MORPHOMETRIC EVOLUTION OF PALEOZOIC BRACHIOPODS - THE EFFECTS OF ENVIRONMENT AND ECOLOGICAL INTERACTIONS ON SHELL MORPHOLOGY

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DEDICATION

This thesis is dedicated to my family.

Thank you all from afar!

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Atrypida (Brachiopoda, Rhynchonellata) are ancient marine invertebrate fossils that are well preserved, abundant and diverse in the mid-Paleozoic (ecological evolutionary unit (EEU) P3). Atrypides thus serve as useful tools for morphological shape study. While qualitative studies have been performed for solving problems in brachiopod taxonomy, phylogeny, evolution and ecology, quantitative studies have been lacking.

After qualitative taxonomic identifications, morphological shape of the Silurian-Devonian Eastern North American atrypids was analyzed using geometric morphometrics, placing the results in evolutionary and ecological perspectives. Landmark analysis was performed on dorsal valves, ventral valves, anterior and posterior regions. These data were used for comparison with morphological distances, calculated as pairwise Procrustes distances. Evolutionary divergence times were determined from atrypide phylogeny and from stratigraphic zonations in the Michigan Traverse Group. Maximum likelihood tests were performed to determine evolutionary rates and modes of morphological divergence within and between genera. Episkeletobionts on hosts were examined to determine how morphological variation affected these assemblages.

Morphometric results suggest that morphological distances within each genus was as large as those observed between genera. Thus, referring individuals to a particular genus, based on shell shape alone is challenging. Diversifying selection has been acting

on morphological divergence of these generic pairs and morphometric distances are consistent with the prior phylogenetic arrangement. Short term changes observed in individual lineages, that gets averaged out in time when compared to other genera, together with considerable morphological overlap observed between genera in P3 EEU, suggests a pattern consistent with stasis, as expected in EEUs.

The Traverse Group atrypid species lineage, which represents a 5 m.y. time span, exhibited lightly constrained morphological evolution, reflecting a stasis-like pattern. Greater encrustation preferences on one of two morphotypes on the dorsal valve and posterior region, suggest greater surface area facilitated by relatively deeper profile hosts in their reclining life orientation. Overall, the integration of various paleontological datasets reveal that the seemingly homogenous group of atrypide brachiopods exhibit subtle but significant evolution in their shell shape that is correlated with several kinds of ecological differences.

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different for *P. lineata* host species which are as follows: PLL = 0.18, PM = 0.138, PRL = 0.18, ALL = 0.147, AM = 0.208, ARL = 0.147. Significantly greater observed episkeletobiont frequency than expected is denoted by a plus symbol and smaller observed episkeletobiont frequency than expected is denoted by a minus symbol across the six regions of the valve; this is described for a) dorsal valve of *P. lineata*, b) dorsal valve of *Pseudoatrypa* sp. A, c) ventral valve of *P. lineata*, and d) ventral valve of *Pseudoatrypa* sp. A 144

CHAPTER I

A GEOMETRIC MORPHOMETRIC APPROACH IN ASSESSING

PALEONTOLOGICAL PROBLEMS IN ATRYPID TAXONOMY, PHYLOGENY,

EVOLUTION AND ECOLOGY

INTRODUCTION

Brief outline

This section is a brief overview of the dissertation. A brief outline of all the dissertation chapters and a few major proposed questions relevant to each chapter is discussed here.

Chapter II follows this Introduction with a detailed morphometric shape analysis of taxonomic and phylogenetic arrangement of atrypid subfamilies from a prior proposed phylogeny by Copper (1973) (Bose et al., 2011). Do morphological shape distances between genera comply with the phylogenetic chart proposed by Paul Copper? Do pairwise Procrustes distances between generic pairs agree with the taxonomic arrangement in atrypid subfamilies as proposed by Copper (1973) in the past? Overall, do these genera reflect stasis within the P3 EEU? Chapter III presents tests for stasis within an atrypid species lineage, *Pseudoatrypa cf. lineata* from the middle Devonian Traverse Group of Michigan, over a period of 5 m.y. period (Bose and Polly, 2011). Does the morphology of this species remain static within the Hamilton EESU stratigraphic units? What could be the possible causes (environment or evolution?) behind the morphological pattern observed? Do we see similar morphological patterns in species lineages in the Traverse Group of Michigan Basin when compared with those of the Hamilton Group of Appalachian Basin? Chapter IV presents a detailed analysis of episkeletobiont interactions with the Genshaw Formation atrypids from the middle Devonian Traverse Group, with further investigation of species, valve and location preference of these episkeletobiont assemblages. Can we reconstruct life orientation of brachiopods from

location preferences of certain episkeletobiont associations on their host valves? Can morphological variation in host species influence the rate of encrustation?

In addition to providing information about factors of evolution, the response of valve morphology to both its physical environment and community interactions is important in reconstructing life histories. Studying the morphology of extinct brachiopod groups, thus, will help reconstruct their evolutionary history in terms of both large scale and small scale temporal intervals. The study presented in this dissertation is important because (a) the Silurian-Devonian is an EEU that has frequently been scrutinized for stasis, (b) the middle Devonian Traverse Group is an EESU which has not been tested for stasis, (c) atrypides are among the most diverse and common macro-invertebrates in these intervals, but (d) with the exception of one athyride and one spiriferide species from the middle Devonian Hamilton Group in the Lieberman et al. (1995) study, the use of morphometrics to evaluate stasis in atrypides is virtually uninvestigated, (e) morphological variation in Devonian brachiopod species *Pseudoatrypa cf. lineata* and their influence on episkeletobiont assemblages using morphometrics has not been examined in the past, and (f) finally, lophophores are the primary feeding and respiratory organ in these organisms and determining their morphological shape could help predict the lophophore shape of these extinct organisms.

Why Silurian and Devonian time periods for this study?

After the Ordovician mass extinction event, many marine taxa rediversified in the Late Ordovician event and a few persisted in the Silurian and Devonian ecosystem. Trilobites almost disappeared, bivalve mollusks invaded non-marine habitats, corals and stromatoporoids diversified in new ways giving rise to massive reef systems in shallow

seas, and graptolites diversified to a great extent. Brachiopods attained the highest diversity during this time. New forms like ammonoids and jawed fishes flourished for the first time. Vascular plants invaded the land in late Silurian period followed by the evolution of more complex land plants in the early and middle Devonian period. Arthropods (insects, scorpions and spiders) and vertebrate animals also evolved during this period. During the Devonian, spore plants were accompanied by seed plants and large trees with roots and abundant foliage arose in the Late Devonian. This initial spread of terrestrial vegetation accelerated weathering rates thus resulting in relatively cooler climates during this time, further providing shelter for early vertebrates (Ausich and Lane, 1999; Stanley, 2005).

The Late Ordovician period was marked by a significant change in the sedimentation pattern in Eastern North America when the newly formed mountains in the east from the Taconic orogenic event caused the deposition of clastic wedges in the west, as reviewed by Stanley (2005). The pattern continued in the Silurian period followed by erosion of the eastern mountains and inundation of the clastic deposits by the shallow epicontinental seas. During the Late Silurian time, shallow water carbonate sediments accumulated along a new passive margin. Carbonate sedimentation that spread along the continent during the Devonian had an abrupt subsidence and was soon replaced by a foreland basin as mountains rose in the east (Acadian orogeny initiation during middle Silurian). During most of the Devonian, eastern North America accumulated little or no sedimentation. The carbonate platforms were covered with sandy beach deposits before subsidence, and then later after subsidence, black muds, turbidites, siltstones and shales deposited in Hudson foreland (New York) basin near the end Devonian time. Shallow

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water sedimentation then lead to the deposition of deep water flysch. Due to an enhanced supply of sedimentation from erosion of adjacent mountain belts in the late Devonian time, these deep water deposits in the foreland basin finally gave way to the deposition of shallow marine and non-marine molasse deposits.

To the west of North America, patterns of sedimentation, however, changed during Early Silurian. The Michigan and Ohio basins accumulated muddy carbonates and were well populated with patchy reefs and bounded by large barrier reefs. The east continued to be filled in with siliciclastic muds. The overall pattern changed with the progression of time; during the Silurian time, siliciclastic sedimentation slowly gave way to carbonate sedimentation in the east. The barrier reefs around the northeastern (Michigan and Ohio) basins had risen very high restricting the supply of water to the basins. This, together with lowering of sea level, caused precipitation of evaporitic deposits in the margins and at considerable depths of the basins. During the Late Silurian, reefs grew only in the southwest (Indiana and Illinois), given the unfavorable conditions in the evaporitic basins. Later in the Devonian time, black mud deposition extended to the west, covering a vast area of eastern and central North America with these sediments, further eliminating nearly all members of the coral-stromatoporid reef community and the placoderm fishes (Stanley, 2005).

Why brachiopods?

Brachiopods are excellent models for testing macroevolutionary and ecological hypotheses due to their increased abundance and diversity during the middle Paleozoic interval after the great Ordovician biodiversification event (Alexander, 1986; Jin, 2001; Leighton, 2005; Novack-Gotshall et al., 2008). Their slow growth rate, low metabolism,

obligate filter feeding, restriction to hard substrates and low energy environments, suggest greater chances of their survival from climatic changes, more likely than any other invertebrate taxa (Rudwick, 1970; Thayer, 1977; Peck, 2008). Brachiopod morphology has been studied using advanced morphometric and statistical techniques in the past two decades (Goldman and Mitchell, 1990; Lieberman et al., 1995; Krause, 2004; Tomasovych et al., 2008; Bose et al., 2010, 2011), further depicting the shape differences at the community and species level. For this study, atrypides have been selected as with their origination in the late Middle Ordovician (Llandeilo) time, they persisted for sometime in the Silurian and Devonian time periods with high generic diversity and abundance, until they were finally wiped out during the late Devonian mass extinction (Frasnian) (Copper 2001). Atrypides were extensively studied in the past by prior researchers (Fenton and Fenton, 1932, 1935; Biernat, 1964; Copper, 1967, 1973, 1977, 1982, 1995, 1997, 2001, 2002, 2004; Day, 1995; Day 1998; Day and Copper, 1998; Ma and Day, 2007), but to date no one has applied advanced quantitative techniques to further address evolutionary, ecological, taphonomic, taxonomic and phylogenetic inquiries. This study was a first attempt in resolving such aspects of paleontological problems by using geometric morphometric methods.

Episkeletobionts, also known as encrusting organisms that adhere to the surface of a shell (Taylor and Wilson, 2002), were mostly restricted to hard skeletons of the host shells during the Devonian geologic period (Taylor and Wilson, 2003). Episkeletobionts on brachiopod hosts have been extensively studied in the past (Rudwick, 1962; Richards and Shabica, 1969; Richards, 1972; Hurst, 1974; Thayer, 1974; Pitrat and Rogers, 1978; Kesling et al., 1980; Spjeldnaes, 1984; Bordeaux and Brett, 1990; Rodland et al., 2004,

2006; Schneider and Leighton, 2007; Rodrigues et al., 2008; Bose et al., 2010; Bose et al., 2011). Thus, quantitative interpretation of abundance, diversity and location preference of these Devonian episkeletobionts on host brachiopod valves could provide insight into the paleoecology and life orientation of these brachiopod hosts.

Why geometric morphometric methods?

Geometric morphometrics provides a great insight into the biological, paleoecological and evolutionary processes that affects the morphology of organisms. Geometric morphometric methods are helpful in solving many complex hypotheses in shape comparative studies. In the past two decades, new methods biological and geometric shape analysis have been elucidated (Bookstein, 1991; Zelditch et al., 2004), and applied in solving evolutionary problems in numerous fields. These techniques have been applied to problems in ontogeny and phylogeny (Fink and Zelditch, 1995; Adams and Rosenberg, 1998; Rohlf, 1998; MacLeod, 1999; MacLeod, 2001; MacLeod et al., 2002; Lockwood et al., 2004; Cardini and O'Higgins, 2004; Rook and O'Higgins, 2005; Caumul and Polly, 2005), hybridization (Hayden et al., 2010), functional morphology (Bonnan, 2004; Kassam et al., 2004; Stayton, 2006; Kulemeyer et al., 2009), genetics (Myers et al., 2006), primate and human cranial anatomy (Frost et al., 2003; Couette et al., 2005; Bernal et al., 2006), mammalian evolution (Polly, 2003, 2004, 2007), trilobite evolution, paleoecology and taphonomy (Webster and Hughes, 1999; Webber and Hunda, 2007; Webster and Zelditch, 2011) and brachiopod ontogeny, evolution, systematics and paleoecology (Haney et al., 2001; Krause, 2004; Adams et al., 2008; Bose et al., 2010; Bose et al., 2011). These references provide a great overview of applications, while those interested in more detailed technical explanations are referred to

the primary reference (Bookstein, 1991; Adams et al., 2004). Collectively, this new set of methods for analyzing landmark-based data is referred to as geometric morphometrics.

Why use geometric morphometrics over any other technique for assessing morphological change in time and space? Geometric morphometrics is an advanced analytical technique that has several advantages over traditional morphometric techniques involving the measurement of interlandmark distances, angles or ratios of distances (Rohlf, 1990). The direct use of landmark data in the analysis allows the incorporation of a unique feature of those data, their spatial organization and the inclusion of average forms, adding statistical power to the various shape space components, allowing pure shape to be analyzed independent of size and allowing results to be depicted visually with representations that resemble the original objects (Bookstein, 1991).

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CHAPTER II

TESTING THE TAXONOMY AND PHYLOGENY OF EASTERN NORTH

AMERICAN ATRYPID BRACHIOPODS: A GEOMETRIC MORPHOMETRIC

APPROACH

(in preparation for submission to *Lethaia*: Bose, R., Leighton, L. R., Day, J., and Polly, P.

D., 2011, A geometric morphometric approach in testing the taxonomy and phylogeny of

eastern North American atrypid brachiopods.)

ABSTRACT

The phylogeny and taxonomy of atrypides as proposed in the past has not been tested in terms of morphometric shape. Here, we investigated external shell shape variation in brachiopod morphology at the subfamily and generic level using geometric morphometrics. We measured valve shape in 1593 atrypid individuals from Silurian-Devonian time intervals from 8 EE subunits from 18 geographic localities in eastern North America. The following representatives of the Atrypida were included in the morphometric analyses: *Atrypa*, *Gotatrypa*, *Kyrtatrypa*, *Oglupes?*, *Joviatrypa*, *Endrea*, *Dihelictera* (Atrypinae); *Pseudoatrypa* (Variatrypinae) and *Spinatrypa* (Spinatrypinae).

We used 8 external landmarks to determine shape differences among genera and subfamilies in time and space and to calculate pairwise distances between them. Phylogenetic divergence time was determined between atrypid generic pairs based on the phylogenetic tree published in prior literature. Maximum-likelihood was used to assess evolutionary rate and mode of morphological divergence.

Results indicate that morphological divergences among these genera are very small compared to their within-genus variation. Thus, while morphometric differentiation is concordant with phylogeny proposed in the past, the small shell shape distances between genera, considerable morphological overlap between subfamilies, considerable variation within one subfamily, and greater morphological variation within genus, suggest that other characteristics such as ribbing, growth lamellae, pedicle opening, etc. prove to be more useful for distinguishing genera in atrypid brachiopods. Thus, a combination of quantified shape, external and internal morphological characters is

essential for future phylogenetic classification in order to understand the evolutionary ecology of these complex organisms in its entirety.

INTRODUCTION

Taxonomy

All atrypide brachiopods in North America were once referred to a single collective species, *Atrypa reticularis* (*e.g.,* Fenton & Fenton 1930). *Atrypa reticularis*

sensu-stricto is now recognized only from the Silurian of Gotland (Copper 2004; P. Copper personal communication, 2009). The group has been radically revised in the last three decades and the understanding of the evolutionary relationships between genera is still in flux. The brachiopods that were once referred to one species are now distributed among 38 genera in 5 subfamilies within the family Atrypidae (Copper 1973, 1996, 2001a, 2002, 2004; Day 1998; Day & Copper 1998; Williams *et al*. 2002). Although the taxonomy of Copper's (1973) phylogeny is now partially out of date, having been revised again by Copper (2001a) based on differences in shell size, shell shape, surface ornamentation and internal morphological features, his phylogenetic hypothesis remains the only one for atrypides. To date, no one has attempted to quantify the morphological characters of these genera to test whether shell shape evolution is consistent with the phylogenetic arrangement. In this study, genera from the Atrypinae, Variatrypinae and Spinatrypinae are studied based on external morphological characters.

The genus *Atrypa* has been revised extensively since 1965 and has been split into several genera (Alvarez 2006). *Atrypa* was most closely related to *Desquamatia* and *Spinatrypa* (Boucot 1964) which were then all referred to Atrypinae (Williams *et al*. 1965). The phylogenetic relationships of *Atrypa*, *Gotatrypa*, *Kyrtatrypa* and many other

atrypids were later studied by Copper (1973) who suggested that *Atrypa* is more closely related to *Gotatrypa* than to *Spinatrypa* or *Pseudoatrypa*. Based on that phylogeny and subsequent work, *Desquamatia* is today referred to Variatrypinae and *Spinatrypa* is referred to Spinatrypinae (Copper *et al*. 2002).

Atrypid individuals that have been measured for this study belong to the Atrypinae, Variatrypinae and Spinatrypinae subfamilies, which have similar dorsally to dorso-medially directed spiralia (Copper 1996, 2002), distinct jugal processes, and distinct types of pedicle collar attachments to deltidial plates (Copper 1967, 1977). These three subfamilies were selected for this study as representatives of the family Atrypidae as they represent the longest stratigraphic ranges within the Silurian and Devonian time periods.

Atrypin adults have wavelike, overlapping or imbricate growth lamellae extended as frills, with loss of pedicle opening during ontogeny in most shells; while variatrypins have widely separated growth lamellae extended as expansive frills or alternatively have reduced growth lamellae but with simple tubular ribs, with most forms retaining the pedicle foramen. Spinatrypinae have commonly spinose, short growth lamellae with ribs disrupted into waves, producing nodular surface macroornament, with all forms retaining the pedicle foramen (Copper 2001a, 2002).

Copper (1973) used rib structure, pedicle structure, structure of jugal processes and dentition type to construct his phylogeny of four atrypide families. Shell shape was not considered as a criterion in his (1973) phylogenetic reconstruction. In our study, atrypid shell shape was evaluated using geometric morphometrics on nine genera representing three subfamilies of Atrypidae recognized by Copper's taxonomy and

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phylogeny. Our data from the Early Silurian to Early Devonian samples consist of individuals that belong to the Atrypinae while the Middle Devonian to Late Devonian samples consist of those from the Variatrypinae and Spinatrypinae subfamilies (Table 1). We analyzed shell shape to see if the patterns of differentiation are consistent with the taxonomic and phylogenetic structure proposed by Copper. A complete phylogenetic analysis based on internal morphological characters of these diverse atrypid genera in the Atrypinae, Variatrypinae and Spinatrypinae subfamilies from the eastern North American region awaits future analysis. Overall, this study tests whether the differences in shell shape between genera are consistent with Copper's classification and whether the quantitative results supports the phylogeny of the atrypid brachiopods.

Hypotheses

Six hypotheses were tested in this study: (1) if the Atrypinae, Variatrypinae and Spinatrypinae are distinct subfamilies, as proposed by Copper (1973) and Williams *et al.* (2002), then the average morphology of these subfamilies should show significant differences between them; (2) likewise, if the genera within subfamilies are truly distinct, then the average shell shape between these genera should show morphometric differences; (3) furthermore, if genera are correctly referred to subfamilies, then average morphological distance between genera in different subfamilies should be greater than that from within one subfamily; (4) If evolutionary stasis is predominant in the P3 evolutionary ecological unit (EEU, see below) caused by ecological interlocking or other environmental influences, then, despite taxonomic replacement, morphology is expected to remain the same with substantial overlap between genera through time; (5) If evolutionary stasis is predominant in the P3 EEU, then minor morphological change is

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expected within each genus through time; (6) If biogeographic differences in shell shape among geographic locations are due to provinciality, then at a given time, genera from the same paleogeographic locations are expected to cluster and morphological distances among paleogeographic locations are expected to be similar to those observed between genera.

Ecological evolutionary units and subunits (EEU and EESU)

The Silurian and Devonian have been classified into a single Paleozoic EEU (designated as P3), which was a time marked by periods of stability (designated as subunits or EESUs) (Boucot 1983, 1986, 1990a, 1990b, 1990c; Sheehan 1991; Sheehan 1996; Holterhoff 1996; Brett *et al*. 2009) interspersed by periods of minor reorganization and extinction (Brett *et al*. 1990; Brett & Baird 1995; Holterhoff 1996; Sheehan 1996; Ivany *et al*. 2009). The major extinction events of the end-Ordovician and Late Devonian mark the P3 EEU boundaries (Sheehan 1996). The 8 P3 EESUs included in the present study are shown in Figure 2.1, Table 2.1. The P3 EESUs have been well studied (Brett & Baird 1995; Brett *et al*. 2009) in the Appalachian Basin with respect to community stability patterns, but studies involving morphological shape change or stasis within brachiopod species lineages from these EESUs are lacking excepting Lieberman *et al*. (1995) who studied two brachiopod species lineages for stasis. In general, brachiopods were abundant, diverse and well-preserved during this time interval, providing plentiful data for morphological shape study. Morphological shape change patterns in P3 EEU atrypid subfamilies and genera are described here to trace both temporal and spatial variation within these brachiopod genera. Thus, this study is designed to determine comparative morphological shape patterns within the atrypid brachiopods belonging to the Atrypinae,

Variatrypinae and Spinatrypinae from the strata making up the P3 EEU from the Appalachian Basin and their stratigraphic equivalents within the Eastern American biogeographic Realm, spanning the entire 64 Myr of the Silurian-Devonian (441–376 Myr) rock record.

Geologic time scale	Sheehan's 9 EEUs	EE subunits (EESUs) Brett and Baird (1995)	Time span (my)
Tertiary	M3	**Gennessee (11.)**	5-6
Cretaceous	M2	**Hamilton**	6-7
Jurassic		**Onondaga**	5-6
Triassic	M1	**Schoharie**	5
Permian		Oriskany	2-3
Carboniferous	P4	**Helderberg**	6
Devonian		**Keyser**	2
Silurian	P3	Salina	3-4
Ordovician	P2	**Upper Clinton-Lockport**	7-8
	P1	**Lower Clinton**	4
Cambrian	C2	Medina	5
	C1		

Figure 2.1: Ecological Evolutionary Unit P3 (circled) showing the major subdivided 11 EE subunits in the Silurian and Devonian (Data sampled from the 8 EESUs are marked in bold). (after Brett and Baird, 1995).

	10	11	12	13	14	15	16	17	18
	Central-east New York, USA	Eastern Tennessee, USA	Central New York, USA	Ohio, USA	Fulton, Central Missouri, USA	Southeastern Indiana, USA	Western New York, USA	NE Michigan, USA	North-central Iowa, USA
	1	151	34	9	33	63	134 23	210	123
	Kyrtatrypa, Atrypinae	Atrypa, Atrypinae	Spinatrypa, Spinatrypin-ae, Pseudoatrypa, Variatrypinae	Pseudoatrypa, Variatrypinae	Pseudoatrypa, Variatrypinae	Pseudoatrypa, Variatrypinae	Spinatrypa, Pseudoatrypa, Variatrypinae, Spinatrypinae	Pseudoatrypa, Variatrypinae	Pseudoatrypa, Variatrypinae
	Schoharie Grit, New Scotland Limestone Helderbergian	Birdsong Shale?, Linden Group,	Onondaga Limestone	Dundee Limestone	Callaway Limestone	Hamilton Silver Creek member of the North Vernon limestone	Hamilton Group	Traverse Group	Cerro Gordo Member, Lime Creek Shale, Hackberry Grove
	Devonian (Early)	Devonian (Early)	Devonian (Middle)	Devonian (Middle)	Devonian (Middle)	Devonian (Middle)	Devonian (Middle)	Devonian (Middle)	Devonian (Late)
	Emsian	Emsian	Lower-Mid Eifelian	Lower-Mid Eifelian	Late Eifelian-Middle Late Givetian	Late Eifelian-Middle Late Givetian	Late Eifelian-Middle Late Givetian	Late Eifelian-Middle Late Givetian	Frasnian
	Schoharie (5 my)	Schoharie (5 my)	Onondaga (5-6 my)	Onondaga (5-6 my)	Hamilton-Tully (6-7 my)	Hamilton-Tully (6-7 my)	Hamilton-Tully (6-7 my)	Hamilton-Tully (6-7 my)	Genesee (5-6 my)
	Northeast-trending folds in the Valley and Ridge Province of the	On the east along flanks of the Nashville Dome	Ridge and valley province of central Appalachian Basin	Northwestern flank of the Findlay Arch	Southern Iowa Basin	Cincinnatian Arch between Illinois and Michigan Basin	Folded ridge valley province of northern Appalachian Basin	Flanks of the northeastern part of Michigan Basin	Southern margin of the Iowa Basin
	Shallow carbonates and	Siliciclastics	Carbonate	Carbonate	Carbonate	Carbonate	Siliciclastics bordered by carbonate shelf	Mixed setting (siliciclastics and carbonates)	Mid-outer carbonate shelf

Table 2.1. Geographic locations for atrypid taxa with specific information on time interval and stage, EE subunit, and depositional environment.

	4	5	6	7	8	9
	West-Central Tennessee, USA	Oklahoma, USA	Oklahoma, USA	Central-east New York, USA	Maryland, USA	West Virginia, USA
64	81 5	10 3	13 2	34 28	11 17	46 4
79						
	Atrypa, Gotatrypa, Endrea, Atrypi-Atrypinae	Atrypa, Gotatrypa, Oglupes? Atrypi-Atrypinae	Atrypa, Kyrtatrypa, Endrea, Atrypinae Atrypina-e	Atrypa, Kyrtatrypa, Atrypi-Atrypinae	Atrypa, Kyrtatrypa, Atrypinae Atrypinae	Atrypa, Kyrtatrypa, Atrypinae Atrypinae
	Waldron Clay member, Wayne Formation	Henryhouse Limestone, Hunton Group	Hunton (Haragan) Limestone (Yellow shale below limestone)	Lower Helderberg Group	Keyser Limestone	Keyser Limestone
	Silurian (Middle)	Silurian (Late)	Devonian (Early)	Devonian (Early)	Devonian (Early)	Devonian (Early)
	Wenlock	Ludlow	Lockhovian	Lockhovian	Lockhovian	Lockhovian
	Upper Clinton-Lockport (7-8 my)	Keyser (2 my)	Helderberg (6 my)	Helderberg (6 my)	Helderberg (6 my)	Helderberg (6 my)
	Northern and western margins of the Central Basin of Tennessee	Surface of Anadarko Basin	'Hunton Ramp' on the margin of the Oklahoma Aulacogen and Ouachita Trough	Northeast-trending folds in the Valley and Ridge Province of the central Appalachian Basin	On a carbonate ramp in the valley and Ridge province of the central Appalachian Basin	On a carbonate ramp in the valley and ridge province of the central Appalachian Basin
	Siliciclastics in the thick limestone sequence	Carbonate	Carbonate ramp	Carbonate	Carbonate	Carbonate

Table 2.1 continued.

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Nos.	1	2	3
Locality	Quebec, Canada	Western New York, USA	Indiana, USA
Sample size	18	54	43
Taxonomy	*Dihelictera* Atrypinae 7; *Joviatrypa* Atrypinae 18; *Gotatrypa* Atrypinae 111; *Atrypa* Atrypi-nae 2; *Oglupes?* Atrypinae 1	*Endrea* Atrypi-nae 3; *Gotatrypa* Atrypinae 54; *Atrypa* Atrypinae 41; *Oglupes?* Atrypina-e 8	*Atrypa* Atrypinae 43; Atrypina-e 18
Formation	Jupiter Formation	Lockport Formation	Niagara Group
Period	Silurian (Early)	Silurian (Middle)	Silurian (Middle)
Stage	Llandovery	Wenlock	Wenlock
EE Unit (duration)	Lower Clinton (4 my)	Upper Clinton-Lockport (7-8 my)	Upper Clinton-Lockport (7-8 my)
Basin	Hudson Bay lowlands (Cliff sections along the southern coast of the Anticosti Island)	Thrusts along ridge and valleys of central Appalachian Basin	Cincinnatian Arch between Illinois and Michigan Basin
Environment	Shallow water shelly packstones to middle-outer shelf micritic mudstones	Siliciclastics	Carbonates

Table 2.1 continued.

Table 2.1. Geographic locations for atrypid taxa with specific information on time interval and stage, EE subunit, and depositional environment.

MATERIALS

Paleogeography

During the Silurian-Devonian time, the Eastern American Realm was relatively isolated from other biogeographic realms and was indeed a realm of its own. Though these realms had established connections between them in this long interval of time during major transgressive events of the trangressive-regressive sea level cycles, much of the evolution of these atrypide lineages possibly occurred within the basin. Boucot (1975) and Boucot & Blodgett (2001) referred to the Eastern American Realm as a warm or hot unit with lower to mid latitudinal strata rich in evaporites, redbeds, carbonate rocks and reef developments. Thus, Silurian and Devonian of Eastern North America, representing high taxic diversity at all taxonomic levels, makes an important biogeographic realm for taxonomic investigation.

The Silurian was a period of marked provincialism for the brachiopod faunas (Boucot & Blodgett 2001) during which the Acadian orogeny occurred (Van der Pluijm *et al*. 1993) and shallow marine carbonate deposition was widespread (Berry & Boucot 1970). During the Llandovery (Early Silurian), sea levels were low and a comparatively cool climate was indicative from the less extensive reef deposits (Copper 2001b) and thus, evolution of some endemic atrypide genera were possibly restricted in their small environmental regimes. Climates warmed up and sea levels started rising during the Wenlock (Middle Silurian) as evidenced by the onset of reef growth (Copper 1973, 2004). Abundant patch reefs occurred in parts of Michigan, Ontario, Ohio and Indiana (Cumings & Shrock 1928; Lowenstam 1957). A shallow marine environmental setting is suggested by the presence of mid-platform carbonates in eastern North America during

this time. Thus, our samples (*Atrypa, Gotatrypa, Endrea*) from the Middle Silurian of Appalachian basin, Cincinnatian Arch and central Tennessee basins were somewhat similar during this time. Some of the Early Silurian genera (*Joviatrypa, Dihelictera*) remained restricted to the Hudson Bay lowlands. Some genera (*Atrypa, Gotatrypa*) in Anadarko basin of Oklahoma localities still persisted in the carbonate platforms during the Ludlow time. By the Pridoli time (Late Silurian), sea level dropped leading to evaporitic conditions in some basins and closure of many sea connections between basins, including between eastern North America and Europe. This provincialization continued during much of the Early Devonian (Copper 1973) of Eastern North America, which gave rise to some endemic genera (*Kyrtatrypa*) in the margins of Oklahoma aulacogen, central Appalachian basin (central-east New York, West Virginia and Maryland) and the eastern Tennessee Nashville Dome localities with continued persistence of the *Atrypa* lineage in these localities. During the Early Devonian and early Middle Devonian (Lockhovian-early Eifelian), sea level was low and most genera (*Atrypa, Kyrtatrypa*) from the Appalachian, Michigan, Iowa and Anadarko basins were most likely separated by geographic barriers (Findley, Kankakee and Cincinnatian Arches) which persisted through the Middle Devonian, thus, giving rise to new evolutionary lineages (*Pseudoatrypa, Spinatrypa*) in some early Eifelian localities (Ohio and central New York). All of these intracratonic arches served as barriers to shallow marine dispersal during the Devonian (Koch & Day 1995; Rode & Lieberman 2005). Later in the Middle Devonian (late Eifelian to early Givetian), sea levels had risen again and climates warmed up with widespread carbonate deposition in this region. This marked sea-level rise during this time possibly breached the Ozark dome, Wisconsin,

Findley, Kankakee, Cincinnatian Arches and Acadian Highlands of Eastern North America further facilitating mixing of faunas within all geographic localities in the Eastern American biogeographic realm. The late Givetian, or early Frasnian (Late Devonian) was thus, a marked period of cosmopolitanism when Appalachian sea lanes were connected all over again and thus similar genera (*Pseudoatrypa*) persisted across various geographic localities (Michigan Basin, Iowa and Missouri localities in Iowa Basin, northern Appalachian Basin and Cincinnatian Arch) during this time. At the end of the Frasnian time, black shales or disconformities were produced locally with sea levels continuing to rise. Eventually, the muddy bottom dwelling and stenohaline atrypides went extinct at the end of the Frasnian more likely due to ecological replacement of these faunas by other higher order organisms (Copper 1973). Thus, this varied biogeographic setting makes it all the more interesting to investigate the taxonomic composition in atrypides during the Silurian-Devonian time period in eastern North America.

Of the eighteen sampled geographic localities in this study, samples from Hudson Bay lowlands represent inner shelf environments, those from Appalachian (New York, Maryland, West Virginia) localities represent inner to middle shelf environments, Tennessee localities represent inner shelf environment with some derived clastics in the north, Michigan locality represents middle shelf environment, Cincinnatian Arch (Indiana) locality represents middle shelf environment, Ohio locality represent environments dominated by eastern derived clastics, Missouri locality represent inner shelf environments, Iowa locality represents inner shelf environments with presence of evaporite beds, and Oklahoma localities represent environments that ranged from inner to middle shelves (Day 1998).

Thus, for this study, geographic variation was examined in a few genera from the Middle Silurian, Early Devonian and Middle Devonian Eastern North American localities. The stratigraphic, lithologic and paleogeographic settings for the sampled atrypids from Silurian-Devonian of Eastern North America in this study are given in Table 2.1.

METHODS

Data Set

We tested morphological variation using a total of 1593 dorsal and ventral valves (Table 2.1) of well preserved atrypid brachiopods. Of those specimens, 1300 specimens were used to test morphological evolution within *Atrypa*, *Gotatrypa* and *Pseudoatrypa*; and 904 specimens were used to assess geographic variation within *Atrypa* from the Middle Silurian and Early Devonian localities, *Kyrtatrypa* from the Early Devonian localities, and *Pseudoatrypa* from the Middle Devonian localities in eastern North America. Specimens were identified to genus level and grouped within their respective subfamilies (Atrypinae=964, Variatrypinae=572, and Spinatrypinae=57). The geographic location and respective sample sizes are reported on the map in Figure 2.2 and in Table 2.1. All specimens were identified based on external morphological characters and ornamentation (Fig. 2.3). The material we used is housed in the Invertebrate Paleontology Collections of the American Museum of Natural History, Yale Peabody Museum, New York State Museum and Indiana University Paleontology Collections.

Figure 2.2: Sampled localities for atrypid brachiopods in eastern North America. Filled triangle in black indicates Silurian localities. Filled square in black indicates Devonian localities. Numbers 1–18 indicate eighteen different localities from where samples were collected. For detailed locality information see table 2.1.
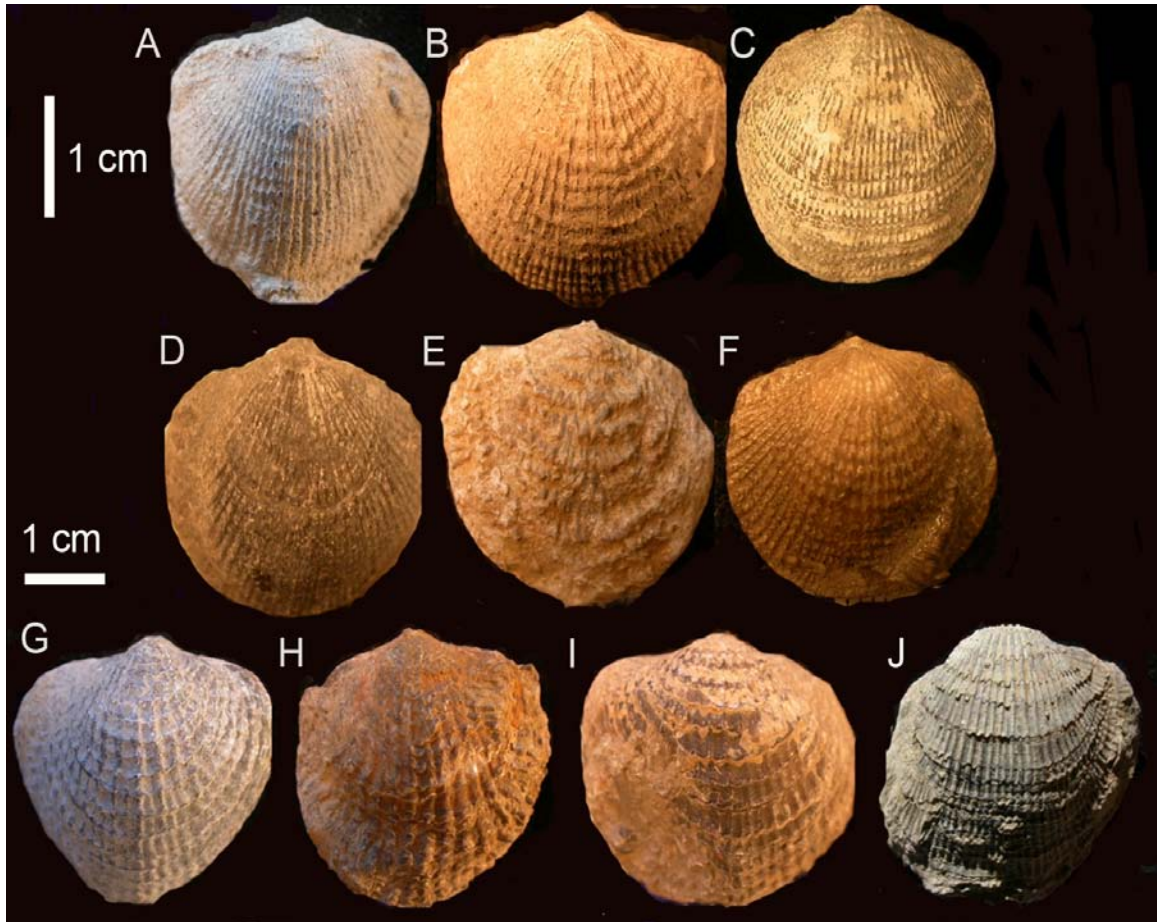
Figure 2.3: Dorsal views of genera from Atrypinae, Variatrypinae, and Spinatrypinae subfamilies: a) YPM 224604, *Atrypa*; b) YPM 224444, *Gotatrypa*; c) NYSM E2341 62-5, *Kyrtatrypa*; d) YPM 224240, *Joviatrypa*; e) YPM 224522, *Endrea*; f) YPM 224450, *Dihelictera*; g) YPM 225957, *Spinatrypa*; h) YPM 226001, *Spinatrypa*; i) YPM 226006, *Spinatrypa* (note the spinose imbricated lamellae in lower right area of the shell in h, and widened spaces between growth lamellae in i); j) YPM 225921, *Pseudoatrypa*. Note: the scale bar is the upper vertical line 1 cm for specimens a-f and the lower horizontal line 1 cm for specimens g-j.

Geometric morphometrics

Geometric morphometrics is the analysis of geometric landmark coordinate points on specific parts of an organism (Bookstein 1991; MacLeod 2002; Zelditch *et al*. 2004; Webster 2011). Morphometric analysis is based on the use of landmarks to capture shape (Rohlf and Marcus 1993); landmarks are points representing the same location on each specimen. In this study, we used 9 two-dimensional landmark points to capture the most meaningful shape differences (Fig. 2.4). Landmarks were digitized from image files using Thin Plate Spline Dig software (Rohlf 2004). When selecting landmarks for analyses, we chose points that not only characterized body shape accurately, but also represented some aspect of the inferred ecological niche. These landmarks represent discrete points that correspond among forms (*sensu* Bookstein 1991) and are appropriate for analyses attempting to capture shape changes or function. These points are at the intersection of articulation of both valves except landmarks 1 and 9 (1= umbo tip on dorsal valve on the plane of symmetry; 2 and 8=left and right posterior marginal tips of the hingeline; also region for food intake from inhalant currents; 3 and 7=mid shell tips along the widest region of the shell; 4 and 6=anterior commissure marginal ends; 5=anterior margin of commissure on the plane of symmetry; 9=beak tip on ventral valve on the plane of symmetry). The same eight landmarks (1-8 on dorsal valves and 2-9 on ventral valves) were used to compare both dorsal and ventral valves (Fig. 2.4).
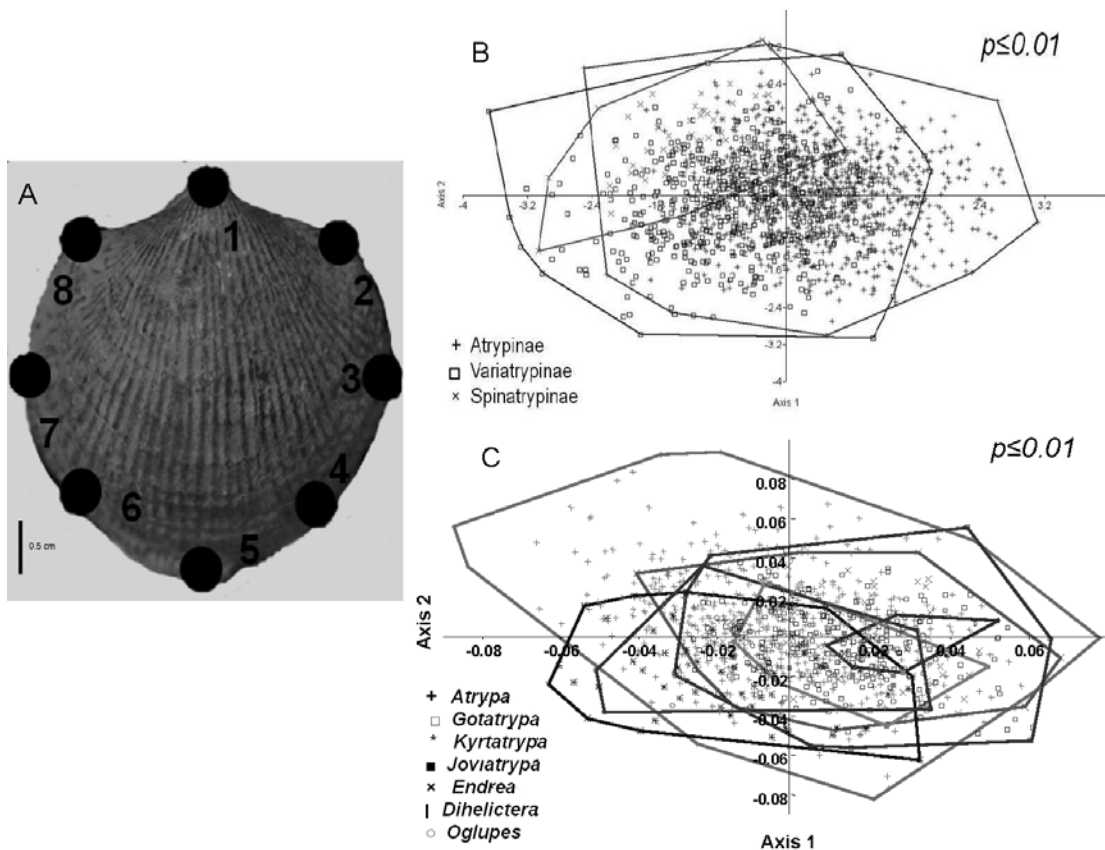
Figure 2.4: a) Location of eight landmarks on the pedicle valve of an atrypid sample for geometric morphometric analysis; b) CVA plot showing morphometric differences between Atrypinae, Variatrypinae, and Spinatrypinae subfamilies (*p<0.01*); c) CVA plot showing morphological differentiation between genera within Atrypinae subfamily (*p<0.01*). Note that *Rugosatrypa* and *Protatrypa* have been removed from analysis as these were only one member from each genus.

Procrustes analysis (Rohlf 1990; Rohlf and Slice 1990; Rohlf 1999; Slice 2001) was performed on original shape data, rotating, translating and scaling all landmarks to remove size effects while maintaining their geometric relationships. Pairwise Procrustes distances were calculated between the mean shapes of genera both within Atrypinae and between Atrypinae, Variatrypinae and Spinatrypinae (Fig. 2.5). Procrustes distances were also calculated between mean shell shapes within each genus from different time units and between mean shell shapes of different geographic localities in the Middle Silurian, Early and Middle Devonian. These distances were all measured in Procrustes units. Procrustes units are measures of shape difference in multivariate space, whose units are arbitrarily derived from the landmark data, but they are comparable across objects with the same number of landmarks (Rohlf 1990; Rohlf & Slice 1990). Principal component analysis was performed on the covariance matrix of Procrustes residuals to determine the morphological variation between the Atrypinae, Variatrypinae and Spinatrypinae and among genera within Atrypinae. Principal component analysis was also performed to determine within genus variation in time and space units.
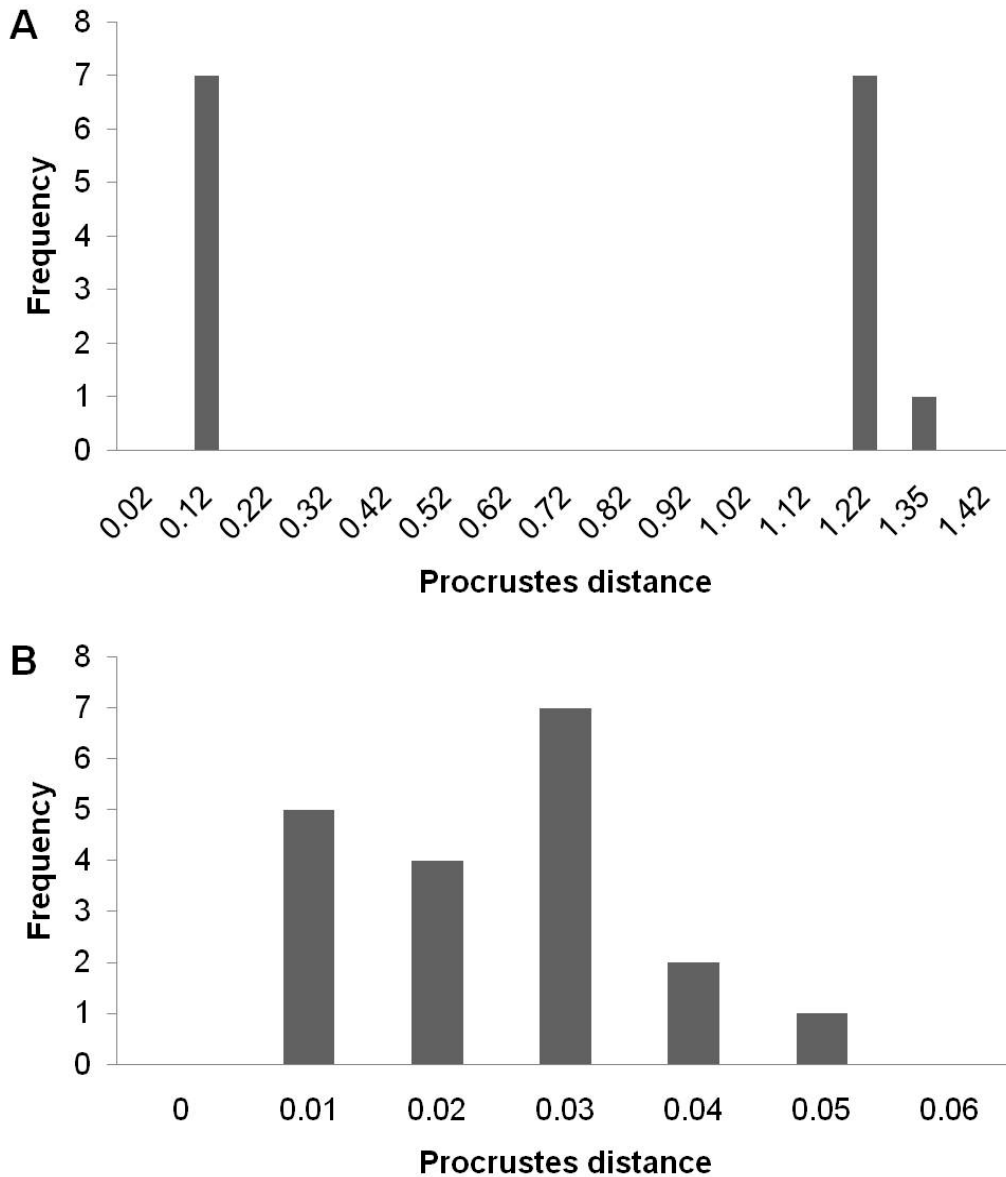
Figure 2.5: a) Histogram for Procrustes distance between genera from three subfamilies. All genera from Atrypinae nearly maintain a small distance with Variatrypinae (0.12) while a large distance with Spinatrypinae (1.22–1.25). A large procrustes distance (1.345) between Variatrypinae and Spinatrypinae; b) Small procrustes distance between genera within Atrypinae subfamily (0.01–0.05).

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Morphometric divergence

Evolutionary rate and mode in morphological divergence were 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 genera (Fig. 2.5) and divergence time was calculated using the patristic distance in millions of years on phylogenetic tree of Copper (1973) (Fig. 2.6), which is an estimate of the total time in millions of years that the two genera have been diverging independently since they last shared a common ancestor. The method uses the following equation to estimate rate and mode simultaneously,

$$D = rt \wedge a, \tag{1}$$

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 to 1, where 0 represents complete stabilizing selection (stasis), 0.5 represents perfect random divergence (Brownian motion) and 1 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. The data were bootstrapped 1000 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 (Lande 1976; Felsenstein 1988; Gingerich 1993; Roopnarine 2003; Hunt 2007).
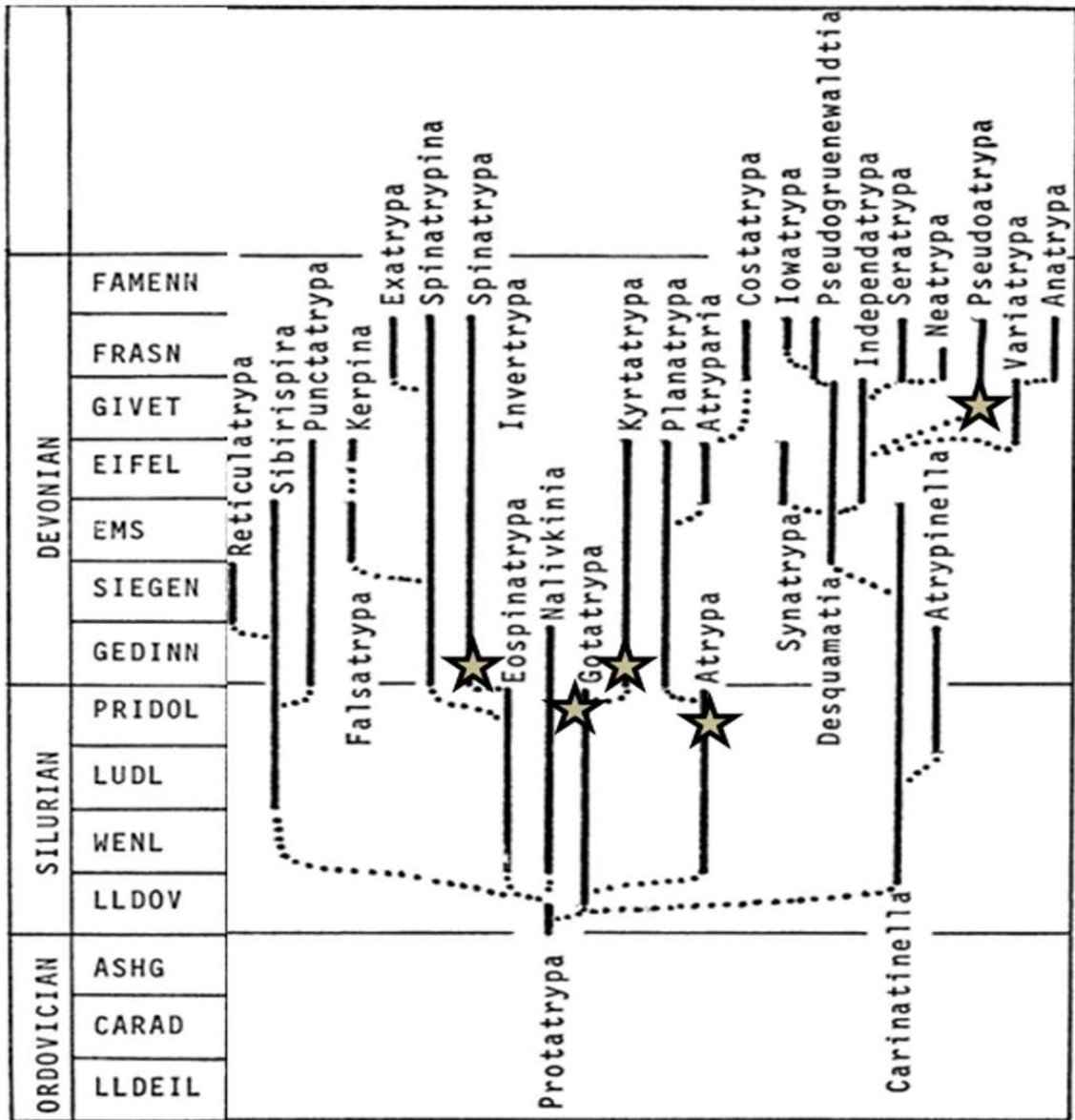
Figure 2.6: Copper's phylogenetic chart from his 1973 paper that was used to calculate evolutionary divergence times (m.y.) between atrypid genera. The five genera used in this study are marked in the figure as star symbols.

Lastly, a few atrypid genera (*Atrypa*, *Gotatrypa*, *Endrea*, *Pseudoatrypa*) were tested for morphological shape differences in specimens from shale and carbonate lithologic settings. For example, *Atrypa* specimens were tested for differences between Lower Devonian Linden Group of Tennessee (siliciclastic) and Keyser Limestone of Maryland (carbonate). Similar tests were performed for other genera.

Statistical analysis

We performed several statistical tests to assess morphological distinctness between atrypin genera, between atrypid subfamilies and to investigate the correctness of the phylogenetic relatedness between these genera. Multivariate analysis of variance (MANOVA) was performed to test for significant morphological shape difference a) between three subfamilies, b) between genera within one subfamily, c) within genera between time and space units, and d) within genera between shale and carbonate environments. Discriminant function analysis (DFA) was also performed to highlight the morphological differentiation within and between subfamilies. Pairwise distance between genera from within a subfamily was then compared with those between subfamilies. A bootstrap test was performed to draw statistical inference regarding the frequency (out of 1000 iterations) of randomly observing the difference in mean sample morphology between time units. The trend in mean shape through time was constructed for individual genera from Principal component scores. Euclidean cluster analysis (UPGMA) was performed to identify similarities in individual genera sampled from different time intervals, and from geographic intervals at a given time. Average Euclidean distances in time and space were also compared to assess whether the

temporal distances are similar to what one would expect from the replacement of one population by a geographically distinct one (Polly 2003).

RESULTS

Taxonomic differentiation

Based on qualitative phenotypic traits, the specimens were identified to genus level (Fig. 2.3, Table 2.1). Atrypin genera were distinguished from other genera by their characteristic closely spaced growth lamellae and loss of the pedicle opening. The most distinguishable phenotypic characters of the variatrypin genera included the long, tubular rib structure, pedicle opening and wide spacing between growth lamellae; while spinatrypin genera possessed spinose growth lamellae with highly imbricated tubular rib structure. Frills were not preserved in most atrypides, so it could not be utilized in distinguishing the atrypid members in various subfamilies. Our sample includes the following genera: Atrypinae **-** *Atrypa*, *Gotatrypa*, *Endrea*, *Joviatrypa*, *Kyrtatrypa, Dihelictera*, *Oglupes?*, *Protatrypa,* and *Rugosatrypa*; Variatrypinae - *Pseudoatrypa*, and *Desquamatia (Independatrypa)*; Spinatrypinae – *Spinatrypa*.   Note that *Protatrypa*, *Rugosatrypa* and *Desquamatia (Independatrypa)* were not included in the morphometric analysis because of their small sample sizes.

Principal component analysis showed significant overlap between the subfamilies and genera. MANOVA found significant differences between mean shell shape in the three subfamilies for dorsal valves (F= 30.7, df1=24, df2=3130, *p<0.01*) (Fig. 2.4b). MANOVA (post-hoc pairwise tests with Bonferroni correction) also found significant differences among mean shape in the following genera within Atrypinae for dorsal valves (F=4.389, df1=72, df2=5060, *p<0.01*) and ventral valves (F=3.628, df1=72, df2=5027,

	Atrypa	Dihelictera	Endrea	Gotatrypa	Joviatrypa	Kyrtatrypa	Oglupes
Atrypa	0	1	*0.000*	*0.000*	1	*0.000*	1
Dihelictera	0.262	0	1	1	1	0.647	1
Endrea	*0.000*	0.616	0	1	1	*0.000*	1
Gotatrypa	*0.000*	0.685	0.084	0	1	*0.000*	0.229
Joviatrypa	0.088	0.950	0.827	0.655	0	0.076	1
Kyrtatrypa	*0.000*	0.031	*0.000*	*0.000*	*0.004*	0	1
Oglupes	0.184	0.780	0.242	0.011	0.444	0.658	0

Table 2.2. 'p' values show distinctness between the genera within Atrypinae subfamily ($p<0.01$).

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p<0.01) (Figure 4c, Table 2.2): *Atrypa-Gotatrypa*, *Atrypa-Endrea*, *Atrypa-Kyrtatrypa*, *Endrea-Kyrtatrypa*, *Gotatrypa-Kyrtatrypa*, *Kyrtatrypa-Joviatrypa*, and *Oglupes?-Gotatrypa*. Significant differences in mean shape were also found between *Pseudoatrypa-Spinatrypa*, from Variatrypinae and Spinatrypinae respectively (*p<0.01*). On average, the mean shape difference between subfamilies ranged from 0.1 to 1.3 Procrustes units, and the difference between genera within the Atrypinae subfamily ranged from 0.01 – 0.05 Procrustes units (Fig. 2.5).

Maximum-likelihood estimation of the rate and mode of evolution given phylogeny of Copper (1973) (Fig. 2.6) yielded a rate of 0.012 ± 0.12 Procrustes units per million years and a mode coefficient *a* of 0.97 ± 0.15, indicating that diversifying selection has made the means of these atrypid genera more different than one would expect by random evolution (Fig. 2.7). In random evolution or Brownian motion, the direction and intensity of selection would have caused change in morphology over time but with changeable conditions (Polly 2004). A general observation suggests that morphometric shape differences between pairs of genera increases with phylogenetic distance with some discrepancy in *Pseudoatrypa* (Variatrypinae) (Table 2.3), which appears to be morphologically closer to the atrypins, more similar to what one would expect for genus-level than sub-family level differentiation.
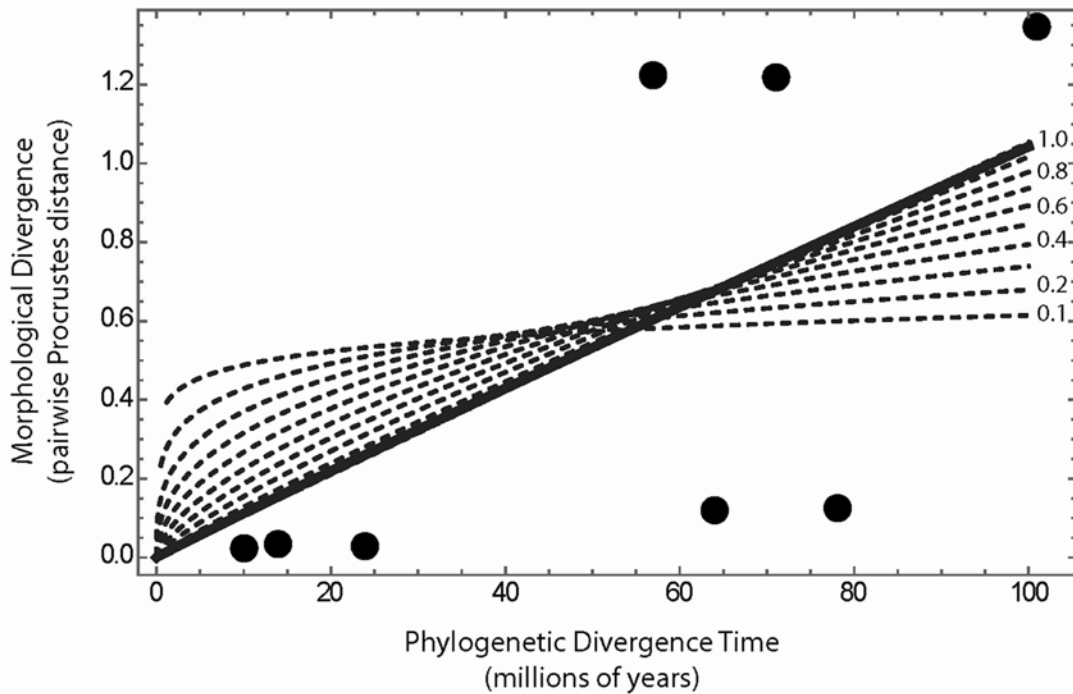
Figure 2.7: Graph showing morphometric divergence (pairwise Procrustes distances) and

phylogenetic divergence (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 these atrypids have experienced diversifying selection.

Atrypide Genera	Evolutionary Divergence Time (m.y.)	Morphological Distance (Procrustes units)
Atrypa-Gotatrypa	10	0.023
Atrypa-Kyrtatrypa	24	0.026
Gotatrypa-Kyrtatrypa	14	0.032
Atrypa-Pseudoatrypa	64	0.121
Gotatrypa-Pseudoatrypa	64	0.122
Kyrtatrypa-Pseudoatrypa	78	0.127
Atrypa-Spinatrypa	57	1.223
Gotatrypa-Spinatrypa	57	1.224
Kyrtatrypa-Spinatrypa	71	1.22
Pseudoatrypa-Spinatrypa	101	1.345

Table 2.3: Procrustes distances between genera within three subfamilies (Atrypinae: *Atrypa, Gotatrypa, Kyrtatrypa*, Variatrypinae: *Pseudoatrypa* and Spinatrypinae: *Spinatrypa*) and evolutionary time between genera calculated from Copper's (1973) phylogenetic chart.

Temporal variation

Principal component analysis of atrypid individuals shows morphological variation within each group with considerable morphological overlap among the six clustered groups of atrypids based on six coarse scale time units (Fig. 2.8). MANOVA found significant shape differences in dorsal valves for individual genus between different time horizons (*Atrypa*: F=4.09, df1=24, df2=1008, *p<0.01*; *Gotatrypa*: F=4.475, df1=24, df2=484, *p<0.01*; and *Pseudoatrypa*: F=10.43, df1= 12, df2=510, *p<0.01*), suggesting short term changes within a lineage. On average, the difference between Early, Middle and Late Silurian time units in *Gotatrypa* shell shape ranges from 1.1 to 1.8 Procrustes units, the difference between Middle Silurian, Late Silurian and Early Devonian time units in *Atrypa* shell shape ranged from 0.7 to 1.1 Procrustes units, and the difference between Middle and Late Devonian time units in *Pseudoatrypa* shell shape was 1.0 Procrustes units (Table 2.4). Overall, these distances were larger than those observed between genera within a subfamily and were comparable to those observed between genera from distinct subfamilies.
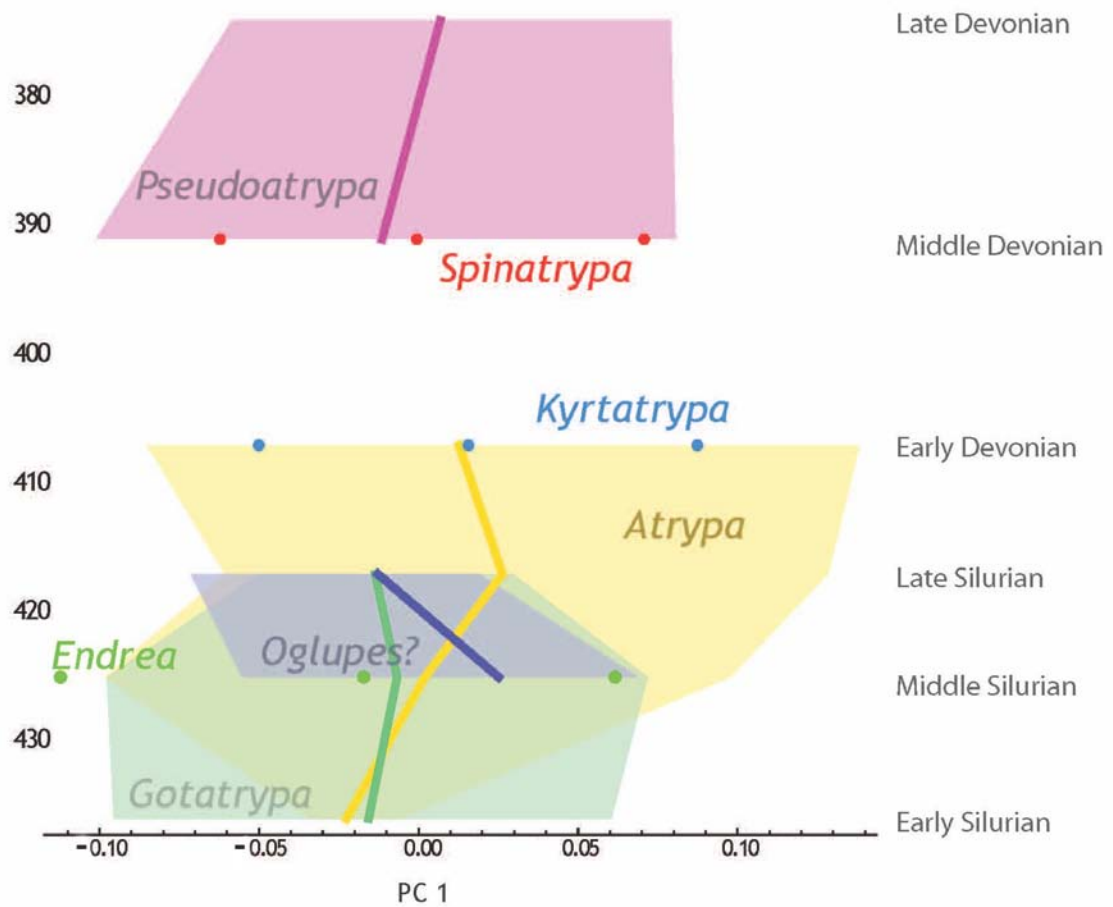
Figure 2.8: Morphological shape trend for dorsal valves with a minimum, mean and maximum PC scores for seven atrypid genera (*Atrypa*, *Gotatryp*a, *Endrea*, *Oglupes?*, *Kyrtatrypa*, *Pseudoatrypa*, *Spinatrypa*) distributed in the six time units (Early Silurian, Middle Silurian, Late Silurian, Early Devonian, Middle Devonian, Late Devonian).

Gotatrypa	Early Silurian	Middle Silurian	Late Silurian
Early Silurian	0	1.1262	1.7833
Middle Silurian	1.1262	0	1.6767
Late Silurian	1.7833	1.6767	0
Atrypa	Middle Silurian	Late Silurian	Early Devonian
Middle Silurian	0	1.0888	0.70276
Late Silurian	1.0888	0	0.86955
Early Devonian	0.70276	0.86955	0
Pseudoatrypa	Middle Devonian	Late Devonian	
Middle Devonian	0	0.992	
Late Devonian	0.992	0	

Table 2.4: Procrustes distance in *Atrypa*, *Gotatrypa*, and *Pseudoatrypa* between time units.

Spatial variation

Multivariate analysis of variance (MANOVA) indicated significant geographic shell shape differences among mean shape in individual genera (Middle Silurian *Atrypa*: F=10.48, df1=24, df2=214, *p<0.01*; Early Devonian *Atrypa*: F=4.18, df1=48, df2=1165, *p<0.01*; Early Devonian *Kyrtatrypa*: F=2.109, df1=36, df2=136.6, *p<0.01*; and Middle Devonian *Pseudoatrypa*: F=5.191, df1=48, df2=1481, *p<0.01*).

Dendograms illustrated in Figure 2.9 depict the similarity in mean valve shape between different geographic localities from the eastern North America region during the three time intervals sampled. Valve morphological shape in the Middle Silurian *Atrypa* shells shows a greater similarity between Tennessee and New York than either region with Indiana (Table 2.5, Fig. 2.9).
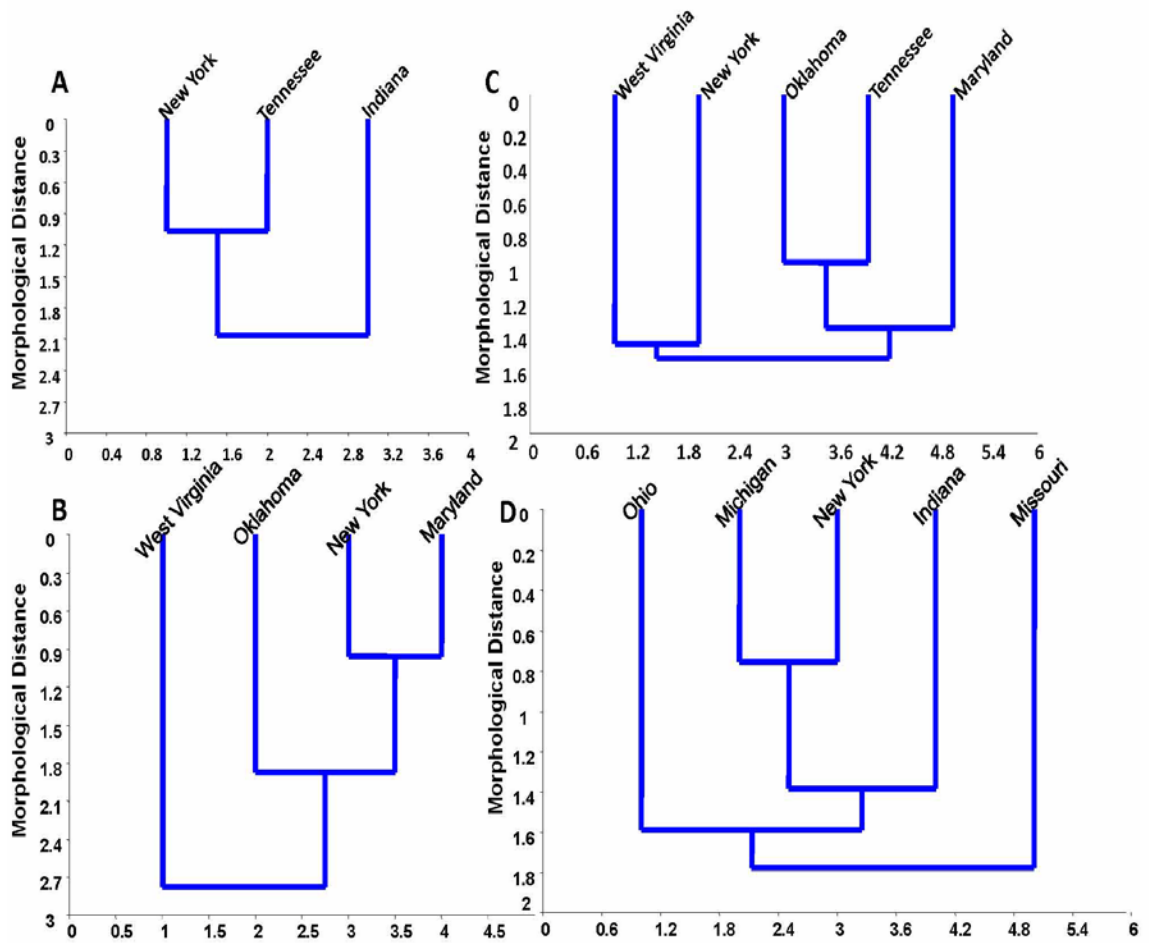
Figure 2.9: Morphological links for dorsal valves of atrypids in various eastern North America biogeographic locations – a) *Atrypa* in Middle Silurian; b) *Atrypa* in Early Devonian; c) *Kyrtatrypa* in Early Devonian; d) *Pseudoatrypa* in Middle Devonian.

Atrypa (Middle Silurian)	Indiana		New York	Tennessee	
Indiana	0		2.2978	1.7388	
New York	2.2978		0	1.78	
Tennessee	1.7388		1.78	0	

Atrypa (Early Devonian)	Maryland	New York	Oklahoma	Tennessee	West Virginia
Maryland	0	1.861	1.400	1.352	2.035
New York	1.861	0	1.274	1.520	1.817
Oklahoma	1.400	1.274	0	0.991	1.537
Tennessee	1.352	1.520	0.991	0	1.256
West Virginia	2.035	1.817	1.537	1.2561	0

Kyrtatrypa (Early Devonian)	Maryland	New York	Oklahoma	West Virginia	
Maryland	0	1.402	2.099	2.474	
New York	1.402	0	1.575	2.827	
Oklahoma	2.099	1.575	0	2.808	
West Virginia	2.474	2.827	2.808	0	

Pseudoatrypa (Middle Devonian)	Indiana	Michigan	Missouri	New York	Ohio
Indiana	0	1.463	2.274	1.656	1.755
Michigan	1.463	0	1.488	0.647	1.588
Missouri	2.274	1.488	0	1.366	2.063
New York	1.656	0.647	1.366	0	1.428
Ohio	1.755	1.588	2.063	1.428	0

Table 2.5: Procrustes distance in *Atrypa* from middle Silurian and early Devonian localities, *Kyrtatrypa* from early Devonian localities, and *Pseudoatrypa* from middle Devonian localities within the Eastern North American province.

During the Early Devonian, *Atrypa* shells from Tennessee and Oklahoma form a close cluster with less morphological distance to the Maryland sample than to the New York and West Virginia samples, which form a cluster with almost similar distance with Maryland (Table 2.5, Fig. 2.9). During the Early Devonian, *Kyrtatrypa* shells from Maryland and New York form a closer cluster with Oklahoma than with West Virginia (Table 2.5, Fig. 2.9). During the Middle Devonian, Missouri samples are more closely linked to those from Michigan and New York than with those from Indiana and Ohio (Table 2.5, Fig. 2.9). Thus, only the Early Devonian *Atrypa* shells shows some biogeographic signal.

On average, the shape difference between Middle Silurian *Atrypa* from different geographic regions ranged from 1.7 to 2.3 Procrustes units and the difference between *Atrypa* from different regions in the Early Devonian ranged from 1.0 to 2.0 Procrustes units. The shape difference between *Kyrtatrypa* from different regions in the Early Devonian ranged from 1.4 to 2.8 Procrustes units. The shape difference between *Pseudoatrypa* samples from different Middle Devonian geographic regions ranged from 0.6 to 2.3 Procrustes units. Overall, geographic variation within genera is greater than temporal variation.

Average Procrustes distance over time suggests that the magnitude of morphological shape change was similar in the dorsal and ventral valves (0.025 and 0.028 Procrustes units respectively). Likewise, average Procrustes distance was similar in the two valves between geographic regions (0.030 and 0.029 for Middle Silurian, 0.027 and 0.029 for Early Devonian, and 0.040 and 0.037 Procrustes units for Middle Devonian respectively). However, geographic variation was slightly greater than temporal variation

within these samples as suggested from the range of Procrustes distances within these units (time: 0.025–0.028; space: 0.027–0.040). Geographic variation (0.6–2.3) was also greater than temporal variation (0.7–1.8) when tested for individual genera (Tables 2.4–2.5).

Lastly, significant statistical differences were observed within each genus between shale and carbonate environments ($p < 0.01$).

DISCUSSION

Taxonomy

In this study, various atrypid genera from the Silurian-Devonian atrypid subfamilies were identified based on phenotypic characters other than shell shape. Overall, significant morphometric differences exist in the shells between subfamilies, thus supporting suggestions put forward by Copper (1973) that these groups are distinct. Significant morphometric differences also exist in the shells between genera within Atrypinae subfamily, also supporting his (Copper, 1973) suggestion that they are distinct. However, the differences in external shell morphology and shell shape among subfamilies and genera are small, further evidenced from smaller morphological distances, with considerable shape overlap at all levels. Thus, this suggests that genera would be difficult to distinguish based on shell shape alone. Overall, morphological distance is greater between subfamilies than between genera from the same subfamily, thereby supporting phylogenetic patterns and taxonomic differentiation proposed by Copper (1973).

Though morphometric differences are statistically significant between the shape means of subfamilies and genera, their overall morphological variation overlaps at all

levels. This study determined the morphological distances between genera from atrypid subfamilies under investigation and evaluated its relationship with the evolutionary divergence time intervals between genera worked out from the phylogenetic chart proposed by Copper in 1973. His (Copper, 1973) phylogeny was the most recent study performed in terms of understanding the generic relationships in atrypides, and so this was used in testing the taxonomy and phylogeny of a few atrypid genera of interest in terms of morphological shape.

The results of the analysis of evolutionary rate and mode indicate that diversifying selection has probably been acting on these atrypid genera, despite the very small morphological divergences among them (Fig. 2.7). Based on the principal component plots (Fig. 2.4), the large degree of morphometric overlap among genera might be interpreted to represent stasis, since none of the atrypid genera have unambiguously diverged from each other. However, the statistical definition of stasis, or stabilizing selection, is that less divergence has occurred than expected under a random-walk (Brownian motion) model of evolution given the amount of time since divergence and the degree of within-taxon variation (Bookstein 1987; Gingerich 1993; Roopnarine 2001). For these atrypid genera, the changes in mean shape are greater than expected given time since divergence and the amount of within-genus variation – the most likely estimate of a in Equation 1 given the data presented in Figure 7 is near 1.0 (dark line). Stasis would produce a pattern where the best fit would have a value near 0.0 for parameter a, which is decidedly not the case for these data, even when bootstrapped to account for the small sample size and seemingly outlying data points. The best interpretation of shape evolution in these genera given the data is that they were diversifying from one another,

but at a rate slow enough that they still overlapped considerably through the time period covered in our study. Our morphometric data are thus consistent with the divisions of taxonomy and the broad strokes of phylogenetic arrangement proposed by Copper (1973), but they indicate that divergences among these genera are very small compared to their within-genus variation, so much so that it is impossible to refer single individuals to a genus on the basis of their geometric shell shape alone. Overall, the scaling between morphological distance and phylogenetic interval generally supports his (Copper, 1973) phylogenetic arrangement.

Some general observations noted for a few genera that were included for the test of evolutionary rates and modes are also described. Morphological relatedness between *Pseudoatrypa* and other genera (*Atrypa, Kyrtatrypa, Gotatrypa*) from Atrypinae shows a discrepancy with the evolutionary divergence time proposed by Copper (1973). The lesser morphological shape distance between atrypin and variatrypin members retrieved from our analysis suggests the possibility of a generic level difference rather than one at the subfamily-level; however, it also confirms that these two subfamilies are closely related. Also, the greater phylogenetic distance between atrypin genera and *Pseudoatrypa* than between atrypin genera and *Spinatrypa* may raise doubts about their phylogenetic arrangement with respect to atrypin genera as retrieved from the phylogenetic chart proposed by Copper (1973). His (Copper 1973) distinctions were made on characters other than shell shape, such as morphology of the pedicle, rib structure and internal features, which may be more diagnostic than simple shell shape. Indeed, the differences in mean shell shape that we found are largely congruent with his (Copper 1973) divisions. In other words, shape analysis has partial bearing on classification, and without

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including other morphological characters into the morphometric analysis, it is challenging to firmly support the correctness of the phylogeny proposed by Copper (1973). Nevertheless, while the atrypid genera might not have been taxonomically oversplit, the large morphological overlap in shell shape raises questions about the level of distinction among the genera. Overall, though morphometric shell shape is a simple morphological measure, it involves multivariate phenotypic traits that can model complex parts of morphologies in genera, further capturing functional constraints among them, thus proving their usefulness in taxonomic studies (Webster & Zelditch 2009).

Temporal variation

Phenotypic traits have been studied in the paleontological fossil record, both qualitatively and quantitatively, in terms of long-term and short-term geologic intervals. No one has quantified morphological characters to study atrypids in long term intervals using geometric morphometrics. Our current understanding is that atrypids originated in the late Middle Ordovician (Llandeilo) and increased in generic diversity and abundance during the Early Silurian (Upper Llandovery to Wenlockian), after which they declined in diversity during the Late Silurian (Pridoli) through the Early Devonian (Lockhovian), followed by another peak in diversity during the Emsian-Givetian when many of these genera had worldwide distributions (Copper 2001). Thus, abundant and well preserved atrypids in the Silurian-Devonian geologic interval, comprise a great case study to test temporal change.

Our data include atrypid subfamilies and the genera within those subfamilies available for investigation from a 64 Myr (Silurian-Devonian) time period. Using geometric morphometrics, in studying temporal variation patterns, besides solving

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taxonomic and phylogenetic problems in Silurian-Devonian well preserved, abundant atrypids, is an entirely novel approach. While morphometric differences existed between atrypid subfamilies and genera and for genera between successive time intervals corresponding to the EE subunits (*p<0.01*; Figs. 2.4, 2.8; Table 2.2), considerable morphological overlap between lowermost and uppermost mean morphological shape occurrences is exhibited with short term changes within lineages in the intermediate time intervals (Fig. 2.8). Overall, smaller morphological distances between atrypids show that the three subfamilies, Atrypinae, Variatrypinae and Spinatrypinae did not differ much based on morphological shape. However, the statistically significant valve shape differences within these subfamilies over time (Fig. 2.4) could have been in response to their adapting to changing paleoenvironmental conditions prevailing in those time periods. On average, atrypids show smaller average morphological distances in time (0.025–0.028), which is representative of little or no morphological change, as expected in an EEU.

The small magnitude of morphological distance between subfamilies (0.12–1.35), although relatively greater than those between genera within Atrypinae (0.01–0.05), concurs with the current classification system in atrypides. Surprisingly, the morphological shape distances within *Atrypa*, *Gotatrypa* and *Pseudoatrypa* in time (0.7– 1.8) are similar or greater than those measured between subfamilies (Table 2.4). This suggests that this difference may be either due to differences in sample size (as the between-genera distances are based on several samples of the same family, whereas the distances through time are based on sub-samples of the same genus), or it may be due to numerous real short-term changes within the lineages, which get averaged out when

comparisons are made between genera. This observed pattern is consistent with stasis. This further suggests that within group variation was greater than between group variation.

Spatial variation

Morphological distances and range of these distances between geographic localities within *Atrypa* (Middle Silurian and Early Devonian), *Kyrtatrypa* (Early Devonian) and *Pseudoatrypa* (Middle Devonian) (0.6–2.8) are similar to greater than those observed for individual genus (*Atrypa, Gotatrypa and Pseudoatrypa*) in time (0.7–1.8) (Tables 2.4–2.5), thus, further confirming greater amount of within-group variation in atrypids. The distances for all these genera also tend to overlap, but the random clustering of geographic localities for each genus and all genera, do not provide a strong biogeographic signal. On average, the smaller average morphological distances in space units (0.027–0.040), suggest little or no morphological change in atrypids spatially.

Environmental effect

Atrypin, variatrypin and spinatrypin genera lived in broad depositional settings ranging from siliciclastics to carbonates to mixed siliciclastic-carbonate settings (Jodry 1957; Droste & Shaver 1975; Cuffey *et al*. 1995). For example, *Joviatrypa* preferred quiet, relatively deeper water, muddy substrate assemblage, *Dihelictera* are known to have been derived from a patch reef assemblage, and *Endrea* are derived from biostromal to reefal units (Copper 1995, 1997), while many smooth to tubular ribbed atrypids preferred high energy reefal settings (Copper 1973). *Spinatrypa* have been commonly found in high energy sandy environments (Leighton 2000), though they have also been accounted from low energy muddy environments (Copper 1973). Some of the atrypids of

the Genshaw Formation of Traverse Group lived in the full range of rough to quieter energy conditions (McIntosh & Schreiber 1971). Thus, there is a wide variation in preference of substrates and energy conditions for atrypid genera to thrive.

Atrypides expanded in diversity and abundance through Emsian to Givetian, and the expansion of reef growth both equatorially and latitudinally could explain their distribution along the shallow water (<100m deep) tropical shelf environments (Copper 2001a, b). Overall, atrypin genera preferred nearshore to slope habitats (Barnes & Zhang 2002; Copper 2001a, b), variatrypin genera preferred middle to outer platform habitats (Day 1995) and spinatrypins preferred outer platform to platform margin habitats (Leighton 2000).

While it is probable that the variation observed within individual atrypid genera in time and space suggests some short term changes and within group variation, it is also important to take into account the paleoenvironmental settings from which these genera were derived that may have caused this variation. Testing for preference of habitats, sedimentology, grain size, and lithology and their correlation with respective atrypid genera may provide a clue for the causes behind the morphological variation observed both within a genus and between the genera in time and space. However, this study mainly focuses on testing the taxonomy and phylogeny using geometric morphometrics, and thus the environmental parameters that may have caused this morphological shape change is the scope of a future study.

Results from one test performed were analysed to determine the morphological shape response to lithologic settings. The same genus (*Atrypa*, *Gotatrypa*, *Endrea*, *Pseudoatrypa*) tested for morphometric shape from shale and carbonate lithologic

settings show statistically significant results ($p<0.01$). However, the temporal patterns observed in genera from three pairs of distinct lithologic settings, Early Silurian packstones and mudstones and Middle Silurian carbonate-silicilastics, Early Silurian packstones and mudstones and Late Silurian carbonate-silicilastics, Middle Devonian carbonate-siliciclastic and Late Devonian carbonates show a slightly higher range of morphological distances (0.99–1.78 Procrustes units) as compared to those from three pairs of similar lithologic settings, Middle and Late Silurian carbonate-siliciclastics, Middle Silurian and Early Devonian carbonate-siliciclastics, and Late Silurian and Early Devonian carbonate-siliciclastics which show a relatively smaller range of morphological distances (0.70–1.09 Procrustes units). Overall, there appears to be no significant relationship between the temporal patterns and lithologic settings, as similar magnitudes (1.1 Procrustes units) of morphological distances result when both overlapping (Middle and Late Silurian carbonate-siliciclastics) and distinct (Early Silurian packstones to mudstones and Middle Silurian carbonate-siliciclastics) lithologic settings were compared in time. Thus, lithological distribution does not explain for the greater similarity in certain time intervals (Middle Silurian-Early Devonian: 0.70 Procrustes units, Late Silurian-Early Devonian: 0.87 Procrustes Units) than other intervals (Middle Silurian-Late Silurian: 1.09 Procrustes units). Similarly, spatial patterns and lithologic settings for genera from the Middle Silurian, Early and Late Devonian time periods exhibit no significant relationship. Magnitudes of morphological distances are similar for both overlapping and distinct lithologies in spatial units. In terms of biogeographic setting, only Early Devonian *Atrypa* genus shows biogeographic signal in that Tennessee and Oklahoma samples are closely linked with more resemblance to Maryland samples than

to New York and West Virginia samples. However biogeographically closely spaced Maryland and West Virginia, and Maryland and New York samples from Early Devonian show less similarity. Other genera from Middle Silurian, Early and Middle Devonian (*Atrypa, Kyrtatrypa. Pseudoatrypa*), show no biogeographic signal. For instance, the greater morphological distances between the Middle Devonian closely spaced Missouri and Indiana-Ohio samples as compared to smaller distances between the distantly spaced Missouri and West Virginia-New York samples, suggest that these derived morphological links cannot be explained by biogeographical setting. Neither can these discrepancies be explained by environmental parameters like lithologic settings. Thus, given that the relationship between change in morphological shape and change in other environmental parameters remain unravelled, the morphometric differences in shape observed within genera, between genera, and between subfamilies in time and space could be attributed to their adaptability to other changing environmental conditions or their differential life habits. An overall morphological shape overlap within these groups in the Silurian and Devonian time intervals suggests a close relationship among the genera and subfamilies.

Considerable mean morphological shape overlap between Lower Clinton and Genesee EESU (both relatively close to the P3 EEU boundaries), is indicative of similar climatic settings during this time, such as lowering of the sea level, and the onset of cold climate. However, it is noteworthy that these were different genera in the respective EESUs (*Atrypa*, *Gotatrypa* represent Lower Clinton and *Pseudoatrypa* represent Genesee) and that they still show considerable overlap, which was probably because they belonged to closely related subfamilies.

If the hypothesis of ecological locking (Morris 1995; Morris *et al*. 1995) within ecological evolutionary units is correct, then morphological stability is expected within these atrypids as these were sampled from the P3 EEU of the Phanerozoic rock record. Atrypides, most likely, maintained their evolutionary stability through ecological interactions within the unit and as there were no major extinction events within that period, the ecosystem must have remained stable throughout with the exception of minor extinction events that separated the EESUs within the P3 EEU. In this study, overall morphological shape overlap observed between atrypid genera in time, though new taxonomic entities replace each time unit, can be referred to as a case of loose stasis. However, individual genera show large amount of distances between time units and thus, evolutionary rates and modes of each genus in time need to be further investigated to confirm whether loose stasis was really the case.

Morphological evolutionary patterns tested in a few atrypid genera (*Atrypa*, *Gotatrypa*, *Pseudoatrypa*) suggest morphological change observed within each lineage is not dramatic as they show some change around the mean which get averaged out in time when compared to other generic pair distances, a pattern similar to stasis. In contrast, these short term changes may be a causal effect of ecophenotypic variation. A few atrypid genera (*Atrypa*, *Kyrtatrypa*, *Pseudoatrypa*) tested in space, also show variation within the same group in space units, and no strong biogeographic signal can be derived from the pattern of clustering observed in eastern North American geographic localities. Overall, atrypids are phenotypically plastic, and often distinguishing one genus from another may be very challenging based on morphological shape alone.

CONCLUSION

Morphological distances between subfamilies were greater than those between genera within a subfamily, thus suggesting the correct reference of these genera to their respective subfamilies. Evolutionary divergence times among genera retrieved from the phylogentic tree proposed by Copper (1973) are consistent with the pairwise distances calculated from our morphological shape data, which further supports the taxonomic arrangement and phylogenetic patterns reported in his (Copper 1973) research article. Evolutionary rate and mode indicate that diversifying selection has probably been acting on these atrypid genera at a very slow rate, despite the very small morphological divergences among them. However, some discrepancy arises, and so further evaluation of phylogenetic distances between atrypin genera with that of *Pseudoatrypa* and *Spinatrypa* as a test of relatedness is necessary. Moreover, the morphological shape distances between variatrypin and atrypin genera were so small that these are more like the generic level differences than subfamily level differences. Thus, these discrepancies needs to be further examined through a phylogenetic analysis using the combination of internal morphological features and quantified morphological shape.

Morphological shape analysis shows considerable overlap in Silurian–Devonian atrypid members within the P3 EEU, representing a case of loose stasis. Moreover, large morphological distances between time units within the same genus suggest the possibility of short term changes within a lineage being averaged out when compared with generic pair distances, representing a pattern similar to stasis. Results from several geometric morphometric techniques (including Procrustes analysis and principal component analysis) suggest a certain degree of morphological variability between subfamilies and

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genera in time and space, which can be attributed to changing paleoenvironmental conditions. Temporal change with some constraints within individual genus (*Atrypa*, *Gotatrypa* and *Pseudoatrypa*) and geographic variation within some genera (*Atrypa*, *Kyrtatrypa* and *Pseudoatrypa*) suggest within group variation was greater than between group variation. Geographic differentiation in morphological shape within atrypids appears to be greater than temporal variation.

Overall, morphological shape change pattern and morphometric divergence in atrypid genera is consistent with the phylogeny proposed by Copper in 1973. Thus, in the 64 myr time scale within the P3 EEU, atrypids in general reflect a high degree of morphological shape conservation in the Silurian-Devonian time interval, regardless of their distinct taxonomic entities.

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CHAPTER III

MORPHOLOGICAL EVOLUTION IN AN ATRYPID BRACHIOPOD LINEAGE

FROM THE MIDDLE DEVONIAN TRAVERSE GROUP OF MICHIGAN, USA: A

GEOMETRIC MORPHOMETRIC APPROACH

(in preparation for submission to *Paleobiology*: Bose, R., and Polly, P. D., 2011, Shape

evolution in a brachiopod species lineage (*Pseudoatrypa cf. lineata*) from the Middle

Devonian Traverse Group of Michigan, USA)

ABSTRACT

Geometric morphometrics were used to assess evolutionary mode and correlation with environmental factors in the shell morphology of an atrypid brachiopod species lineage. Seven landmark measurements were taken on the dorsal valve, ventral valve, anterior and posterior regions of over 1100 specimens of *Pseudoatrypa cf. lineata* taxon from the Middle Devonian Traverse Group of Michigan State to quantify shell shape. Specimens were partitioned by their occurrence in four stratigraphic horizons (Bell Shale, Ferron Point, Genshaw and Norway Point) from the Traverse Group of northeastern Michigan outcrop. Geometric morphometric and multivariate statistical analyses were performed to test patterns and processes of morphological shape change of species over 5 m.y. interval of time. Maximum-likelihood method was used to determine the evolutionary rate and mode in morphological divergence in this species over time.

Three hypotheses were tested regarding patterns of evolutionary change: (1) if the species conforms to a punctuated equilibrium model, there should be no significant differences between successive stratigraphic samples; (2) if the species evolved in a gradual, directional manner, then samples from successive stratigraphic units should be more similar than ones more separated in time; (3) if morphological shape was affected by change in environmental factors like water depth, etc. then we would expect a strong correlation between changes in such factors and changes in shell shape. MANOVA showed significant shape differences in mean shape between stratigraphic units ($p \leq 0.01$), but with considerable overlap in morphology. There was little change in the lower part of the section, but a large jump in morphology between the Genshaw Formation and the overlying Norway Point Formation at the top of the section. Maximum likelihood

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estimation suggests that morphological evolution was lightly constrained, but was not subject to strong stasis. Rates of evolutionary change were slow to moderate. Euclidean based cluster analysis demonstrated that samples from successive units were more similar than widely separated ones. Changes in water depth do not show any statistical correlation with changes in shell shape. However, shallow water depth samples were significantly different than medium depth samples.

Collectively, these results suggest that shell morphology did not change through the lower 61 meters, but made a sharp jump between the Genshaw and Norway Point formations. Erosional unconformities below Norway Point Formation coupled with environmental heterogeneity during this time interval, may have lead to provinciality in the Michigan Basin sections, thus resulting in greater morphological change. Thus, the change in the Norway Point samples could be interpreted as the origin of a new species, either from environmental selection pressure or by an immigration event. Comparison of Michigan Basin sections with the contemporary Appalachian Basin sections suggests that morphologies from the uppermost intervals in the Traverse Group show abrupt deviation from the lowermost intervals unlike the Hamilton Group where morphological overlap was prominent between lowermost and uppermost units. Thus, the morphological trend observed in the *P. cf. lineata* lineage in the Michigan Basin appears to be local in scope.

INTRODUCTION

The mode and rate of morphological change in lineages over geologic time has been a hotly debated topic in paleontology and biology over the last three decades. The punctuated equilibrium model (Eldredge and Gould, 1972; Gould and Eldredge, 1977; Stanley, 1979) has had a major impact on the study of Paleozoic faunas, and many studies have confirmed punctuated patterns of change in Paleozoic species. Lieberman et al. (1995) found a pattern of punctuated stasis in brachiopods from the Middle Devonian Hamilton Group of the Appalachian Basin. In this study, we examine contemporary brachiopods from the Traverse Group of the Michigan Basin to see whether the patterns found in the Appalachian Basin are regional or local in scope.

The paleontological record of the lower and middle Paleozoic Appalachian foreland basin demonstrates ecological and morphological stability on geological time scales (Brett and Baird, 1995). 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). Though studying the community stability patterns is beyond the scope of this study, it would be

interesting to examine whether similar morphological stability is exhibited in the Michigan Basin Traverse group setting.

Models of stasis and gradual change have previously been tested in Devonian taxa from the Appalachian Basin. Isaacson and Perry (1977) did not find any significant change in *Tropidoleptus carinatus*, an orthide brachiopod from the Givetian of the Hamilton Group from the lowest to its highest occurrence, spanning some 40 m.y. 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. Eldredge further tested the same fauna studied by Goldman and Mitchell (1990) using morphometrics and found almost no significant morphological change in this unit (Brett and Baird, 1995). Later workers (Lieberman et al., 1995) tested two common brachiopod species lineages using size measurements on the pedicle valves of 401 *Mediospirifer audaculus* and 614 *Athyris spiriferoides* from successive stratigraphic horizons in the Hamilton Group, a section which has a five million year duration. They found morphological overlap within these species between the lowermost and uppermost strata with some variations in the intervening samples of the Hamilton Group and concluded that the pattern of change was one of stasis. All of the Hamilton brachiopod species lineages that were studied showed stasis or, at most, minor evolutionary changes.

This study tests the hypothesis of stasis in the Michigan Basin, a biogeographically separate setting from the Appalachian Basin. These two basins are separate sub-provinces of Eastern North America, formerly a part of the eastern Laurentian paleocontinent. Michigan Basin is a large intracratonic basin of Eastern North

America situated south of the Canadian Shield, containing Paleozoic sedimentary rocks (Cambrian-Carboniferous) and a thin surface layer of Jurassic sediments at the center of the basin. The basin is centered in Michigan's Southern Peninsula including parts of Michigan's Northern Peninsula, northern and eastern edges of Wisconsin, northeastern Illinois, northern parts of Indiana and Ohio, and extreme western part of Ontario, Canada. The Appalachian Basin is a foreland basin situated southeast of the Michigan Basin, containing Paleozoic sedimentary rocks and extending from New York, Pennysylvania, eastern Ohio, West Virginia, western Maryland in the north to eastern Kentucky, western Virginia, eastern Tennessee, northwestern Georgia, and northeastern Alabama in the south. The Findlay–Algonquin Arch separates the intracratonic basin from the foreland basin, which were connected by shallow seas to varying degrees during the late Eifelian to Givetian interval (Bartholomew et al., 2007; Brett et al., 2010).

Based on biostratigraphic evidence and sequence stratigraphic analysis, the Traverse EE subunit correlates with the Hamilton EE subunit (Brett and Baird, 1995; Bartholomew, 2006; Brett et al., 2009; Brett et al., 2010). The Traverse fauna within the Middle Devonian of the Michigan Basin subprovince displays a high level of faunal and compositional persistence and thus is defined as the Traverse EE subunit (Bartholomew, 2006). The small-scale community stability of the Hamilton fauna within the Middle Devonian of the Appalachian Basin subprovince is defined as the Hamilton EE subunit (Brett and Baird, 1995). Thus, the morphological trends observed in this study of the Traverse Group can be compared to previously studied patterns in the contemporary Hamilton Group.

In this study, changes in morphological shape over time were assessed in the *Pseudoatrypa cf. lineata* lineage from a 5 m.y. long section of the Givetian in the Traverse Group. The 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 four richly fossiliferous formations in the Alpena and Presque Isle Counties of the northeastern outcrop of Michigan: Bell Shale, Ferron Point, Genshaw and Norway Point (Fig. 3.1). The stratigraphy and paleoenvironment of the Traverse Group have been the subject of many detailed studies (e.g., Ehlers and Kesling, 1970; Kesling, Segall and Sorensen, 1974; Wylie and Huntoon, 2003), allowing fossil specimens collected from the Traverse Group to be placed in a paleoenvironment setting. These data were used to evaluate the environmental context of these four samples, especially to determine whether changes in water depth are correlated with observed changes in the brachiopods (Wylie and Huntoon, 2003).
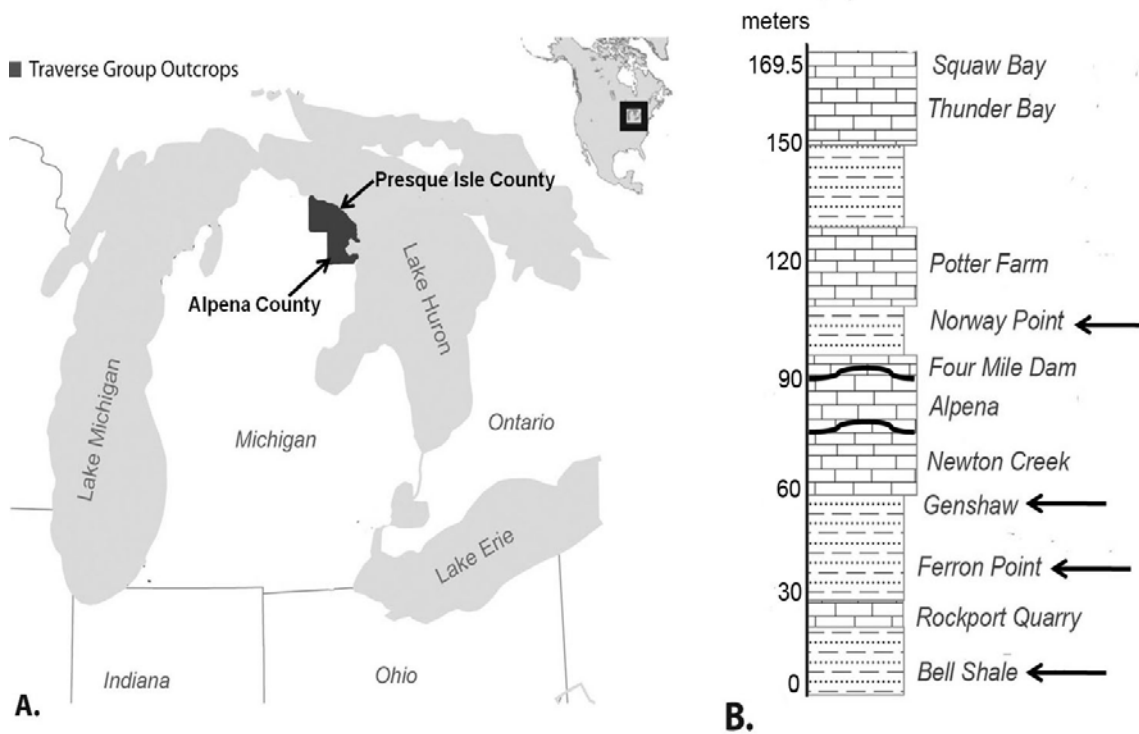
Figure 3.1: a) Map showing location of Michigan quarries of the Middle Devonian Traverse Group, namely the Alpena and Presque Isle Quarries, from which the samples used in this study were collected, b) Simplified stratigraphic section of the Traverse Group at Alpena Quarry showing the eleven stratigraphic intervals exposed on the northeastern outcrop of Michigan. Arrows show the four stratigraphic intervals from where the specimens used in this study were collected. Curved lines show the location of unconformities (after Wylie and Huntoon, 2003).

Hypotheses

(1) If the species lineage *P. cf. lineata* evolved according to the punctuated equilibrium model, in which morphological change occurs predominantly at speciation and otherwise remains static through the rest of its history, then we would expect no significant differences between samples of the species from successive stratigraphic units of the 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; and (3) if morphological shape was affected by change in environmental factors like water depth, etc. then we would expect a strong correlation between changes in such factors and changes in shell shape.

GEOLOGIC SETTING

The geologic setting used to test the proposed hypotheses in the *Pseudoatrypa cf. lineata* species lineage is the Traverse Group, a package of rocks from Michigan that spans roughly 6.0 m.y. of the Middle Devonian (Givetian) and the lower Upper Devonian (Frasnian). The appearance of rocks 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). Depending upon the frequency of these 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.

The Traverse strata comprise a nearly 169.5-meters 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 21.0 meters in thickness, consists of a basal crinoid rich lag and shales, which were deposited with water depth ranging from 25.0-44.0 meters. The Ferron Point, about 13.0 meters in thickness, consists of soft shales and limestones, deposited with water depth approximately 39.0 meters. The Genshaw Formation, 35.0 meters in thickness, consists of soft shales and argillaceous limestones, with water depth ranging from 25.0-39.0 meters. Norway Point Formation, 13.5 meters in thickness, consists of abundant shales and claystones, with limestones, deposited at approximately, <7.0 meters 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. Regarding water depths, these samples represent nearshore low energy environments from shallow to medium water depths (7.0-50.0 m) which may have been interrupted by occasional storms.

The patterns of shape change in these Michigan Basin samples will be compared with the patterns found by previous workers in the Appalachian Basin from the contemporary Hamilton Group units, which the Traverse units have been correlated based on sequence stratigraphic analysis (Brett et al., 2010). The Michigan Basin is separated from the Appalachian Basin by a basement arch system, the northeastern segment of which is called the Algonquin Arch, and the southwestern segment called the Findlay

Arch (Carlson, 1991). The Traverse Group lies on the flanks of the Michigan Basin and my study area is located in the northeastern part (Northern Peninsula) of the Michigan Basin in Alpena and Presque Isle Counties, Michigan. The Hamilton Group lies on the flanks of the Appalachian Basin, with samples studied in the past for stasis coming from western and central New York, northwestern part of Appalachian Basin.

Conodont-based correlation and sequence stratigraphic analysis of the Middle Devonian strata from the Michigan and Appalachian Basin shows that the Bell Shale is coeval with the upper Marcellus Shale, the Ferron Point and Genshaw formations are coeval with the Skaneateles, and the Norway Point Formation with the lower Windom Member of the Moscow Formation (Brett et al., 2009, 2010). Thus the Traverse Group and Hamilton Group fauna thrived during similar geologic time periods within the Hamilton EESU (Orr, 1971; Cooper and Dutro, 1982; Bartholomew and Brett, 2007; Brett et al., 2010).

MATERIALS AND METHODS

Bulk atrypid samples were first qualitatively examined and identified to species level based on external morphological characteristics. 1124 specimens of *P. cf. lineata* were 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. Most of the samples used in this study are from the Michigan Museum of Paleontology Collections, the rest are from the collections of Alex Bartholomew from State University of New York that have now been deposited at the Indiana University Paleontology Collections.

Seven landmark points were chosen for morphological analysis (Fig. 3.2, Table 3.1), each landmark point representing the same location on each specimen to capture the biologically most meaningful shape. These landmark points are geometrically homologous (*sensu* Bookstein, 1991), which is appropriate for analyses attempting to capture morphological shape changes (Rohlf and Marcus, 1993). 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, one side of anterior and posterior views) (Fig. 3.2). Data were captured using the TPSdig program for digitizing landmarks for geometric morphometrics. Procrustes analysis (Rohlf, 1990; Rohlf and Slice, 1990; Rohlf, 1999; 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). Principal component analysis was performed to determine the morphological variation between samples from the four stratigraphic intervals using the principal component axes 1 and 2. Multivariate analysis of variance (MANOVA) was performed to test for differences in mean shape between stratigraphic units.
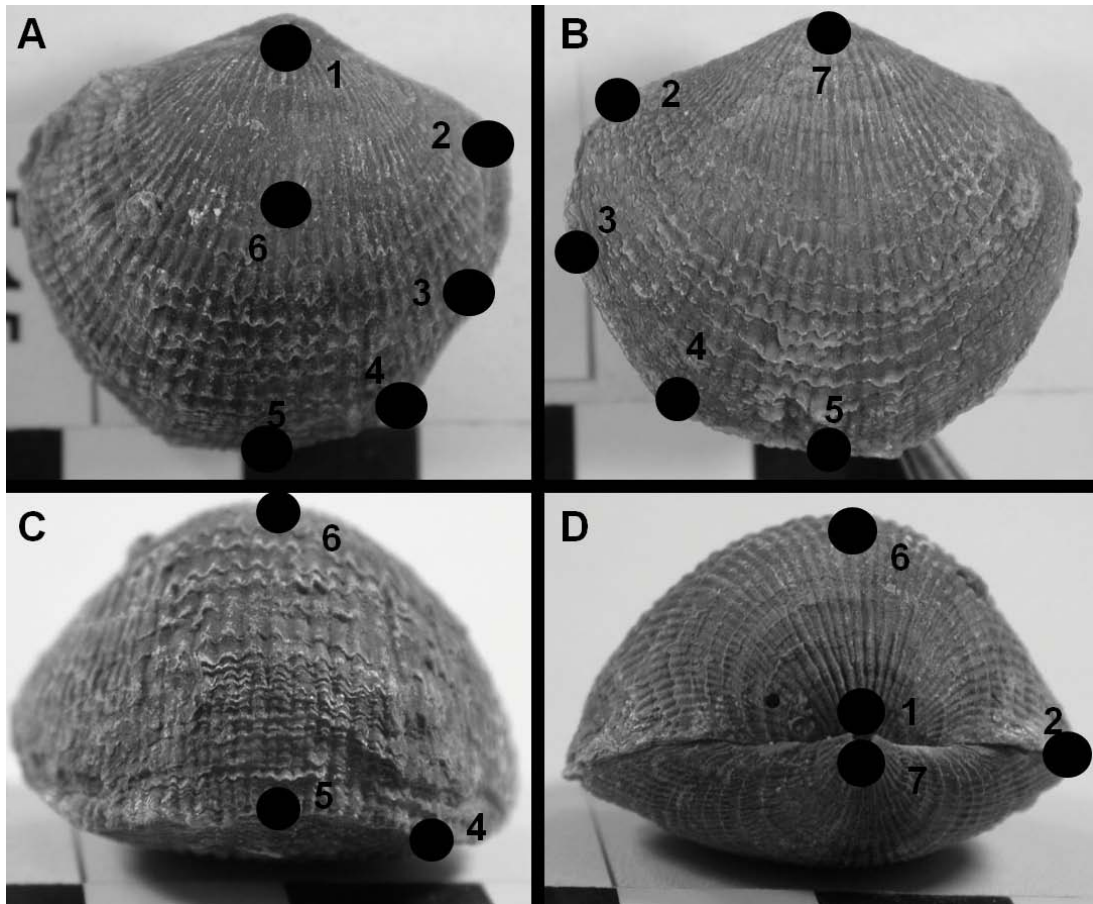
Figure 3.2: Seven landmark points on *Pseudoatrypa cf. lineata* shells with distribution of a) six landmark points on right side of dorsal valve, b) five landmark points on left side of ventral valve, c) three landmark points on right side of anterior margin area of shell, and d) four landmark points on right side of posterior hinge view of shell.

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

Table 3.1: Landmark points on the *Pseudoatrypa cf. lineata* shell representing geometric

positions that are biologically functional. D=dorsal and V=ventral.

Cluster analysis based on Euclidean distances was performed to illustrate shape similarities among the stratigraphic units. The relationship between change in mean shape and time was used to estimate the rate of change and evolutionary mode. Appropriate absolute age dates are not available for the individual stratigraphic units, so their durations and the intervals of time between them were estimated based on the total thickness and duration of the Traverse Group using the section thicknesses reported by Wylie and Huntoon (2003) (Tables 3.2-3.3).

Evolutionary rate and mode in morphological divergence was assessed using maximum-likelihood (Polly, 2004, 2008). This method estimates the mean per-step evolutionary rate and the degree of stabilizing or diversifying selection from the time-distance 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 taken from the estimates of the total time in millions of years between strata that the species have been diverging independently. The method uses the following equation to estimate rate and mode simultaneously,

$$D = rt \wedge a \qquad\qquad (1)$$

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. The data were bootstrapped 1000 times to generate standard errors for these

estimates. This method is derived directly from the work presented by Polly (2004, 2008) and is mathematically related to other methods in evolutionary genetics (Felsenstein, 1988; Gingerich, 1993; Hunt, 2007; Lande, 1976; Roopnarine, 2003).

Morphological shape in *Pseudoatrypa cf. lineata* individuals were tested against the shallow (Bell Shale=34.35m, Ferron Point=39.3m, Genshaw Fm=31.95m) and medium (Norway Point=1.9m) classes of water depth with respect to the water depth data from Wylie and Huntoon (2003). Multivariate analysis of variance (MANOVA) was performed between water depths and principal component scores of the shape co-ordinates of the valve morphology of individual shells from the Traverse Group strata to test for a statistical significant relationship between the two. In addition, the mean morphological PC scores for the samples were statistically correlated with water depth using linear regression analysis.

	Stratigraphic units	Thickness (meters)	Time (m.y.)
T **R** **A** **V** **E** **R** **S** **E** **G** **R** **O** **U** **P**	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**

Table 3.2: Eleven stratigraphic units of the Traverse Group showing their thickness in meters and their estimated duration in million years. Time in million years for each unit was estimated by the proportional thickness relative to the entire Traverse Group, which is estimated to have been deposited over 6 million years. *Pseudoatrypa cf. lineata* samples are from the stratigraphic units in bold.

	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

Table 3.3: Matrix showing time differences (million years) between the four stratigraphic units used for this study estimated from thicknesses of the strata.

RESULTS

The material from the Bell Shale, Ferron Point, Genshaw and Norway Point strata of the Traverse Group studied here was referred to *Pseudoatrypa cf. lineata* based on distinctive qualitative characters. Webster (1921) first described this taxon as *Atrypa lineata* from the late Givetian-early Frasnian Cedar Valley Group of Iowa, material which was later recognised as *Pseudoatrypa lineata* species of the new genus *Pseudoatrypa* (Copper, 1973; 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 (Day, 1992, 1996). *Pseudoatrypa* also occurs in the Traverse Group of the Michigan Basin (Stumm, 1951; Copper, 1973; Koch, 1978) and in the Silica Formation and equivalent rocks from northern Indiana (Wiedman, 1985). Copper (1973) described *Pseudoatrypa* as medium-sized with dorsiconvex to convexiplanar, subtriangular to subrectangular shaped shells. These shells were usually strongly uniplicate with subtubular to sublamellar rib structure, 2-3 mm spaced growth lamellae and either lacking frills or containing very short projecting frills. They have a small ventral beak with a foramen commonly expanding or enlarging into the umbo, with small interarea and tiny deltidial plates. Their internal features contain small dental cavities with delicate tooth and socket plates, disjunct jugal processes and spiralia with 8-12 whorls. *P. lineata* is described as medium- to large-sized (up to 37 mm in length, 35 mm in width) 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 towards 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 towards anterior and lateral margins in larger adults (20 mm length), short frills rarely preserved (Fenton and Fenton, 1935; Day and Copper, 1998). *P. lineata* ranged from late Givetian to early Frasnian of North America (Day and Copper, 1998).

Samples in this study from all the four stratigraphic intervals of the Givetian age Traverse Group agree well with the overall morphology of *P. lineata* and were referred to *Pseudoatrypa cf. lineata* for the purpose of this study. These samples are characterised by shell maximum width of 2.1-3.3 ± 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/1mm 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.

Principal component axis 1 (PC1) explained 36.0% of shape variation in dorsal valves, 28.8% of variation in ventral valves, 62.6% variation in anterior margin area, and 82.9% variation in posterior hinge area. PC2 explained 21.6% of variation in dorsal valves, 23.9% variation in ventral valves, 35.8% variation in anterior margin area, and 13.1% variation in posterior hinge area. There is some shape variation between stratigraphic intervals, mostly in the deviation of the Norway Point sample from the underlying stratigraphic horizons (Fig. 3.3).
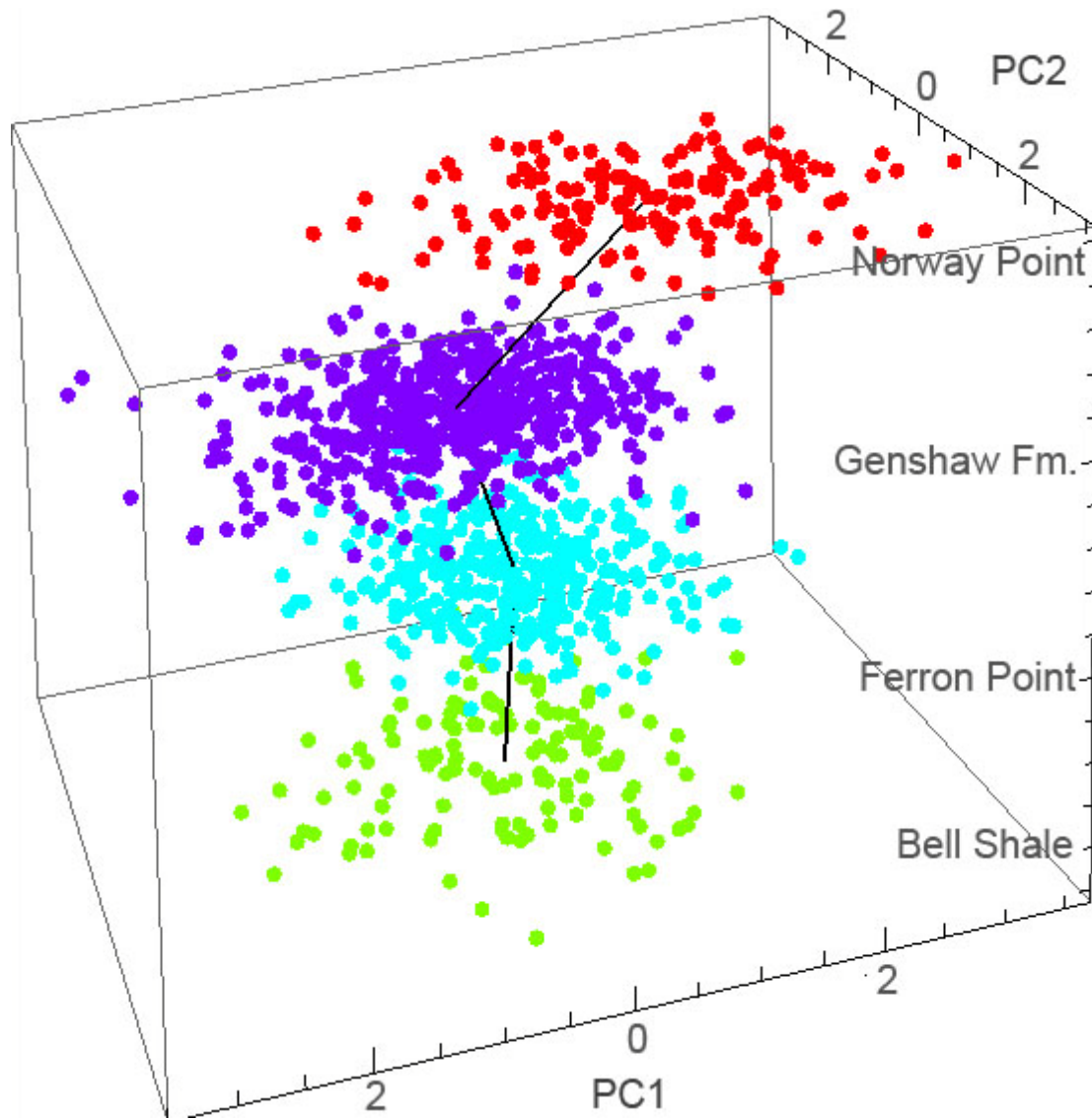
Figure 3.3: Morphological variation (PC1=36.02% and PC2=21.62%) and mean morphological shape trend in dorsal valves of *P. cf. lineata* along four Traverse Group formations (Bell Shale, Ferron Point, Genshaw Formation and Norway Point).

MANOVA indicated that differences in mean shape between stratigraphic intervals were significant for dorsal valves (F=39.58, df1=24 , df2=3336, *p<0.01*), ventral valves (F=29.65, df1=18, df2=3345, *p<0.01*), anterior (F=38.72, df1=6, df2=2228, *p<0.01*) and posterior (F=90.48, df1=12, df2=3339, *p<0.01*) (Table 3.4). The statistical significance of the MANOVA (post-hoc pairwise tests with Bonferroni correction) demonstrates that there is some real differentiation between the samples from the four stratigraphic horizons in shell shape (Table 3.4), 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. 3.3-3.4). However, abrupt deviation in mean morphological shape of the Norway Point samples (Fig. 3.3) gives some evidence of morphological change in this species later in time.
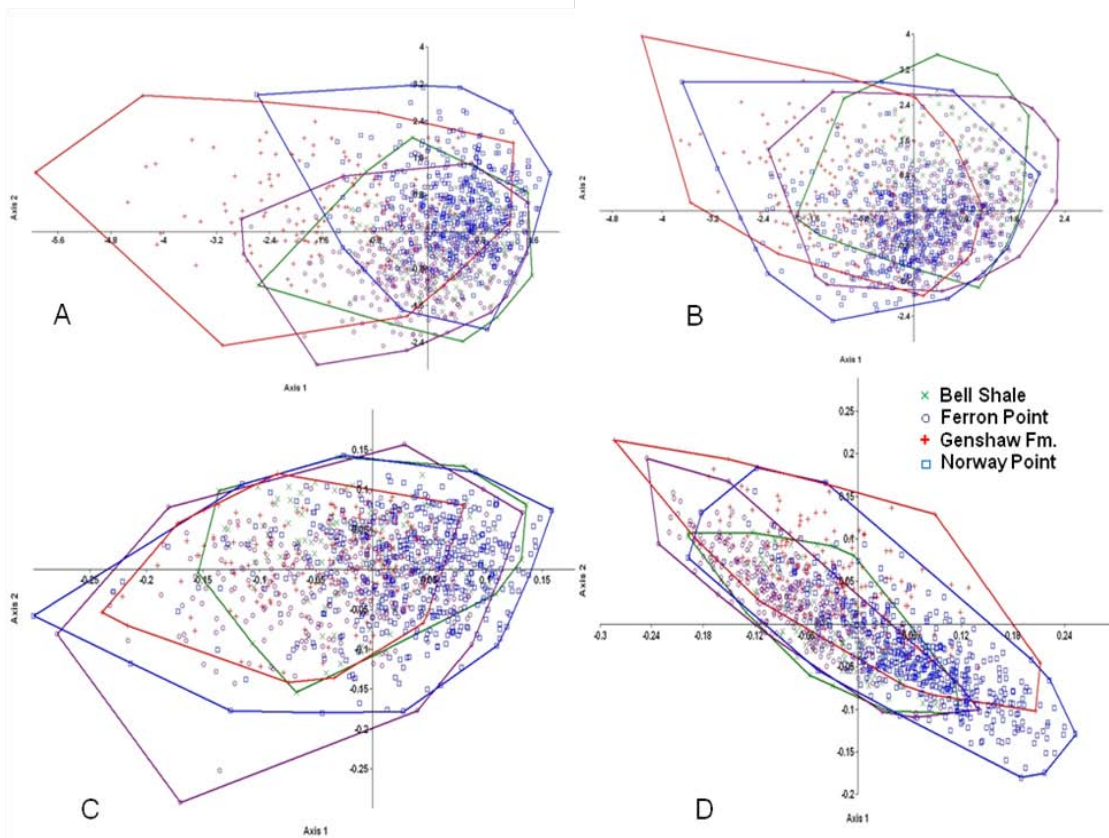
Figure 3.4: CVA plot showing morphometric differences between samples from Bell Shale, Ferron Point, Genshaw Formation and Norway Point (*p<0.01*) in a) dorsal valves, b) ventral valves, c) anterior margin area, and d) posterior hinge area.

DORSAL	Bell	Ferron	Genshaw	Norway
Bell	0	*0.000*	*0.000*	*0.000*
Ferron	*0.000*	0	*0.000*	*0.000*
Genshaw	*0.000*	*0.000*	0	*0.000*
Norway	*0.000*	*0.000*	*0.000*	0

VENTRAL	Bell	Ferron	Genshaw	Norway
Bell	0	*0.000*	*0.000*	*0.000*
Ferron	*0.000*	0	*0.000*	*0.000*
Genshaw	*0.000*	*0.000*	0	*0.000*
Norway	*0.000*	*0.000*	*0.000*	0

ANTERIOR	Bell	Ferron	Genshaw	Norway
Bell	0	*0.000*	*0.000*	*0.000*
Ferron	*0.000*	0	*0.000*	*0.001*
Genshaw	*0.000*	*0.000*	0	*0.000*
Norway	*0.001*	*0.001*	*0.000*	0

POSTERIOR	Bell	Ferron	Genshaw	Norway
Bell	0	*0.000*	*0.000*	*0.000*
Ferron	*0.000*	0	*0.000*	*0.000*
Genshaw	*0.000*	*0.000*	0	*0.000*
Norway	*0.000*	*0.000*	*0.000*	0

Table 3.4: 'p' values show distinctness between *Pseudoatrypa cf. lineata* samples from four stratigraphic units in time for a) dorsal valve, b) ventral valve, c) anterior marginal area, and d) posterior hinge area ($p<0.01$).

Morphological differences between stratigraphic samples ranged from 0.47-1.97 Procrustes units (the units of difference in the principal components space) (Table 3.5). Closely spaced samples had smaller morphological distances than did widely separated samples. Overall, the morphological distances concur with the stratigraphic succession (Fig. 3.5).

DORSAL	Bell	Ferron	Genshaw	Norway
Bell	0	0.943	1.112	1.970
Ferron	0.943	0	1.317	1.807
Genshaw	1.112	1.317	0	1.823
Norway	1.970	1.807	1.823	0

VENTRAL	Bell	Ferron	Genshaw	Norway
Bell	0	0.845	1.198	1.686
Ferron	0.845	0	0.794	1.701
Genshaw	1.198	0.794	0	1.295
Norway	1.686	1.701	1.295	0

ANTERIOR	Bell	Ferron	Genshaw	Norway
Bell	0	0.630	0.751	0.567
Ferron	0.630	0	0.855	0.472
Genshaw	0.751	0.855	0	1.139
Norway	0.567	0.472	1.139	0

POSTERIOR	Bell	Ferron	Genshaw	Norway
Bell	0	0.747	1.122	1.720
Ferron	0.747	0	1.549	1.804
Genshaw	1.122	1.549	0	1.646
Norway	1.720	1.804	1.646	0

Table 3.5: Procrustes pairwise distances for *Pseudoatrypa cf. lineata* lineage between stratigraphic units in time for a) dorsal valve, b) ventral valve, c) anterior marginal area, and d) posterior hinge area.
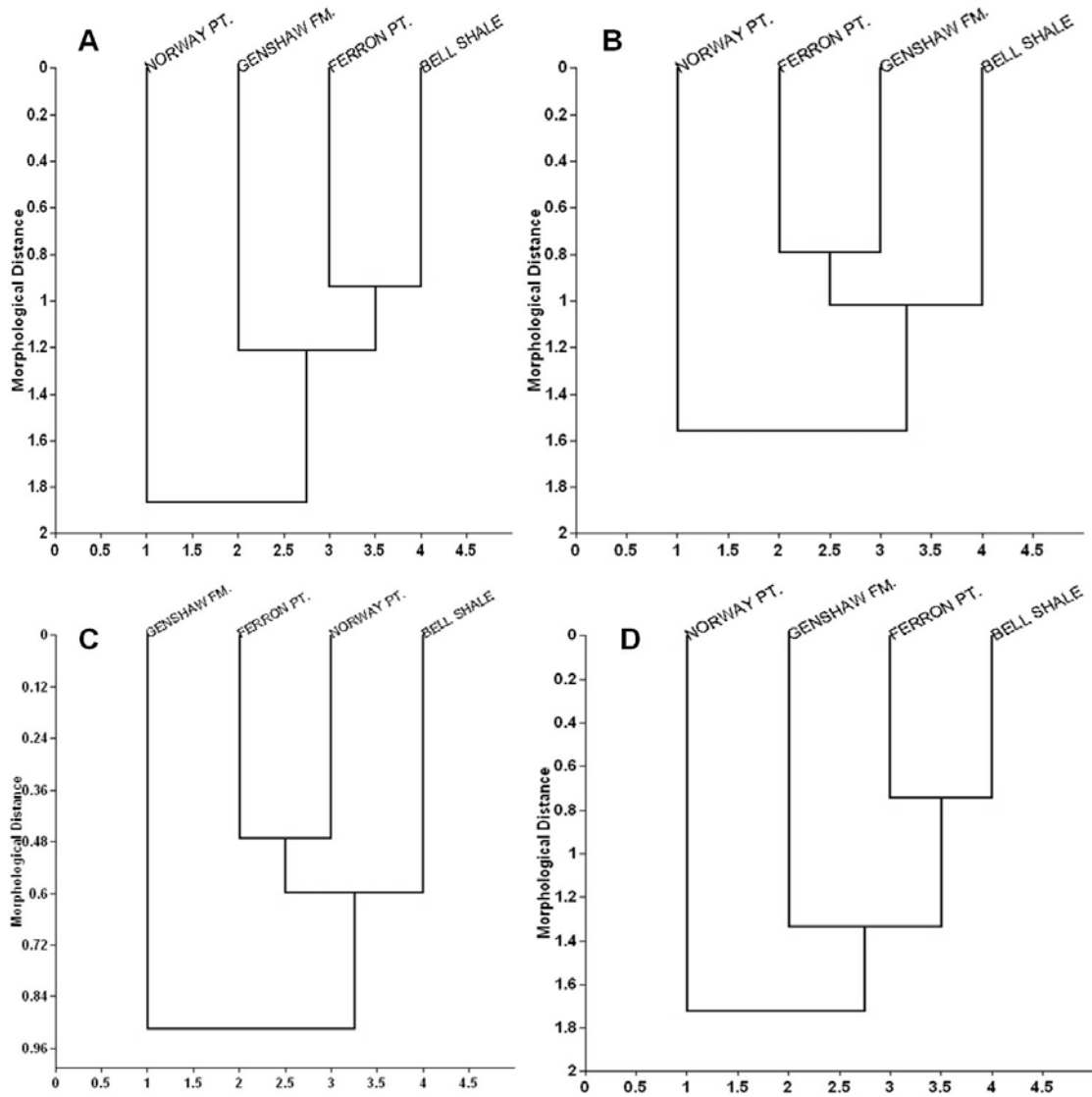
Figure 3.5: Morphological links for *P. cf. lineata* in Traverse group formations of a) dorsal valves, b) ventral valves, c) anterior margin area, and d) posterior hinge area.

Procrustes pairwise distances were plotted against time calculated from stratigraphic thicknesses and maximum likelihood used to estimate the rate and mode of evolution (Fig. 3.6). Perfectly random Brownian-motion change corresponds to a mode coefficient of 0.5, perfectly directional change to a coefficient of 1.0 and perfect stasis to a coefficient of 0.0. All four data sets had coefficients less than 0.5, indicating that morphological divergence was less than expected with random changes and suggesting that morphology is constrained in a stasis-like pattern. The anterior and posterior landmarks were nearest to stasis, and the ventral valve showed less constraint than the dorsal valve.

MANOVA and regression analysis shows significant difference between medium and shallow water depth brachiopod samples for dorsal valves ($p<<0.01$), ventral valves ($p<<0.01$), anterior ($p<<0.01$) and posterior ($p<<0.01$). Water depth correlated only weakly with the individual sample mean principal component scores of *P. cf. lineata* for dorsal valves (r=-0.14), ventral valves (r=0.33), anterior (-0.11) and posterior (-0.07).
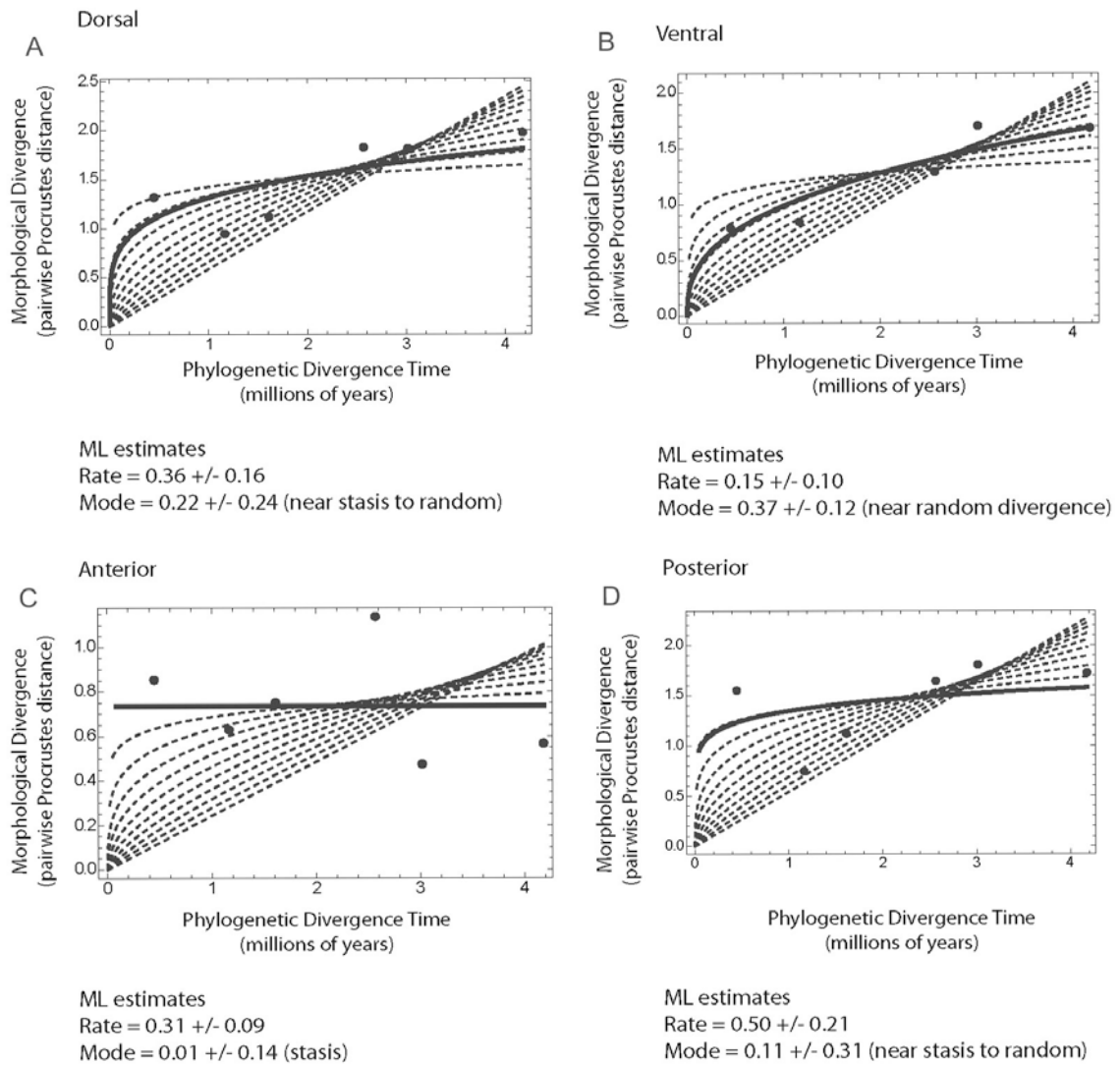
Figure 3.6: Graph showing morphometric divergence (pairwise Procrustes distances) and phylogenetic divergence time (millions of years). The series of dashed lines show the expected relationship between morphological and phylogenetic divergence time from strong stabilizing selection (0.1), through random 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.

DISCUSSION

Patterns of stasis and change and their possible causes

Despite the fact that there were significant differences in shell shape between Norway Point and the lower units of the Michigan Basin, the morphological variation within individual units is very large and there is considerable morphological overlap between units. The lower three units show considerable morphological overlap suggestive of stasis-like patterns while the upper Norway Point unit shows abrupt deviation, suggestive of a number of possible causes that are explained later in this section of study.

The morphology of *Pseudoatrypa cf. lineata* was very similar between the three lowermost successive strata (Bell Shale, Ferron Point, Genshaw Formation) with some difference between them and the uppermost strata (Norway Point) (Fig. 3.3). The morphometric shape distances concur with the stratigraphic arrangement of the Traverse Group in that the Euclidean cluster analysis shows that morphological samples from closely spaced strata are more similar than those that are widely spaced in time (Fig. 3.5), thus matching our expectation for gradual change. However, this morphological trend alone is insufficient evidence for determining whether the pattern of change is stasis or gradualism because morphological shape change may be oscillating around a mean. Stronger evidence is required that determines the rate and mode of evolution to test whether this shape change pattern is consistent with directional selection. The test based on morphological shape distances plotted against evolutionary divergence time suggests random to static evolution in this taxon with light constraint on morphologies (Fig. 3.6).

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Stabilizing selection is one of several processes thought to explain patterns of morphological stasis (Vrba and Eldredge, 1984; Maynard Smith et al. 1985; Lieberman et al. 1995; Polly, 2004). However, later investigation has shown that a stasis-like pattern may be produced when different selection pressures act on species belonging to different ecosystems, overall, producing no net morphological trend (Lieberman et al., 1994, 1995, 1996). Similarly, when morphological fitness is influenced by many independent environmental variables (e.g., nutrient availability, water depth, storm intensity), 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, narrow range of water depths, and similar sea level cycles 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 shows evidence of evolving 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 *Pseudoatrypa cf. lineata* evolved statically to randomly, with light constraint on morphologies. The major change in morphology in the upper stratigraphic interval is suggestive of a punctuated change after stable morphologies in the lower stratigraphic intervals.

Four possible causes for the change in the Norway Point sample can be evaluated in this study and are each discussed below. First, this abrupt change may be indicative of

either an evolutionary change or a species immigration event, with the Norway Point sample being a different species altogether. Second, this change may have been in response to a somewhat different paleoenvironmental setting represented by the Norway Point interval. Third, the samples from the upper Norway Point may belong to a different EE subunit succession, other than the Hamilton EE subunit. Fourth, the abrupt change may have resulted from a long time interval that elapsed between the lower Genshaw and the Norway Point intervals.

The Norway Point brachiopods were quantitatively different from the Bell Shale, Ferron Point and Genshaw samples. In addition, there seems to be a significant morphological difference between shallow and medium water depth brachiopods. Norway Point brachiopods that preferred shallow water settings were significantly different from those that preferred medium water depths. Thus, this change in morphology may be indicative of an evolutionary change where a new species may have arisen or an immigration event in which another species moved into the Michigan Basin from elsewhere.

Amongst other environmental parameters, water depth has been analysed in correspondence to each stratigraphic interval sampled and it seems that the overall range of water depth for these units varies from <7.0–50.0 meters. Notably, Norway Point is shallower (<7.0-8.0 meters) than the lower three formations. However, morphology was not correlated with water depth, suggesting that this factor did not cause the observed change. The eustatic curve, in contrast, depicts overall sea level rise punctuated by regression during the final subcycle of Cycle If (Johnson et al., 1985; Wylie and Huntoon, 2003), later interpreted as one of the major third order cycles. The Norway

Point sequence was deposited during what Brett *et al.* referred to as the Ih Cycle (Brett et al., 2010). However, sequence stratigraphic data shows that the strata analysed in the Traverse Group represents similar environments throughout with the lower Bell Shale representing the Eifelian-Givetian falling (FSST) sea level, Ferron Point and Genshaw representing Givetian-1 early highstand to falling sea levels (EHST, HST and FSST) and Norway Point representing Givetian-3 highstand (HST) (Brett et al., 2010). Based on detailed correlation records of high order sea level cycles across these basins in Eastern North America, Bell Shale falls within the lower Ie cycle (Johnson et al., 1985), while Ferron Point and Genshaw falls within the If cycle (Brett et al., 2010). Thus, sea level oscillations were probably not responsible for causing this morphological effect either. Lithologically, Norway Point and Ferron Point is made mostly of soft shales with few layers of claystones, Genshaw is made of limestones with shales in the basal part, and Bell Shale is completely shale with a few limestone lenses. Thus, with the samples coming from lithostratigraphically similar settings, it is less likely that this was causing the morphological change. It is however noteworthy, that Norway Point is separated by a thick sequence of limestones below with two erosional unconformities, which is further suggestive of sea level shallowing and the region been subaerially exposed between Genshaw and Norway Point intervals.

Interestingly, environments around the Michigan Basin during the Norway Point time interval show considerable heterogeneity (Dorr and Eschman, 1970; Ehlers and Kesling, 1970; Wylie and Huntoon, 2003) as compared to the other lower stratigraphic intervals (Detroit River Group, Dundee Limestone, lower Traverse formations like the Bell Shale and Alpena Limestone in the Michigan Basin) across different regions (upper,

northern, central lower and southeastern lower Peninsula) in the Michigan Basin based on the stratigraphic columns described in Dorr and Eschman (1970). This suggests provinciality in the Michigan Basin during Norway Point time, which raises the possibility that smaller populations may have been isolated in small different local environmental regimes facilitating the greater morphological change observed in the Norway Point sample. Perhaps there were some real environmental changes in the Norway Point interval of the Traverse Group section that may have resulted in environmental selection and thus, leading to evolutionary change.

Samples studied herein are from the Traverse Group of the Michigan Basin that correlates with the Hamilton ecological evolutionary subunit (Bartholomew, 2006; Brett et al., 2009, 2010), thus, a good case study to determine morphological patterns in a species lineage from an EESU. However, correlation of the Michigan Basin and Appalachian Basin sections show that Norway Point interval is contemporary with the lower Windom Member of the Moscow Formation of the Hamilton Group based on Orr (1971) and Brett and others (2010), thus ruling out the possibility for existence of a separate EESU during this time. Though this was the same EESU, the abrupt change observed in Norway Point samples could be due to an immigration event in the Traverse Group caused by transgression after major regression below the Norway Point. Thus, this further suggests that if the Norway Point samples were a different species, then there was a pulse of anagenetic change within *P. cf. lineata* giving rise to a new species (speciation) within the same Hamilton EESU or there was an abrupt change due to species immigration into the Michigan Basin from elsewhere during this time. In either way, the results from this study do not support the ecological locking hypothesis.

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Finally, stratigraphic gaps, unconformities and lack of sampling may result in deviation in morphologies. 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 except for two erosional unconformities observed between Genshaw and Norway Point intervals (Fig. 3.1, Table 3.3). However, the time elapsed in sampling between Genshaw and Norway Point samples, which equals 51.0 meters in stratigraphic thickness, is more than that observed between other successive strata (Bell Shale-Ferron Point: 25.0 meters, Ferron Point-Genshaw: 35.0 meters). Thus, a major change in the Norway Point interval is expected than in any other stratigraphic interval. But it is important to note that the time elapsed between Bell Shale and Genshaw samples, is also nearly 60.0 meters; however there is no substantial morphological difference observed between them as observed in the case of Genshaw and Norway Point samples. Thus, the abrupt deflection in morphological variation in Norway Point interval is simply not due to a long interval between Norway Point and other lower strata. In fact, this change may have to do with some kind of anagenetic change in morphological shape pattern as proposed in prior studies (Roopnarine et al., 1999) caused by isolation effects in the Michigan Basin subprovince or due to an immigration event during this time.

The relative importance of stasis has been studied for many fossil lineages (Hunt 2007, Gingerich 2001, Roopnarine 2001, Polly 2001). This study reports for morphological stasis within the *Pseudoatrypa cf. lineata* lineage in the lower Traverse Group units with the advent of abrupt change in the uppermost unit. Though significant

statistical differences exist between units, stasis-like patterns evidenced from morphological overlap between lower units followed by change in the uppermost unit samples and results from detailed evolutionary mode analysis, suggest constraint on morphologies in time followed by change. Overall, this is a pattern of punctuated stasis, where there is a long term stasis interrupted by a transitional population later in time. Cases of punctuated stasis have been commonly described from lower Devonian graptolite populations of central Nevada in prior studies (Springer and Murphy, 1994). Thus, the pattern observed in this study partially agrees with the punctuated equilibrium model.

Shell function and shape change

Morphological shape change in a species lineage may result from differential functional responses of the various part of the shell during its life. In this study, anterior and posterior morphologies showed more stability relative to other parts of the shell and ventral valves reflect more random change relative to dorsal valves, which showed stasis-like homogeneity. Of the different regions of the shell, the anterior margin was the most stable in contrast to posterior hinge, dorsal and ventral valve area. This anterior margin stability may be related to 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). Other parts reflecting less constraint may be related to their different episodes of life orientation where they were possibly exposed to environmental vagaries during various life stages.

The rate of change also varied with respect to different regions in the shell. The posterior region evolved faster than the dorsal valve, ventral valve and anterior of the

shell, while the dorsal valve and anterior evolved even faster than the ventral valve. The posterior region is the hinge of the brachiopods which provides stability to certain life orientations of the animals through pedicle attachment to the substrate during life. During pedicle attachment, immature atrypids are observed in a reclined orientation with their ventral valve facing up and young adults oriented in vertically upright or inclined position, with mature adults oriented with their dorsal valves facing up after pedicle atrophy (Fenton and Fenton, 1932; Alexander, 1984). Thus, before atrophy, the atrypid brachiopods are attached to the substrate by the pedicles that emerge from the pedicle foramen. The lateral extremes of the hinge line are the regions in which the shell filter feeds on suspended food particles from the host inhalant currents. Thus, this region of the shell must be constantly evolving a) to resist any strong currents that may be responsible for pedicle atrophy, b) in response to any encruster settlement on the host that may benefit from host feeding currents acting as parasites, and c) in response to any predatory attack. The dorsal valve and anterior are probably exposed for greater times during their life in their hydrodynamically stable life position (Fenton and Fenton, 1932), thus susceptible to evolving moderately to compensate for any environmental or ecological changes occurring during their life. The ventral valves of the atrypids are facing up during the immature stages of their life (Alexander, 1984) with probably less exposure time, thus susceptible to fewer episodes of selection, which further explains the slow rate of evolution of this region as compared to other regions in the shell.

Comparison of the Michigan Basin with the Appalachian Basin

The Traverse Group sections of the Michigan Basin are correlated with the Hamilton Group of western and central New York sections in the Appalachian Basin (Ehlers and

Kesling, 1970; Brett et al., 2009, 2010) (Fig. 3.7). Patterns of morphological shifts in *Pseudoatrypa cf. lineata* species lineage from this study have been compared with the patterns in the *Athyris* and *Mediospirifer* lineages documented by Lieberman et al. (1995). Lieberman et al. (1995) studied samples from various horizons of the Hamilton Group formations (Fig. 3.7). These include Chittenango and Cardiff members of the Upper Oatka Creek formation, Centerfield, Ledyard, Wanakah and Jaycox members of the Ludlowville Formation, and Tichenor-Kashong and Windom members of the Moscow Formation. The upper Oatka Creek Formation is coeval with the Bell Shale, middle-upper Skaneateles Formation with the Genshaw and Ferron Point, and the lower Windom member of the Moscow Formation with the Norway Point of the Traverse Group (Fig. 3.7). Lieberman et al. (1995) observed morphological overlap between the lowermost (Oatka Creek Formation) and uppermost (Moscow Formation) occurrences with some variations in the intervening samples. In this study, atrypid samples show stasis-like patterns in the lower stratigraphic intervals (Bell Shale, Ferron Point, Genshaw) in the Traverse Group with a large change recorded in the uppermost (Norway Point) interval. Samples have not been analysed from Traverse sections contemporary to the Ludlowville of the Hamilton. Thus, though sampling from intermediate units (Newton Creek and Alpena) of the Traverse may have been ideal for comparing the Michigan and Appalachian Basin sections for accounting morphological patterns in its entirety, the comparative analysis in this study still holds value as the sampled stratigraphic intervals from the Traverse correlates with the lower, upper and intermediate units of the sampled stratigraphic horizons in the Hamilton Group (Fig. 3.7). The middle stratigraphic horizons of the Hamilton Group has been previously accounted for

morphological oscillations with common reversals and considerable overlap in species occurrences in the lowermost and uppermost intervals, while within single biofacies (based on water depth and sedimentation rates), morphological change was evident (Lieberman et al., 1995; Brett et al., 2007). While detailed biofacies analysis has not been performed for the Traverse Group samples, temporal data from the Traverse stratigraphic horizons show that their intermediate horizons overlap in morphological patterns with the lowermost ones but deviate from the uppermost intervals. Thus, while these units of the Michigan and Appalachian Basin sections are contemporary, though being separate geographic subprovinces in the Eifelian-Givetian time with some interconnections by shallow seas, the morphological change observed in the lower peninsula of the Michigan Basin section could be interpreted as a local phenomenon in response to the changing environmental conditions. Small populations may have remained isolated in their own small ecological demes, thus resulting in evolution into new populations with increasing provinciality within the Basin later in time.

In the Hamilton Group, the Moscow Formation is separated from the lower stratigraphic intervals with a major disconformity, which is the most distinctive sequence boundary in the Hamilton Group which was further terminated with a widespread shallowing-upward succession. Similarly, the Norway Point was also separated by two major unconformities from the lower stratigraphic intervals further resulting in major regression after transgression. Thus, interestingly, both these formations represent the overall shallowest point in the entire succession. Thus, while similar eustatic sea level changes were noted within the Michigan and Appalachian Basin succession, it is interesting that Lieberman et al. (1995) found considerable morphological overlap

between the Norway Point equivalent Moscow Formation and Bell Shale equivalent upper Oatka Creek Formation of the Hamilton succession while this study found morphological dissimilarity between the Norway Point and Bell Shale formations of the Traverse succession.
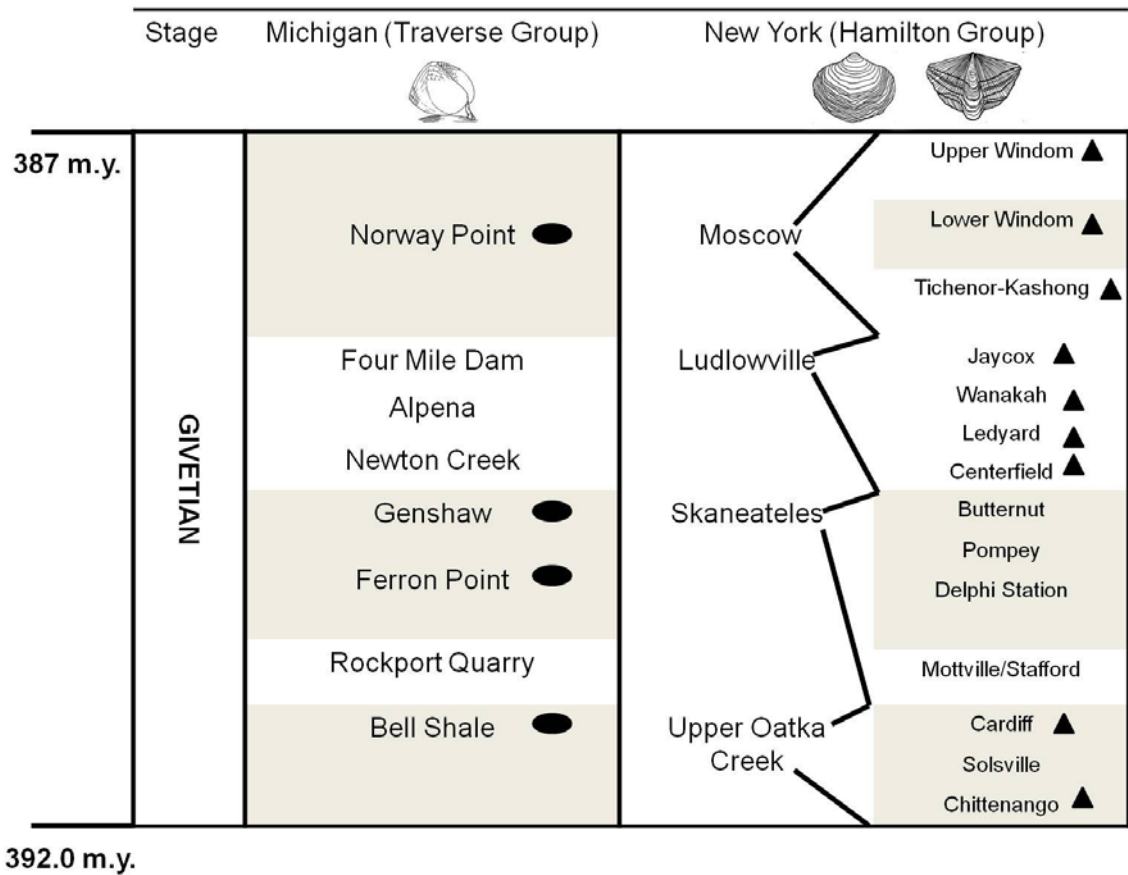
Figure 3.7: Chart showing stratigraphic correlation between Traverse Group and Hamilton Group units (modified after Brett et al., 2010). Shaded region shows the Traverse Group units sampled and their Hamilton Group equivalents. Solid triangles show the sampled horizons from Lieberman et al. (1995) study and solid circles show the sampled horizons for this study. Dark solid lines for each Hamilton Group formation marks all the members within. A brachiopod sketch of *Pseudoatrypa sp*. is inserted next to the Traverse Group column and brachiopod sketches of *Athyris sp.* and *Mediospirifer sp.* is inserted next to the Hamilton Group column.

CONCLUSION

Landmark measurements in atrypid species lineage *Pseudoatrypa cf. lineata* from the Middle Devonian Traverse Group of Michigan State has been analysed in this study to determine whether morphological shape trends in a lineage can be explained by punctuated equilibrium model. Geometric morphometric and multivariate statistical analyses reveals significant statistical differences in morphological shape between Traverse group stratigraphic units with considerable overlap in widespread morphologies over 5 m.y. interval of time. Notably, the samples from the uppermost strata, Norway Point formation show an abrupt morphological shift from the lower stratigraphic units, Bell Shale, Ferron Point, and Genshaw Formation. Thus, this suggests that morphological shape, a species diagnostic character, underwent very little change in the lower Traverse Group stratigraphic intervals with major change been reflected in the upper Norway Point formation. This change may be attributed to the environmental heterogeneity observed during this time with two erosional unconformities below the Norway Point, further leading to high provinciality in the Michigan Basin sections during the Norway Point time interval. Thus, two possible explanations for this abrupt change may be real evolutionary change due to environmental selection or new species immigration to the Michigan Basin from elsewhere.

The maximum-likelihood method suggests a slow to moderate rate of evolution with near stasis to random divergence mode of evolution in the *Pseudoatrypa cf. lineata* species lineage. However, different parts of the shell show light constraint on morphologies with anterior and posterior showing greater constraint than ventral valves and ventral valves even more constraint than dorsal valves. Evolutionary stasis in anterior

region may be a response of the stabilizing function of the frills in their anterior margin. Ventral valves evolving at a lesser magnitude than all other shape measurements (dorsal valves, posterior hinge area and anterior margin), is indicative of its being subject to fewer episodes of selection as a result of lower residence time in its ventral valve facing up early stage life orientation. While ventral valves show maximum fluctuation in their evolutionary mode, anterior margin is most stable in morphology over time.

Overall, the mean shape morphological trend suggests considerable morphological overlap between the lower 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 either anagenetic evolution may have caused the rise of new descendant populations or new species from elsewhere may have replaced the native species later in time.

Morphology of *Pseudoatrypa cf. lineata* weakly correlates with variation in water depth. Samples from shallow versus medium water depths show significant difference in morphology. This difference in morphology could be attributed to the difference in species, one of which preferred shallow water depths and others which preferred medium water depths. Since testing other environmental variables is beyond the scope of this study, it was challenging to infer if any abiotic or biotic factors were behind these mechanisms of evolutionary selection. Thus, this suggests, that the morphological shape trend can be explained only by stabilizing selection and/or by randomly fluctuating selection mechanisms trigerred by environmental changes occurring in that regime.

Thus, the results from this study appear to partially comply with the punctuated equilibrium model as morphological shape response in *Pseudoatrypa cf. lineata* in the

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Traverse Group of the Michigan Basin is more in agreement with near stabilizing to random selection processes with constraint on morphologies rather than directional selection process. Stasis is represented in the *P. cf. lineata* species with evidence of morphological change later in time. This abrupt change may be attributed to either an evolutionary change resulting from environmental selection or an immigration event that occurred during that time.

Comparison of Michigan Basin sections with the contemporary Appalachian Basin sections suggests that morphological trend observed in the *P. cf. lineata* lineage in the Michigan Basin appears to be local in scope in that the uppermost intervals of the Traverse Group show deflection from the lowermost intervals unlike overlap recorded in the Hamilton Group lowermost and uppermost intervals.

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CHAPTER IV

MORPHOLOGICAL SHAPE, EPISKELETOBIONT ANALYSIS, AND LIFE
ORIENTATION STUDY IN *PSEUDOATRYPA CF. LINEATA* (BRACHIOPODA)
FROM THE LOWER GENSHAW FORMATION OF THE MIDDLE DEVONIAN
TRAVERSE GROUP, MICHIGAN: A GEOMETRIC MORPHOMETRIC APPROACH

ABSTRACT

Atrypids examined from the lower Genshaw Formation of the Middle Devonian (early middle Givetian) Traverse Group include a large assemblage of *Pseudoatrypa* bearing a rich fauna of episkeletobionts. We identified two species of *Pseudoatrypa* – *Pseudoatrypa lineata* and *Pseudoatrypa* sp. A based on ornamentation and shell shape. Qualitative examination suggested that the former had fine-medium size ribbing, narrow hinge line, widened anterior, gentle to steep mid-anterior fold, a more domal shaped dorsal valve, and an inflated ventral valve in contrast to the coarse ribbing, widened hinge line, narrow anterior, gentle mid-anterior fold, arched shape dorsal valve, and flat ventral valve of the latter. Geometric morphometric analysis supported two statistically different shapes ($p<0.01$) for the two distinct species.

This study further examined these atrypids to investigate the influence of morphology on episkeletobiont settlement on the two *Pseudoatrypa* species. Among the 343 atrypid hosts examined, nearly 50% were encrusted by episkeletobionts. Common encrusters included microconchids, bryozoan sheets, and hederellids. Less common encrusters included auloporid corals, cornulitids, tabulate corals, *Ascodictyon*, craniid brachiopods, and fenestrate bryozoans. Hederellids, auloporid corals, cornulitids, and tabulate corals encrusted a few living *Pseudoatrypa* hosts, but determination of pre- or post-mortem encrustation by the majority of episkeletobionts is equivocal. In a very few cases, episkeletobionts crossed the commissure indicating the death of the host.

Some episkeletobionts, microconchids and the sheet bryozoans, were more common on *Pseudoatrypa lineata*, which exhibited more dorsal-ventral convexity than

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Pseudoatrypa sp. A. Perhaps, *P. lineata* may have provided a larger surface area for episkeletobiont settlement relative to *Pseudoatrypa* sp. A.

In both the host species, encrustation was heaviest on the convex dorsal valve. This suggests that most of the encrustation occurred in a reclining, dorsal-valve-up life orientation of both species, in which the convex dorsal valve was exposed in the water column and the ventral valve remained in contact with the substrate. However, life orientations of these atrypid species could not be confidently predicted simply from the location preferences of episkeletobionts alone, as the life orientation of the host would also have been a hydrodynamically stable orientation of the articulated shell after death.

Most episkeletobionts encrusted the posterior region of both dorsal and ventral valves of the two species, which suggests that the inflated areas of these valves, when exposed, favored the settlement of most episkeletobiont larvae.

INTRODUCTION

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 Genshaw Formation (Kelly and Wendell Smith, 1947; Koch, 1978). Here we focus on material from the lower Genshaw Formation to: 1) analyze morphological shape patterns in two *Pseudoatrypa* species, and, 2) investigate episkeletobiont interactions with these species to determine how the distinct morphological shapes of the two species may have influenced their settlement.

Pseudoatrypa* is frequently encountered in Devonian Midcontinent basins. Webster (1921) first described the taxon as *Atrypa devoniana* from the late Frasnian Independence Shale of Iowa; his specimens were later designated as the type species of the new genus *Pseudoatrypa* (Copper, 1973; Day and Copper, 1998). *Pseudoatrypa* also occurs in the Traverse Group of the Michigan Basin (Stumm, 1951; Copper, 1973; Koch, 1978) and in the Silica Formation of Ohio and equivalent rocks from northern Indiana (Wiedman, 1985). Webster (1921) described the species *Atrypa lineata* from the late Middle Devonian (late Givetian) upper Osage Springs Member of the Lithograph City Formation of the Upper Cedar Valley Group of Iowa, which was later included in *Pseudoatrypa* by Day and Copper (1998). Fenton and Fenton (1935) described a subspecies and growth variant forms of this species from the late Givetian Cedar Valley of Illinois. Herein we test both qualitatively and quantitatively whether distinct species exist within *Pseudoatrypa* from the Lower Genshaw Formation of Michigan, and whether these external morphology influences episkeletobiont assemblages.

Episkeletobionts are organisms that adhere to, or encrust, the surface of a shell (Taylor and Wilson, 2002). Episkeletobionts are useful as ecological and life status indicators of their hosts—whether the host was living at the time of encrustation or was dead (Watkins, 1981; Anderson and Megivern, 1982; Brezinski, 1984; Gibson, 1992; Lescinsky, 1995; Sandy, 1996; Sumrall, 2000; Morris and Felton, 2003; Schneider, 2003, 2009a; Zhan and Vinn, 2007; Rodrigues et al., 2008). Episkeletobionts have been used to infer the life orientation of brachiopods (Rudwick, 1962; Hurst, 1974; Pitrat and Rogers, 1978; Kesling et al., 1980; Spjeldnaes, 1984; Lescinsky, 1995), the preferred orientation of host water currents (e.g., Kesling et al., 1980), potential camouflage for hosts (Schneider, 2003, 2009a), the attracting or antifouling nature of ornamentation (Richards and Shabica, 1969; Richards, 1972; Carrera, 2000; Schneider, 2003, 2009a; Schneider and Leighton, 2007), and the function of the valve punctae (Thayer, 1974; Curry, 1983; Bordeaux and Brett, 1990). Brachiopod hosts are useful for investigating host influences on episkeletobiont preferences such as shell texture (Schneider and Webb, 2004; Rodland et al., 2004; Schneider and Leighton, 2007), size of host (Ager, 1961; Kesling et al., 1980), and antifouling strategies (Schneider and Leighton, 2007). Although other Paleozoic marine organisms were frequently encrusted, brachiopods remain one of the best understood hosts for Paleozoic episkeletobionts.

In the present study, the settlement of a live episkeletobiont during the life of the host is called a live–live association (pre-mortem encrustation) and the settlement of a live encruster on a dead host is called a live-dead association (post-mortem encrustation). Taylor and Wilson (2003) provided the following criteria for distinguishing between pre- and post-mortem associations: (a) If the episkeletobiont fossil overgrows (crosses) the

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commissural margin, or if there is evidence of internal valve encrustation, then the brachiopod host was dead when the organism overgrew the commissure - this is evidence of a live-dead association; (b) if the episkeletobiont and the host both have a similar degree of preservation, and if there is evidence of scars representing the repair of damage inflicted by episkeletobionts, then the brachiopod host was alive during encrustation - this is evidence of live-live association; and (c) if certain episkeletobionts repeatedly encrust specific locations on host shells, e.g., if branching fossils, like auloporid corals or hederellids, branch towards or are aligned parallel to the commissure or if solitary organisms, such as cornulitids, grow with their apertures pointing towards the commissure, then hosts and their episkeletobionts experienced live-live associations. In other cases, there is no way to tell for certain whether the host was alive or dead at the time of encrustation.

Our purpose herein is twofold: (1) to quantitatively assess putatively distinct species of *Pseudoatrypa* from the Genshaw Formation, herein described as *Pseudoatrypa lineata* and *Pseudoatrypa* sp. A; and (2) to examine the influence of species morphology on encrustation by episkeletobionts. We structured the study by testing the following hypotheses:

1) two species of *Pseudoatrypa* - *Pseudoatrypa lineata* and *Pseudoatrypa* sp. A, previously distinguished on qualitative features, must have statistically distinct shell shapes and are validly different species;if not they will be considered growth variants of the same species;

2) episkeletobionts are influenced by morphology and will preferentially encrust the two species differently; and

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3) given the preferred orientation of atrypid adult shells—convex dorsal valve raised into the water column and flat ventral valve in contact with the substrate (as inferred by Fenton and Fenton (1932)) —the extent of encrustation coverage on the ventral valve will be limited by physical contact with the substrate and thus statistically less than on the dorsal valve.

These hypotheses were tested using geometric morphometric assessment of shell shape and statistical analysis of the location of encrusting organisms.

GEOLOGIC SETTING

Pseudoatrypa brachiopods were collected from the lower Genshaw Formation of the Middle Devonian Traverse Group. The Traverse Group ranges in thickness from ~25.0–169.5 meters (Ehlers and Kesling, 1970; Wylie and Huntoon, 2003), with depositional environments ranging from shallow water carbonate lagoons with coral-stromatoporoid reefs to storm-dominated mixed carbonate-siliciclastic shelf deposits and offshore muddy shelf to slope environments (Ehlers and Kesling, 1970). The Genshaw Formation was named by Warthin and Cooper (1935) for strata overlying their Ferron Point Formation and underlying their Killians Limestone, later revised by the same stratigraphers to include the Killians Limestone as the upper member of the Genshaw Formation (Warthin and Cooper 1943). Warthin and Cooper (1943) placed the new upper contact at the base of the overlying Newton Creek Limestone. The Genshaw Formation remained one of the least studied units of the lower Traverse Group until recently, when the LaFarge Quarry in the Alpena area began to mine into this unit and exposed nearly the entire Formation (Bartholomew, 2006). The Genshaw Formation accumulated during

the highstand of a third-order sea level sequence (Wylie and Huntoon, 2003; Brett et al., 2010).

The Genshaw Formation, which is ~30.0 meters thick (Fig 4.1), is subdivided into informal lower, middle, and upper (formerly Killians Member) portions (Wylie and Huntoon, 2003). The lower unit of the Genshaw Formation begins with a 0.5 m-thick crinoidal grainstone, which locally contains burrows on its lower surface. Overlying this basal bed of the Genshaw Formation is a thin, argillaceous succession capped by a limestone-rich interval to the top of the lower Genshaw. The brachiopods used in this study were collected from the argillaceous beds of this lower unit (Fig. 4.1).
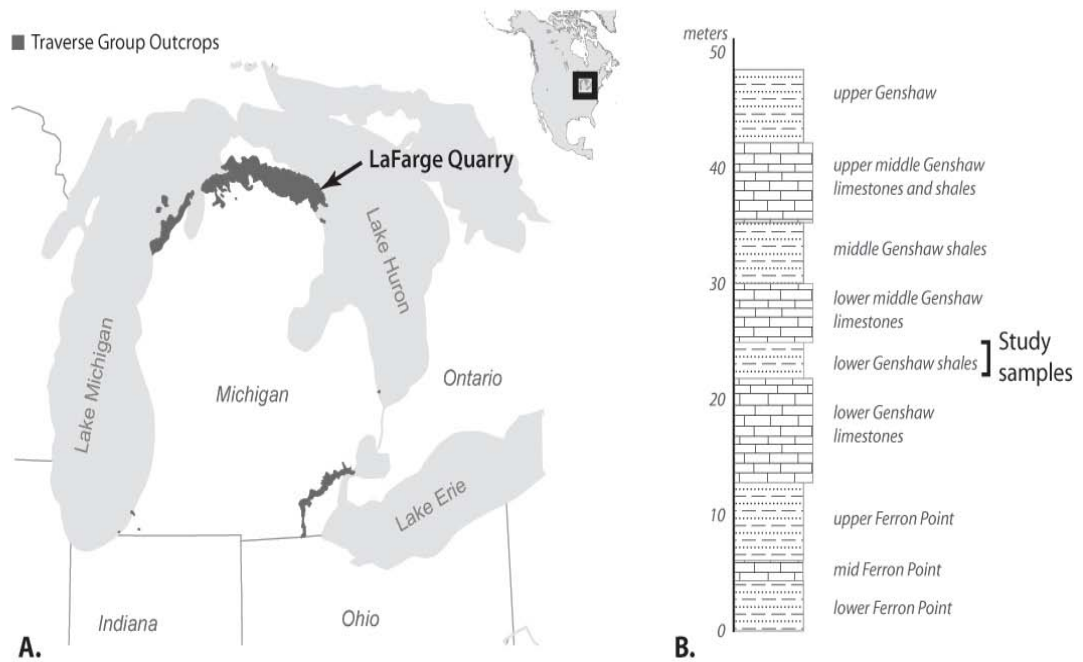
Figure 4.1: a) Map showing Michigan surface exposures of the Middle Devonian Traverse Group and the location of the La Farge Quarry, Alpena area, from which the samples used in this study were collected, b) Simplified stratigraphic section of the Traverse Group at La Farge Quarry showing the horizons of the Genshaw Formation where the specimens used in this study were collected (after Bartholomew, 2006).

MATERIALS AND METHODS

Sampling

Samples examined were collected by A. Bartholomew of State University of New York, New Paltz from the northeastern outcrop of the Lafarge Alpena Quarry, Alpena County, Michigan (Fig. 4.1). He extensively sampled all brachiopods from a shale bed of the lower Genshaw Formation. The 185 well-preserved atrypids examined for encrustation in this study have been deposited in the Indiana University Paleontology Collection (IU 100059 – IU 100243). Use of ammonium chloride spray in a dry environment helped distinguish morphological features of the species.

Species recognition

The atrypid sample was first divided into two populations based on the qualitative traits examined in this study. The two populations are similar in that they have an apical foramen, hinge line with incurved extremities, orbicular to subquadrate shell outline, ribbing with implantations and bifurcations, and somewhat similar spacing between growth lamellae or frills, with frills crowding more at the anterior. However, *Pseudoatrypa lineata* is different from *Pseudoatrypa* sp. A in having a) a smooth, arcuate, domal curvature to the dorsal valve as opposed to the arched shape in the latter, b) slightly inflated ventral valve with an inflation near the umbo as opposed to a more flattened ventral valve in the latter, c) relatively lower dorsal valve curvature height, d) fine to medium closely spaced ribs in contrast to coarse ribs in the latter, e) angular to subrounded hinge line as opposed to the widened hinge in the latter, f) widened median deflection (fold and sulcus) on the commissure as opposed to the narrow deflection in the latter, and g) gentle to steep mid-anterior fold as opposed to the gentler fold in the latter.

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Morphometrics

We performed geometric morphometric analysis to determine morphological variation within and between the two qualitatively distinguished populations assigned to *Pseudoatrypa lineata* and *Pseudoatrypa* sp. A. No crushed specimens were used for morphometrics.

Geometric morphometrics is the analysis of geometric landmark coordinates points on specific parts of an organism (Bookstein 1991; MacLeod and Forey, 2002; Zelditch et al., 2004). We based our morphometric analysis on the use of landmarks to capture shape (Rohlf and Marcus, 1993); landmarks represent discrete geometric points on each specimen that correspond among forms (*sensu* Bookstein 1991). In this study, we used 10 two-dimensional landmark points on the external shell to capture the most meaningful shape differences (Fig. 4.2). When selecting landmarks for analyses, we selected points that not only characterized body shape accurately, but also represented some aspect of the inferred ecological niche. All landmarks were defined by geometric position on host shells (1=beak tip on brachial valve; 2 and 8= intersection points of the commissure and the hingeline; also region for food intake from inhalant currents; 3 and 7= length midpoint projected onto the commissure; these points are perpendicular to, and crosses the midline of the shell; 4 and 6= lowest point of median deflection (fold and sulcus) on the commissure; 5=middle point of commissure; 9=tip of umbo on pedicle valve; 10=maximum height on brachial valve). These landmarks are appropriate for analyses attempting to capture shape changes or function. For this study, we conducted four different analyses operating on ten landmarks in four different orientations of the shell. Two analyses were conducted in the x-y plane of the dorsal and ventral valves;

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these analyses capture only the view in that plane (Figs. 4.2A-B). These analyses of the dorsal and ventral valve views, included nine landmarks, which were selected to encompass the outline of the entire specimen in the x-y plane. Although brachiopods are bilaterally symmetrical, landmarks were included from both the left and right sides of the specimens to record the functional response of these hosts to the then existing ecological conditions and to encrusting episkeletobionts. Capturing both the postero-lateral distal extremities of the hingeline and the lowest points of median deflection on the commissure, even of a bilaterally symmetrical organism may be important for determining shape changes in the host species, as each of these locations may possess unique specific abundances of distinct episkeletobiont assemblages (Bookstein, 1991; Kesling et al., 1980). Two separate analyses operating on landmarks in the y-z plane were conducted from the anterior and posterior views of the shells (Figs. 4.2C-D). For posterior and anterior regions of the shell, landmark measurements (four landmarks on posterior and three landmarks on anterior) were taken only on half of the specimen (anterior/posterior view left or right) (Figs. 4.2C-D). Overall, these two orientations measure not only the shape of the valves, but also capture the shape of the brachiopod lophophore support, the spiralia (Bookstein, 1991; Haney, 2001). The four views (dorsal, vental, anterior, and posterior) were analyzed separately.
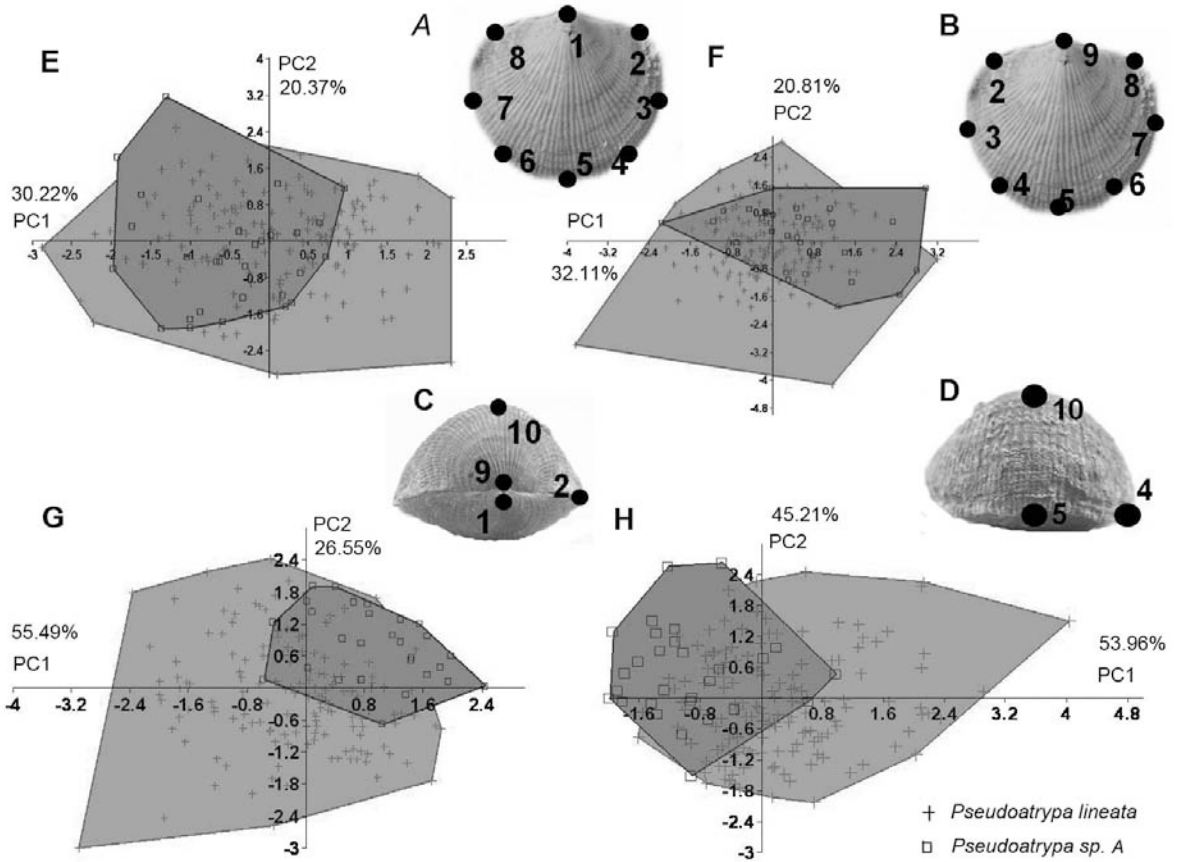
Figure 4.2: a) Location of eight landmark points on dorsal valves of host species, b) location of eight landmark points on ventral valves of host species, c) location of four landmark points on posterior region of host species, d) location of three landmark points on anterior region of host species; morphological shape variation between the two host species *Pseudoatrypa lineata* and *Pseudoatrypa* sp. A along e) dorsal vales, f) ventral valves, g) posterior region, and h) anterior region.

Procrustes analysis (Rohlf, 1990; Rohlf and Slice, 1990; Rohlf, 1999; 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). Principal component analysis of the covariance matrix of the residuals of the Procrustes superimposed coordinates was performed to determine the morphological variation of the two species along their major principal component axes (1 and 2) in the shape morphospace (Fig. 2) and to provide a set of uncorrelated shape variables for further statistical analysis. Procrustes distances, which are the sum of the distances between corresponding landmarks of Procrustes superimposed objects (equal to their Euclidean distance in the principal components space if all axes are used), were calculated as a measure of difference between mean morphological shapes of the dorsal valves, ventral valves, posterior and anterior regions of *Pseudoatrypa lineata* and *Pseudoatrypa* sp. A and thin plate spline plots (Bookstein, 1989) were used to visualize those differences. Multivariate analysis of variance (MANOVA) and discriminant function analysis (DFA) of the shape variables was used to test for significant shell shape differences between the two species along the dorsal, ventral, anterior and posterior regions of the shells (Hammer and Harper, 2005). Multivariate analysis of variance (MANOVA) was performed to test shape variation between the two species. Adult shells of the two species, larger than 1.9 cm in size, were used for geometric morphometric analyses to avoid any misinterpretation in comparative shape study between the two species that could have resulted from not controlling for ontogenic development.

Episkeletobiont analysis

Brachiopods were first examined microscopically for encrustation data (100x magnification). Episkeletobiont distribution was tabulated for each species, for valve preference within each species, and for position on each valve. The relationship between these episkeletobionts and the host atrypids were investigated based on their placement on the host shell. The *Chi-square* test was used to determine whether differences in most abundant episkeletobiont assemblages were significant between the two host species and between the dorsal and ventral valves of each species. Furthermore, species and valve preference by episkeletobionts was reconstructed based on the abundance and location of episkeletobionts, as described below.

Mean encrustation frequency per species was determined to compare encrustation abundance on the dorsal and ventral valves of the two species as

$$\mathbf{A_C} = [(\textstyle\sum E_T / \sum V_E)/N] * 100, \tag{1}$$

where A_C is the mean encrustation frequency with respect to episkeletobiont count, E_T is the total number of episkeletobiont colonies, and V_E is the total number of valves encrusted.

The total area of the valve that was encrusted was measured on each individual host, and the proportion of the valve that was encrusted was calculated using the equation:

$$\mathbf{A_A} = A_E/A_V * 100, \tag{2}$$

where A_A is the encrustation area per valve (A_E) with respect to total valve area (A_V). Relationship between encrustation area (A_A) and principal component (PC axis 1) scores of the shape co-ordinates of the valve morphology was tested using the product-moment

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correlation (r). A *p-value* was also reported for this correlation method to determine if 'r' was significantly different from 0.0.

Following the methods previously established by Bose et al. (2010), each valve of the atrypid hosts was divided into six regions (Fig. 4.3). The six regions were defined as postero-left lateral (PLL), posteromedial (PM), postero-right lateral (PRL), antero-left lateral (ALL), anteromedial (AM), and antero-right lateral (ARL). These six divisions, i.e., six different surface areas of host, were selected such that they represent biologically functional grids for both the host and the episkeletobiont. The PLL and PRL regions were selected based on the idea that host inhalant currents in those regions may attract episkeletobionts, and these currents may also partially influence episkeletobiont settling along the PM region. Similarly, the AM region was selected based on the host exhalant current criteria, which may also partially influence the ALL and ARL regions. Thus, selecting these six regions and recording the frequency of episkeletobionts on each of these regions will help infer host-episkeletobiont relationships in live-live associations.

Area ratios for each region of the shell was determined using the following equation (Fig. 4.3):

$$\mathbf{R} = A_R / A_T, \tag{3}$$

where R is the area ratio, A_R is the area of each region, and A_T is the total area.
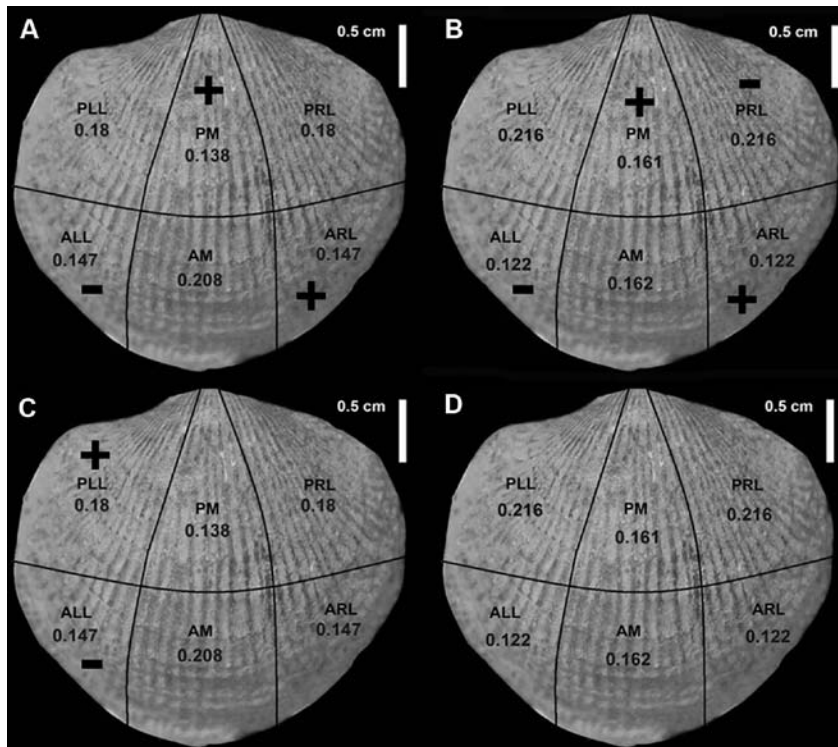
Figure 4.3: *Pseudoatrypa* specimen divided into six regions for episkeletobiont frequency study; PLL = postero-left lateral, PM = posteromedial; PRL = postero-right lateral; ALL = antero-left lateral, AM = anteromedial; and ARL = antero-right lateral. Numbers represent the area ratios of each grid across the *Pseudoatrypa lineata* and *Pseudoatrypa* sp. A host valve. Scale bar 0.5 cm. Note that the area ratios are slightly different for *P. lineata* host species which are as follows: PLL = 0.18, PM = 0.138, PRL = 0.18, ALL = 0.147, AM = 0.208, ARL = 0.147. Significantly greater observed episkeletobiont frequency than expected is denoted by a plus symbol and smaller observed episkeletobiont frequency than expected is denoted by a minus symbol across the six regions of the valve; this is described for a) dorsal valve of *P. lineata*, b) dorsal valve of *Pseudoatrypa* sp. A, c) ventral valve of *P. lineata*, and d) ventral valve of *Pseudoatrypa* sp. A.

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The frequency of encrustation in each region was recorded by counting individual colonies as one occurrence and then summing for all atrypid hosts. For comparison with the actual frequency of episkeletobiosis, expected episkeletobiosis for each region was calculated by:

$$E = NR_i , \qquad\qquad (4)$$

in which the expected number of episkeletobionts (E) is calculated by multiplying the total number of episkeletobionts (N) for all *Pseudoatrypa* specimens by the area ratio (R) for a given region on the atrypid shell (i). The null hypothesis used here for developing the expected value is as follows: Given that we have six regions for one valve, and each region has a chance of being encrusted based on their proportion of available surface area (assuming as a null hypothesis a random distribution of encrusters), then if one region accounts for x% of the surface area on the valve, then the expected value for that region is x% of the total number of episkeletobionts encrusting that valve (all six regions) for that species. The same approach is used to determine the expected value for the other regions. Colonial episkeletobionts—sheet-like and branching—posed a problem for calculations because these specimens often crossed borders into adjacent regions. For these specimens, colonization of an episkeletobiont that extended into two or more regions was divided among the total number of regions it inhabited. For example, branching auloporid corals and hederellids that were observed in all the three anterior regions were counted as 1/3 for each region.

We then quantified common episkeletobionts (i.e., microconchids, bryozoans sheets, and hederellids) for their distribution on six regions of the shell of both dorsal and ventral valves of each host, using Equation 2 above. Distribution of rare episkeletobionts

on host shells was also examined, but only for dorsal valves, as episkeletobiont abundance of rare encrusters is negligible on ventral valves. A *chi-square* test was also performed for the total observed and expected episkeletobiont activity along the six regions to determine the episkeletobiont location preference on the atrypid valve within each species.

RESULTS

Morphology and morphometrics

Two-hundred and thirty two specimens of atrypids were assigned to *Pseudoatrypa lineata* and 111 specimens of atrypids were assigned to *Pseudoatrypa* sp. A. Representatives of the two species from this study are shown in Figure 4.4. The first two principal component axes (axes 1 and 2) explained a total of 50.2% of the variation in dorsal valves, 52.9% of the variation in ventral valves, 82.0% of the variation in the posterior region and 98.0% of the variation in the anterior region (Fig. 4.2). Principal component analysis of dorsal and ventral valves indicates that there is considerable shape variation within each species and that the two species overlap considerably in the morphology of both valves in the x-y plane (Fig. 4.2E-F). Procrustes distances between the mean shape of the two species are 0.023 for the dorsal valves and 0.028 for ventral valves, suggesting that ventral valves show slightly greater morphological differentiation than dorsal valves. Principal component analysis of posterior and anterior regions also indicates that there is considerable variation in morphology between the two species in the y-z plane (Figs. 4.2G-H). Procrustes distances between the mean shape of the two species are 1.69 for the posterior region and 1.53 for anterior region.
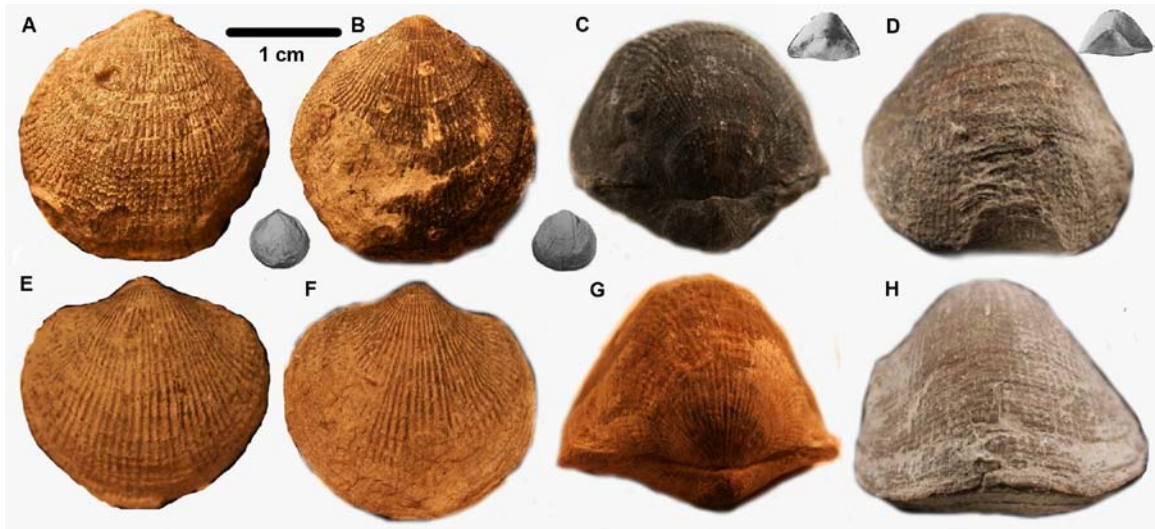
Figure 4.4: *Pseudoatrypa lineata* a) Dorsal view, b) ventral view, c) posterior view, d) anterior view (IU#100069); *Pseudoatrypa* sp. A e) dorsal view, f) ventral view, g) posterior view and h) anterior view (IU#100220). The small inset illustrations next to dorsal and ventral views of *P. lineata* represent the type specimen of *Atrypa lineata var. inflata* as described in Fenton and Fenton, 1935 and the posterior and anterior views represent the type specimen of *Atrypa lineata* as described in Day and Copper, 1998.

MANOVA detects a small significant difference in mean shape of dorsal, ventral, posterior and anterior regions ($p<0.01$). DFA detects a small but significant difference in mean shape of dorsal and ventral valves ($p<0.01$) and a large significant difference in mean shape of the posterior and anterior regions ($p<<0.01$) (Fig. 4.5). The significance of the MANOVA and the DFA demonstrates that the two populations can be distinguished as separate species, based on shell shape.
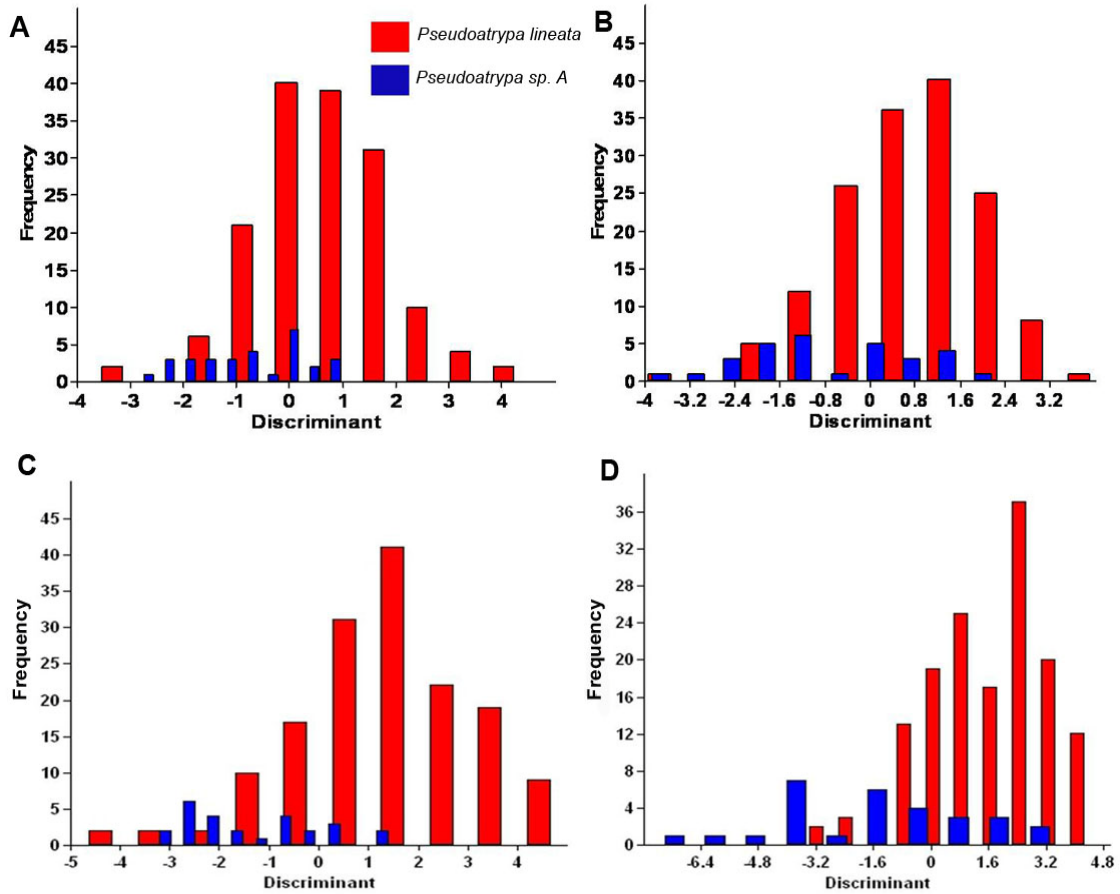
Figure 4.5: Discriminant function analysis showing the morphological distinctness between *P. lineata* and *Pseudoatrypa* sp. A for a) dorsal valves: Hotelling's t2 P= 0.00759 (Dorsal valves DFA) b) ventral valves: Hotelling's t2 P= 0.002113 (ventral valves DFA), c) posterior region: Hotelling's t2 P= 6.304×10-9 (posterior region DFA), and d) anterior region: Hotelling's t2 P=   1.973×10-12 (anterior region DFA).

Thin plate spline visualisation plots show the mean morphological shapes of these two species are different (Fig. 4.6). Dorsal valves show a difference in the shape of the posterior hinge line and anterior commissure. The distances between the umbo tip and the posterior left and right lateral margins in the dorsal valve plots are less in *Pseudoatrypa lineata* than in *Pseudoatrypa* sp. A, confirming the observation of a more widened hinge line in the latter. Similarly, the distances between the middle point of commissure and the lowest point of the median deflection (fold and sulcus) on both halves of the specimen suggesting a widening of the deflection in *Pseudoatrypa lineata* and narrowing in *Pseudoatrypa* sp. A. Ventral valves, however, do not show much significant difference in shape, except for the widened hinge line in *Pseudoatrypa* sp. A relative to the narrow hinge line in *Pseudoatrypa lineata*. The posterior region plots show greater distance between the dorsal umbo and ventral beak tip and lesser distance between dorsal umbo and maximum curvature point in *P. lineata* than in *Pseudoatrypa* sp. A, consistent with the visual observation of a domal, relatively shallower dorsal valve and inflated ventral valve in *P. lineata* and arched, relatively deeper dorsal valve and flattened ventral valve in *Pseudoatrypa* sp. A. The mean shape plots for the anterior region show less distance between the mid-anterior and right anterior margin in *P. lineata* than *Pseudoatrypa* sp. A and the lateral margin is higher in *Pseudoatrypa* sp. A than in *P. lineata*. This demonstrates that the two species are substantially different in morphological shape (Fig. 4.6).
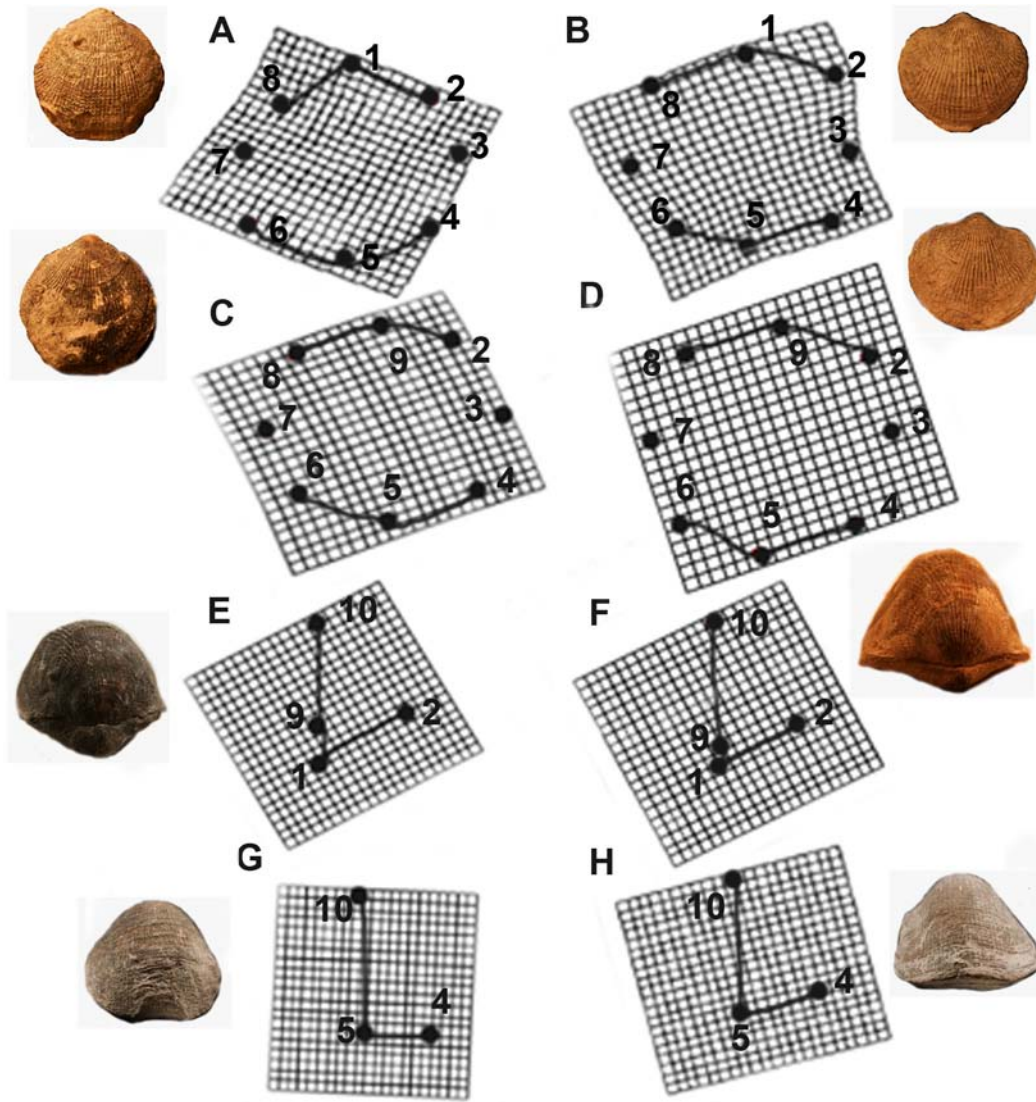
Figure 4.6: Thin Plate Spline visualisation plots for mean morphological shape of a) dorsal valves of *P. lineata*, b) dorsal valves of *Pseudoatrypa* sp. A, c) ventral valves of *P. lineata*, d) ventral valves of *Pseudoatrypa* sp. A, e) posterior region of *P. lineata*, f) posterior region of *Pseudoatrypa* sp. A, g) anterior region of *P. lineata* and h) anterior region of *Pseudoatrypa* sp. A.

Frequency of episkeletobionts

Pseudoatrypa lineata and *Pseudoatrypa* sp. A are hosts to many colonial episkeletobionts – hederellids, sheet-like bryozoans, tabulate corals, fenestrate bryozoans and *Ascodictyon* – as well as many solitary episkeletobionts - microconchids, craniid brachiopods, and *Cornulites* (Fig. 4.7). Episkeletobionts encrusted 155 specimens (out of 232 total specimens) of *Pseudoatrypa lineata* and 30 specimens (out of 111 total specimens) of *Pseudoatrypa* sp. A, for a total of 185 encrusted specimens. Episkeletobionts encrusted more frequently on *Pseudoatrypa lineata* than *Pseudoatrypa* sp. A. On *Pseudoatrypa lineata*, 125 dorsal valves (81%) and 65 ventral valves (42%) out of 155 encrusted specimens were encrusted, compared with 30 dorsal valves (100%) and 22 ventral valves (74%) out of 30 encrusted specimens of *Pseudoatrypa* sp. A.
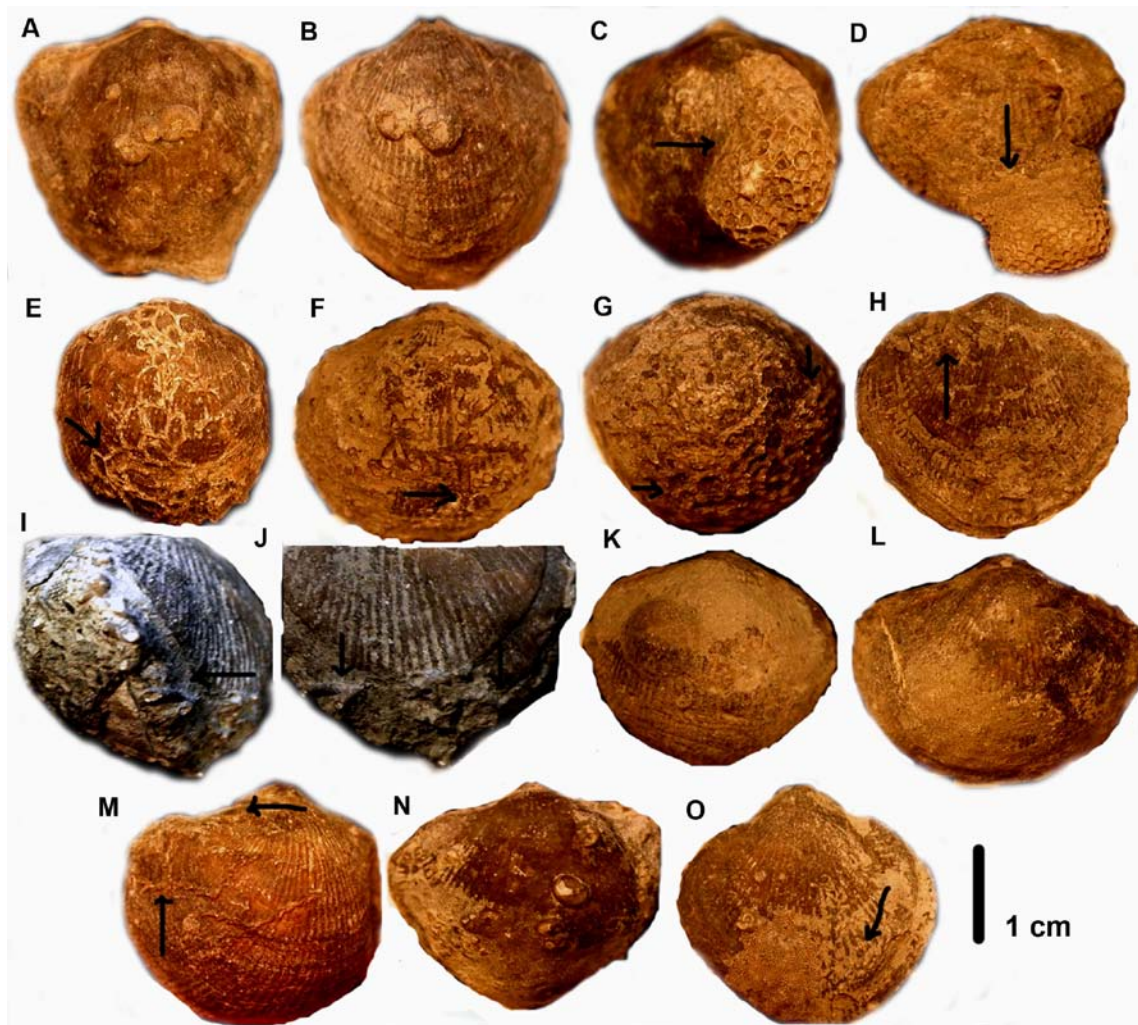
Figure 4.7: Different types of episkeletobionts on *P. lineata* and *Pseudoatrypa* sp. A hosts – a-b) (IU#100196, IU#100211) Microconchid tube-worms; c-d) (IU#100179, IU#100122) tabulate sheet corals; e-j) (IU#100061, IU#100109, IU#100164, IU#100177, IU#100241) auloporid coral colonies; k) (IU#100222) craniid brachiopod; l) (IU#100174) bryozoans sheet; m) (IU#100077) hederellid colony; n-o) (IU#100138, IU#100226) mutual co-occurrences of hederellid, bryozoan sheet and microconchid tube worms. Black arrows indicate the episkeletobiont extension to the posterior or anterior edges of the host valve.

A total of 354 episkeletobionts encrusted *Pseudoatrypa lineata* dorsal valves (A_C= 2.83%) and 74 episkeletobionts encrusted ventral valves (A_C= 1.14%). On *Pseudoatrypa* sp. A, 152 episkeletobionts encrusted dorsal valves (A_C= 5.07%) and 61 encrusted ventral valves (A_C= 2.77%). Dorsal valves are more heavily encrusted for both species (Fig. 4.8; Table 4.1). However, average encrustation frequency (A_A) was only weakly correlated with the principal component (PC1) scores for both *Pseudoatrypa lineata* (dorsal view: r = -0.08, p=0.36; posterior view: r=0.08, p=0.40; anterior view: r=0.01, p=0.87) and *Pseudoatrypa* sp. A (dorsal view: r = 0.09, p=0.63; posterior view: r=-0.06, p=0.75; anterior view: r=-0.10, p=0.62), implying that episkeletobionts did not have a strict preference for shape.
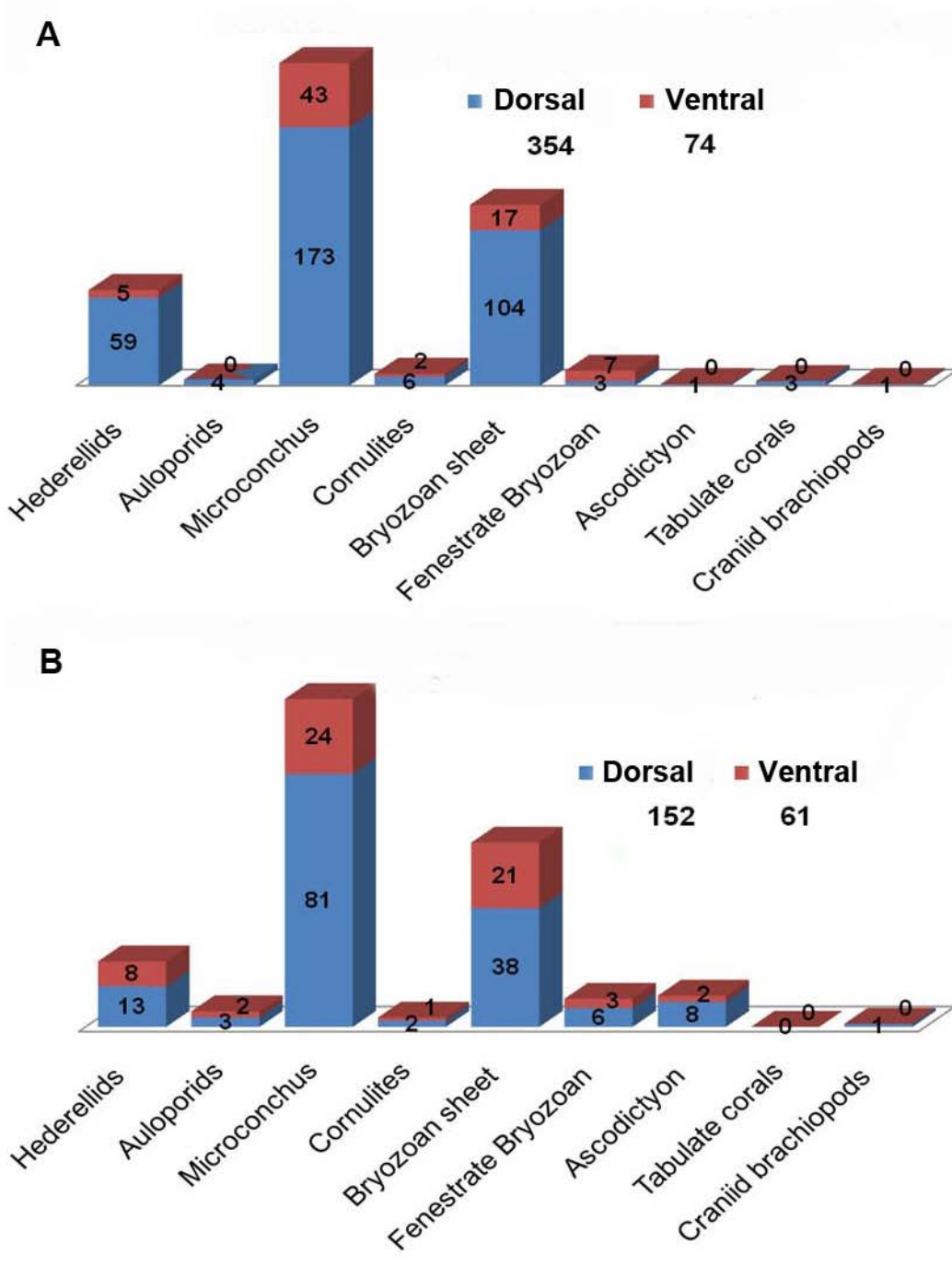
Figure 4.8: Total episkeletobiont count on a) *P. lineata* and b) *Pseudoatrypa* sp. A.

Episkeletobiont type	*Pseudoatrypa lineata* (dorsal)	*Pseudoatrypa lineata* (ventral)	*Pseudoatrypa* sp. A (dorsal)	*Pseudoatrypa* sp. A (ventral)
Hederellids	**0.3**	0.05	**1.44**	1.21
Auloporids	0.02	0	0.33	0.3
Microconchus	**0.89**	0.43	**9.00**	3.64
Cornulites	0.03	0.02	0.22	0.15
Bryozoan sheet	**0.54**	0.17	**4.22**	3.18
Fenestrate Bryozoan	0.02	0.07	0.67	0.45
Ascodictyon	0.01	0	0.89	0.3
Tabulate corals	0.02	0	0	0
Craniid brachiopods	0.01	0	0.11	0

Table 4.1: Mean encrustation frequency (A_C) results of each episkeletobiont type on *Pseudoatrypa lineata* and *Pseudoatrypa* sp. A.

Microconchids, hederellids and sheet bryozoans were the most abundant epizoans, while tabulate corals, auloporid corals, craniid brachiopods, fenestrate bryozoans, *Cornulites* and *Ascodictyon* were present but rarer. Overall, dorsal valves of both species were encrusted more frequently by microconchids, sheet bryozoans and hederellid colonies (*Chi-square* test, *p<0.05*) (Table 4.2). Frequencies of each episkeletobiont taxon on both valves of the two species are illustrated in Table 4.2 and Figure 4.8. For each episkeletobiont taxon, mean frequency based on encrustation count (A_C) is presented in Table 4.1.

Episkeletobiont	Fenestrate Bryozoan	Bryozoan sheet	*Cornulites*	*Microconchus*	Auloporids	Hederellids
Pseudoatrypa lineata						
Shells encrusted	3	64	2	55	4	23
%	1.9	41.3	1.3	35.5	2.6	14.8
Dorsal encrusters	3	104	6	173	4	59
Ventral encrusters	7	17	2	43	0	5
P		*<0.01*		*<0.01*		*<0.01*
Pseudoatrypa sp. A						
Shells encrusted	2	6	2	10	2	5
%	6.7	20.0	6.7	30.0	6.7	16.7
Dorsal encrusters	6	38	2	81	3	13
Ventral encrusters	3	21	1	24	2	8
P		*<0.01*		*<0.01*		*<0.01*
Grand Totals						
shells	5	70	4	64	6	28
encrusters	19	180	11	321	9	85

Table 4.2. Summary of encrustation by episkeletobiont type.

Total	Craniid brachiopods	Tabulate corals	Ascodictyon
155	1	2	1
354	0.7	1.9	0.7
74	1	3	1
30	0	0	0
152	1	0	2
61	3.3	0.0	6.7
185	1	0	8
	0	0	2
641	2	3	3
	2	3	11

Table **4.2**. continued.

Table 4.2: Summary of encrustation by episkeletobiont type. The number of brachiopods encrusted by each episkeletobiont (shells encrusted) and the percentage of encrusted shells that had that particular episkeletobiont (%) are reported. The total number of encrusters of each episkeletobiont are reported for each valve. *p* values report the probability that the rate of encrustation is the same on dorsal and ventral valves. Grand totals give the total number of shells encrusted by each episkeletobiont in both species and the total number of encrustations by each episkeletobiont.

Location of episkeletobionts

The frequency of biotic interactions varies among the six regions on both valves of the *Pseudoatrypa lineata* and *Pseudoatrypa* sp. A hosts; dorsal valves of each are illustrated in Figures 4.9 and 4.10. Dorsal valves are more heavily encrusted than the ventral valves with relatively greater episkeletobiont concentration on all the grids (*p<0.01*).

Dorsal valves

In dorsal valves, the posteromedial region contains the most frequent occurrence of episkeletobionts on both *Pseudoatrypa lineata* and *Pseudoatrypa* sp. A. Microconchids, the most frequent episkeletobiont, is noticeably abundant on all of the six shell regions of both species (Fig. 4.9).
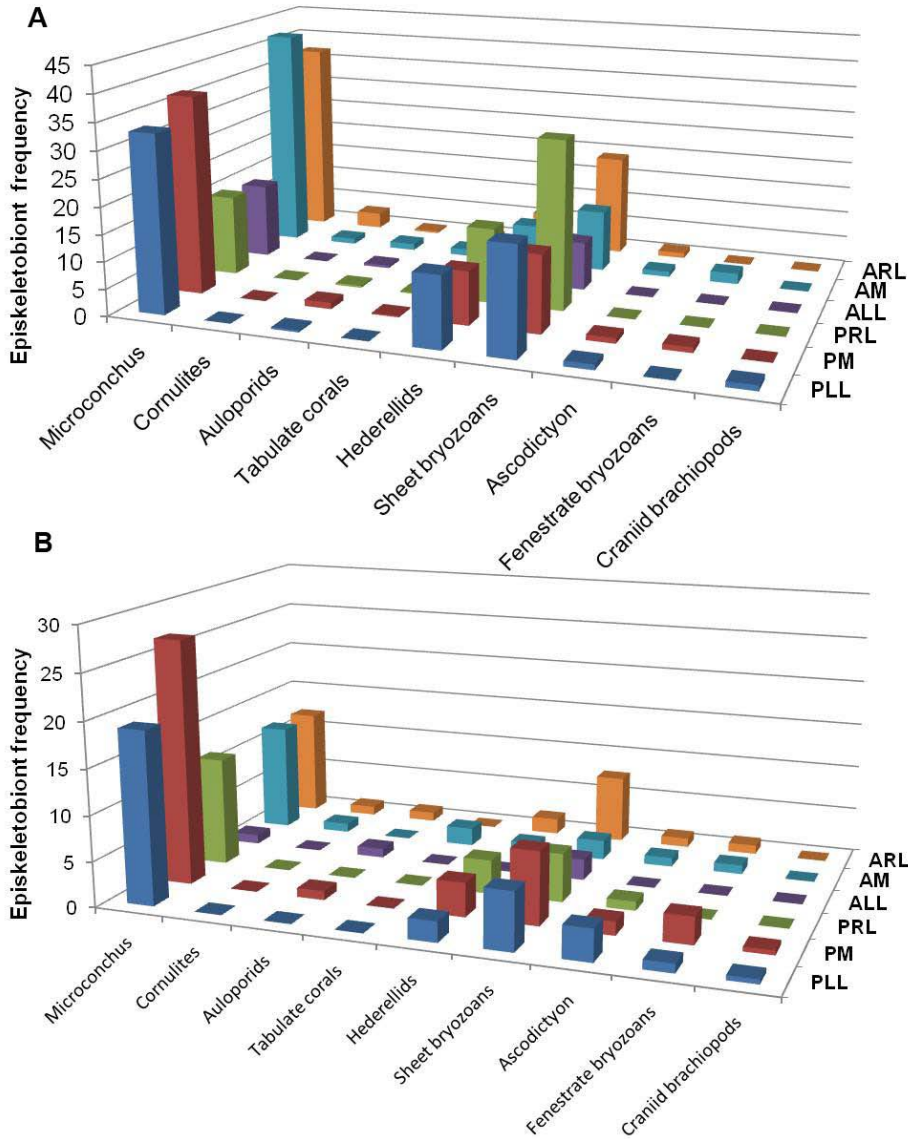
Figure 4.9: Total standardized frequency of each episkeletobiont activity on dorsal valves across each region for a) 125 *P. lineata* and b) 30 *Pseudoatrypa* sp. A hosts. (Note: Standardized frequency = Frequency of colonized episkeletobionts on host species). The six regions are as follows: PLL = postero–left lateral region; PM = posteromedial region; PRL = postero–right lateral region; ALL = antero–left lateral region; AM = anteromedial region; and ARL = antero–right lateral region.
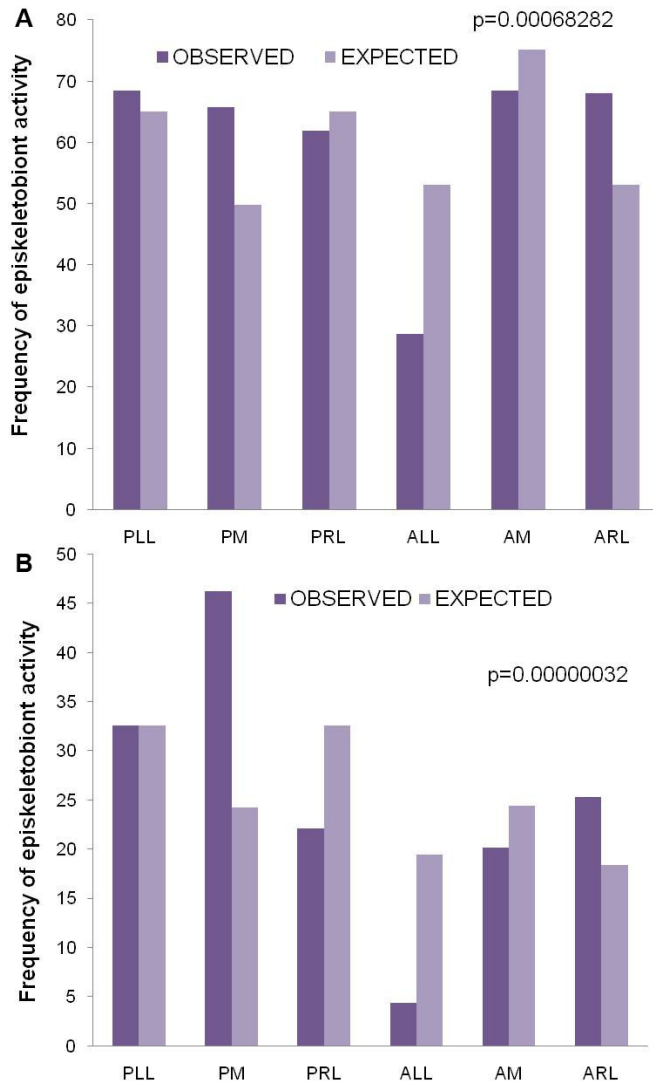
Figure 4.10: Observed versus expected episkeletobiont activity in dorsal valves across each region. Observed values are the actual frequency of encrustation for each region of the shell; expected values are calculated as described in the text. a) 125 count P. lineata hosts and b) 30 count *Pseudoatrypa* sp. A hosts. The six regions are as follows: PLL= postero–left lateral region; PM = posteromedial region; PRL= postero–right lateral region; ALL= antero–left lateral region; AM= anteromedial region; and ARL= antero–right lateral region.

The episkeletobiont distribution was non-random on dorsal valves. The observed frequency of total episkeletobionts across all regions of the two *Pseudoatrypa* species is significantly different than expected if episkeletobionts randomly encrusted any portion of the shell (*Chi-square*; *p<<0.01*) (Table 4.3). Specifically, the antero-left lateral region of *P. lineata* was encrusted at a lower rate than expected (*Chi-square*, *p<<0.01*) whereas the postero-right lateral and antero-left lateral regions were encrusted at a lower than expected rate on *Pseudoatrypa* sp. A (*Chi-square*, *p=0.04, p<<0.01*) respectively (Table 4.4; Fig. 4.3). Conversely, the diagonally opposite posteromedial and antero-right lateral regions were encrusted at a greater frequency than expected in both the species (*Chi-square*, *p=0.015* and *p<0.027* in *P. lineata*; *p<<0.01* and *p=0.08* in *Pseudoatrypa* sp. A) (Table 4.4; Fig. 4.3). The remaining regions do not show any significant difference between expected and observed episkeletobiont frequency (Table 4.4; Fig. 4.10).

DORSAL	*Pseudoatrypa lineata*		*Pseudoatrypa* sp. A	
Regions	**Observed**	**Expected**	**Observed**	**Expected**
PLL	68.4	65.0	32.584	32.544
PM	65.7	49.8	46.25	24.26
PRL	61.9	65.0	22.08	32.54
ALL	28.7	53.1	4.333	19.43
AM	68.4	75.1	20.17	24.41
ARL	68.0	53.1	25.25	18.38
SUM	361.1	361.1	150.667	151.564

VENTRAL	*Pseudoatrypa lineata*		*Pseudoatrypa sp. A*	
Regions	**Observed**	**Expected**	**Observed**	**Expected**
PLL	15	9.18	11	6.696
PM	6	7.038	7	5.006
PRL	10	9.18	4	6.696
ALL	2	7.497	2	3.782
AM	9	10.608	4.83	5.022
ARL	9	7.497	2.17	3.782
SUM	51	51	31	30.984

Table 4.3: Sum of the observed and expected values for episkeletobiont activity across six shell regions of a) dorsal valves and b) ventral valves of *Pseudoatrypa lineata* and *Pseudoatrypa* sp. A. The six grids are as follows: PLL postero–left lateral region; PM posteromedial region; PRL postero–right lateral region; ALL antero–left lateral region; AM anteromedial region; ARL antero–right lateral region. Note that in ventral valves, many rare episkeletobionts were absent, so only the most abundant episkeletobionts is considered.

A) *Pseudoatrupa lineata*	*p* values	Observed is — than expected
PLL vs. sum of other areas	0.6410	
PM vs. sum of other areas	0.0150	MORE
PRL vs. sum of other areas	0.6710	
ALL vs. sum of other areas	0.0003	LESS
AM vs. sum of other areas	0.3850	
ARL vs. sum of other areas	0.0270	MORE
A) *Pseudoatrypa* **sp. A**	*p values*	Observed is — than expected
PLL vs. sum of other areas	0.9300	
PM vs. sum of other areas	$9.4 \times 10\text{-}7$	MORE
PRL vs. sum of other areas	0.042	LESS
ALL vs. sum of other areas	0.0003	LESS
AM vs. sum of other areas	0.3639	
ARL vs. sum of other areas	0.0822	MORE
B) *Pseudoatrypa lineata*	*p values*	Observed is — than expected
PLL vs. sum of other areas	0.0300	MORE
PM vs. sum of other areas	0.6700	
PRL vs. sum of other areas	0.5400	
ALL vs. sum of other areas	0.0300	LESS
AM vs. sum of other areas	0.5800	
ARL vs. sum of other areas	0.5500	
B) *Pseudoatrypa* **sp. A**	**p values**	Observed is — than expected
PLL vs. sum of other areas	0.0600	MORE
PM vs. sum of other areas	0.3300	
PRL vs. sum of other areas	0.2400	
ALL vs. sum of other areas	0.3200	
AM vs. sum of other areas	0.9200	
ARL vs. sum of other areas	0.3700	

Table 4.4: Results of *Chi-square* test of observed versus expected episkeletobiont activity for *Pseudoatrypa lineata and Pseudoatrypa* sp. A a) dorsal and b) ventral valves. A *p-value* < 0.05 indicates either more or less biological activity in that shell region than expected, as indicated.

Ventral valves

On ventral valves, the postero-left lateral region bears abundant episkeletobionts on both species. Microconchids are common to all of the six shell regions of *P. lineata*, but absent in postero-right lateral and antero-right lateral regions of *Pseudoatrypa* sp. A.

The ventral valve episkeletobiont distribution was too low to infer whether the distribution was random or non-random in the six regions. The observed frequency of total episkeletobionts across all regions of the two *Pseudoatrypa* species for ventral valves is not significantly different than expected (*Chi-square*, *P. lineata*, *p=0.13* and *Pseudoatrypa* sp. A, *p=0.29*) (Table 4.3). However, the postero-left lateral region of *P. lineata* was encrusted at a greater rate than expected (*Chi-square*, *p=0.03*) and the antero-left lateral region was encrusted at a lower rate than expected rate on *P. lineata* (*Chi-square*, *p=0.03*) (Table 4.4; Fig. 4.3). The remaining regions do not show any significant difference between expected and observed episkeletobiont frequency on *P. lineata* (Table 4.4). None of the six regions of the ventral valve show any significant difference between expected and observed episkeletobiont activity in *Pseudoatrypa* sp. A (Table 4.4).

DISCUSSION

Morphology of *Pseudoatrypa lineata* and *Pseudoatrypa* sp. A

The two species *Psueudoatrypa lineata* and *Pseudoatrypa* sp. are different enough to warrant splitting into separate species. These samples show significant morphological differences, especially in their dorsal convexity, that are sufficient to designate them as two distinct species based on qualitative traits and significant morphometric shape. Thus, in addition to the visually distinguishing characteristic differences in shell shape, morphometric results suggest that the two morphotypes

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deserve species-level distinction. In this study, morphological shape variation exists within each species. Principal component analysis indicates morphologies of the two species overlap when dorsal and ventral valves are considered. However, the morphological differences between the two species is best observed in the posterior and anterior views, which is also observed in overall qualitative traits of these species (Figs. 4.2, 4.4, 4.5). The morphological differences between the two species are clearly visible in the thin plate spline plots and the differences in mean are significant using MANOVA, when the posterior and anterior regions are assessed. The two species are separable by DFA (Fig. 4.5). These differences were in the shape of the hinge line and commissure, height of dorsal valve curvature, and ventral valve inflation (Figs. 4.4-4.5). Thus, we consider the two morphotypes to be different species.

Pseudoatrypa lineata (Webster, 1921), was described by Fenton and Fenton (1935) and Day and Copper (1998) as a medium-large sized atrypide with dorsibiconvex to convexoplanar shells with inflated dome-like dorsal valves. *Pseudoatrypa lineata* from Cedar Valley of Iowa possessed fine radial, subtubular to tubular rib structure (1-2/1 mm at anterior margin), irregularly spaced concentric growth lamellae (more like wrinkles or lines) crowding towards the anterior and lateral margins in larger adults (20 mm length), with very short projecting frills or almost absent. Day and Copper (1998) grouped *Atrypa lineata*, a growth variant form of *A. lineata* and a subspecies of this species, *Atrypa lineata var. inflata* (described earlier by Fenton and Fenton (1935)), all under *Pseudoatrypa lineata*. In our study, one of the species sampled from the Givetian age Traverse Group resemble the overall shape and morphology of *P. lineata* described

previously from the late Givetian Cedar Valley of Iowa by Fenton and Fenton (1935) and hence are called *P. lineata* for the purpose of this study.

In contrast, the other species do not resemble *P. lineata* type specimens in that they possess a highly arched dorsal valve in contrast to the dome shaped dorsal valve, a flat ventral valve in contrast to the slightly inflated ventral valve, coarser ribs in contrast to the fine-medium ribs, and a subquadrate shell outline in contrast to the rounded outline of *P. lineata*. *P. devoniana* has an elongated shell outline and is Late Frasnian in age (Day and Copper, 1998). *P. witzkei* has a rounded shell outline, a shallow dorsal valve profile and is middle Frasnian in age (Day and Copper, 1998). *Desquamatia (Independatrypa) scutiformis* has a subrounded shell outline, shallow dorsal valve and highly imbricate tubular ribs in contrast to the subtubular ribs in this species. Thus, the species described in this study is referred to *Pseudoatrypa* sp. A, as it does not resemble *P. lineata* or other species of late Givetian time.

P. lineata diagnosed in this study clearly resembles *A. lineata var. inflata* of Fenton and Fenton (1935) in having similar shell size (2.1-2.4 ± 0.2 cm), shell thickness and convexity (slightly convex ventral valve), ribs with implantations and bifurcations, and numerous growth lines crowding at the anterior. However, *Pseudoatrypa* sp. A resembles *A. lineata* described by Fenton and Fenton (1935) in having larger sized shells (2.3-3.3 ± 0.2 cm), flattened ventral valve, etc. but is significantly different from *A. lineata* in its dorsal valve shape. Thus, both *P. lineata* and *Pseudoatrypa* sp. A in this study are described as two distinct species of *Pseudoatrypa* (Fig. 4.4) based on ornamentation and overall shell shape differences (Figs. 4.4-4.6).

Several studies have speculated possible causes (e.g., sedimentation rates, current stimuli, oxygen level, substrate conditions, etc.) behind the observed morphologies for brachiopod shell shape (Lamont, 1934; Bowen, 1966; Copper, 1967; Alexander, 1975; Richards, 1969, 1972; Leighton, 1998). Copper (1973) suggested *Pseudoatrypa* was a soft muddy bottom inhabitant favoring quieter water, though in later studies (Day, 1998; Day and Copper, 1998), *Pseudoatrypa* has been reported from carbonate environments of the Upper Devonian Cedar Valley group of Iowa. In this study, the samples of the two species were collected from a thin succession of argillaceous shales representing middle shelf environments. These argillaceous beds contained large atrypids with encrusters attached on both valves, which suggests that these shells might have been subject to agitated currents from time to time that were capable of occasionally flipping the shells over in a moderate-low water energy conditions, thus enabling the growth of encrusters on both sides. Thus, as the *P. lineata* and *Pseudoatrypa* sp. A both existed in the same sedimentological regime and were exposed to similar environmental conditions (similar oxygen-level, energy, and substrate conditions), the causes of the difference in shape of the two species are more likely genetic rather than ecomorphic.

Species preference of episkeletobionts

Episkeletobionts more frequently encrusted *Pseudoatrypa lineata* over *Pseudoatrypa* sp. A (Tables 4.1-4.2). In particular, microconchids and sheet bryozoans, the two most abundant episkeletobionts, were more common on *P. lineata* than *Pseudoatrypa* sp. A. No strict species preference was observed for the third-most abundant taxon, hederellids, or for any of the rarer episkeletobionts (*Cornulites*, auloporid corals, tabulate corals, fenestrate bryozoans, *Ascodictyon*, craniid brachiopods).

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Among the abundant episkeletobionts, the greatest episkeletobiont activity on the two species can be attributed to the calcareous spirorbiform microconchid tube worms. These spiral worm tubes (0.5-5.0 mm) on *Pseudoatrypa* hosts resemble those encrusting the Middle Devonian Hamilton Group brachiopod hosts (Bordeaux and Brett, 1990: Fig 4.2). A few tube worms, as shown in Fig. 4.7, were very large (>3 mm).

Bryozoan sheets, the second most abundant episkeletobiont, generally encrusted *Pseudoatrypa* hosts over large surface areas (Figs. 4.7L, N, O). They were more common on *P. lineata* than *Pseudoatrypa* sp. A. The surface covering patterns and colonial morphology of the trepostome bryozoans was similar to those encrusting Middle Devonian brachiopods from the Kashong Shale (Bordeaux and Brett, 1990). In a few instances, bryozoans even overgrew spirorbiform microconchids and hederellids (Figs. 4.7N-O).

Hederellids, the third most abundant episkeletobiont, were common on both species and did not show a strict preference for either host. Hederellids, originally defined as suborder Hederolloidea (Bassler, 1939), are characterized by tubular, calcitic branches. Hederellids have been traditionally referred to bryozoans, but the true affinity of hederelloids has been called into question by some recent workers (Wilson and Taylor, 2001; Taylor and Wilson, 2008). These Genshaw Formation hederellids (Figs. 4.7M, O) resemble the hederellid species *Hederella canadensis* that encrusted brachiopods from the Devonian Silica Formation of northwestern Ohio (Hoare and Stellar, 1967; Pl. 1), brachiopods from the Middle Devonian Kashong Shale of New York (Bordeaux and Brett, 1990, Fig. 2) and *Paraspirifer bownockeri* from the Michigan Basin (Sparks et al., 1980).

Coarse ribs and spines on brachiopod shells have been considered anti-predatory and anti-fouling tools (Richards and Shabica, 1969; Vermeij, 1977; Alexander, 1990; Leighton, 1999, 2003; Carrera, 2000; Dietl and Kelley, 2001; Schneider, 2003, 2009a; Schneider and Leighton, 2007; Voros, 2010) and in some cases have been avoided by epizoans (Richards, 1972). Consistent with this hypothesis, finer ribbed taxa in modern (Rodland et al., 2004) and Devonian (Hurst, 1974; Thayer, 1974; Anderson and Megivern, 1982; Schneider and Webb, 2004; Zhan and Vinn, 2007; Schneider, 2009b) brachiopod assemblages experienced greater encrustation frequency than more coarsely ribbed taxa. . In this study, there may be a similar preference for finer ribs. As there is no relationship between shell shape and encrustation, but episkeletobionts did prefer *P. lineata*, the data suggest that ornamentation may have been the determining factor in encruster preference for hosts. The fine-medium rib structure of *P. lineata* may have attracted more episkeletobionts than the coarsely ribbed *Pseudoatrypa* sp. A specimens.

Thus, although most episkeletobionts do not exhibit a preference for one of the species, the microconchids, and sheet bryozoans clearly exhibited a preference for *P. lineata*. Surprisingly, *Pseudoatrypa* sp. A, which possesses a relatively larger shell size than *P. lineata*, is less preferred by the most abundant episkeletobionts. One possible explanation for this could be the greater surface area provided by the inflated geometry of the dorsal valve of *P. lineata*, despite its smaller overall shell size. In other words, *P. lineata* may have facilitated heavier encrustation by providing a larger surface area for settlement.

Live-dead and live-live associations

Both live and dead hosts could be used as a substrate for episkeletobiont settlement. While live hosts might attract encrusters through their feeding currents, dead hosts, obviously, can only be used as a substrate for encrustation.

For some episkeletobionts, hosts would serve merely as hard substrates. In an epizoan ecology study performed by Watkins (1981), it was observed that some epizoans had a very weak preference for live hosts. There is evidence of hederellids and sheet bryozoa encrusting dead hosts or wood (Thayer, 1974). There is also evidence of microconchids encrusting dead brachiopod hosts from the Upper Devonian Cerro Gordo Member of the Lime Creek Formation of Iowa (Anderson and Megivern, 1982). In contrast, in other studies (e.g., Ager, 1961; Hoare and Steller, 1967; Richards, 1974; Kesling and Chilman, 1975; Morris and Felton, 1993), auloporids, hederellids and cornulitids frequently displayed preferential growth along or toward the commissure, particularly on Devonian alate spiriferides and large atrypides, possibly in order to take advantage of feeding and respiration currents actively generated by the host's lophophore.

Because post-mortem encrustation cannot be ruled out, it is critical to interpret whether the brachiopod host was alive concurrently with the episkeletobionts. We observed that in rare cases, episkeletobionts oriented themselves on the brachiopod host in specific directions or encrusted particular regions to benefit from feeding currents (Fig. 4.7). These instances may indicate live-live associations.

Sparks et al. (1980), suggested a commensal relation between *Paraspirifer bownockeri* hosts and the spirorbiform microconchids, whereas Barringer (2008) noted

no preferred location or orientation of microconchids on host valves, and suggested that they simply infested the hard substrates of the brachiopods. In the present study, microconchids randomly encrusted both valves (Figs. 4.7A-B), with no particular concentration along the commissure area nor any particular orientation of their apertures, thus leaving the host-episkeletobiont relationship ambiguous. Their random orientation on the host valves may indicate that they fed from ambient water currents, rather than requiring currents induced by live brachiopods, a result consistent with other studies (Ager, 1961; Pitrat and Rogers, 1978; Hurst, 1974; Kesling et al., 1980; Fagerstrom, 1996). Encrusting bryozoans rarely indicate live-live episkeletobiont-host interactions (Fagerstrom, 1996). Microconchids or sheet bryozoa in this study could have encrusted the two species whether live or dead, possibly because of the availability of their hard substrate.

Hederellid colonies that encrusted brachiopods with their apertures oriented towards the anterolateral commissure may have been in that position to benefit from host exhalant currents as described by Bordeaux and Brett (1990). *Hederella* has been reported to have a commensal relationship with its host by Sparks et al. (1980), whereby the episkeletobiont benefited from the hard surface for attachment and from the elevation above the soft substrate but this would be also true for a dead host. In our study, orientation of the apertures of hederellid colonies towards the postero-left lateral end of the host and their termination towards the lateral margin could indicate that the hederellid was taking advantage of host-induced currents (Fig. 4.7M). Such an orientation of hederellids indicates that these organisms may have either benefited from host's feeding inhalant currents, and possibly may have harmed the host by taking in too much of the

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host's food supply, thus implying a commensal, or parasitic relationship. In one particular instance, however, hederellid colonies were found to parallel the anterior commissure, which would support a commensal relation with the host (Fig. 4.7O). Thus, some of these associations of hederellids and host brachiopods provide evidence of a real, biological interaction.

Some of the rare episkeletobionts also possibly encrusted live hosts. Although auloporid corals were rare, four colonies grew from the medial region of the host towards the anterior commissure suggesting the possibility of mutualism in which corals would benefit from the host feeding currents and protect the host from predators by using possible stinging cells (Fig. 4.7E). Another colony grew parallel to its host's commissure, suggesting a commensal relationship in which the encruster may have benefited from host feeding currents (Fig. 4.7G). On another specimen (Fig. 4.7H), the hinge-proximal location of the corallites with their termination towards the postero-left lateral end of the host suggests possible live-live association with a mutualistic relation between the host and the episkeletobiont. In one instance, the tabulate coral colony, located along the anterior commissure and extending upright suggests a possible live-live association (commensal relation) between the host and the episkeletobiont, where the encruster may have benefited from host exhalant currents (Fig. 4.7D). *Cornulites* attached along the anterior commissure of one host, suggesting encrustation of a live host. Based on the encruster location preference, these instances suggest a live-live association between the host and the episkeletobiont, thus providing further evidence of real, biological interactions. For other host-encruster associations (*Ascodictyon*, fenestrate bryozoans, craniid brachiopods), the live or dead status of the host remains unknown.

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Overall, the preferred location of the most abundant episkeletobionts (microconchids, sheet bryozoans and hederellids) and the rare episkeletobionts that show possible evidence of live-live associations (*Cornulites*, auloporid corals, and tabulate corals)is for the posterior region of both dorsal and ventral valves, regardless of host species (described in next section), suggesting that larval settlement of the episkeletobionts may have occurred at the highest point of inflation on brachiopod valves, regardless of whether the brachiopod was dead or alive.

Distribution of episkeletobionts on *P. lineata* and *Pseudoatrypa* sp. A

Distribution of episkeletobionts has assisted in interpretations of life orientation of brachiopod hosts in the past (Hurst, 1974). Encrustation frequency (A_C) on hosts assessed from encrustation count (Table 4.2) were preferentially greater for dorsal valves than ventral valves for both species. This suggests that the dorsal valves probably facilitated greater encrustation due to their domal shell geometry relative to the flattened ventral valve, or possibly because the dorsal valve was "up" and so more exposed to settlement by encrusters.

Episkeletobionts may have settled randomly or non-randomly on the host surface of both valves. In this study, episkeletobiont occurrence varies among the six regions sampled on the dorsal valve of the hosts of the two species (Fig. 4.10). On dorsal valves, microconchids had no preference for posterior or anterior, sheet bryozoans preferred the posterior region over the anterior, and hederellids also preferred the posterior region. Microconchids had a high preference for postero-medial and second-most preference for the antero-medial region on dorsal valves of both species and a high preference for postero-left lateral region and secondmost preference for postero-medial region on

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ventral valves. Sheet bryozoans frequently encrusted the postero-right lateral region of the dorsal valve of both species with a secondary coverage on postero-left lateral, postero-right lateral and antero-right lateral regions (Fig. 4.9). Sheet bryozoans frequented the postero-left and postero-right lateral regions and secondarily encrusted the anteromedial and antero-right lateral regions of the ventral valves. Hederellids often occupied a vast area along the brachiopod host, often along the posterior edge (Figs. 4.7M, O) in both hosts. Although the ventral valve had a comparatively lower concentration of episkeletobionts as compared to dorsal valves, the most abundant episkeletobionts showed similar preferences for posterior versus anterior regions on both valves.

The rare episkeletobionts, *Cornulites*, auloporids and tabulate corals, preferred the anterior regions while *Ascodictyon*, fenestrate bryozoans and craniid brachiopods had no strict preference for anterior or posterior regions of dorsal valves. Tabulate corals and craniid brachiopods were absent on ventral valves, and *Ascodictyon,* fenestrate bryozoans, *Cornulites* and auloporid corals were too low in abundance to determine their preference for a specific region on the valve. Cornulitids, where present, dominated the anterior (antero-medial and antero-right lateral) commissural margin of the host valves with their aperture pointing away from the hinge margin. Auloporid corals most frequently grew their branching colonies along the anterior commissure (antero-left lateral and antero-right lateral) of dorsal valves od both host species with some occurrences in the postero-medial region (Fig. 4.9); the same pattern is also observed for ventral valves. This could simply be a preference of auloporids for settling and growing near their hosts' exhalant currents, a suggested phenomenon for other brachiopod-

auloporid associations (e.g., Shou Hsin, 1959; Pitrat and Rogers, 1978; Alvarez and Taylor, 1987; Taylor and Wilson, 2003; Zapalski, 2005). Tabulate sheet-like corals, craniid brachiopod, *Ascodictyon*, and fenestrate bryozoans were too low in abundance to determine whether they were random or non-randomly distributed along the grids of the dorsal valve of the two species. Overall, the greater abundance of episkeletobionts on the posterior region of dorsal and ventral valves may have been due to the greater chances of encruster larval settlement on the highest point of the shell geometry, simply because they are higher above the substrate and so more likely to be encountered first by settling larvae. Alternatively, episkeletobiont settlers possibly selected those regions to benefit from host feeding currents. This pattern held true for both hederellid colonies and sheet bryozoans. In addition, hederellids may have selected the posterior edges of the host to benefit from host feeding currents. Although fewer in abundance, the preference of auloporid corals, tabulate corals and cornulitids along the anterior region of the hosts suggest that these episkeletobionts may have selected that region possibly to benefit from the host feeding (exhalant) currents. In general, most episkeletobionts preferred margins of posterior and anterior areas of the valves, an encrustation pattern worth noting. Thus, this nonrandom distribution of episkeletobionts on *Pseudoatrypa* is a real, biological signal.

Inference of life orientation in *P. lineata* and *Pseudoatrypa* sp. A

Atrypids that were dorsibiconvex (dorsal valve more convex than the ventral valve) to planoconvex (dorsal valve flat and ventral valve convex), lived attached by a pedicle in their early stages of life in an almost reclining life orientation, probably with the dorsal valve closest to the substrate and ventral valve facing upwards (Alexander,

1984), and later with increasing convexity of the dorsal valve through ontogeny, they attained an inclined or a vertically upright life orientation (Fenton and Fenton, 1932) (Figs. 4.11A-C). When the pedicle later atrophied in their adult stage, they attained a hydrodynamically stable resting life position (Fenton and Fenton, 1932) by falling on their relatively flattened ventral valve with their convex dorsal valves facing upright into the water column (Fig. 4.11D), such that the commissure was subparallel to the substrate. In this resting life position, the roughly domal shape of the shell would provide an optimally streamlined condition for receiving currents from potentially any direction (Copper, 1967). Problematically for interpretation of live-live episkeletobiont-host interactions, this last orientation was also the most likely orientation for the brachiopod after death. In this study, encrustation distribution patterns and frequency suggest that, at the time when most encrustation occurred, these hosts were oriented with their dorsal valves up after pedicle atrophy. Whether these species were alive or dead at the time of encrustation cannot be discerned. Thus, our results from location preference of episkeletobionts on host species alone cannot suggest if these host species were encrusted pre- or post-mortem. In addition, these shells preserved no frills, which would have provided stability to the organism in a particular orientation. Frills, characteristic of atrypid brachiopods, are large growth lamellae that can project beyond the contour of the valves and can assist as anchors in high energy, mobile substrates (Copper, 1967). Thus predicting their life orientation without such evidence is difficult based on encrustation distribution pattern alone.
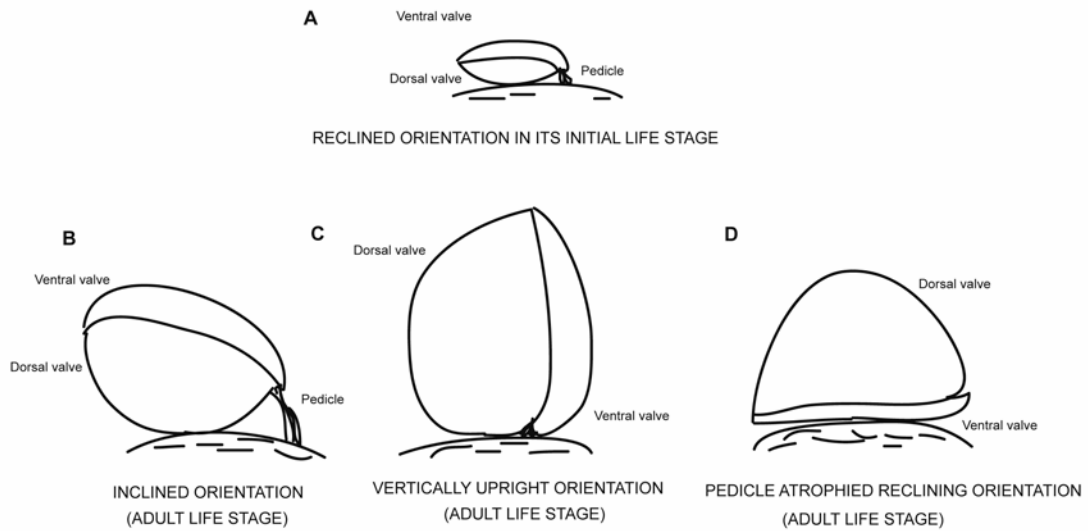
Figure 4.11: Possible stages of life and death orientation in *P. lineata* and *Pseudoatrypa* sp. A – a) initial immature life stage where the host remain attached by its pedicle to the substrate in a reclining orientation with the ventral valve up and dorsal valve down, b) mature adult life stage where the host remain attached by its pedicle to the substrate in an inclined orientation with the increasingly convex dorsal valve facing the substrate and the ventral valve facing up, c) mature adult life stage where the host remain attached by its pedicle to the substrate in a vertically upright orientation, d) mature adult stage with a reclining orientation with dorsal valve up and ventral valve down after the pedicle has atrophied – this could represent both life and death orientations in atrypids.

The difference in morphology of the two species poses the question of whether they had similar life orientations. If these species were living in soft substrates, then the shape difference in *P. lineata* (inflated pedicle valve) and *Pseudoatrypa* sp. A (flattened pedicle valve) would have had little or almost no effect in their stability patterns in life or in availability of cryptic surface area, once the brachiopod was in its dorsal-valve-up orientation. However, if these species were resting on hard substrates in the same orientation, then the inflated ventral valves in *P. lineata* would have had a greater surface area exposed along the umbo region for encruster settlement than *Pseudoatrypa* sp. A. Both species would not have had much difference in stability though because of their relatively flattened ventral valve. Given that both these species lived in similar environments, life orientations may also have been similar regardless of whether they lived on soft or hard substrates. Thus, encrustation may have occurred on the shell surface of these species specific to each of their multiple life or death orientations.

CONCLUSION

Pseudoatrypa lineata and *Pseudoatrypa* sp. A (Variatrypinae) dominated the atrypide assemblage recovered from the Lower Genshaw Formation of the Middle Devonian Traverse Group of Michigan. The two species were identified based on differences in qualitative traits and statistical shape analysis. *Pseudoatrypa lineata* differs from *Pseudoatrypa* sp. A in having a relatively smaller shell size, domal shape with a relatively shallower dorsal valve curvature, slightly convex ventral valve with inflation near the umbo, narrower hinge line, wider commissure with a pronounced gentle to steep fold, and fine-medium sized closely spaced ribs. Statistically significant shape values and

large morphological distances between the two species, supports the distinct shapes of the two species identified.

Of the 343 *Pseudoatrypa* hosts examinedfrom both species, 185 of them bore episkeletobionts. The most abundant episkeletobionts were the microconchids, hederellids and the sheet bryozoans. Auloporid corals, *Cornulites*, tabulate corals, *Ascodictyon*, craniid brachiopods, and fenestrate bryozoans were very rare. Several episkeletobionts in this study provide evidence of encrusting a live host based on the location preference of the episkeletobionts. Hederellids, auloporid corals, tabulate corals, and *Cornulites* had a live-live episkeletobiont-host relationship. The majority of other episkeletobionts, notably microconchids, sheet bryozoans, and *Ascodictyon,* were enigmatic in determining whether their relationship was with a live or a dead host. Very few epizoans crossed the commissure of the host after the host's death.

Most episkeletobionts (microconchids and sheet bryozoans) preferred *P. lineata*, despite the fact that this species is generally smaller. This differential effect in epibiosis could be due to the nature of ribbing structure (fine to medium) and greater exposed area facilitated by the shell shape of *P. lineata*. Overall, the episkeletobiont preference for one species over another strongly suggests that the overall episkeletobiont distribution was influenced by shape and ornamentation variation in atrypid samples. Abundant encrusting organisms – microconchids, sheet bryozoans and hederellids, had a preference for *P. lineata* dorsal valves. This greater abundance of episkeletobionts on dorsal valves and lower abundance on ventral valves is suggestive of most of the encrustation occurring when the host species were oriented with their convex dorsal valves up and ventral valves down with most of the ventral valve surface in contact with the sediment substrate.

Whether encrustation was pre- or post-mortem was challenging to discern for the majority of host-episkeletobiont associations as life orientation of the host would also be a hydrodynamically stable orientation of the articulated shell after death. Additionally, the most abundant episkeletobionts showed a preference for the posterior region on both dorsal and ventral valves of both species. This suggests that the posterior umbonal region may have provided an inflated surface that remained exposed, thus, favoring the settlement of most episkeletobiont larvae in that region.

The present study of the Genshaw Formation documents epibiosis on two species of atrypids, which significantly enhances our understanding of morphological influence on episkeletobiont distribution.

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CHAPTER V

SUCCESS OF GEOMETRIC MORPHOMETRICS IN DEDUCING

MORPHOLOGICAL SHAPE CHANGE PATTERNS IN PALEOZOIC ATRYPIDS

CONCLUSION

Brief inferences

This section concludes all the major findings accomplished during the course of this study. This study described the effects of evolution, ecology and environment on shell morphology of extinct Paleozoic brachiopods both in large scale and small scale temporal and spatial units. Geometric morphometric methods were used to quantify shell shape which further helped in assessment of a) morphological shape differences in atrypid brachiopods at the subfamily, genus and species level, b) correctness of a previously constructed phylogeny of atrypids, c) evolutionary rates and modes in atrypid generic and species lineages, d) correlation with environmental factors, e) influence of episkeletobionts on morphological shape, and f) derive ecology and life habit of these extinct brachiopods.

The taxonomic arrangement and phylogenetic patterns examined from morphological shape distances complies with Copper's (Copper, 1973) phylogenetic tree. Morphologies appear to be constrained in the generic lineages in the ~70 m.y. time scale with slow rate of evolution, however, diversifying selection has been acting on them. Morphology in an atrypid species lineage from a ~5 m.y. strata, exhibits stasis like patterns in the lower stratigraphic intervals with abrupt change occurring in the uppermost interval. Evolutionary rates are slow to moderate with stabilizing selection acting on the species lineage. The abrupt change in the uppermost occurrence could be due to change in environmental conditions during that time. This observed morphological pattern in the Michigan Basin when compared to the Hamilton Group of the Appalachian Basin, suggests that this pattern is unique to the Traverse Group. Morphological shape

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and ornamentation has influenced episkeletobiont settlement on Genshaw Formation atrypid brachiopod species. The greater concentration of episkeletobionts on convex dorsal valves suggests their dorsal valve facing up life orientation. The posterior region was inflated on both valves of atrypid species, thus, facilitating greater exposed area for encrustation.

Atrypid taxonomy, evolution and ecology

The study in Chapter II provides evidence for greater morphological shape distances between subfamilies than within a subfamily. This result agrees with the phylogenetic arrangement of Copper (1973); however, within genus morphological distances in time and space is as large as between genera, suggesting within group variation is greater than between group variation in atrypids, so much so, that referring individuals to a genus based on morphological shape alone is challenging. Despite the very small morphological divergences among genera within the three atrypid subfamilies, evolutionary rate and mode indicate that diversifying selection has probably been acting on them. Short term changes in individual genus lineages, gets averaged out when compared with other genera, a pattern similar to loose stasis. Distinct taxonomic entities within Atrypidae, show considerable overlap in morphological shape between them, which is also similar to a case of loose stasis. Thus, morphologies in atrypid brachiopods appear to be conserved to a great extent within the P3 EEU.

Chapter III study suggests the evolution of the *Pseudoatrypa cf. lineata* at a slow to moderate rate with morphologies lightly constrained within this species lineage. Samples from the lower stratigraphic units in the Traverse Group reflect stasis-like patterns while the uppermost stratigraphic occurrences shows greater morphological

change. This abrupt change in morphology may be attributed to the provinciality in the Michigan Basin section during that time interval. This pattern observed in Traverse Group is however, local in scope, unlike the Hamilton Group (correlatable section of Traverse Group) stratigraphic section, that shows overlap in lowermost and uppermost morphological occurrences. Overall, the qualitative similarity noted in morphologies between samples and considerable overlap in morphological variation observed between samples from successive strata suggests that these samples belong to the same species *P. cf. lineata*. The abrupt deviation of the uppermost occurrences from the mean is suggestive of greater environmental change during that time.

The study presented in Chapter IV shows that while in a very few cases, live-live associations between host brachiopods and episkeletobionts could be discerned, the abundance of most common episkeletobionts on the convex dorsal valves suggest that these brachiopods were most likely oriented with their dorsal valve facing up and ventral valve facing the substrate during life. Greater encrustation abundance on one species over another suggests that episkeletobiont settlement was influenced by variation in morphological shape and ornamentation. Their preferential settlement on the posterior region suggests that the exposed inflated area of the shells may have facilitated encrustation in those regions.

This study supports or contradicts EEU, EESU and PE model?

Paleontological data reported in this study supports the EEU model and is in partial agreement with the EESU and the punctuated equilibrium model. Morphological dataset of atrypid subfamilies and genera, show overall morphological stability in lineages within the P3 EEU. Morphological dataset of atrypid species lineage in the

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Traverse Group EESU shows stasis like patterns in the lowermost and middle stratigraphic units, however, marked by abrupt change in the uppermost unit. Morphology of this atrypid species was relatively static during most of its evolutionary history with change occurring at a later time where an associated event of environmental change occurred during that time, which could perhaps be a speciation event. Thus, the datasets from this study largely complies with the EEU and EESU model and thus, provides a great database for future researchers to compare these results with other Phanerozoic EEU and EESUs. Overall, in a broader perspective, brachiopods served as great tools to test models of EEU, EESU and punctuated equilibrium.

This morphometric dataset may also be of future assistance to researchers interested in phylogenetic reconstruction of the complex atrypid brachiopod group, where morphometric shape may be incorporated as an important character in phylogenetic coding coupled with other external and internal morphological characters.

Evolutionary ecology in Silurian-Devonian brachiopods

Ecological interactions are thought to have maintained a static adaptive landscape and prevented both the long-term establishment of exotic invading species and evolutionary change of native species within EEUs and EESUs while when disturbance exceeds the capacity of the ecosystem, ecological crashes occur and evolution proceeds at high rates of directional selection (Morris et al., 1995). In this study, species exhibited morphological stability in the Silurian and Devonian time periods. Similar stable pattern was observed in a species lineage from the Middle Devonian time which exhibited sudden change in morphology later in its life history. This change in morphology coincided with environmental heterogeneity in the Michigan Basin during that time

interval (Dorr and Eschman, 1970; Ehlers and Kesling, 1970; Wylie and Huntoon, 2003). This atrypid species lineage, thus, correlated well with environmental conditions persisting during that time, with change being evident of either an immigration or speciation event. Morphology of these shells also influenced episkeletobiont settlement.

All of these combined observations suggests that morphological shape of extinct Paleozoic atrypid brachiopods correlated well with evolutionary, ecological, and environmental factors, providing further insight into the evolutionary ecology of these extinct organisms.

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CURRICULUM VITAE
RITUPARNA BOSE

EDUCATION

- **Doctor of Philosophy (PhD)**, Geological Sciences (specialization in Geobiology and Paleontology), 2011

  Dept. of Geological Sciences, Indiana University, Bloomington, IN

  Advisor: Dr. P. David Polly

  Dissertation: Morphometric evolution of Paleozoic brachiopods: a geometric morphometric approach

- **Master of Science (MS),** Geology, 2006

  Bowling Green State University, Bowling Green, OH

  Advisor: Dr. Margaret Yacobucci

  Thesis: Epibionts on brachiopods from the Devonian Dundee formation of Ohio

- **Master of Science (MSc),** Applied Geology, 2003

  Jadavpur University, Calcutta, India, 1st class Honors

  Advisor: Dr. Ananda Deb Mukherjee

  Thesis: Study of the Physico-Chemical Parameters of the Coastal Waters in two Neighboring Rivers in the Bengal Delta: Impacts of Coastal Water Pollution

- **Bachelor of Science (BSc),** *Major*: Geology (Honors); *Minors*: Maths. & Chem., 2001

  University of Calcutta, India, 1st class Honors

RESEARCH INTERESTS

The prerequisite to developing effective strategies for conserving biodiversity is a profound understanding of the taxonomy and phylogeny of all life forms. Most studies deal with understanding the taxonomy and phylogeny of extant organisms. This is of obvious importance and biochemical or genetic approaches are often used to determine their ancestry. However, it is equally important to appreciate the significance of such studies in extinct organisms, especially in organisms that were abundant in a certain geologic era, but have subsequently dwindled or become extinct. Such studies should help to understand extinction, accurately gauge the underlying causes behind loss of biodiversity and make predictions about future distribution of biodiversity. Ideally these models should also serve as a starting point for conservation.

My primary interest lies in understanding the taxonomy and phylogeny of extinct fossil marine invertebrate groups. I also want to understand the coordinated morphological response of extinct marine invertebrate species lineages, both from an evolutionary and an ecological perspective. I apply novel techniques of geometric morphometrics to quantify morphology, taxonomy, phylogeny, evolution, ecology and paleoenvironment of invertebrates ranging from the Paleozoic era to the present time period. My past research involved investigating the effects of evolution, ecology and environment on Paleozoic brachiopods. Other research interests involve micropaleontology, sedimentary geochemistry and paleoceanography.

AWARDS AND HONORS

- **Theodore Roosevelt Memorial Grant**, American Museum of Natural History, 2009, (*$2000*)

- **Schuchert and Dunbar Grant**, Yale Peabody Museum of Natural History, 2009, (*$1000*)

- **Dissertation Year Research Fellowship**, Indiana University College of Arts and Sciences, 2010-2011, (*$18,000*)

- **Galloway-Horowitz Summer Research Grant** Recipient, Dept. of Geological Sciences, Indiana University, Bloomington, 2008 and 2009 (*$3000* and *$1500*)

- **North American Paleontology Convention (NAPC) Travel Award** Recipient, funded by BP Global Energy Group, 2009, (*$250*)

- **Graduate Fellowship**, Indiana University, 2006, (*$1000*)

- **Graduate Research Scholarship**, Jadavpur University, India, 2003, (Rs. 1000)

RESEARCH EXPERIENCE

- **Museum research**: National Museum of Natural History, Yale Peabody Museum, National Museum of Natural History, American Museum of Natural History, Michigan Museum of Paleontology at Ann Arbor, New York State Museum (Albany and New Paltz), Indiana University Paleontology Collections, 2006-present

- **Field Geology**, Sedimentology, Stratigraphy, Paleontology, etc., 1998-present

- **Science writing**: Extensive experience in reading, writing and publishing in the field of Science, 2003-present

- **Peer-review**: Reviewing, critiquing, and editing other research papers, 2003-present
- **Stereomicroscopy**, Geological specimens, 1998-present

- **Scanning electron microscopy**, Biological study, 2006-present

- **3-D laser scanner imaging, Morphometric study**, 2006-present

- ➢ **Environmental and geological modeling (ArcGIS)**, 2006-present

- ➢ **Biostatistics (use of statistical softwares R, PAST, TPS, GIMP, etc.)**, 2007-present

- ➢ **Photography** and **digitizing** samples using microscope, high resolution camera and SPOT software

- ➢ **Analytical skills in Geochemistry, Hydrogeology**, 2006-2008

TEACHING EXPERIENCE

- ➢ **Adjunct Assistant Professor**, 2011-present
  Department of Earth and Atmospheric Sciences
  The City College of New York, CUNY, New York, NY
  Course sections taught: Global Natural Hazards using GIS applications (EAS328), Earth System Science (EAS106)

- ➢ **Adjunct Assistant Professor**, 2011-present
  Department of Biological Sciences and Geology
  Queensborough Community College, CUNY, New York, NY
  Course sections taught: Physical Geology (GE101), Historical Geology (GE102), Earth Science (GE125)

- ➢ **Guest lecturer**, 2010
  Department of Geological Sciences
  Indiana University, Bloomington, IN
  Course section taught: Evolutionary Ecology (GEOL 690)

- ➢ **Principal Instructor**, 2009 and 2010
  Department of Geological Sciences
  Indiana University, Bloomington, IN
  Course taught: Earth, Our Habitable Planet (GEOL105)

- ➢ **Principal Instructor**, SU 2007
  Upward bound Program
  Smith Research Center, School of Education
  Indiana University, Bloomington, IN
  Course taught: Geology

- ➢ **Associate Instructor/Teaching Assistant,** 2006-2010
  Department of Geological Sciences
  Indiana University, Bloomington, IN
  Courses taught: General Geology, Physical Geology, Historical Geology, Theory of the Earth (Honors topic), Earth Science - Materials and Processes, Dinosaurs and their relatives, Evolution of the Earth

- ➢ **Teaching Assistant**, 2004-2006
  Department of Geology

Bowling Green State University, Bowling Green, OH
Courses taught: Historical Geology, Dinosaurs

LIST OF PUBLICATIONS

SCIENTIFIC MONOGRAPH

- ➢ **Bose, R.**, 2008. Paleoecology of brachiopods in carbonate settings. ISBN: 978-3-8364-7741-3. *VDM Verlag Dr. Muller*.

PUBLICATIONS

- ➢ **Bose, R.**, Schneider, C., Leighton, L. R., and Polly, P. D., 2011. Influence of atrypid morphological shape on Devonian episkeletobiont assemblages from the lower Genshaw Formation of the Traverse Group of Michigan: a geometric morphometric approach. *Paleogeography, Paleoecology and Paleoclimatology* 310: 427-441.

- ➢ **Bose, R.**, 2011. Integrated qualitative and quantitative approaches in distinguishing two Paleozoic brachiopod species from the middle Devonian Traverse Group of Michigan, USA. Manuscript under review in *Historical Biology*.

- ➢ **Bose, R.**, 2011. Accuracy review of qualitative taxonomic classification: implications in conserving biodiversity. Manuscript under review in *Nature communications*.

- ➢ De, A., and **Bose, R.**, 2011. Smart Science Investment in India. *Reply to* India's Vision: From Scientific Pipsqueak to Powerhouse. *Science E-letters*. http://www.sciencemag.org/content/330/6000/23.1/reply

- ➢ **Bose, R.**, De, A., Mazumdar, S., Sen, G., & Mukherjee, A. D., 2011. Comparative study of the physico-chemical parameters of the coastal waters in river Matla and Saptamukhi: impacts of coastal water coastal pollution. Manuscript in press in *Journal of Water Chemistry and Technology*.

- ➢ **Bose, R.**, 2011. Impacts of coastal water pollution in Matla and Saptamukhi rivers of the Bengal delta. Manuscript accepted in *Geochemistry International*.

- ➢ **Bose, R.**, and De, A., 2011. Arsenic contamination - unavoidable natural phenomenon or an anthropogenic crisis. Manuscript under review in *Environmental Earth Sciences*.

- ➢ **Bose, R.**, Schneider, C., Polly, P. D., and Yacobucci, M., 2010. Ecological interactions between *Rhipidomella* (Orthides, brachiopoda) and its endoskeletobionts and predators from the Middle Devonian Dundee Formation of Ohio, United states. *Palaios* 25:196-208.

- ➢ De, A., Mozumdar, S., and **Bose, R**. 2010. Taste receptors, chemical kinetics and equilibrium. *The Scepticalchymist, The Nature Chemistry Blog*. http://blogs.nature.com/thescepticalchymist/2010/06/

- ➢ De, A., Mathur, R. K., and **Bose, R.**, 2009. Can molecular biology and bioinformatics be used to probe an evolutionary pathway? *Proceedings of the National Academy of Sciences* 106:E141 http://www.pnas.org/content/106/52/E141.full.pdf+html

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- ➢ **Bose, R.**, and Schneider, C., 2010. Episkeletobionts on *Pseudoatrypa* (brachiopoda) from the lower Genshaw Formation of the Middle Devonian Traverse Group of Michigan, USA, *Geological Society of America Abstracts with Programs,* 42: 98.
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- ➢ **Bose, R.**, and Polly, P. D., 2009. Evolutionary change and geographic variation in Silurian-Devonian *Atrypa reticularis*: A geometric morphometric approach. Presented at *9th North American Paleontological Convention*.

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- ➢ Journal of Coastal Research
- ➢ Environmental Earth Sciences

IN THE NEWS

- Short story on **"Prehistoric finds"**, Mississipian spiriferids, a new finding from Mooresville locality, Indiana published in **MD times newspaper**, 2009 (8th April)
  http://www.reporter-times.com/stories/2009/04/08/news.nw-206161.sto

- Participation in **Friday Zone Episode** 'Indiana Fossils', 2009

SOCIETY MEMBERSHIPS

- Geological Society of America
- Paleontological Society