Point, Genshaw, and Norway Point) such that it provides enough stratigraphic coverage to recognize potential temporal trends in morphology (Fig. 2.1). Finally, abundant samples are available for a statistical significant analysis across time.

In this study, morphological analyses have focused on seven landmark points (Fig. 2.2), each landmark point representing the same location on each specimen to capture the biologically most meaningful shape. These landmark points represent discrete juxtapositions, functional equivalents, and extremal points (Table 2.1) (Bookstein 1991; MacLeod and Forey 2002; Zelditch et al. 2004).

Though these landmark points are not biologically homologous, they correspond among diverse forms (sensu Bookstein 1991), which is appropriate for

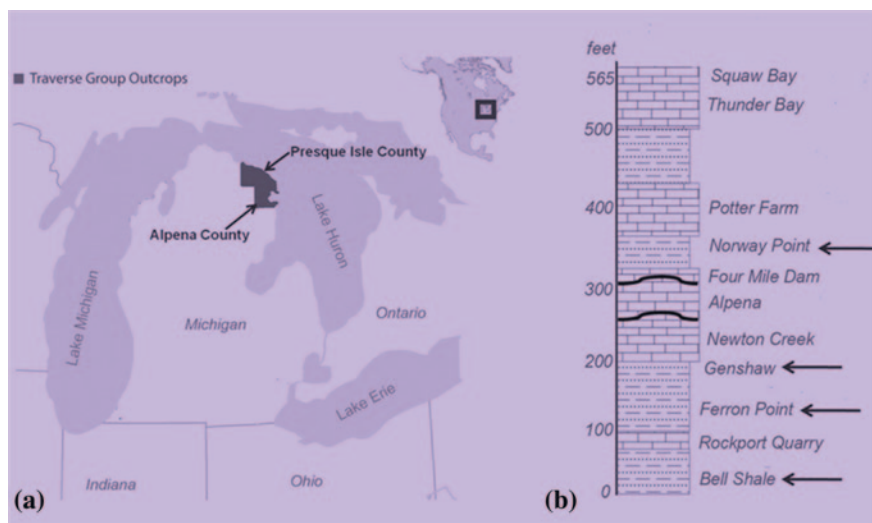


Fig. 2.1 **a** Study area map showing sample field site collection locations in the Michigan State. **b** Stratigraphy of the Traverse Group of Michigan. *Arrows* indicate sampled strata from where brachiopod fossils were collected

Table 2.1 Landmark points on the *Pseudoatrypa cf. lineata* shell representing geometric positions that are biologically functional

Landmark points	Area of the shell	Landmark descriptions
1	D	Tip of umbo
2	D/V	Junction on the hinge of dorsal valve interarea, ventral valve interarea, and commissure
3	D/V	Midpoint of specimen length projected onto commissure, length midpoint based on length of baseline
4	D/V	Extreme edge of anterior commissure adjacent to L5
5	D/V	Edge of commissure perpendicular to hinge, in line with L1 (on sulcate specimens, this point coincided with the lowest point of the sulcus)
6	D	Maximum height of curvature
7	V	Lowest point of interarea/on the pedicle foramen

D dorsal and *V* ventral

analyses attempting to capture morphological shape changes (Rohlf and Marcus 1993) or any functional aspects of the species. Brachiopods are bilaterally symmetrical organisms and each side is a mirror image of the other, i.e., each half captures the shape of the organism. Thus, for all individuals, measurements were taken on half of the specimen (dorsal view right, ventral view left, and one side of anterior and posterior views) (Fig. 2.2).

Data were captured using Thin Plate Spline dig (TPSdig) software for digitizing landmarks for geometric morphometrics. Procrustes analysis (Rohlf 1990, 1999; Rohlf and Slice 1990; Slice 2001) was performed on original shape data, rotating, translating, and scaling all landmarks to remove all size effects, while maintaining their geometric relationships (Procrustes superimposition). The Procrustes coordinates were used in all morphometric analyses. Principal component analysis was performed to determine the morphological variation between samples from four stratigraphic intervals (Bell Shale, Ferron Point, Genshaw, and Norway Point) along their major principal component axes (1 and 2) in the shape morphospace. Mean morphological shape trend was constructed from principal component scores for both dorsal and ventral valves along the stratigraphic units of the Traverse Group (Fig. 2.3). Thin Plate Spline (Bookstein 1989) visualization plots were created to detect morphological shifts in individual landmark points over time. Multivariate analysis of variance (MANOVA) was performed to test shape variation between these samples (Fig. 2.4).

Euclidean based cluster analysis was performed to determine Procrustes pairwise distances from mean morphological shape of samples between the Traverse Group stratigraphic intervals (Table 2.2, Fig. 2.5). Due to the lack of appropriate absolute age dates, time matrix was constructed by calculating time in million

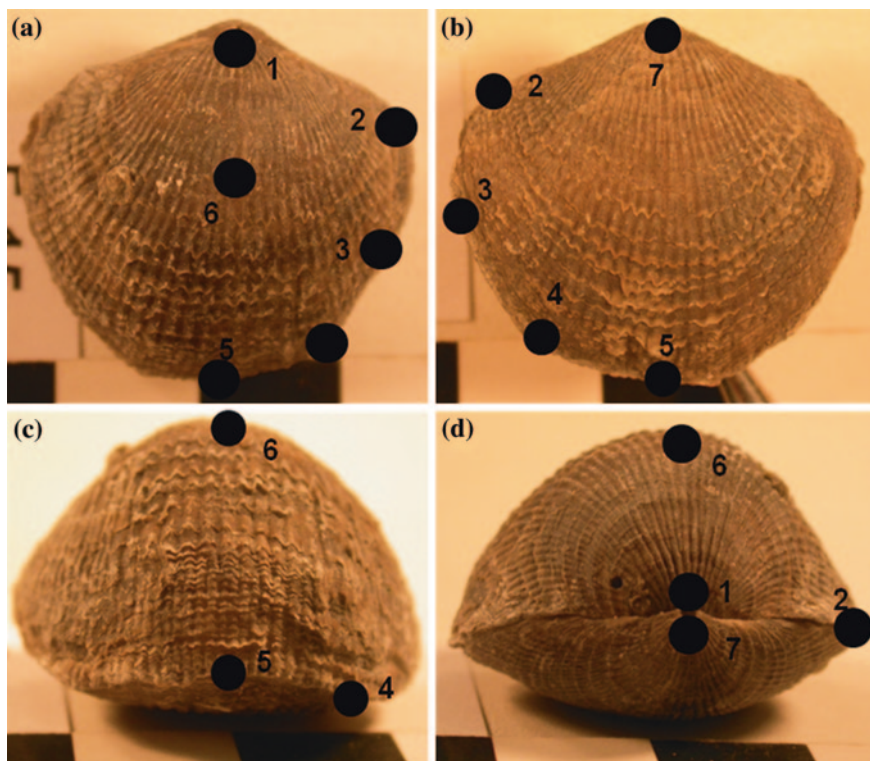
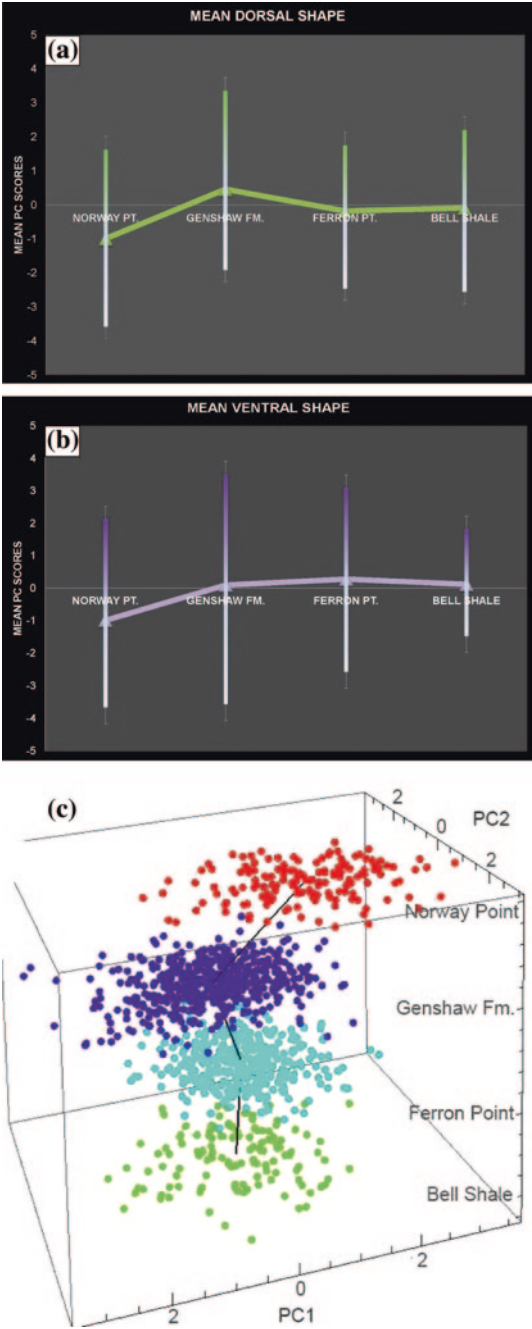


Fig. 2.2 Seven landmark points on *Pseudoatrypa cf. lineata* shells with distribution of **a** six landmark points on right side of dorsal valve, **b** five landmark points on left side of ventral valve, **c** three landmark points on right side of anterior margin area of shell, and **d** four landmark points on right side of posterior hinge view of shell

years among each of the four stratigraphic intervals of the Traverse Group based on the stratigraphic thicknesses of the formations obtained from Wylie and Huntoon (2003) (Tables 2.3, 2.4). Thus, the morphological distances and time data accumulated from morphometric and stratigraphic differences were used to construct time distance matrix.

Evolutionary rate and mode in morphological divergence was assessed using the maximum-likelihood method of Polly (2008). This method estimates the mean per-step evolutionary rate and the degree of stabilizing or diversifying selection from a matrix of pairwise morphological distances and divergence times. Morphological distance was calculated as pairwise Procrustes distances among *P. cf. lineata* taxon and divergence time was calculated from the stratigraphic thickness converted to millions of years on Wiley and Huntoon's (2003) stratigraphic column, which is an estimate of the total time in millions of years between strata that the species has been diverging independently. The method uses the following equation to estimate rate and mode simultaneously,

Fig. 2.3 Mean morphological shape trend in **a** dorsal and **b** ventral valves of *P. cf. lineata* along four Traverse Group formations (Bell Shale, Ferron Point, Genshaw Formation and Norway Point); **c** morphological variation in dorsal valves along the four units representing percent variation along principal component axes 1 and 2 (PC1 = 36.02 % and PC2 = 21.62 %)



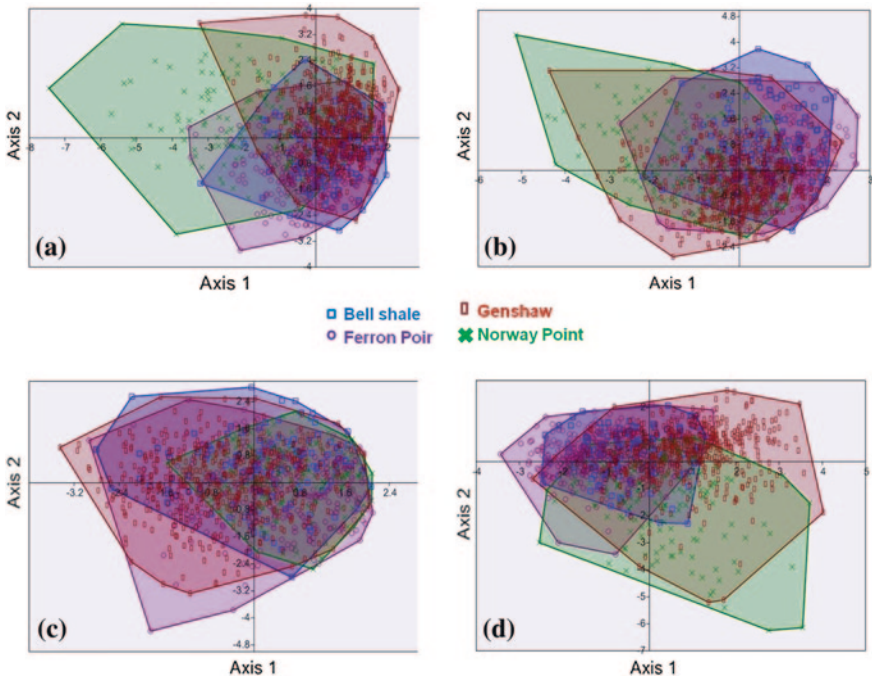


Fig. 2.4 Canonical Variate Analysis showing morphometric differences between samples from Bell Shale, Ferron Point, Genshaw Formation, and Norway Point ($p < 0.01$) in **a** dorsal valves, **b** ventral valves, **c** anterior margin area, and **d** posterior hinge area (Note Bell Shale = blue square, Ferron Point = purple circle, Genshaw = dark red rectangle, Norway Point = green cross)

$$D = rt^a \quad (2.1)$$

where D is morphological divergence (Procrustes distance), r is the mean rate of morphological divergence, t is divergence time, and a is a coefficient that ranges from 0.0 to 1.0, where 0.0 represents complete stabilizing selection (stasis), 0.5 represents perfect random divergence (Brownian motion), and 1.0 represents perfect diversifying (directional) selection (Polly 2008). Maximum-likelihood is used to find the parameters r and a that maximize the likelihood of the data, and are thus the best estimates for rate and mode (Fig. 2.6). The data were bootstrapped 1,000 times to generate standard errors for these estimates. This method is derived directly from the work presented by Polly (2004) and is mathematically related to other methods in evolutionary genetics (Felsenstein 1988; Gingerich 1993; Hunt 2007; Lande 1976; Roopnarine 2003).

Morphological patterns in *Pseudoatrypa cf. lineata* are compared with water depth data from Wylie and Huntoon (2003). The mean morphological PC1 scores for the samples are statistically correlated with water depth using linear regression analysis.

Table 2.2 Procrustes pairwise distances for *Pseudoatrypa cf. lineata* lineage among stratigraphic units in time for (a) dorsal valve, (b) ventral valve, (c) anterior marginal area, and (d) posterior hinge area

	Bell	Ferron	Genshaw	Norway
<i>Dorsal</i>				
Bell	0	0.94315	1.1128	1.9706
Ferron	0.94315	0	1.3173	1.8075
Genshaw	1.1128	1.3173	0	1.8232
Norway	1.9706	1.8075	1.8232	0
<i>Ventral</i>				
Bell	0	0.84557	1.1987	1.686
Ferron	0.84557	0	0.79457	1.7012
Genshaw	1.1987	0.79457	0	1.295
Norway	1.686	1.7012	1.295	0
<i>Anterior</i>				
Bell	0	0.63057	0.75156	0.5672
Ferron	0.63057	0	0.85516	0.47276
Genshaw	0.75156	0.85516	0	1.1393
Norway	0.5672	0.47276	1.1393	0
<i>Posterior</i>				
Bell	0	0.74795	1.1225	1.7207
Ferron	0.74795	0	1.5494	1.8043
Genshaw	1.1225	1.5494	0	1.6468
Norway	1.7207	1.8043	1.6468	0

2.4 Results

Among the atrypid samples, *Pseudoatrypa cf. lineata* was recognized from four Traverse Group formations based on qualitative traits. Main characteristics used for identification included medium- to large-size shells with globose dorsibiconvex-convexiplanar shells and an inflated hemispherical dome-like dorsal valve, shell length exceeding width slightly in all growth stages, subquadrate shell outline, broad to angular fold developed posterior of mid-valve, becoming more pronounced toward anterior margin in large adult shells (30 mm), exterior of both valves with fine radial tubular ribs (9–10/5 mm at anterior margin), regularly spaced concentric lamellae crowding toward anterior and lateral margins in larger adults (20 mm length), and short frills rarely preserved.

Eleven hundred and twenty four specimens of *P. cf. lineata* were analyzed for morphological shape change pattern over time. Geometric morphometric analysis was used to test the morphological differences in shell shape between the Traverse Group stratigraphic intervals. The major principal component axis, axis 1, explained for 36.02 % variation in dorsal valves, 28.80 % variation in ventral valves, 62.59 % variation in anterior margin area, and 82.87 % variation in posterior hinge area. The second major principal component axis, axis 2, explained for 21.62 % variation in dorsal valves, 23.85 % variation in ventral valves, 35.83 % variation in anterior margin area, and 13.07 % variation in posterior hinge area. Principal component

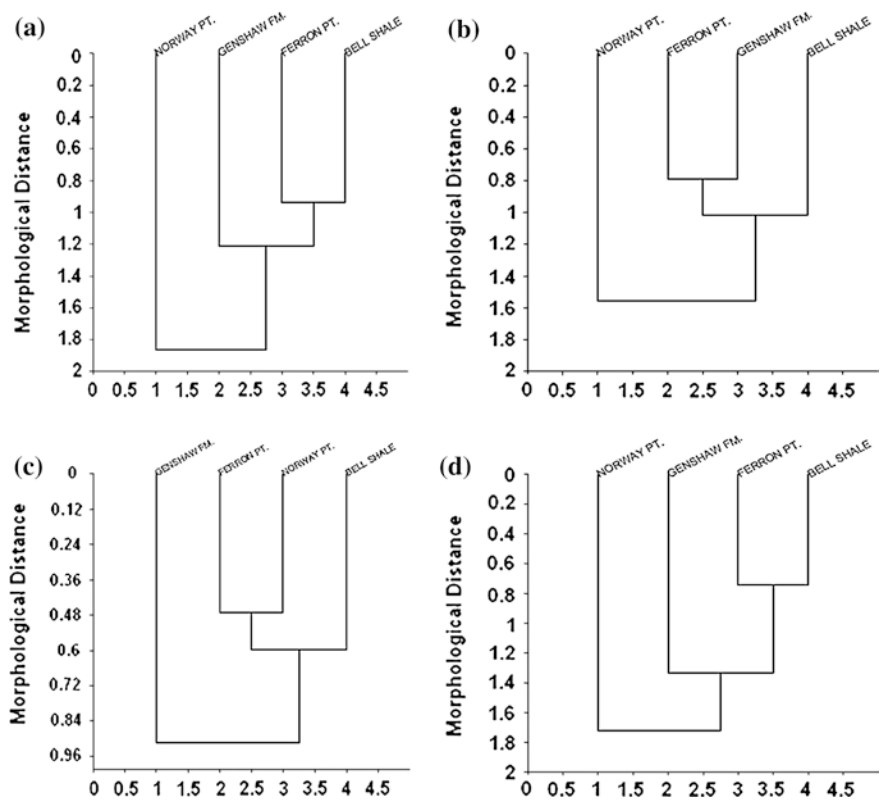


Fig. 2.5 Morphological links for *P. cf. lineata* in Traverse group formations of **a** dorsal valves, **b** ventral valves, **c** anterior margin area, and **d** posterior hinge area

Table 2.3 Eleven stratigraphic units in the Traverse Group representing various thicknesses in feet and time in million years

	Stratigraphic units	Thickness (m)	Time (million year)
Traverse group	Squaw Bay	2.85	0.10
	Thunder Bay	4.8	0.17
	Potter Farm	30.6	1.08
	Norway	13.5	0.48
	Four Mile Dam	6.3	0.22
	Alpena	23.7	0.84
	Newton Creek	7.5	0.27
	Genshaw	34.95	1.24
	Ferron	12.6	0.45
	Rockport	12.6	0.45
	Bell	20.4	0.72
	Total thickness	169.5	6.02

Time in million years for each unit calculated from thickness estimates of each unit w.r.t the total thickness of the Traverse Group (169.5 m). *Pseudoatrypa cf. lineata* samples represent the stratigraphic units in bold

Table 2.4 Time matrix (million years) calculated for the four stratigraphic units used for this study from thicknesses of the strata in time

	Bell	Ferron	Genshaw	Norway
Bell	0	1.16	1.61	4.18
Ferron	1.16	0	0.45	3.02
Genshaw	1.61	0.45	0	2.57
Norway	4.18	3.02	2.57	0

analysis indicated that there is considerable shape variation within samples from each stratigraphic interval and that the lower three stratigraphic horizons overlap considerably in the morphology of both valves with some deviation in Norway Point samples (Fig. 2.3a–c). Thin Plate Spline visualization plots show the mean morphological shape of these samples from the four stratigraphic intervals are quite similar, which along with the overlap in morphological variation, demonstrates the samples from the four strata are not substantially different in morphological shape.

MANOVA, however, detects a small but significant statistical difference in mean shape ($p < 0.01$) between the stratigraphic intervals (Fig. 2.4) based on Hotelling's p values. The statistical significance of the MANOVA demonstrates that there is some real differentiation between the samples from the four stratigraphic horizons in shell shape, but the substantial overlap in variation and the difficulty in visually distinguishing the differences in shell shape suggests to us that all these samples of *P. cf. lineata* species show little morphological change over time (Figs. 2.3, 2.4). However, abrupt deviation in mean morphological shape of the Norway Point samples (Fig. 2.3a–c) suggests gives some evidence of morphological change in this species later in time.

Procrustes distances, which are the units of difference in the principal components space, between the mean shape of the brachiopod shell, ranged from 0.47 to 1.97 Procrustes units for the stratigraphic intervals of the Traverse Group (Fig. 2.5, Table 2.2). Closely spaced stratigraphic units represent smaller Procrustes distance while widely separated units represent larger Procrustes distance (Table 2.2). Overall, the morphological distances between the Traverse Group formations concur with the stratigraphic succession of the Traverse Group (Fig. 2.5).

Procrustes pairwise distances were plotted against time calculated from stratigraphic thicknesses of Traverse Group strata (Tables 2.3, 2.4, Fig. 2.6).

Maximum-likelihood estimation of the rate and mode of evolution of *P. cf. lineata* dorsal valve shape given the Traverse group stratigraphy, yielded a rate of 0.36 ± 0.16 Procrustes units (the standard measure of geometric shape change) per million years and a mode coefficient a of 0.22 ± 0.24 , indicating near stasis to random mode of shape evolution for the means of this atrypid species lineage. *P. cf. lineata* ventral valve shape yielded a rate of 0.15 ± 0.10 Procrustes units per million years and a mode coefficient a of 0.37 ± 0.12 indicating near random divergence mode of shape evolution. *P. cf. lineata* anterior of the shell shape yielded a rate of 0.31 ± 0.09 Procrustes units per million years and a mode coefficient a of 0.01 ± 0.14 indicating stasis. *P. cf. lineata* posterior of the shell shape yielded a rate of 0.50 ± 0.21 Procrustes units per million years and a mode coefficient a of 0.11 ± 0.31 indicating near stasis to random mode of shape evolution (Fig. 2.6).

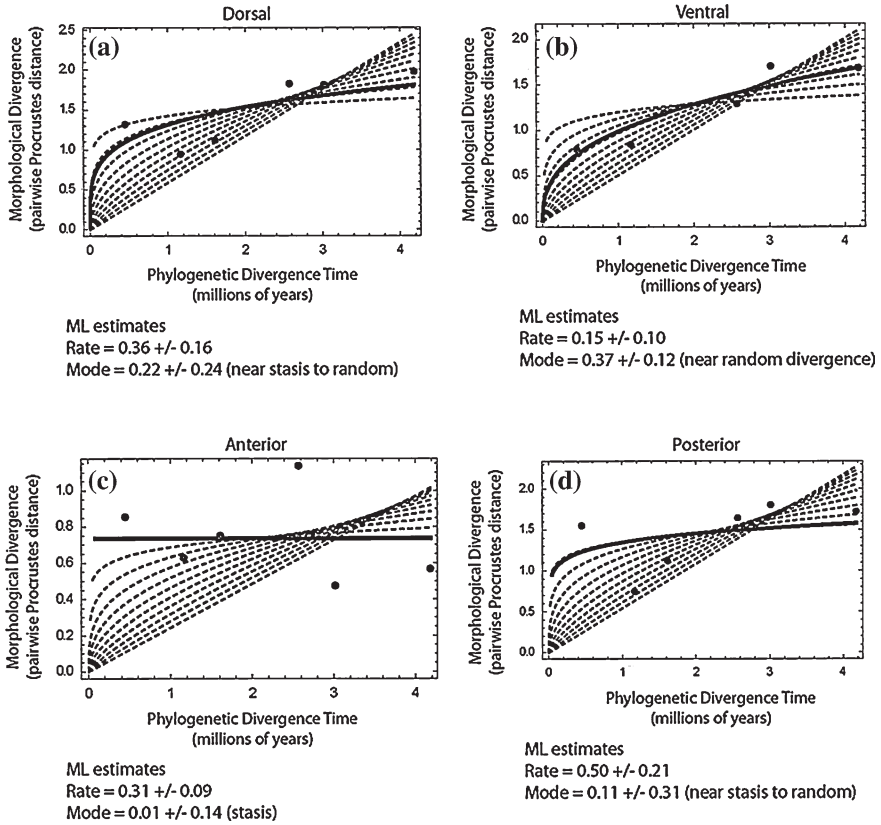


Fig. 2.6 Graph showing morphometric divergence (pairwise Procrustes distances) and phylogenetic divergence time (millions of years). The series of *dashed lines* show the expected relationship between morphological and phylogenetic divergence time from strong stabilizing selection (0.1), through random divergence (0.5), to diversifying (directional) selection (1.0). The maximum-likelihood estimate of this relationship, shown by the *dark line*, suggests that *P. cf. lineata* has experienced **a** near stabilizing selection to random divergence in dorsal valves, **b** near random divergence in ventral valves, **c** stabilizing selection in anterior margin area of valves and **d** near stabilizing selection to random divergence in posterior hinge area (modified from Bose 2012)

Mean principal component scores of the *P. cf. lineata* dorsal valves regressed on water depth values show a high positive correlation with insignificant results ($r = +0.79$, $p > 0.01$); for those of ventral valves show a very high positive correlation with significant results ($r = +0.99$, $p < 0.01$); for those of anterior margin area show a moderate positive correlation with insignificant results ($r = +0.53$, $p > 0.01$) and posterior hinge area shows a low positive correlation with insignificant results ($r = +0.22$, $p > 0.01$). Thus, overall, only the ventral valve morphological shape of this species shows a strong correspondence with the ranges of water depth temporally (Table 2.5). While other morphological shape data (dorsal valve, anterior, and posterior areas) show a low to moderately high linear correlation with water depth ranges, they do not show any significant correspondence with changing water depth.

Table 2.5 Multivariate analysis of variance between morphological principal component scores of individual samples corresponding to medium and shallow water depths

		Mean water depth (m)	Correlation	<i>P</i> values
<i>PC1 (dorsal)</i>				
Norway Point	−0.99918424	1.95	<i>r</i> = −0.14	<i>p</i> = 1.156 × 10 ^{−96} MANOVA <i>p</i> = 4.74 × 10 ^{−07} Regression
Genshaw Fm.	0.457945261	31.95		
Ferron Point	−0.1882791	39.3		<i>r</i> = −0.15
Bell Shale	−0.08658585	34.35		
<i>PC1 (ventral)</i>				
Norway Point	−0.99427466	1.95	<i>r</i> = 0.3267	<i>p</i> = 5.49 × 10 ^{−22} MANOVA <i>p</i> = 2.57 × 10 ^{−29} Regression
Genshaw Fm.	0.09912704	31.95		
Ferron Point	0.275272864	39.3		
Bell Shale	0.118146437	34.35		
<i>PC1 (anterior)</i>				
Norway Point	0.561290195	1.95	<i>r</i> = −0.11455	<i>p</i> = 4.17 × 10 ^{−16} MANOVA
Genshaw Fm.	−0.41474042	31.95		
Ferron Point	0.34338073	39.3		<i>p</i> = 0.0001238
Bell Shale	0.058519641	34.35		
<i>PC1 (posterior)</i>				
Norway Point	−0.51941632	1.95	<i>r</i> = −0.07	<i>p</i> = 2.65 × 10 ^{−75} MANOVA <i>p</i> = 0.0087
Genshaw Fm.	0.646570066	31.95		
Ferron Point	−0.6960508	39.3		
Bell Shale	−0.11861116	34.35		

Statistical correlation (linear regression) between mean morphological principal component (PC axes) scores and water depth values retrieved from Fig. 2.5 of Wylie and Huntoon (2003). ‘r’ values indicate the linear correlation coefficient between the two variables (mean PC scores of individual samples and water depth). P values report the probability that morphological shape change corresponds with the change in water depth

2.5 Discussion

2.5.1 Qualitative and Quantitative Recognition of Taxa

Pseudoatrypa is a common brachiopod from the Givetian to late Frasnian of North America. This genus occurs throughout much of the Traverse Group in the Michigan Basin, including the Bell, Ferron Point, Genshaw, Norway Point, and Potter Farm formations (Kelly and Smith 1947; Koch 1978). Here we focus on material from the Bell Shale, Ferron Point, Genshaw, and Norway Point of the northeastern outcrop of Michigan.

Webster (1921) first described the taxon *Pseudoatrypa* as *Atrypa lineata* from the late Givetian-early Frasnian Cedar Valley Group of Iowa, material which was later recognized as *Pseudoatrypa lineata* species of the new genus

Pseudoatrypa (Day 1992; Day and Copper 1998). The holotype of *Atrypa lineata* (Webster 1921) came from the upper Osage Springs and Idlewild members of the Lithograph City Formation of Iowa (Stumm 1951; Day 1996). Samples in this study from all the four stratigraphic intervals of the Givetian age Traverse Group agree well with the overall morphology of type specimen of *P. lineata* and were called *Pseudoatrypa cf. lineata* for the purpose of this study. These samples are characterized by shell maximum width of $2.1\text{--}3.3 \pm 0.2$ cm, width almost equal to the length of the shell, subquadrate shell shape, dorsibiconvex-convexiplanar shell, flattened with/without umbonal inflation in ventral valves, fine to coarse ribs with implantations and bifurcations, 1–2 plicae/1 mm spacing, somewhat consistent 2–4 mm spacing between growth lines with their crowding at the anterior margin. However, based on morphometric results derived from quantification of morphological shape, the Norway Point samples appear to be different from the lower Traverse Group samples.

When quantitatively examined, the samples of this species from the Traverse group stratigraphic intervals overlap in morphological shape with significant statistical differences between them, in addition to morphological variation within samples from each interval. Principal component analysis indicates morphologies of *P. cf. lineata* samples show considerable overlap, which is also observed in overall phenotypic traits of these specimens (Figs. 2.3, 2.4). Notably, samples show some deviation in morphological shape in the uppermost sampled strata of the Traverse group. However, statistically significant morphometric differences clearly exist between the mean shapes of the samples from these intervals using MANOVA tests ($p < 0.01$) and as illustrated by CVA (Fig. 2.4). Thin Plate Spline Real warp plots show that these differences were in the shape of the shell from the mid-point of the specimen to the anterior commissure on both dorsal and ventral valves (landmark points 3, 4, and 5) suggesting shape deflection in the whole anterior region of the shell as these are bilaterally symmetrical organisms. However, this deflection was not so much, so as to count for change. Further tests show that anterior region of the shells remained static through time unlike dorsal valve and posterior region that were near static to randomly diverging through time. Ventral valve randomly diverged in time. This, further, suggests that anterior margin was the most stable in contrast to posterior hinge, dorsal, and ventral valve area. Anterior margin stability reflects a functional significance as evident from studies related to frills in atrypids where they are known to stabilize the shells in the substrate (Copper 1967).

2.5.2 Punctuated Equilibrium Hypothesis

The punctuated equilibrium model of evolution predicts that the morphology of a species will be relatively static during most of the species history of evolution with change occurring at rapid and episodic events of speciation (Eldredge and Gould 1972; Gould and Eldredge 1977). In this case study, *Pseudoatrypa*

cf. lineata species lineage was traced in the Traverse Group stratigraphic intervals of Michigan to test the punctuated equilibrium model, in fact to test for stasis, since it persisted through that time range. If this model is true, then very little or no morphological change is expected between samples in successive strata as this is only one species lineage with no evidence of species splitting. However, if data could be retrieved with greater stratigraphic resolution, that is, if samples could be collected from numerous successive finer scale units, then the chances are that the morphological trend could be more reasonably evaluated. Morphological shape trend illustrated for four broad scale stratigraphic units along the major principal component axes shows a large degree of morphological overlap between the lower three stratigraphic intervals (Bell Shale, Ferron Point, and Genshaw Formation) with some deflection in Norway Point samples (Fig. 2.3a–c). MANOVA and CVA show significant statistical differences between samples from all four stratigraphic intervals ($p < 0.01$) (Fig. 2.4); however, the morphological variation within samples in individual units also shows considerable overlap. This suggests, that while there is phenotypic variation within *Pseudoatrypa cf. lineata* itself, there is still considerable overlap in their extent of morphological variation among stratigraphic intervals. Incorrect recording of spacing between stratigraphic units due to lack of absolute ages and presence of stratigraphic gaps often gives an impression of abrupt change within a species (Sheldon 1987). In this study, samples were collected from units with known differential spacing between them and with almost rarely present stratigraphic gaps between them (Fig. 2.1, Table 2.4); however, there is a lack of sampling between Genshaw and Norway Point formations which equals 42.0 m (125.0 feet) in thickness. Thus, while the abrupt deflection in morphological variation in Norway Point formation may appear to be due to sampling bias to some extent, it cannot be further proved without illustrating the morphological trend of the samples from the intermediate stratigraphic units between Genshaw and Norway Point formations. This change may have to do with some kind of anagenetic change in morphological shape pattern within this species lineage as proposed in prior studies by Roopnarine and others (1999).

Lieberman et al. 1995 observed morphological overlap between the lowermost and uppermost occurrences with some variations in the intervening samples within *Mediospirifer audaculus* and *Athyris spiriferoides* species lineages sampled from successive stratigraphic horizons of the Hamilton Group (5 million year) of New York. They performed this study using traditional morphometrics and interpreted the results as a case of stasis without performing real tests for determining evolutionary modes within those two species lineages. In this study, morphological distances retrieved from geometric morphometric analysis were further used to plot morphological shape against evolutionary divergence time. *P. cf. lineata* samples, an atrypid species lineage was studied using geometric morphometric technique, from a 6 million year time interval, from the Middle Devonian period that has never been tested for stasis or other evolutionary patterns. Thus, whether results testing evolutionary patterns support the stasis hypothesis or not, is discussed under another section, called rate and mode of evolution.

2.5.3 *Phyletic Gradualism Hypothesis*

The phyletic gradualism hypothesis is that species continue to adapt to new environmental and biological selection pressures over the course of their life history, gradually becoming new species. During this process, chances are that anagenetic evolution occurs at a smooth, steady, and incremental (not necessarily constant or slow) rate on a geological timescale (Darwin 1859). Sheldon (1987) reported evidence of parallel gradualistic evolution in eight lineages of 15,000 Ordovician trilobites from central Wales over a 3 million year interval based on evidence of increasing number of pygidial ribs in more than one species lineage. However, in a later study, Sheldon (1996) proposed the Plus ~ca change model that predicts a tendency for continuous, gradualistic evolution in narrowly fluctuating, relatively stable environments, and more stasis with episodic punctuations in widely fluctuating environments with its application in more physical environmental variables like sea level, substrate, temperature, etc., on a geologic time scale (Sheldon 1990, 1996). Nevertheless, the traditional conception of Darwin's gradualistic evolution has been persisting as the mainstream idea among evolutionary biologists through the last two centuries. However, observed patterns in the fossil record alone are not sufficient to confirm the theory of phyletic gradualism; the mechanisms behind the pattern must also be described and demonstrated (Gould and Eldredge 1977). Therefore, while some fossil evidence supports Darwin's more traditional concept of phyletic gradualism, overwhelming evidence from the fossil record and theoretical studies now implies that punctuated equilibrium (punctuation and stasis) is the foremost pattern in macroevolution (Eldredge and Gould 1972; Gould and Eldredge 1977; Williamson 1981; Stanley and Yang 1987; Gould 1988; Barnosky 1990; Lich 1990). Here we tested for evolutionary patterns in a single species lineage, to see if stasis or change predominates the Traverse Group stratigraphic units.

In this study, close morphological links were established in *P. cf. lineata* taxon among the three lowermost successive strata (Bell Shale, Ferron Point, and Genshaw Formation) with some distance with the uppermost strata (Norway Point) under investigation. The morphometric shape distances concur with the stratigraphic arrangement of the Traverse Group (Fig. 2.5). Results from Euclidean cluster analysis in part appear to support the phyletic gradualism hypothesis in that the closely spaced intervals show smaller morphological distances than those widely spaced in time. However, morphological trend alone cannot give evidence for gradual evolution in this species over time. While morphological shape change appears to be oscillating around the mean and morphological distances appear to be incremental in time, a more strong evidence is required that tests the rate and mode of evolution to prove that this shape change pattern is driven by directional selection.

2.5.4 *Tempo and Mode of Evolution*

The evolution of dorsal valve, ventral valve, anterior margin, and posterior hinge shape morphology in *Pseudoatrypa cf. lineata* is investigated under three different

evolutionary modes: (1) stabilizing selection; (2) randomly fluctuating selection; and (3) directional selection. Stabilizing selection, is a type of selection, in which the morphology in the given unit is adjusted or pushed back with respect to the earlier morphologies, in cases where it moves too far away from the mean morphology. Randomly fluctuating selection is a type of random walk, or Brownian motion, in which the direction and magnitude of change in any given generation or time is not influenced by that in earlier or later ones. Directional selection, is the type of selection, in which selection often causes changes in one direction than another (Polly 2004).

The results of the analysis of evolutionary rate and mode in this case study indicate that stabilizing to near random divergence has probably been acting on these *P. cf. lineata* taxon, which concurs with the very small morphological divergences among them (Fig. 2.6). The large degree of morphometric overlap among the *P. cf. lineata* individuals from the four stratigraphic units of Traverse Group might be interpreted by some to represent stasis, since mean shell shape among none of the strata have unambiguously diverged from each other, except for the Norway Point samples. However, the statistical definition of stasis, or stabilizing selection, is that less morphological divergence has occurred than expected under a random-walk (Brownian motion) model of evolution given the amount of time since divergence. The statistical definition of random divergence is that similar morphological divergence has occurred as expected under a random-walk model of evolution given the amount of time since divergence. For this atrypid taxon, the changes in mean shape tested in four different views are less than or equal to that expected given time since divergence (since lowest strata in Traverse Group succession)—the most likely estimate of a in Eq. 2.1 given the data presented in Fig. 2.6 ranges between <0.01 and ≤ 0.50 (dark line). Stasis would produce a pattern where the best fit would have a value near 0.0 for parameter a , and random selection would produce a pattern where the best fit would have a value near 0.5 for parameter a . The rate of divergence in this brachiopod species over stratigraphic intervals is not linear as expected with directional selection. The best interpretation for these data is that they produce a pattern which ranges from near stasis to near random mode of evolution.

Stabilizing selection is one of the several processes thought to explain patterns of morphological stasis (Vrba and Eldredge 1984; Smith et al. 1985; Lieberman et al. 1995; Polly 2004). However, later investigation has shown that stasis like patterns is produced when different selection pressures act on species belonging to different ecosystems, overall, producing no net morphological trend (Lieberman et al. 1994, 1995, Lieberman and Dudgeon 1996). When morphological fitness is influenced by many independent environmental variables (e.g., nutrition, winter temperature, and predator density), morphologies can oscillate in time with changing environments (Polly 2004). Thus, randomly fluctuating selection can explain patterns of morphological change in species over time. Here, we have selected samples from more stable environmental regimes with similar lithologic settings, water depth, and sea-level cycle to detect morphological patterns across time. In this study, an evaluation of real morphological distances on brachiopod morphological shape against geologic time suggests that they have evolved predominantly

by stabilizing to randomly fluctuating selection. The dorsal valve had chances of evolving both via near stabilizing to random selection, ventral valve via near random selection, anterior margin via stabilizing selection, and posterior hinge via near stabilizing to random selection. This suggests that morphologies from ancestral to descendant populations in this species lineage evolved statically to randomly, which does not support completely either of the evolutionary models (gradual evolution and punctuated equilibrium).

Over 250 documented cases of phenotypic traits evolving within fossil lineages were depicted by Hunt (2007) in his study where he observed only 5 % cases indicated directional evolution, 95 % cases involved random walk and stasis patterns with equal chances for each. In this study, the best interpretation of shape evolution in *P. cf. lineata* taxon, given the data, is that these were statically to randomly evolving over time at a rate slow to moderate enough that they still overlapped considerably through the time period covered in our study. However, morphological shape of descendant populations in Norway Point samples depicts an enormous deflection from the ancestral populations suggesting somewhat anagenetic shape evolution may have occurred in this species later in time. Overall, our morphometric data for the *P. cf. lineata* species lineage are consistent with the stratigraphic succession of Traverse Group.

2.5.5 Morphology and Environment

The paleontological record of the lower and middle Paleozoic Appalachian foreland basin demonstrates ecological and morphological stability on geological time scales. Some 70–80 % of fossil morphospecies within assemblages persisted in similar relative abundances in coordinated packages lasting as long as 7 million years despite evidence for environmental change and biotic disturbances (Morris et al. 1995). This phenomenal evolutionary stability despite environmental fluctuations has been explained by the concept of ecological locking. Ecological locking provides the source of evolutionary stability that is suggested to have been caused by ecological interactions that maintain a static adaptive landscape and prevent both the long-term establishment of exotic invading species and evolutionary change of native species (Morris 1995; Morris et al. 1995). For example, competition plays an important role in mediating stasis by stabilizing selection (Lieberman and Dudgeon 1996).

When disturbance exceeds the capacity of the ecosystem, evolution proceeds at high rates of directional selection during the organization of a new stable ecological hierarchy (Morris et al. 1995). Thus, ecological evolutionary units (EEUs) and subunits (EESUs) have been used to explain why many fossil species appear to persist unchanged morphologically for long periods, punctuated by short bursts of rapid change. My samples are from the Traverse Group of the Michigan Basin that falls within the Hamilton ecological evolutionary subunit, thus, a good case study to determine morphological patterns in a species lineage from an EESU.

A better understanding is required as of how environment can affect the morphology of a species. Vrba (1980) found that the ultimate driving force for evolutionary change was the environment that includes both the physical and biotic conditions surrounding an organism. Webber and Hunda (2007) quantified environment from faunal abundance data in each bed of Kope and lower Fairview Formations spanning over 2 million year interval using DCA ordination scores and used it as a proxy for water depth. They observed morphological shape in Upper Ordovician trilobite *Flexicalymene granulosa* changes with change in paleoenvironmental conditions. In contrast, for lineages in a single locality, when environments were more narrowly fluctuating and relatively stable, net directional change and/or more widely fluctuating morphologies were predicted (Sheldon 1996, Fig. 2.2). In this study, *Pseudoatrypa cf. lineata* sample collection was from six different localities in Michigan, confined to the shale units of Bell Shale, Ferron Point, Genshaw and Norway Point formations of the Traverse Group (Fig. 2.1). Water depths in the Michigan Basin during transgressive–regressive cycle If, decreased from approximately 50 to <2 m (Bell Shale through Norway Point deposition) and the eustatic curve, in contrast, depicts overall sea level rise punctuated only by regression during the final subcycle of transgressive–regressive cycle If (Wyllie and Huntoon 2003). Shallow water depth and onset of regression in the transgressive–regressive cycle If in the upper Traverse Group, somewhat coincides with the morphological shape fluctuation in the Norway Point samples with greater water depth and overall transgression coinciding with the lower Traverse Group strata. However, the overall range of water depth, 2–50 m, and the Middle Devonian eustatic curve represented by transgression–regression cycle during this time, was considered to be stable in general.

Morphological shape in four different views, when regressed onto the shallowing trend of water depth from basal Bell Shale to upper Norway Point formation, shows a low to high positive correlation with significant results only for ventral valve ($p < 0.01$). Other views do not show significant correlation between the two ($p > 0.01$). While it is challenging to discuss morphological shape change patterns in terms of just one or two environmental variables, it is still quite noteworthy, to see the correspondence of Norway Point samples with shallow water depth (<2 m) and Bell Shale, Ferron Point, and Genshaw Formation samples with relatively deeper (40–50 m) water levels. In other words, the small morphological deflection of Norway Point samples from the lower stratigraphic intervals could be in conjunction with the sudden outburst of transgressive–regressive cycle in the whole transgression cycle If and abrupt shallowing of the water level from 50 to <2 m during deposition of the Norway Point Formation.

Atrypids are phenotypically plastic (Fenton and Fenton 1935), and thus it is very challenging to distinguish between true evolution in a species and phenotypic plasticity. Controlling for environment while sampling, to some extent, may help in interpreting true morphological shifts and evolutionary patterns in this species lineage. In anyway, if change in morphological shape in *P. cf. lineata* was only an ecophenotypic phenomenon, one would expect far closer correlation between morphological shape and water depth variable which is clearly not the case in this study.

2.6 Conclusions

Landmark measurements in atrypid species lineage *Pseudoatrypa cf. lineata* from the Middle Devonian Traverse Group of Michigan State have been analyzed in this study to determine whether morphological shape trends in lineage can be explained by phyletic gradualism, punctuated equilibria, and/or ecophenotypic variations. Geometric morphometric and multivariate statistical analyses reveal significant statistical differences in morphological shape between Traverse group stratigraphic units, but a considerable overlap is noticed among morphologies over 6 million year interval of time. Though, the samples from the uppermost strata, Norway Point formation shows an abrupt morphological shift from the lower stratigraphic units, Bell Shale, Ferron Point, and Genshaw Formation. Thus, over a period of 6 million years, morphological shape, a species diagnostic character, underwent very little change in the lower Traverse Group formations with some change been reflected in the upper Norway Point formation.

Maximum-likelihood method suggests slow to moderate rate of evolution with near stasis to random divergence mode of evolution in *P. cf. lineata* species lineage. Overall, the mean shape morphological trend suggests considerable morphological overlap between the successive stratigraphic units of the lower Traverse Group with small morphological oscillations in the species life history. However, samples in the uppermost strata deviate from the mean so far, such that some kind of anagenetic evolution appears to be acting on the descendant populations in this species.

Morphological shape in dorsal valves and posterior hinge area suggests evolution by near stasis to random divergence with similar magnitudes of rates (moderate) of evolution. Morphological shape in ventral valves suggests evolution by random divergence with relatively slower rate of evolution. Morphological shape in anterior margin suggests evolutionary stasis with moderate rate of evolution. Overall, this suggests, that ventral valves evolve at a lesser magnitude than all other shape measurements that include dorsal valves, posterior hinge area, and anterior margin. While ventral valves show maximum fluctuation in their evolutionary mode, anterior margin is most stable in morphology over time.

Changes in morphological shape patterns in *P. cf. lineata* weakly correlates with variation in water depth, except for ventral valves. Thus, this suggests, that the morphological shape trend can be explained by stabilizing selection and/or by randomly fluctuating selection, and not by ecophenotypic variations. Since other environmental variables were not tested, it was challenging to infer if any abiotic or biotic factors were behind these mechanisms of evolutionary selection.

Thus, the results from this study, in a complete sense, are neither in full favor of the punctuated equilibrium model nor the phyletic gradualism model. Static evolution is represented in the species early life history with anagenetic evolution, most likely, predominating the later stages in the species life.

References

- Barnosky AD (1990) Evolution of dental traits since latest Pleistocene in meadow voles from Virginia. *Paleobiology* 16:370–383
- Bookstein FL (1989) Principal warps: thin-plate splines and the decomposition of deformations. *IEEE Trans Pattern Anal Mach Intell* 11:567–585
- Bookstein FL (1991) *Morphometric tools for landmark data: geometry and biology*. Cambridge University Press, Cambridge 435 p
- Bose R (2012) *Biodiversity and evolutionary ecology of extinct organisms*. Palaeoenvironmental Sciences. Springer, New York 100 p
- Brett CE (1986) The Middle Devonian Hamilton group of New York: an overview. In: Brett C (ed) *Dynamic stratigraphy and depositional environments of the Hamilton Group (Middle Devonian) in New York State, Part 1*. New York State Museum Bulletin, vol 457, pp 1–4
- Brett CE, Baird GC (1995). Coordinated Stasis and Evolutionary Ecology. In: Erwin DH, Anstey RL (eds) *New approaches to Speciation*. Columbia University Press, New York, pp 285–315
- Cooper GA, Butts C, Caster KE, Chadwick GH, Goldring W, Kindle EM, Kirk E, Merriam CW, Swartz FM, Warren PS, Warthin AS, Willard B (1942) Correlation of the Devonian sedimentary formations of North America. *Bull Geol Soc Am* 53:1729–1794
- Copper P (1967) Adaptations and life habits of Devonian atrypid brachiopods. *Palaeogeogr Palaeoclimatol Palaeoecol* 3:363–379
- Darwin C (1859) *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. John Murray, London
- Day J (1992) Middle-Upper Devonian (late Givetian-early Frasnian) brachiopod sequence in the Cedar Valley Group of central and eastern Iowa. In: Day J, Bunker BJ (eds) *The stratigraphy, paleontology, depositional and diagenetic history of the Middle-Upper Devonian Cedar valley group of central and eastern Iowa*, vol 16. Iowa Department of Natural Resources Guidebook Series, pp 53–105
- Day J (1996). Faunal signatures of Middle-Upper Devonian depositional sequences and sea level fluctuations in the Iowa Basin: U.S. midcontinent. In: Witzke BJ, Ludvigson GA, Day J (eds) *Paleozoic sequence stratigraphy, views from the North American Craton*. Geological Society of America Special Paper, vol 306, pp 277–300
- Day J, Copper P (1998) Revision of latest Givetian-Frasnian Atrypida (Brachiopoda) from central North America. *Acta Palaeontol Pol* 43:155–204
- Ehlers GM, Kesling RV (1970) Devonian strata of Alpena and Presque Isle counties. Michigan Basin Geological Society, Michigan, p 130
- Eldredge N, Gould SJ (1972) Punctuated equilibria. In: Schopf (ed) *Models in Paleobiology*. Freeman, Cooper, pp 82–115
- Ettensohn FR (1985) The Catskill Delta complex and the Acadian orogeny: a model. In: Woodrow DL, Sevon WD (eds) *The Catskill Delta*. Geological Society of America Special Paper 201. Boulder, Colorado, pp 39–50
- Felsenstein J (1988) Phylogenies and quantitative characters. *Annu Rev Ecol Syst* 19:445–471
- Fenton CL, Fenton MA (1935) Atrypae described by Clement L. Webster and related forms (Devonian, Iowa). *J Paleontol* 9:369–384
- Geary DH (1995) Investigating species-level transitions in the fossil record: the importance of geologically gradual change. In: Erwin DH, Anstey RA (eds) *New approaches to speciation in the fossil record*. Columbia University Press, New York, pp 67–86
- Geary DH, Hunt G, Magyar I, Schreiber H (2010) The paradox of gradualism: phyletic evolution in two lineages of lymnocardiid bivalves (Lake Pannon, central Europe). *Paleobiology* 36:592–614
- Gingerich PD (1993) Quantification and comparison of evolutionary rates. *Am J Sci* 293A:453–478
- Gingerich PD (1976) Paleontology and phylogeny: patterns of evolution at the species level in early Tertiary mammals. *Am J Sci* 276:1–28

- Gingerich PD (1985) Species in the fossil record: concepts, trends and transitions. *Paleobiology* 11:27–41
- Gingerich PD (2001) Rates of evolution on the time scale of the evolutionary process. *Genetica* 112–113:127–144
- Goldman D, Mitchell CE (1990) Morphology, systematics, and evolution of Middle Devonian Ambocoeliidae (Brachiopoda), Western New York. *J Paleontol* 64:79–99
- Gould SJ, Eldredge N (1977) Punctuated Equilibria: the tempo and mode of evolution reconsidered. *Paleobiology* 3:115–151
- Gould SJ (1988) Prolonged stability in local populations of *Cerion agassizi* on Great Bahama bank. *Paleobiology* 14:1–18
- Hunt G (2007) The relative importance of directional change, random walks, and stasis in the evolution of fossil lineages. *Proc Natl Acad Sci* 104:18404–18408
- Isaacson PE, Perry DG (1977) Biogeography and morphological conservatism of *Tropidoleptus* (Brachiopoda, Orthida) during the Devonian. *J Paleontol* 51:1108–1122
- Kelly WA, Smith GW (1947) Stratigraphy and structure of Traverse Group in Afton-Onaway area, Michigan. *Bull Am Assoc Petrol Geol* 31:447–469
- Kesling RV, Segall RT, Sorensen HO (1974) Devonian strata of Emmet and Charlevoix counties, Michigan. Michigan Museum of Paleontology Papers on Paleontology, vol 7, pp 1–187
- Koch WF (1978) Brachiopod paleoecology, paleobiogeography, and biostratigraphy in the upper middle Devonian of Eastern North America: an ecofacies model for the Appalachian, Michigan, and Illinois basins. Dissertation, Oregon State University, Oregon
- Lande R (1976) Natural selection and random genetic drift in phenotypic evolution. *Evolution* 30:314–334
- Lich D (1990) *Cosomys primus*: a case for stasis. *Paleobiology* 16:384–395
- Lieberman BS, Brett CE, Eldredge N (1994) Patterns and processes of stasis in two species lineages from the Middle Devonian of New York State. American Museum of Natural History Novitates, vol 3114, New York, NY
- Lieberman BS, Brett CE, Eldredge N (1995) A study of stasis in two species lineages from the Middle Devonian of New York State. *Paleobiology* 21:15–27
- Lieberman BS, Dudgeon S (1996) An evaluation of stabilizing selection as a mechanism for stasis. *Palaeogeogr Palaeoclim Palaeoecol* 127:229–238
- Mayr E (1963) Animal species and evolution. Harvard University Press, Cambridge
- Macleod N, Forey PL (2002) Morphology, shape, and phylogeny. Taylor and Francis, New York
- Morris PJ (1995) Coordinated stasis and ecological locking. *Palaio* 10:101–102
- Morris PJ, Ivany LC, Schopf KM, Brett CE (1995) The challenge of paleoecological stasis: reassessing sources of evolutionary stability. *Proc Natl Acad Sci* 92:11269–11273
- Polly PD (2001) Paleontology and the comparative method: ancestral node reconstructions versus observed node values. *Am Nat* 157:596–609
- Polly PD (2004). On the simulation of morphological shape: multivariate shape under selection and drift. *Palaeontol Electron* 7:L7A (Coquina Press)
- Polly PD (2008) Adaptive zones and the pinniped ankle: a three-dimensional quantitative analysis of carnivoran tarsal evolution. In: Sargis E, Dagosto M (eds) Mammalian evolutionary morphology: a tribute to Frederick S. Szalay. Springer, Dordrecht, pp 167–196
- Rohlf FJ (1990) Fitting curves to outlines. In: Proceedings of the Michigan morphometrics workshop, pp 167–177
- Rohlf FJ, Slice DE (1990) Extensions of the procrustes method for the optimal superimposition of landmarks. *Syst Zool* 39:40–59
- Rohlf FJ (1999) Shape statistics: procrustes superimpositions and tangent spaces. *J Classif* 16:197–223
- Rohlf FJ, Marcus LF (1993) A revolution in morphometrics. *Trends Ecol Evol* 8:129–132
- Roopnarine PD, Byars G, Fitzgerald P (1999) Anagenetic evolution, stratophenetic patterns, and random walk models. *Paleobiology* 25:41–57
- Roopnarine PD (2001) The description and classification of evolutionary mode: a computational approach. *Paleobiology* 27:446–465

- Roopnarine PD (2003) Analysis of rates of morphologic evolution. *Annu Rev Ecol Evol Syst* 34:605–632
- Sheldon PR (1987) Parallel gradualistic evolution of Ordovician trilobites. *Nature* 330:561–563
- Sheldon PR (1990) Shaking up evolutionary patterns. *Nature* 345:772
- Sheldon PR (1996) Plus ça change—a model for stasis and evolution in different environments. *Palaeogeogr Palaeoclimatol Palaeoecol* 127(209):227
- Simpson GG (1953) The major features of evolution. Columbia University Press, New York
- Slice DE (2001) Landmark coordinates aligned by procrustes analysis do not lie in Kendall's shape space. *Syst Biol* 50:141–149
- Smith MJ, Burian R, Kauffman S, Alberch P, Campbell J, Goodwin B, Lande R, Raup D, Wolpert L (1985) Developmental constraints and evolution. *Quart Rev Biol* 60:265–287
- Stanley SM (1979) Macroevolution. WH Freeman, San Francisco
- Stanley SM, Yang X (1987) Approximate evolutionary stasis for bivalve morphology over millions of years: a multivariate, multilineage study. *Paleobiology* 13:113–139
- Stumm EC (1951) Check list of fossil invertebrates described from the middle Devonian traverse group of Michigan. *Contrib Mus Paleontol Univ Mich* 9:1–44
- Vrba ES (1980) Evolution, species and fossils: how does life evolve? *S Afr J Sci* 76:61–84
- Vrba ES, Eldredge N (1984) Individuals, hierarchies and processes: towards a more complete evolutionary theory. *Paleobiol* 10:146–171
- Webber AJ, Hunda BR (2007) Quantitatively comparing morphological trends to environment in the fossil record (Cincinnatian series; Upper Ordovician). *Evolution* 61:1455–1465
- Webster CL (1921) Notes on the genus *Atrypa*, with description of new species. *Amer Midl Nat* 7:13–26
- Williamson PG (1981) Paleontological documentation of speciation in Cenozoic mollusks from Turkana Basin. *Nature* 293:437–443
- Wylie AS, Huntton JE (2003) Log-curve amplitude slicing: Visualization of log data and depositional trends in the Middle Devonian Traverse Group, Michigan basin, United States. *Am Assoc Pet Geol Bull* 87:581–608
- Zelditch ML, Swiderski DL, Sheets HD, Fink WL (2004) Geometric morphometrics for biologists, A primer. Elsevier Academic Press, New York

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