

THE NATURE OF EVOLUTIONARY RADIATIONS WITH A
SPECIAL FOCUS ON DEVONIAN CALMONIID TRILOBITES

by

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ABSTRACT

Trilobites were a diverse group of arthropods that left an extensive fossil record which are today used today to study macroevolutionary patterns and processes. A new species and form of olenelloidea trilobites (*Nevadella keelensis* n. sp. and *Esmeraldina rowei*) are described from the lower Cambrian Sekwi Formation, Canada. One particular clade of trilobites, the Devonian calmonioid trilobites of the Malvinokaffric Realm, was hailed as a classic paleontological example of an adaptive radiation. Three aspects of the radiation were examined in detail: diversification rates, biogeography, and morphological change. The rates of speciation calculated from stratigraphy were highest when sea level was lowest suggesting causal effect of abiotic factors in speciation. A phylogenetic biogeographic analysis indicated a geographically complex area, and this geographic complexity created various opportunities for speciation via allopatry through sea level changes. The geometric morphometric analysis of morphological change during the radiation did not show a signal of ecological filling. Ultimately, adaptive radiations—including some classic cases—may be caused primarily by abiotic factors of speciation.

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This is for my parents. Casuco Ito Abe and Sergio Diyodi Abe have been my greatest supporters and heroes as they have striven day in and day out to make me and my brothers happy. *Saudades*—it's a word with no direct translation in English, and yet it embodies exactly the feeling that has lingered in me from the day I stepped out of home.

I came to KU confused and yet completely clear-headed; I knew that I wanted to study the big questions of large scale evolution—I just had absolutely no idea how to go about this. As a biologist who shied away from rocks (mainly because my geologist father joked that he'd disown any geologist child of his), I was reticent to become a paleontologist. So, I was in the exceptional circumstance of being interdisciplinary and having two advisors. Two advisors for most people mean that they only have one real advisor. The truth is that I have been lucky to actually have two co-advisors: Bruce Lieberman and Ed Wiley. Being a student of two labs has also meant that I have double the academic families, and thus, double the graduate student academic siblings. Yeah, I think I got the best of both worlds, actually.

I have to thank Ed Wiley, my EEB adviser, for the hours of stimulating discussion about science, life, the universe, and everything. It was always encouraging to know that whatever question I had, I could expect an interested ear and an insightful response. If I had to pick a way to age out my academic career, it would follow in the footsteps of a fine vintage like Ed.

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CHAPTER 1

THE NATURE OF EVOLUTIONARY RADIATIONS: A CASE STUDY INVOLVING DEVONIAN TRILOBITES

INTRODUCTION

Evolutionary radiations are macroevolutionary-level phenomena that can be studied in the extant biota and the fossil record. Given that one of the basic aspects of evolutionary radiations is the production of new species, a taxic approach *sensu* Eldredge (1979) to the study of these radiations, with a focus on calculating rates of speciation and analyzing biogeographic patterns, can yield important information on the processes that drive them (Eldredge and Cracraft 1980). Further, a phylogenetic framework is very useful for studying radiations because phylogenetic information is crucial for calibrating underlying rates of diversification. Phylogenies can also be used to tease apart the relative roles that intrinsic factors (such as competition and adaptation) and extrinsic factors (such as climate and geology) play in generating evolutionary radiations. There has been some difficulty in divorcing process from pattern in studies of evolutionary radiations; this is apparent by the pervasive usage of the term *adaptive radiation* (Eldredge and Cracraft 1980, Givnish and Sytsma 1997, Schluter 2000, Vogler and Goldstein 1997). While it is important to examine the intrinsic mechanisms of divergence, such as adaptation, studies of evolutionary radiations have often overlooked the extrinsic factors—the geological,

climatic, and environmental aspects which are key mechanisms to speciation (Cracraft 1982a, Mayr 1942). One important way of examining extrinsic factors is to consider the biogeographic patterns in the radiating clade. In particular, geographic range is known to affect speciation and extinction rates and is in turn very much affected by environmental and geological changes (Rode and Lieberman 2005). Here we use phylogenetic information in concert with biogeographic and evolutionary rate studies to analyze a clade of Devonian trilobites, the calmoniids, that has been hailed as a classic example (see Eldredge and Cracraft, 1980 and Lieberman, 1993) of an adaptive radiation preserved in the fossil record.

Biogeographic analyses, when performed in a phylogenetic context, make it possible to infer mode of speciation and determine the relative prevalence of vicariant differentiation or range expansion associated with diversification. Ultimately, if a primary reason for rapid diversification is a multitude of allopatric events, it may suggest that it was not adaptive phenomena that solely or even primarily motivated the radiation, although at all times the organisms must have maintained their adaptive character.

Analyses of taxonomic rate patterns during evolutionary radiations are also useful. The general pattern of evolution can be deconstructed into components of evolutionary rates (Gilinsky and Bambach 1987, Rode and Lieberman 2005, Sepkoski 1998, Stanley 1979, Vrba 1987). While an increase in taxonomic diversity can be caused by unusually high rates of speciation, normal rates of speciation coupled with exceptionally low rates of extinction could also cause such patterns. Thus far, however, it appears that evolutionary rates during evolutionary radiations are generally associated with high speciation rates, at

least early in the radiation, and these subsequently decline, often quite rapidly (Eldredge and Cracraft 1980, Hulbert 1993b, Lieberman 2001b, Lieberman et al. 1991).

Eldredge and Cracraft (1980) identified a number of patterns expected in a clade undergoing an adaptive radiation: rapid appearance of numerous closely related species; monophyletic status of the clade; confinement to an endemic area; and high morphological diversity. These prerequisites all appear to be present in the calmoniids. In particular, they are a morphologically diverse group of acastid trilobites endemic solely to the Malvinokaffric Realm (Fig. 1.1) (Eldredge and Ormiston 1979). This study focuses on a diverse monophyletic clade within the calmoniids—the *Metacryphaeus* group—which contains over 40 species; furthermore, they have been subjects of cladistic analysis (Lieberman 1993, Lieberman et al. 1991).

Here, we characterize the dynamics of speciation and extinction rates in this clade of calmoniids during its evolutionary radiation. Further, we determine the role biogeographic and geologic factors played in motivating its diversification. The calmoniid radiation appears to follow a pattern of explosion followed by evolutionary quiescence, and these dynamics seem to be related to the geographic and geologic setting of their area of endemism: the Malvinokaffric Realm. This suggests that adaptation did not play the formative role in this radiation, although clearly it was involved at some level.

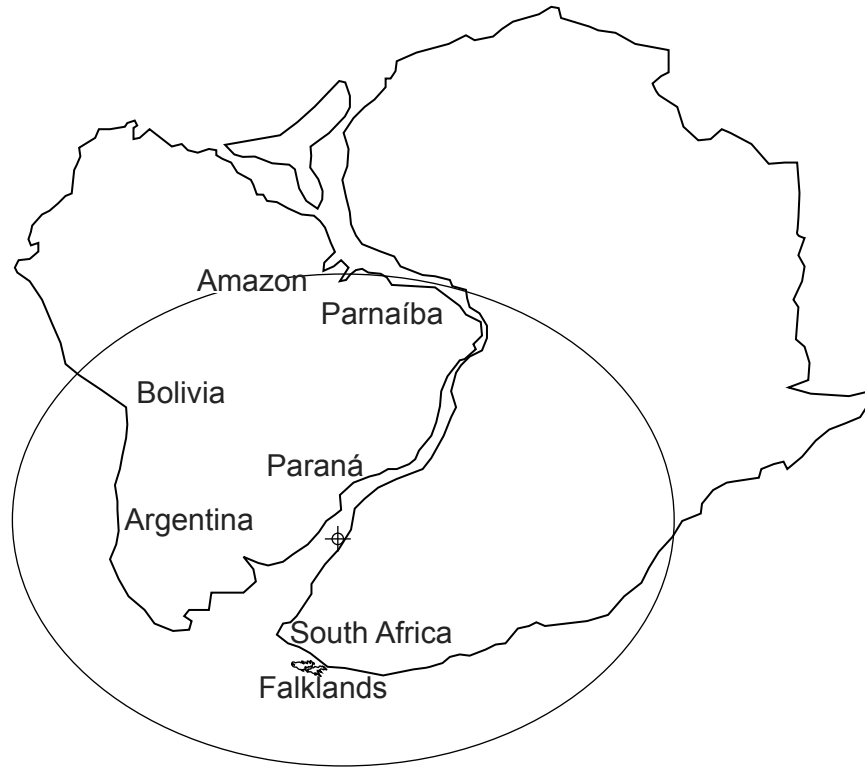


FIGURE 1.1. Map of the Malvinokaffric Realm ca. 400 Ma (modified from Cocks and Torsvik 2002) with the position of the South Pole indicated by a cross. Position of areas used in the biogeographic analysis of Devonian trilobites also shown.

MATERIALS AND METHODS

Phylogeny of Metacryphaeus group

The analyses of paleobiogeography and evolutionary rates utilized the phylogenetic framework of the *Metacryphaeus* group calmoniids presented in Lieberman *et al.* (1991) and Lieberman (1993). More recently described species were appended to the phylogeny, in particular: *Metacryphaeus kegei* and *M. meloi* from the Parnaíba Basin of Brazil (Carvalho *et al.* 1997); *M. australis* from the Paraná Basin of Brazil (Carvalho and Edgecombe 1991); *Eldredgeia eocryphaeus*, *Wolfartaspis liebermani*, and the genus *Gemellus* from the *Scaphocoelia* assemblage and Icla Formation of Bolivia (Carvalho *et al.* 2003); *Talacastops zarelae* and *T. sp. nov. A* from the Talacasto Formation of Argentina (Edgecombe *et al.* 1994); and *M. caffer* from the Fox Bay Formation of the Falkland Islands (Carvalho 2006). The resulting phylogeny incorporated 44 species (Fig. 1.2).

Paleobiogeography

The method used in this study was a modified version of Brooks Parsimony analysis (hereafter mBPA) which can capture information about congruent speciation events resulting from either a contraction of distributional range (vicariance) or range expansion (Lieberman 2000, Lieberman and Eldredge 1996). This method has been

described in detail in Lieberman and Eldredge (1996), Lieberman (2000, 2003, 2005) and Maguire and Stigall (2008). A brief discussion is given here and the interested reader is referred to these papers and the references therein for additional discussion. This historical biogeographic method discovers relationships between biogeographic areas and determines whether speciation events coincide with geologic processes separating or joining areas, such as tectonic events and changes in relative sea level.

mBPA replaces the terminal taxa of a cladogram with their area of occurrence and then performs unordered Fitch parsimony optimization on each of the ancestral nodes. Two matrices can be constructed that are used to uncover evidence for congruence in both vicariance (Table 1.1) and geodispersal (Table 1.2) respectively. A parsimony analysis is then conducted on the matrices using equally weighted, ordered, multistate characters. In this particular case, the exhaustive search option of the PAUP* 4.0b10 software was utilized to determine the most parsimonious cladogram(s) (Swofford 2002). Then, a bootstrap analysis with 1000 replicates was used to test the robustness.

The areas used in the biogeographic analysis were defined based on geological criteria and history of endemism of the basins (Fig. 1.1). In particular, because they contained large numbers of endemic taxa, Eldredge and Ormiston (1979) recognized several valid biogeographic regions within the Malvinokaffric Realm, and our area designations basically follow theirs. However, the Sub Andean areas in Bolivia and southern Peru were considered as a single area, as these locations have strong geological associations and co-occurring endemic species (Eldredge and Ormiston 1979, Isaacson and Sablock 1988). While some Eastern Americas Realm faunal elements have been found in

the middle Amazon Basin (Boucot 1988) and in the Parnaíba Basin, typical Malvinokaffric Realm calmoniids are also found there (Copper 1977), and thus for this analysis the areas were considered discrete and separate biogeographic units within the Malvinokaffric Realm.

Taxonomic Rates

A phylogeny can be used to constrain the timing of cladogenetic events if it is assumed that sister-taxa diversify concurrently (Edgecombe 1992, Smith 1994). As there are no grounds for inferring that any one of the taxa considered was the direct ancestor of any other taxon, this assumption seems reasonable (cf. Engelmann and Wiley 1977). Speciation and extinction rates were calculated (Table 1.3) using a standard birth-death exponential growth model; (Stanley 1979) was an early advocate for the applicability of the exponential model and it has been used extensively with fossil data to study speciation and extinction rates (Lieberman 2001b, Weiss-Schneeweiss et al. 2006). In our study the methods of taxonomic rate calculations proposed by Foote (2000a, 2000b) were applied as these measure diversity crossing interval boundaries, providing a more seamless estimation of rate over time that is unaffected by interval lengths and presence of singleton taxa. Artificial edge effects (see Foote 2000b) are unlikely to play an important role in the origination and extinction rate values derived herein because the taxa being analyzed originate in the Lochkovian and disappear in the Frasnian.

TABLE 1.1. Matrix derived from biogeographic character states for a modified Brooks Parsimony analysis for geodispersal patterns. The ancestor denotes the ancestral biogeographic condition and served as an outgroup. The other locations used in the biogeographic analysis are discrete areas in the Malvinokaffric Realm. Character states 1 and 2 are derived states. The 80 characters refer to the nodes within the phylogenetic tree from the root to the leaves.

	10	20	30	40	50	60	70	80
Ancestor	000000000	000000000	000000000	000000000	000000000	000000000	000000000	000000000
Bolivia	110011111	111111111	111111111	111111111	111111111	111111111	111111111	110011111
Argentina	111000000	200000000	000000000	000000002	020000000	000000000	000000000	000000000
Falkland	000000000	000000000	000000000	000000000	000000000	000000000	000000021	100100000
S. Africa	110111000	000002000	000000000	000000000	000000000	000000000	000000000	200000000
Paraná	000000000	000000000	000000000	000000000	000000000	000000000	000000002	000000000
Parnaíba	000000000	000020000	000000000	000000000	000000000	000000000	000000021	011000002
Amazon	000000000	000200000	000000000	000000000	000020000	200002000	000000000	000000000

TABLE 1.2. Matrix derived from biogeographic character states for a modified Brooks Parsimony analysis for vicariance patterns. The ancestor denotes the ancestral biogeographic condition and served as an outgroup. The other locations used in the biogeographic analysis are discrete areas in the Malvinokaffric Realm. Character states 1 and 2 are derived states. The 80 characters refer to the nodes within the phylogenetic tree from the root to the leaves.

	10	20	30	40	50	60	70	80
Ancestor	000000000	000000000	000000000	000000000	000000000	000000000	000000000	000000000
Bolivia	111121211	011000111	111111111	111111110	101101111	011110111	111111110	021111110
Argentina	112110000	100000000	000000000	000000001	010000000	000000000	000000000	000000000
Falkland	000000000	000000000	000000000	000000000	000000000	000000000	000000010	111200000
S. Africa	111221100	000001000	000000000	000000000	000000000	000000000	000000000	100000000
Paraná	000000000	000000000	000000000	000000000	000000000	000000000	000000001	000000000
Parnaíba	000000000	000010000	000000000	000000000	000000000	000000000	000000010	022100001
Amazon	000000000	000100000	000000000	000000000	000010000	100001000	000000000	000000000

TABLE 1.3. Speciation and extinction rates were calculated using a standard birth-death exponential growth model.

	N _o	N _f	#sp	#ext	t	Total rate of diversity Δ (r)			Rate of speciation (S)			Rate of extinction (E)			
						<u>GSA</u>	<u>Kauffm an</u>	<u>GSA</u>	<u>Kauffman</u>	<u>GSA</u>	<u>Kauffma n</u>	<u>GSA</u>	<u>Kauffma n</u>	<u>GSA</u>	<u>Kauffma n</u>
Famennian	2	2	0	2	<u>GSA</u> 15.3	<u>Kauffm an</u> 15.4	-	-	-	-	-	-	-	-	-
Frasnian	5	5	0	3	10.8	7.6	-0.085	-0.121	0.000	0.000	0.085	0.000	0.000	0.085	0.121
Givetian	22	22	0	17	6.5	4.4	-0.228	-0.337	0.000	0.000	0.228	0.000	0.000	0.228	0.337
Eifellian	35	35	0	13	5.7	3.8	-0.081	-0.122	0.000	0.000	0.081	0.000	0.000	0.081	0.122
Emsian	36	36	0	1	9.5	17.2	-0.003	-0.002	0.000	0.000	0.003	0.000	0.000	0.003	0.002
Pragian	8	56	48	20	4.2	3.2	0.358	0.470	0.463	0.608	0.105	0.608	0.105	0.138	0.138
Lochkovian	1	32	31	24	4.8	5.8	0.433	0.359	0.722	0.598	0.289	0.598	0.289	0.239	0.239

The number of first and last appearances was tabulated using the stratigraphic occurrence data for each species (Fig. 1.3). Cladogenesis was also interpreted to involve some extinction, following the discussion above, as the ancestor ceases to exist after the speciation event. Correlation of the different sections was obtained from temporal stratigraphic correlations of palynomorphs (Grahn 2005, for South American basins) and event stratigraphy (Cooper 1986, for South Africa and Falkland). Consensus on the absolute chronology of the Devonian is still debated; thus, to avoid any potential biases and to increase the potential resiliency of the results, a number of different time scales were used, in particular, House and Grady (2004), Tucker *et al.* (1998), and Kaufmann (2006).

RESULTS

Biogeographic analysis

The phylogeny with biogeographic states mapped to terminals and nodes indicated most speciation events in calmoniids transpired within individual areas of endemism. Many of the transitions between nodes on the tree are associated with no major changes in geographic range (Fig. 1.2), at least not at the scale of major tectonic barriers and areas of endemism. Whether this actually represents sympatric differentiation, or smaller scale within-region vicariance, could not be determined at this time. However, there is some evidence for vicariance and geodispersal (see Fig. 1.2) as indicated by contractions and

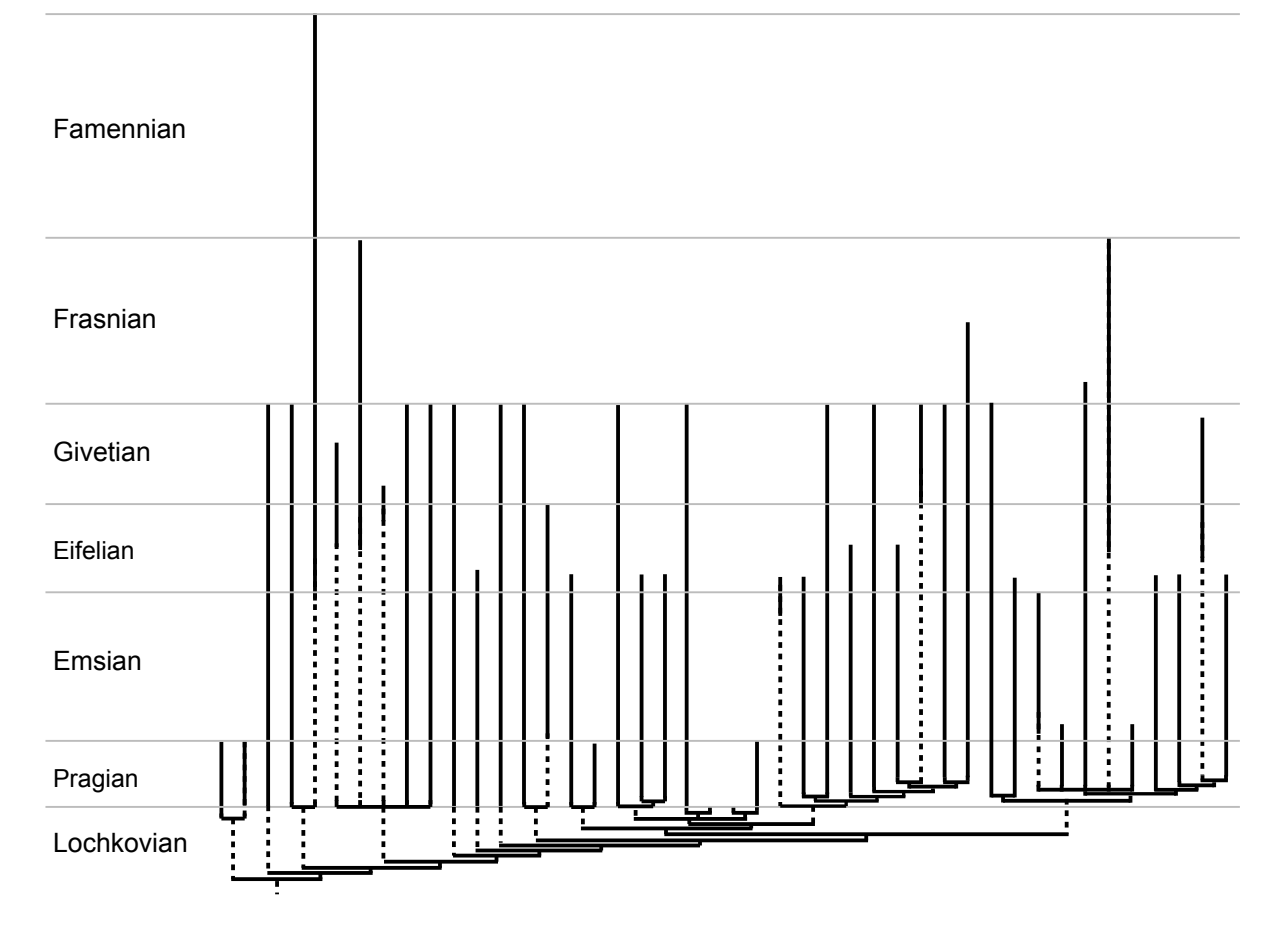


FIGURE 1.3. Phylogeny of the *Metacryphaeus* group calmoniid trilobites modified from Lieberman et al. (1991) and Lieberman (1993). Solid lines indicate known occurrence of species sampled in the fossil record. Dotted lines indicate inferred origination based on the ghost-lineage methodology (Edgecombe 1992b, Smith 1994) of sister taxa divergence. Devonian time calibrations were obtained through radiometric dating (House and Gradstein 2004, Kaufmann 2006, Tucker et al. 1998) and stratigraphic correlations were based on analysis of palynomorph and event stratigraphy (Cooper 1986, Grahn 2005).

expansions (respectively) of the geographic regions occupied by ancestors and their descendents.

Application of mBPA to the data matrix in Table 1.1 yielded a single best vicariance tree with a number of well-resolved branches (Fig. 1.4). There were 12 parsimony informative characters and the tree length was 93 steps, with a consistency index of 0.936, a retention index of 0.739, and a $g_I = -0.62$. The g_I value supports a left skewed tree distribution at a $p = 0.01$ (Hillis and Huelsenbeck 1992). A bootstrap analysis showed high support for area relationships between Bolivia and South Africa, Argentina and Bolivia-South Africa, and the Falklands and Parnaíba Basin. The parsimony analysis of the geodispersal matrix (Table 1.2) produced one best tree of length 106 steps with a consistency index of 0.877, a retention index of 0.48, and a $g_I = -0.265$. The g_I statistic also shows a left skewed tree distribution, though the p -value does not show statistical significance (Hillis and Huelsenbeck 1992). Only the Falkland and Parnaíba branch and the Bolivia-South Africa-Argentina branch had a bootstrap support value over 50 on the geodispersal tree. Except for the failure of Paraná to consistently associate with the Parnaíba-Falkland branch in the vicariance tree, the vicariance and geodispersal area cladograms are identical. (Note, the two trees are not in conflict as the position of Paraná in the vicariance tree simply reflects absence of evidence.) When the vicariance and geodispersal trees are similar, it suggests the biogeographic processes controlling vicariance are the same as those governing geodispersal (Lieberman 2000, 2003, Lieberman and Eldredge 1996). This typically implicates cyclical processes that may at times cause vicariance and other times geodispersal. In the case of marine invertebrates

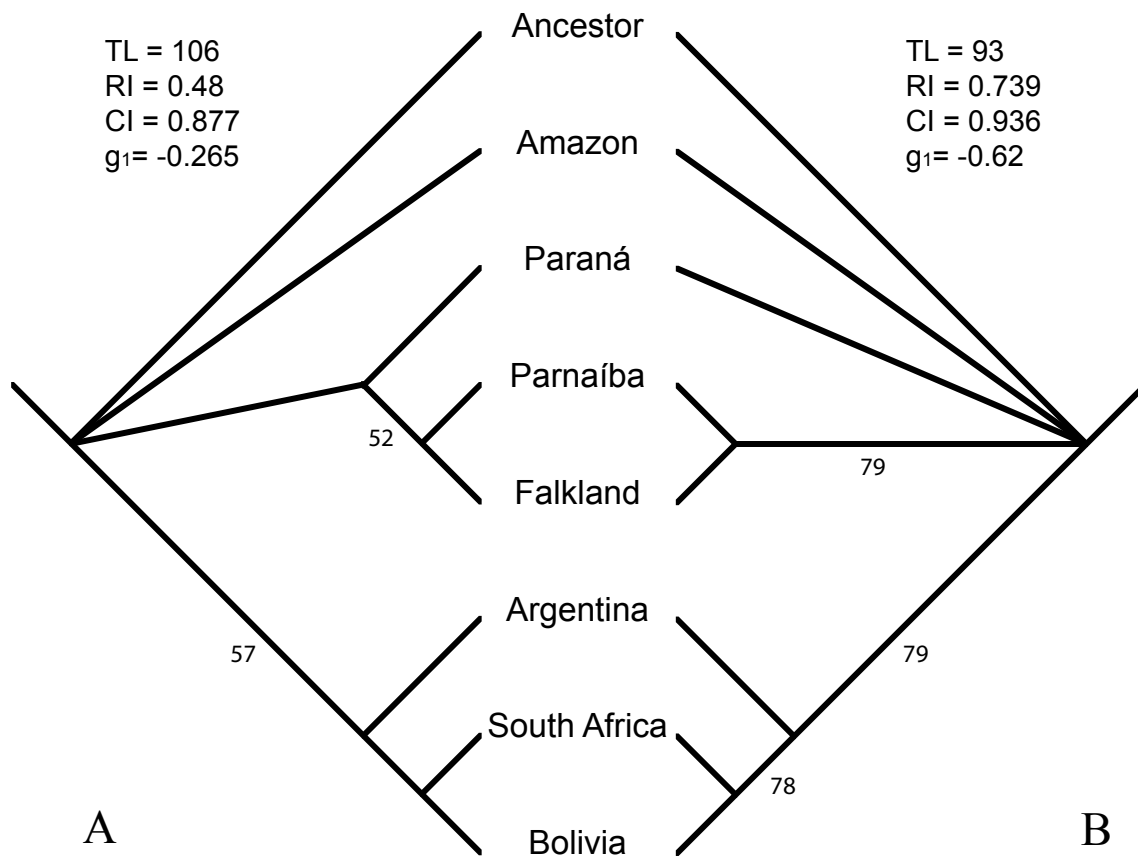


FIGURE 1.4. Results of a modified Brooks Parsimony Analysis examining the biogeographic relationships of areas within the Malvinokaffric Realm during the Devonian. Numbers on branches indicate bootstrap support over 50. A, Area cladogram derived from analysis of the geodispersal matrix. B, Area cladogram derived from analysis of the vicariance matrix. Abbreviations TL, RI, CI, g_1 are used for tree length, retention index, consistency index, and skewness.

like trilobites, those cyclical processes likely involved repeated episodes of sea level rise and fall (Lieberman 2000, 2003, 2005, Lieberman and Eldredge 1996).

Taxonomic rates

There are only two stages in the Devonian over which any speciation transpires. Results for speciation rate basically agree for the Kaufmann (2006) and House and Gradstein (2004) timescales. In particular, in both cases there is a very high initial speciation rate during the Lochkovian, which declines during the second stage of the Devonian. By the Emsian speciation rate falls to zero. Using dates from Tucker *et al.* (1998), speciation rate starts lower, and plateaus during the Early Devonian (Fig. 1.5).

The different timescales show very similar patterns in extinction rate (Fig. 1.6). The initial moderate extinction rate is—for the most part—due to cladogenetic extinction. There are no recorded last appearances during the Emsian, but the rate of extinction increases during the Middle Devonian, peaks during the Givetian and stays moderately high into the Late Devonian.

The pattern of diversity change during the evolutionary radiation appears to be divided into three discrete phases: initial high speciation rate for the early Devonian; an interval of stability with no speciation or extinction events for about 9-17 Ma during the Emsian; and a final phase of no speciation rate coupled with moderate extinction rate.

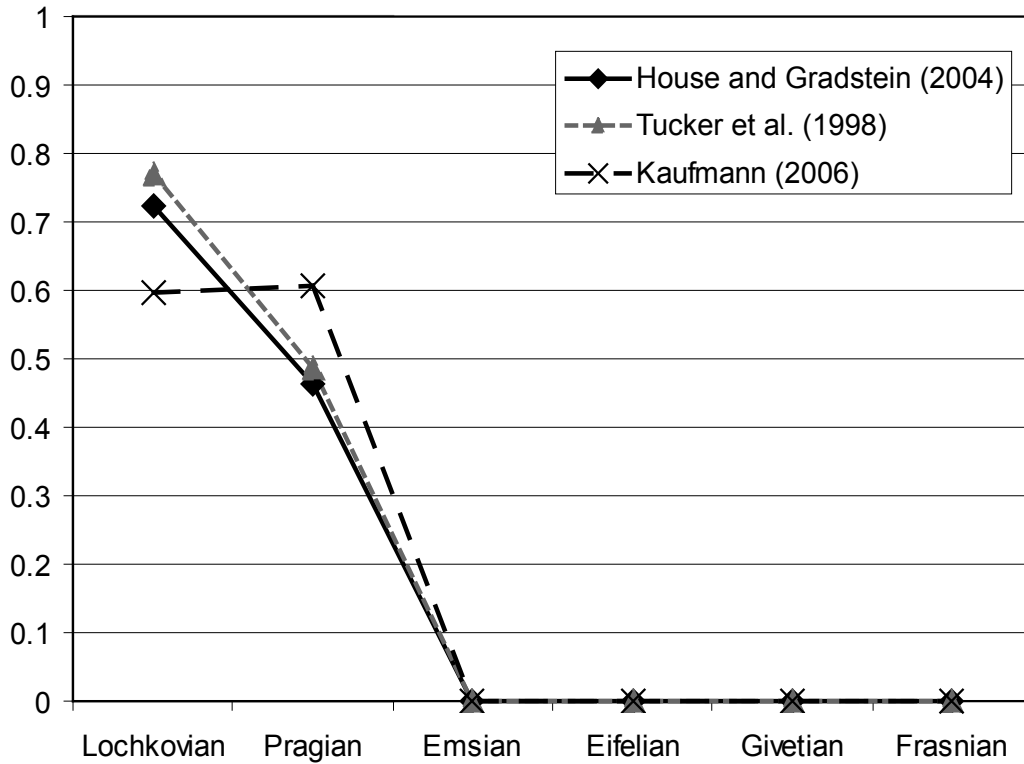


FIGURE 1.5. Speciation rates of calmoniid trilobites plotted against stages of the Devonian. Rates were calculated based on a birth-death model using the first appearance of fossil taxa coupled with sister-taxa divergence to constrain the origination times to a phylogeny. Calculations were performed using three different Devonian time scales: Tucker et al. (1998); House and Gradstein (2004); and Kaufmann (2006).

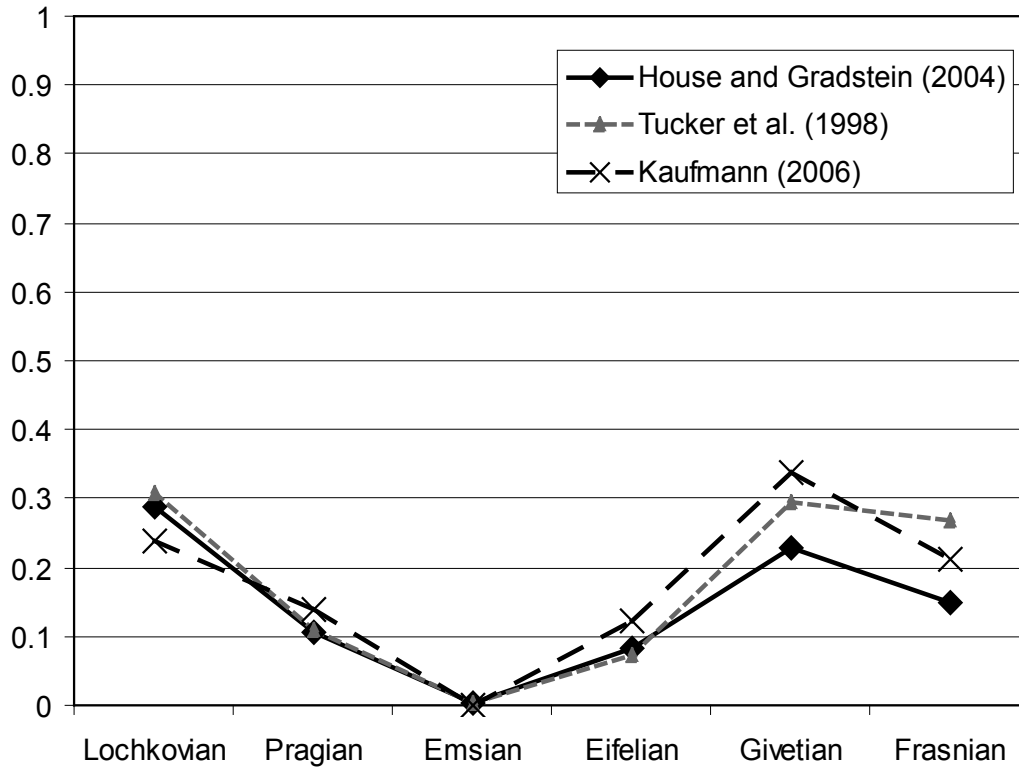


FIGURE 1.6. Extinction rates in calmoniid trilobites plotted against stages of the Devonian. Rates were calculated based on a birth-death model and the inferred appearance of fossil taxa as shown in Figure 4. Calculations were performed using three different Devonian time scales: Tucker et al. (1998); House and Gradstein (2004); and Kaufmann (2006).

DISCUSSION

We have employed a taxic approach (*sensu* Eldredge 1979) to study an evolutionary radiation, emphasizing analyses of rates of speciation and biogeographic patterns. Results using mBPA suggest that the context of speciation events in the Malvinokaffric Realm was crucial for this particular radiation: Earth history factors played a fundamental role in the radiation, with a complex geographic setting, and changing climatic factors overlaid, setting the stage for the calmoniid radiation. As such, the radiation seems to represent an excellent example of species sorting mediated by Vrba's (1984) effect hypothesis—processes operating at the organismal level initiates species diversification within the clade. In particular, early on there were multiple opportunities for geographic barriers to form and fall as sea level fell and rose, allowing for vicariance and geodispersal to effectively multiply opportunities for speciation events in trilobites manifold (Fig. 1.7a and b). Our biogeographic results indicate strong signal in both the geodispersal and vicariance matrices, which suggests some overlying congruent geological or climatic processes were influencing the radiation. Further, we note that the strong support for a close association of Bolivia, South Africa, and Argentina (Fig. 1.2) in the area cladograms makes sense given the geographic position of these basins during the Devonian (Isaacson and Sablock 1988). (The only divergent relationship in this regard is the position of the Falkland Islands. Although they grouped biogeographically with the Parnaíba Basin, the Falklands may have been on the eastern side of South Africa at the time [Torsvik and Cocks 2004]). Moreover, most of the speciation events appeared to have occurred *in situ* in Bolivia, probably involving repeated vicariance and geodispersal within the smaller basins contained therein (although there were also geodispersal and

vicariance events between Bolivia and other parts of the Malvinokaffric [Fig. 1.2]). Bolivia seems to have served as the biodiversity hotspot of the Malvinokaffric Realm. Others have advanced the idea that evolutionary radiations involve a centralized biodiversity hotspot (Erwin 1979); however, these ideas have usually focused on adaptive shifts as the mode, without considering allopatric speciation as the primary mechanism (Vogler and Goldstein 1997).

Not only do the congruent patterns in the individual area cladograms indicate Earth history factors played a key role in the radiation, but the similarity between the vicariance and geodispersal trees suggest it was repeated episodes of sea level rise and fall that played the primary role. This provides a means for explaining why the radiation happened, but it also provides a means for explaining why the evolutionary rates subsequently subsided and the radiation ended. In particular, not only were there several major episodes of sea level rise and fall in the Devonian, but overall, relative sea level was increasing throughout the Devonian. (Cooper 1986, Johnson et al. 1985).

A breakdown of the taxonomic rates during the diversification of the *Metacryphaeus* group shows high initial speciation rates for the first 9 myrs, followed by no speciation events (Fig. 1.5). It appears that speciation rates were highest when sea level was relatively low. In a sense, oscillations in sea level, facilitated by oscillations in climate and geological changes, may be what was turning on and turning off the speciation faucet. However, when sea level became too high (Fig. 1.7c), subsequent oscillations in sea level no longer caused geographic isolation and vicariance and formerly endemic regions stayed homogenized and the speciation faucet remained in the off position.

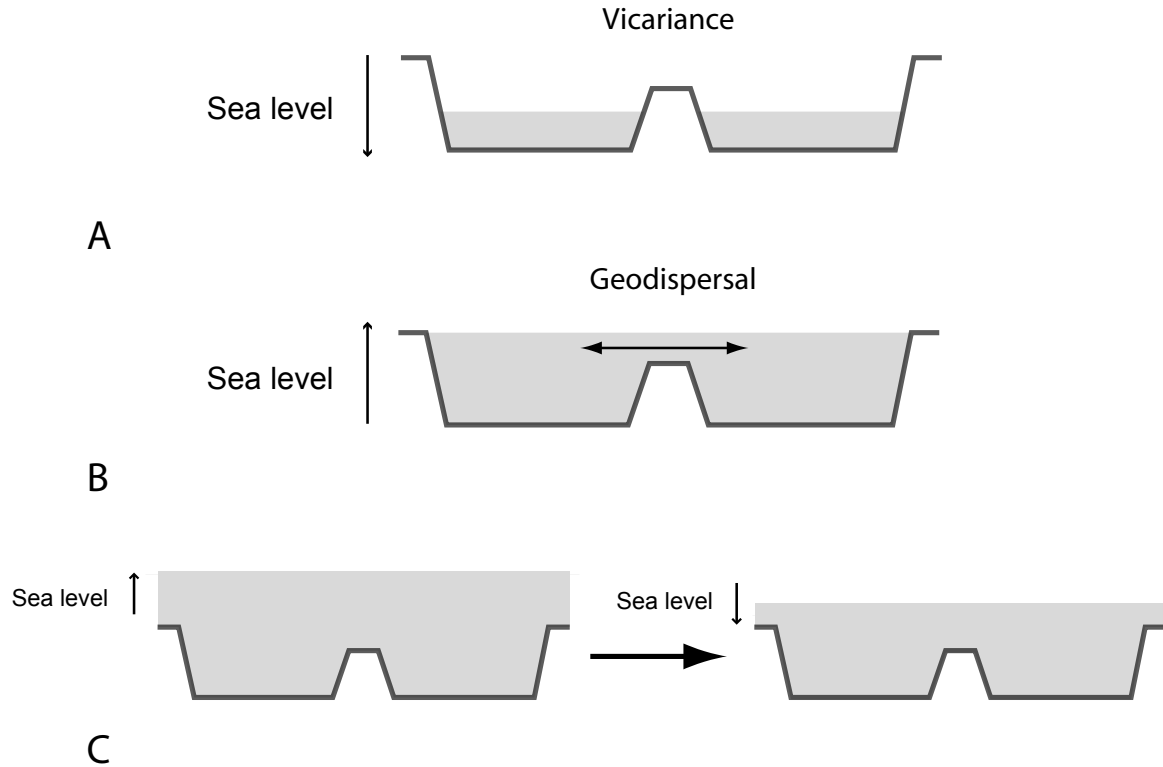


FIGURE 1.7. A model showing how sea-level changes might affect biogeographic patterns and episodes of speciation in species such as trilobites inhabiting different marine basins. Regression allows for physical separation of the basins leading to vicariance (A). Transgression joins formerly isolated basins and allows for range expansion of taxa leading to geodispersal (B). If overall sea-level becomes too high, sea level rise and fall may no longer be sufficient to cause vicariant events (C).

Notably, a pattern of initial peak in rates of evolution, with subsequent decline, was recognized previously in the calmoniids (Eldredge and Cracraft 1980) and has been described for other evolutionary radiations. In these other radiations, this was generally explained by invoking the initial filling of ecological space in an adaptive radiation sense (Phillimore and Price 2008, Simpson 1953). The types of taxa considered in our study make it very difficult to consider the ecological aspects of the radiation, and we would not preclude these as playing some role in the radiation. However, biogeographic patterns in the calmoniids also indicate the important influence of external physical factors.

The flip side of the radiation is of course the demise of the calmoniid group. Extinction rates in the calmoniids show bimodality with time. Early on in the Devonian, extinction rates were high. However, this was due to cladogenetic extinction associated with divergence of ancestral lineages. Extinction falls to zero in the early part of the Middle Devonian, and then there is an uptick later in the Middle and in the Late Devonian (Fig. 1.6). Over these intervals, rates of extinction involved true lineage disappearance. Still, these extinction rates in the late Middle Devonian and Late Devonian can only be considered moderate and were not dramatically high (Lieberman 2001b, e.g. Stanley 1979, Vrba 1987). It would appear that it was the absence of speciation after the Early Devonian, coupled with moderate extinction that caused the ultimate demise of the calmoniids. This matches a more general pattern documented for the Late Devonian biodiversity crisis: it was not precipitated by a dramatic increase in extinction rates, but instead by a decline in speciation rates associated with a decline in geographic provincialism (McGhee 1996b, Rode and Lieberman 2004, 2005). This pattern may be due to the lack of opportunities for

allopatric differentiation caused by the global rise in relative sea level (Rode and Lieberman 2004, 2005).

Given the apparent association between external physical factors—sea level changes and climate—and speciation rates in this radiation, this vindicates the important role these play in the history of life (Eldredge 1989, Lieberman 2000, Vrba 1980). Often, the adaptive character of evolutionary radiations is stressed (though not always, e.g. Cracraft 1982a, Eldredge and Cracraft 1980, Lieberman 1993, Platnick 1992) and clearly these must have played some role. Ultimately, though, “adaptive” radiations are also likely a product of geologic complexity coupled with recurrent union and separation of areas causing multiple allopatric events. Subsequent morphological divergence may have caused the uniquely adapted forms, with apparent adaptive patterns, but an initial cause is the abiotic processes facilitating isolation.

This examination of an evolutionary radiation finds important associations between abiotic processes and rapid speciation through multiple events of geodispersal and vicariance in a geographically complex area. A future promising avenue for research may be examining other evolutionary radiations to take into account the geographic setting and abiotic factors affecting speciation via opportunities for allopatry.

CHAPTER 2

NEW INFORMATION ON OLENELLINE TRILOBITES FROM THE EARLY CAMBRIAN SEKWI FORMATION, NORTHWESTERN CANADA

INTRODUCTION

Olenellines are a diverse and biogeographically, biostratigraphically and evolutionarily significant Early Cambrian trilobite group. The Lower Cambrian of the Mackenzie Mountains, Canada, has yielded a number of species of olenelline trilobites described in Fritz (1972, 1973). This study presents new material collected from N63°31.160' W 128°10.285', approximate altitude 1768 meters (Fig. 2.1), the *Nevadella* zone of the Early Cambrian (Branchian) Sekwi Formation, Mackenzie Mountains, Northwestern Territories, Canada. The material of interest hails from a locality that has facies of a distinctive lithology relative to other localities in the Sekwi Formation: they are principally red siltstones whereas the Sekwi Formation regionally is composed principally of shallow to deep-water carbonate interbedded with black shale (Fritz 1976a, 1976b; Krause and Oldershaw 1978; Dilliard et al. In press). Material occurs in the units 230-240 meters above the base of the section (Fig. 2.2). Olenelline genera known from the *Nevadella* zone of the Sekwi Formation include the eponymous *Nevadella* Raw, 1936, along with *Bradyfallotaspis* Fritz, 1972, and *Holmiella* Fritz, 1972.

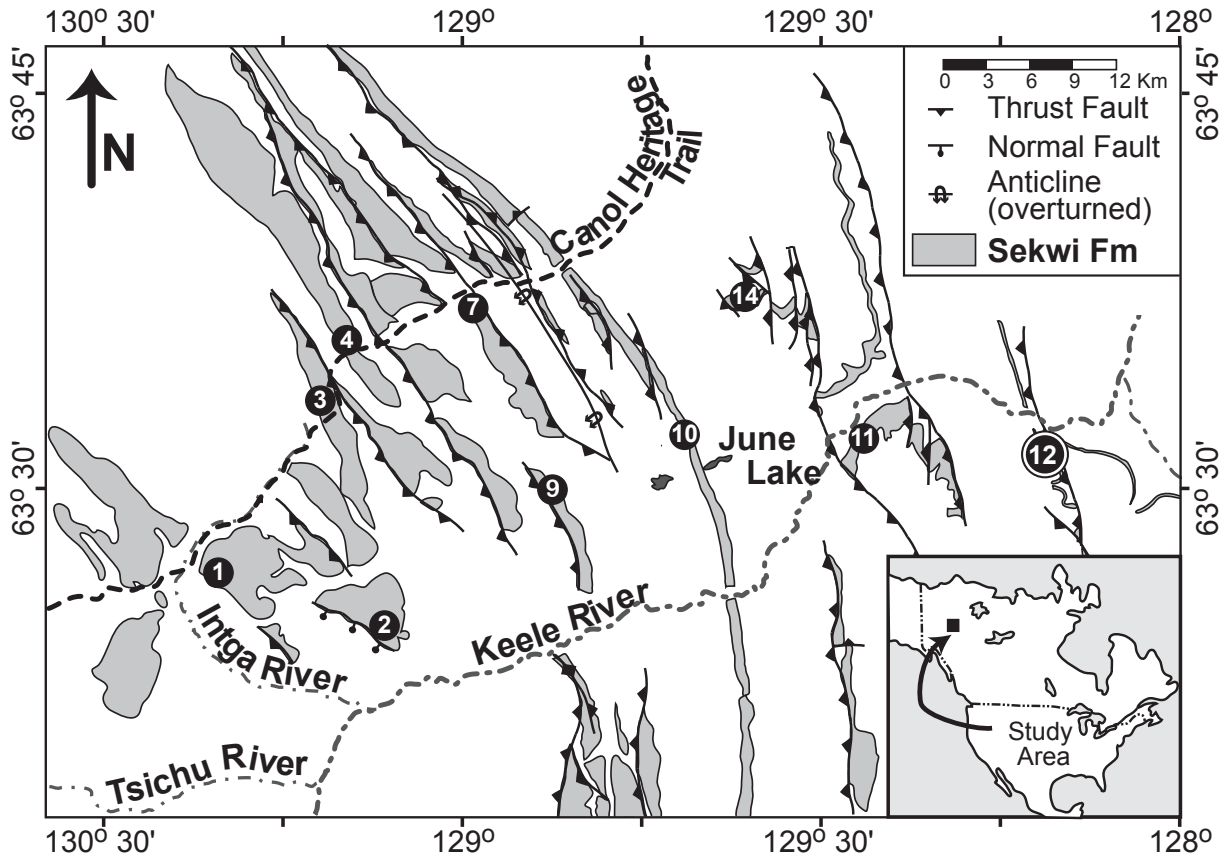


FIGURE 2.1. Geographic position of locality, indicated by a circle, which lies approximately 30 km east of the locality discussed and figured in Randell et al. (2005).

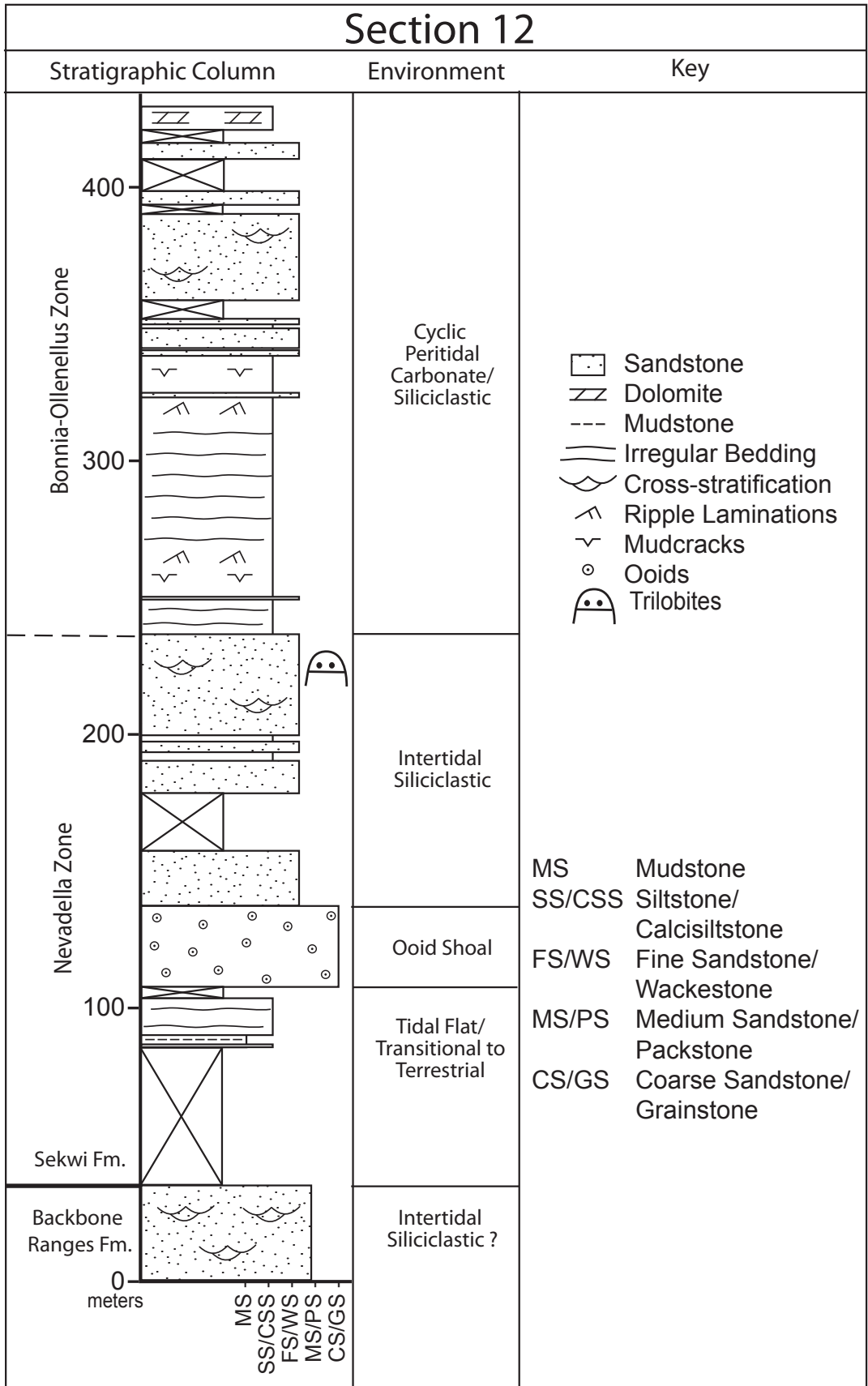


FIGURE 2.2. Measured stratigraphic section of Lower Cambrian Sekwi formation at locality containing new material.

SYSTEMATIC PALEONTOLOGY

Terminology used follows Lieberman (1998, 1999, 2001). Specimens are housed in the Prince of Wales Northern Heritage Center, Yellowknife, Northwest Territories, Canada (PWNHC) and the University of Kansas Natural History Museum and Biodiversity Institute, Division of Invertebrate Paleontology (KUMIP). Quotation marks around taxon name denotes a paraphyletic group, following Wiley (1979).

Order Redlichiida Richter, 1932

Suborder Olenellina Walcott, 1890

Superfamily “Nevadioidea” Hupé, 1953

Genus *Nevadella* Raw, 1936

Nevadella keelensis new species

(Figs. 2.3c and 2.3d)

= ?*Nevadella* sp. 2 Fritz, 1972, p. 24, pl. 5, figs. 12-15.

TYPES: Holotype cephalon KUMIP 319926 and paratype PWNHC 2009.20.47 from locality given above (Figs. 2.1, 2.2).

OTHER MATERIAL EXAMINED: Fragmentary cephalata PWNHC 2009.20.48 and 2009.20.49 from same locality.

ETYMOLOGY: Named after the Keele River, the large river that the locality overlooks.

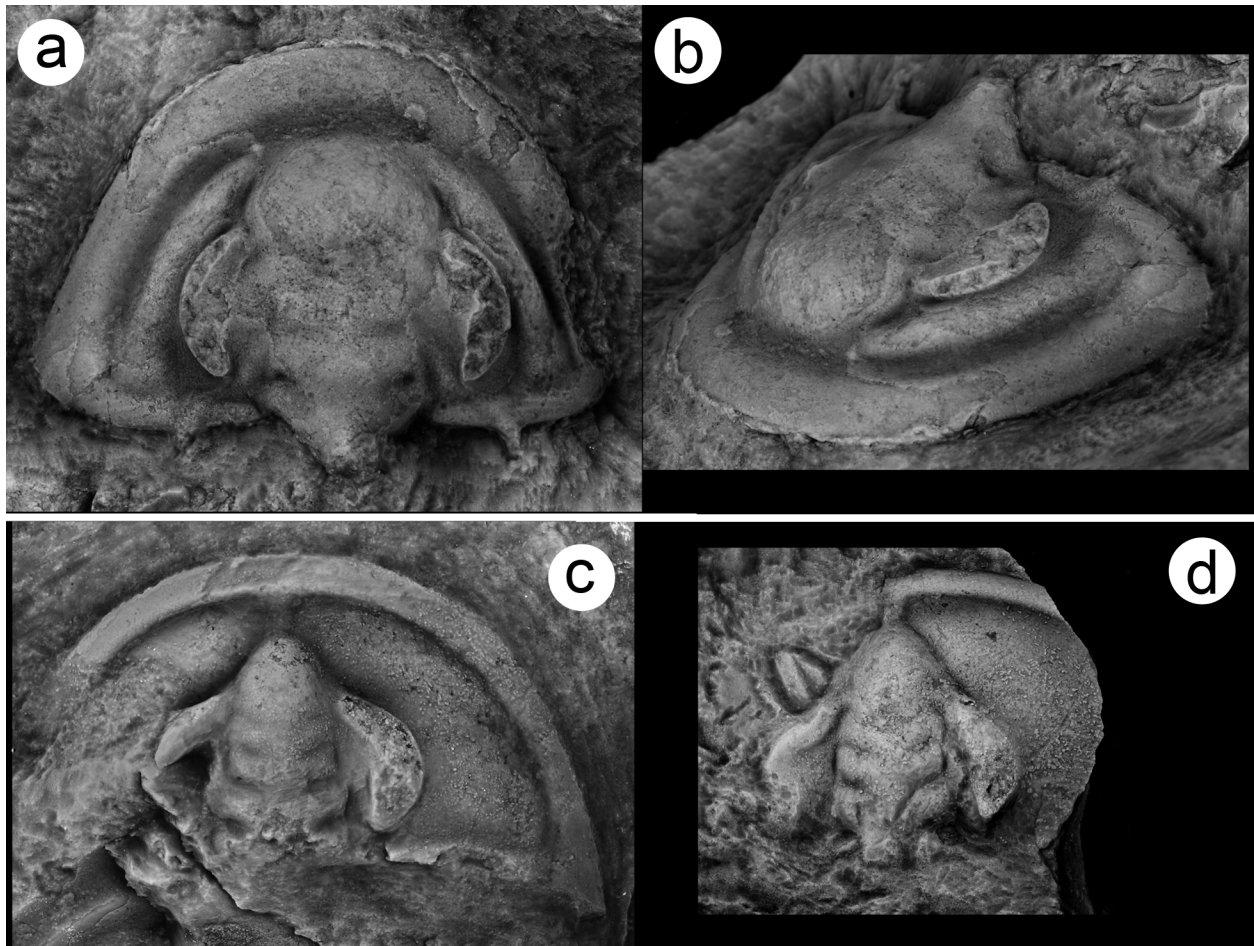


FIGURE 2.3. Specimens collected from Lower Cambrian Sekwi Formation, Northwest Territories, Canada. a,b, *Esmeraldina* sp. aff. *rowei* (Walcott, 1910). a, cephalon, dorsal view, KUMIP 319926, x 2.0; b, oblique view of a, x 2.0. c, d, cephalons of *Nevadella keelensis* n. sp. c, dorsal view of holotype, KUMIP 319927, x 2.0. d, partial cephalon, dorsal view, PWNHC 2009.20.47, x 2.0.

DIAGNOSIS: Glabella tapering evenly and slightly anteriorly. Anterior border relatively wide, length (exsag.) approximately equal to length (sag.) of L0. Frontal lobe does not contact anterior border furrow; plectrum present. S2 straight and not conjoined medially. Extraocular region broad, width (tr.) approximately 100-120 percent width of glabella at L1.

DESCRIPTION: Cephalic length (sag.) 45-55 percent of width (tr.). Anterior cephalic border moderately long, length (exsag.) equal to length (sag.) of L0, may be rounded ridge or flattened ledge. Frontal lobe does not contact anterior border furrow; plectrum present. Anterior margins of frontal lobe at each side of midline deflected posteriorly at roughly 40 degree angle relative to transverse line. Length (sag.) of LA long, equal to 1.5 times length of L0 and L1 medially. Lateral margins of LA proximal to lateral margins of L0. Ocular lobes contact frontal lobe at posterior parts of frontal lobe; outer band of ocular lobe near lateral margin of LA does not expand prominently exsagittally; ocular lobes gradually increase dorso-ventral elevation between axial furrows and mid-point of ocular lobes; region of anterior part of ocular lobe between putative visual surfaces is in contact with LA. Line from posterior tip of ocular lobe to junction of posterior margin of lobe with glabella forms 15-20 degree angle with sagittal line. Posterior tips of ocular lobes developed opposite medial part of distal margin of L0 or S0. Width of interocular area approximately equal to 1.0-1.4 times width of ocular lobe at its midlength. Distal margins of L3 is straight. S3 either not prominently incised or poorly preserved, not conjoined. Lateral margins of glabella between L0-L2 convergent. S2 not conjoined medially, straight, and directed inward and posteriorly at roughly 35-45 degrees to transverse line. L2 and L3 do not merge distally. Distal margins of L2 when proceeding anteriorly

converge. S1 convex anteriorly and sinuous. Distal sector of S0 is convex anteriorly with proximal end well posterior of distal end. Extraocular region opposite L1 broad, width (tr.) approximately 100-120 percent width of glabella at L1. Genal spine angle developed opposite medial part of distal margin of L0. Intergenal angle relative to transverse line deflected at roughly -10 to 5 degrees. Posterior cephalic border transverse.

DISCUSSION: *Nevadella keelensis* shares characters of both *Nevadella* and the closely related *Nevadia*, and a future revision of the two genera may be necessary. In this case, the bulk of the character information supports an assignment of this species to *Nevadella*. For instance, LA is relatively long (sag.) which is typical of *Nevadella* and not *Nevadia* according to the phylogenetic hypothesis and generic assignments presented in Lieberman (2001). Further, S0 is convex anteriorly as in *Nevadella*, and the anterior and lateral borders are relatively longer (sag.) and wider (tr.). However, there are some characters more consistent with an assignment to *Nevadia*. For instance, the cephalon is relatively broad (tr.) and S2 is straight, as in *Nevadia*. Unfortunately, no intergenal ridge is preserved in this material—another character used to distinguish between the genera. *Nevadella keelensis* n. sp. can be distinguished from *Nevadia weeksi* Walcott, 1910 by having a relatively shorter (tr.) extraocular area and longer (exsag.) anterior border. *Nevadella keelensis* also does not have a conjoined S3 and S2, contra the condition in *Nevadia weeksi*. *Nevadia fritzi* (Lieberman 2001a) differs from *N. keelensis* by having a relatively shorter ocular lobe; conjoined S3; and the glabella constricting at L1. Note that several other species have the glabella constricting at approximately L1 or L2 including *Nevadella mountjoyi* Fritz, 1992, *N. eucharis* (Walcott 1913), *N. perfecta* (Walcott 1913), *N. parvoconica* (Fritz 1992), and *Nevadia bacculenta* (Fritz 1972). Also, *N. keelensis*

differs from *Nevadia bacculenta* in having a more evenly tapering glabella and relatively longer ocular lobes. *Nevadia faceta* (Fritz 1972), another species found in the Mackenzie Mountains, has a shorter extraocular area relative to *N. keelensis* and the glabellar furrows are more prominently conjoined. Fritz (1972) described and illustrated *Nevadella* sp. 2 from the Sekwi Formation and although this material is poorly preserved and incomplete it appears closely similar to *N. keelensis* in the form and shape of the anterior border, the glabellar furrows, and the plectrum, and they are questionably treated as conspecific.

Superfamily Olenelloidea Walcott, 1890

Family Holmiidae Hupé, 1953

Subfamily Holmiinae Hupé, 1953

Genus *Esmeraldina* Resser and Howell, 1938

Esmeraldina sp. aff. *rowei* (Walcott 1910)

(Figs. 2.3a and 2.3b)

= *Holmia rowei* Walcott, 1910 (partim), p. 292, Pl. 29, figs. 2-4, 7-11.

= *Esmeraldina rowei* Fritz, 1995, p. 714, figs. 5.1, 6.1-6.12, 7.1-7.3, 10.10, 10.11;

Lieberman, 1998, p. 71, fig. 3.4; Lieberman, 1999, p. 86. figs. 15.1, 15.3;

Hollingsworth, 2006, p. 319, figs. 9.1-9.9, 9.12 (see for more complete synonymy).

= ?*Holmia rowei* Walcott. Fritz, 1973, p. 12.

= ?*Esmeraldina rowei* (Walcott). Fritz, 1992, p. 17.

= ?*Esmeraldina rowei* (Walcott). Fritz, 1995, p. 714.

MATERIAL EXAMINED: Cephalon KUMIP 319927 from locality described above.

DISCUSSION: This specimen can be assigned to the Holmiidae based on a number of diagnostic characters including, but not limited to, a forward expanding glabella, the convex and prominently vaulted extraocular area, and the presence of a spine or node at the axial part of L0. Further, it possesses a number of characters also shared by *Esmeraldina rowei* as described by Fritz (1995). However, poor preservation of some features precludes definitive assignment to this species. A prominent difference from the description of Fritz (1995) is in the occipital spine which does not jut out narrowly and abruptly from the occipital ring, but tapers dorsally from the posterior border of the occipital ring (Fig. 2.3a). This may be an artifact of the variation within the species as discussed by Hollingsworth (2006). This specimen bears the shape of the narrower form (Hollingsworth 2006) where the ocular lobes are close to the glabellar axial furrows and the posterior border is transverse. *Esmeraldina rowei* is discussed in greater detail in (Fritz 1995, see Hollingsworth 2006 for a full discussion of *E. rowei* forms, Lieberman 1998, 2001a)

Fritz (1973, p. 12) mentioned that he had observed *E. rowei* (or a species closely similar to it) in the Mackenzie Mountains. Fritz later (1992, p. 17, and 1995, p. 714) questionably synonymized his material with *E. rowei*. It could not be determined whether his material is indeed conspecific with the material presented here, so we have only questionably synonymized these. Fritz (1973, p. 12) also described and illustrated an incomplete cephalon as *Holmia?* sp. 1 from the Mackenzie Mountains, Sekwi Formation. *Holmia?* sp.

1 differs from *E. sp. aff. rowei* presented herein in having deeper axial furrows and more distinct glabellar furrows, less prominent lateral lobes at L0; little constriction of glabella at S1; a narrower anterior border (exsag.), and a less dorsally prominent extraocular area; thus, at this time we do not synonymize them. However, Hollingsworth (2006) has shown that *E. rowei* can be problematic to identify, as the species can vary in form.

CHAPTER 3

QUANTIFYING MORPHOLOGICAL CHANGE DURING AN EVOLUTIONARY RADIATION OF DEVONIAN TRILOBITES

INTRODUCTION

Numerous evolutionary radiations are preserved in the fossil record, and indeed, many of the early theoretical considerations, specifically in the context of adaptive radiations, were based on studies of the fossil record (e.g., Osborn 1902, Simpson 1944). Hypotheses about such evolutionary radiations have largely focused on how ecological mechanisms could cause the rapid speciation events. The prevailing model for adaptive radiation requires open ecological opportunities that allow species (and sometimes, it has been argued, even higher taxa) to occupy empty and new niches and subsequently proliferate (Phillimore and Price 2008, Schluter 2000, Simpson 1953). This mechanism has been invoked to explain evolutionary radiations as small as the 15 species of Darwin's finches (Grant and Grant 2007, Lack 1947) and as large as the Cambrian radiation (Bambach et al. 2007). Such ecologically driven speciation would be expected to generate identifiable patterns of morphological diversification, and the fossil record provides excellent opportunities to study patterns of morphological change during evolutionary radiations as they play out through macroevolutionary time scales (e.g., Foote 1993, Foote 1997, Smith

and Lieberman 1999, Wagner 1995, 2000, Wagner and Erwin 2006, Zelditch and Fink 1996). Here we consider patterns of morphological change during the radiation of the Devonian calmoniid (Calmoniidae: Phacopida) trilobites; this group has been hailed as a classic example of an evolutionary radiation in the fossil record (Eldredge and Cracraft 1980, Fortey and Owens 1990, Lieberman 1993). We specifically focus on the monophyletic *Metacryphaeus* Group within this clade; it consists of more than 40 species that diversified rapidly into myriad morphological forms, even at a time when global trilobite diversity was waning (Eldredge and Cracraft 1980). They occurred in the cooler southern waters of the Malvinokaffric Realm, which was a geographically complex region that possessed high endemism. The rapid diversification of the group was mediated by high initial speciation rates coupled with low to moderate extinction rates; an abrupt decrease of speciation rates in the face of moderate extinction rates caused the eventual demise of the group, coincident with the Late Devonian biodiversity crisis (Abe and Lieberman 2009, see also McGhee 1996a, Rode and Lieberman 2004). Our study considers the tempo of this radiation and how rates of speciation, extinction, and morphological change are associated with various abiotic and biotic factors including biogeography, paleoenvironment, and ecological association. Using a phylogenetic framework, a geometric morphometric approach is used to quantify morphological change throughout the evolutionary radiation.

A pattern of rapid initial morphological diversification that subsequently declines (Fig. 3.1A) has been found in many taxa (Foote 1993, 1997). One possible interpretation of such a pattern is that early morphological diversification is associated with initial rampant ecological opportunities, followed by a decrease in morphological diversification as the

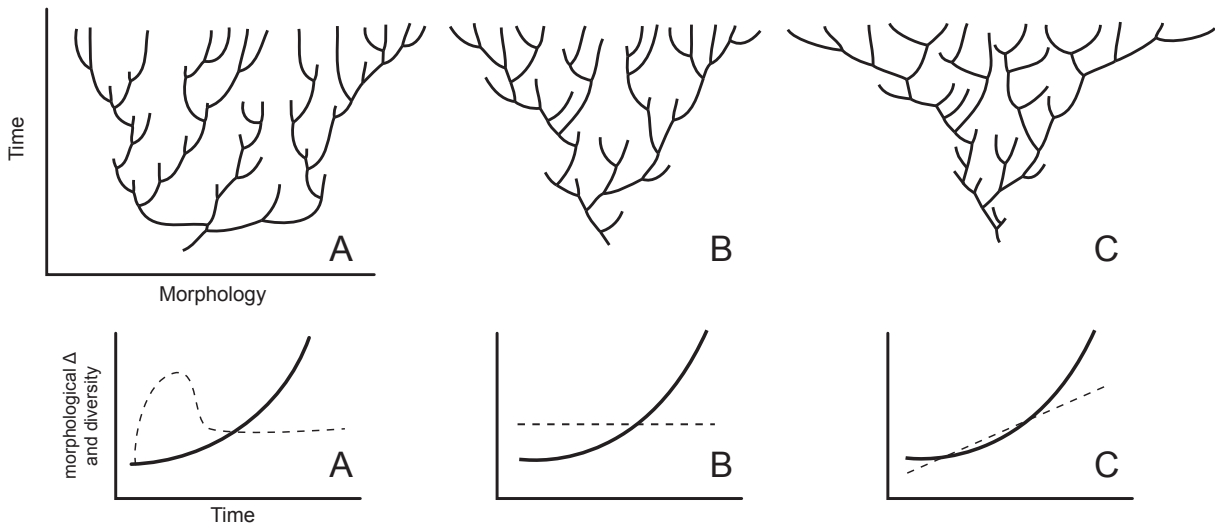


FIGURE 3.1. Models with predicted morphological change and exponential diversity curves. Dashed lines denote morphological change and solid lines show diversity. A) Rapid early morphological diversification followed by stable or decreasing morphological change. B) Morphological change constant over the diversification of the clade. C) Morphological change increases during diversification. Modified from Foote (1993), although there disparity curves were shown.

available ecological niches are filled. “Key innovations” (*sensu* Simpson 1953) might be associated with such a pattern as the acquisition of a trait would allow invasion into new ecological space. In another model of morphological diversification driven by ecology, there is a change from a generalist form to specialized (stenotopic) forms (Eldredge and Cracraft 1980). Specialization due to ecological processes could yield early morphological change (Fig. 3.1A) or increasing ecological divergence into specialized roles (Fig. 3.1C). (This assumes that the evolution of different specializations might be associated with the acquisition of distinctive morphologies).

Quantitative analyses of morphology of taxa during evolutionary radiations have focused mainly on indices of disparity (Erwin 2007, Foote 1993, 1997), which measure occupation of morphospace at a given time. Some analyses employ phylogenetic relationships to measure disparity differences between and among clades (Clabaut et al. 2007 for cichlid fishes; Harmon et al. 2003 for iguanid lizards) or between cladogenetic events (Wagner 1995 for rostroconch mollusks; Smith and Lieberman 1999 for olenelloid trilobites; see also Harmon et al. 2003). The phylogenetic information permits the evolutionary radiation to be examined through time at the level of morphological changes at speciation events, and also allows for comparison with diversification rates and biogeographic patterns.

Previous analyses of the biogeographic context of the calmoniid trilobite evolutionary radiation: (1) supported a widespread and geographically complex setting for speciation (Abe and Lieberman 2009, Eldredge and Ormiston 1979, Lieberman 1993); (2) suggested most speciation occurred in the biogeographic hotspot of Bolivia; and (3) indicated that

there were congruent patterns of vicariance and geodispersal (*sensu* Lieberman 2000) between different parts of the Malvinokaffric Realm related to episodes of sea-level rise and fall (Abe and Lieberman 2009). These all suggest that changes in earth history, in particular geological and climatic changes, played a fundamental role in causing the radiation, matching aspects of Grant and Grant's (2007) discussion of the radiation of Darwin's finches. However, an important role for earth history in the calmonioid radiation does not preclude a role for ecological factors. Indeed, the argument has been made that ecological processes are the main factors affecting other cases of adaptive radiation. For instance, the aforementioned Darwin's finches as well as examples involving cichlids (Clabaut et al. 2007), Hawaiian spiders (Gillespie 2005), and *Anolis* lizards (Losos et al. 1998) seem to be rife with instances of ecological processes involving convergence, character displacement, competition, and reinforcement (Schluter 2000). By focusing on the morphological changes during the calmonioid radiation, we aim to tease apart the role ecological factors played by examining (1) whether morphological change seems to increase or decline through time and with cladogenetic rank, and (2) how morphological change varies relative to various biogeographic factors, including cases when closely related trilobite species have sympatric or allopatric distributions.

MATERIALS AND METHODS

Calmonioids of the *Metacryphaeus* Group are well-preserved, abundant trilobites from the Devonian Malvinokaffric Realm (Eldredge and Branisa 1980). A phylogenetic

hypothesis of the group was proposed by Lieberman et al. (1991) and Lieberman (1993) based on an analysis of 44 species and 50 characters. A biogeographic analysis of the group and calculation of speciation and extinction rates was presented in Abe and Lieberman (2009).

Geometric morphometrics

Morphological change in the group was quantified using Bookstein coordinate landmark data of the trilobite cephalon. Shape analysis commonly is based on measurements of the cephalon in the morphometric literature (e.g., Foote 1989, 1990, Foote 1991, Smith and Lieberman 1999, Webster and Zelditch 2005) because the cephalon have easily recognized homologous landmarks. Moreover, the cephalon contain the bulk of character information used for species identification. Although Lieberman et al. (1991) and Lieberman (1993) used characters of the cephalon to generate the phylogeny of the *Metacryphaeus* group, these characters were not identical to the shape-change landmarks; in addition, thoracic and pygidial characters were used in the analysis. Thus, the phylogenetic and morphometric databases can be considered to be at least partially, though not completely, independent.

Interpreting the functional or ecological meaning of changes in the morphology of trilobites (or any long extinct taxon) is far from straightforward. For instance, the grooves and bumps on the cephalic exoskeleton seem in part to reflect sites of muscle attachment leading to the stomach and limbs, such that differences in the configurations of these bumps and grooves could relate to differences in diet, motility, and lifestyle (Eldredge 1971, Fortey and Owens 1990, Whittington 1997); still, the ecological and functional

significance of any of these differences among species is indeterminate. Here we are quantifying differences in morphospace, not assuming that they must imply a difference in ecology, ecospace, or function. However, we follow various authors (e.g. Foote 1991, 1993, 1997, Harmon et al. 2003, Wagner 1995, 2000, Yoder et al.) in positing that morphometric data (broadly construed) can provide some indication of ecospace occupation.

Landmark data were collected from digital photos of cephalons (in standard dorsal orientation) representing 37 species (Appendix 1). All available holaspids with no apparent deformation or prominent diagenesis (a total of 109 cephalons) housed in the two major calmonioid repositories (American Museum of Natural History, AMNH; National Museum of Natural History, USNM) were analyzed. Features that are commonly preserved and that have served as the basis for previous landmark studies of trilobites were selected as landmarks (e.g., Smith and Lieberman 1999). A total of 19 landmarks (5 midpoints, 14 symmetrical pairs) was chosen (Bookstein 1997; Fig. 3.2; Appendix 2); these are at points that are easily homologized (MacLeod 2001). When possible, points were digitized on both sides of the sagittal symmetry plane using TPSDig2 (Rohlf 2010a), and symmetrical pairs of points were reflected and averaged across the sagittal plane using BigFix6 (IMP Package, Sheets 2002); points without symmetrical pairs were used without averaging. Baseline points for the axis were the anteriormost point of the cephalon including the anterior border, and the posteromedian point of the occipital ring (Fig. 3.2). To remove the non-affine effects of shape (i.e., orientation, size, translation), a generalized least-square Procrustes superimposition analysis was applied in TPSRelw (Rohlf 2010b). All data are

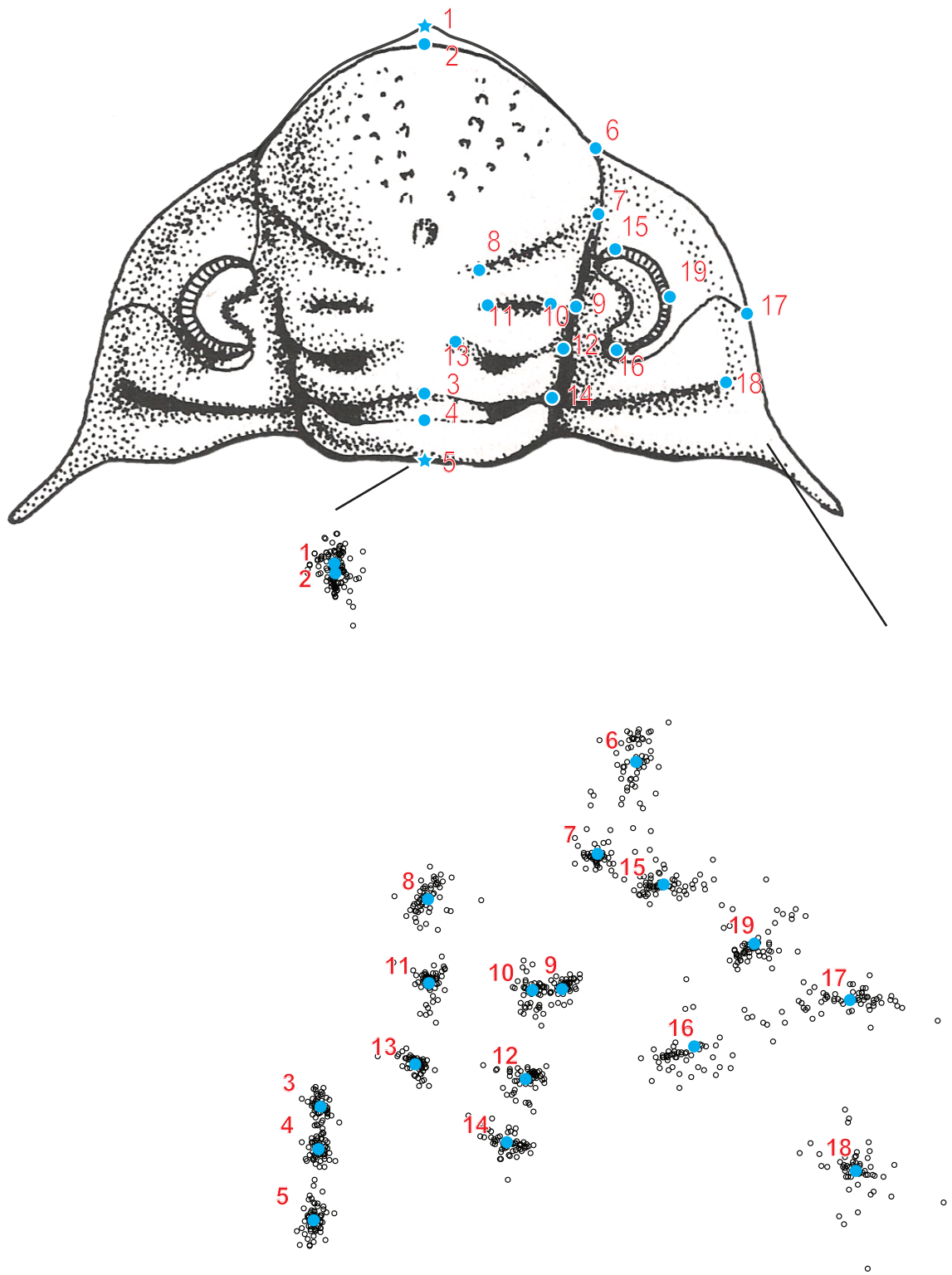


FIGURE 3.2. Landmarks used in geometric morphometric analyses shown on cephalon of *Metacryphaeus giganteus* (drawn from Cooper 1977). Points used corresponded to midpoints, maxima of curvatures and intersection of furrows. Star-shaped points denote the baseline (symmetry axis) from which the symmetrical pairs (not shown) were reflected. Procrustes superimposed results with consensus without effects of size, rotation, and translation are shown below the cephalon.

available on the Paleobiology web archive at <http://www.paleobiology.org> and by request from the authors.

Morphological change

Not only is it difficult in general to identify actual ancestral descendant pairs of species in the fossil record (MacLeod 2001, Smith 1994), but in the particular case of the calmoniids, none of the criteria needed to identify specific ancestors was met (see Engelmann and Wiley 1977). For this reason, geometric morphometric methods were used in conjunction with ancestral character-state reconstructions to quantify morphological change along edges of the best available phylogenetic hypothesis for the *Metacryphaeus* Group.

Ancestral character-state reconstruction of continuous characters is considered more reliable if no overall trend is affecting the evolution of the group (Oakley and Cunningham 2000, Polly 2001, Webster and Purvis 2002). In the case of the calmoniids, there do not appear to be any particular trends in morphology, because various species gain and lose ornamentation, change the vaulting of the cephalon, etc. Estimates of ancestral shape were calculated using an unweighted square-change parsimony based on the Procrustes superimposed landmark data and using Mesquite (Maddison and Maddison 2010). Square-change parsimony assumes a Brownian motion model of evolutionary change and minimizes the sum of squares of the differences between nodes (Maddison 1991, Maddison and Maddison 2010). For each internal node, an ancestral shape was reconstructed based on descendent morphometric data, when available. A measure of morphological transition distance was calculated based on the Euclidean distances using the first three dimensions of relative warps that explained 70.64% of the total variation (41.37%, 15.69%, 13.58% for top three axes). Most of this variation was expressed in

differences in the position and shape of the eyes. The Euclidean distances were calculated between available reconstructed nodes and descendents. There were some species for which no landmark data were available, owing to poor preservation or dearth of specimens. Those ancestral nodes that lacked morphometric data for their direct descendents were excluded from transition calculations because this makes the analyses of character change more conservative and less reliant on ancestral state reconstruction.

Analyses of morphological change through time and in relation to biogeographic patterns

Comparisons were made between the magnitude of morphological change at cladogenetic events associated with: (1) allopatric differentiation involving vicariance; (2) allopatric differentiation involving range expansion (most akin to peripatric speciation); and (3) no change in area, possibly involving sympatric differentiation. The statistical analysis used was a non-parametric Kruskal-Wallis analysis of variance for comparisons.

Morphological transition distance also was considered through time to determine if larger morphological changes occurred earlier in the radiation. Analyses of transition distances against cladistic rank also offer a measurement of morphological diversification through the evolution of a clade (Smith and Lieberman 1999). The node (n) at the root of the tree was assigned a rank of one and each descendent node is given a rank of (n + 1). For parts of the tree where branches were not fully pectinate, ranks were duplicated accordingly, following standard practice (e.g., Norell and Novacek 1992). Non-parametric analyses using Kendall's coefficient of rank correlations between transition distance and cladistic rank were used. Finally, morphological transition was compared relative to

speciation rates. Speciation in the calmoniids was confined to the first two stages (Lochkovian and Pragian) of the Devonian (~9 myrs; Fig. 3.3), limiting our chances for comparisons. A non-parametric Mann-Whitney U test was used to look for significant differences between morphological transition distances during these two stages.

RESULTS

A visualization of the total morphological diversity is shown on Figure 4 as the first two principal component scores of the relative warps. This representation captures a great deal of the shape variation of calmoniid cephalae, including the shape of the glabella, and the position and size of eyes, indicating that differences in morphology are being reflected by different geometric morphometric patterns. As an example, *Typhloniscus baini* is part of the basal-most branch on the tree and is a morphological outlier with its unusual anterior facing ocular lobes that are rotated 90°; moreover, its eyes appear to lack lenses (Cooper 1982). This departure from the typical calmoniid eye position, together with its flattened anterior margin of the glabella and relatively wide cephalon is captured in the geometric morphometric analysis (Fig. 3.4). It is worth noting that the relatively distinctive eye morphology of *Typhloniscus* did not unduly influence the results of our morphological distance analyses because the absence of *Typhloniscus* n. sp. did not allow for reconstruction of the ancestral *Typhloniscus* node. The reconstructed ancestor of the rest of the *Metacryphaeus* Group shows relatively small, standard eyes (for trilobites),

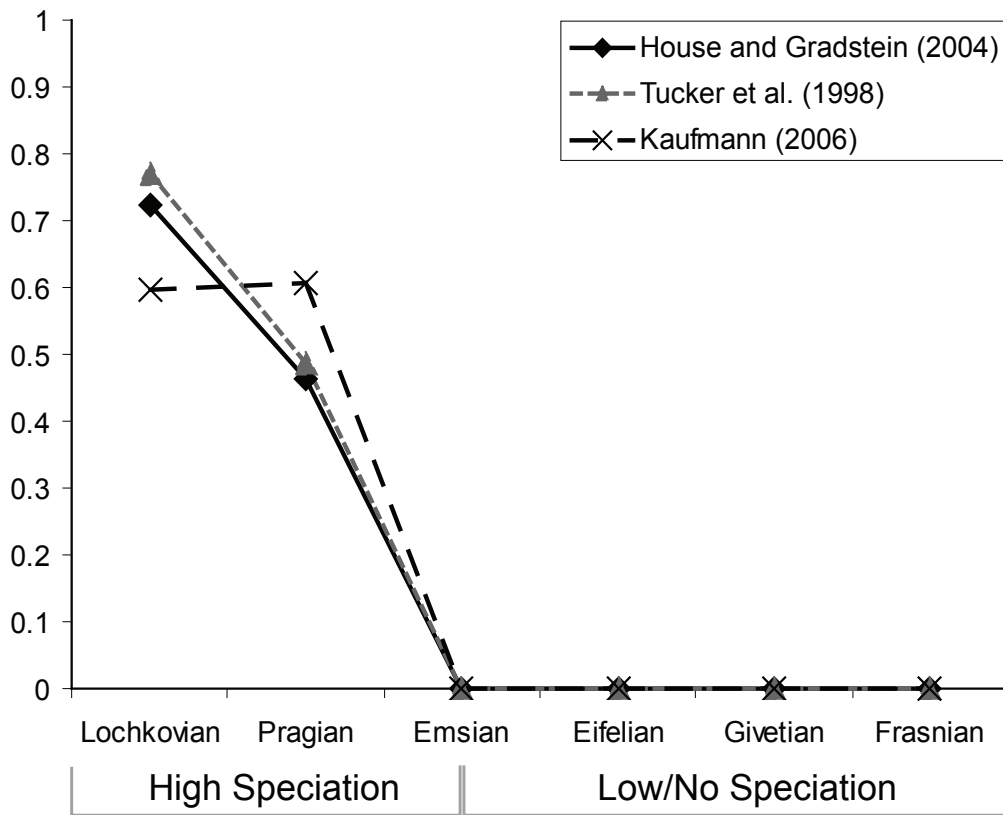


FIGURE 3.3. Speciation rates during the diversification of the Metacryphaeus Group calmoniids. Rates were high during the first two stages of the Devonian (~9 myrs), but no speciation was recorded after the Emsian (from Abe and Lieberman 2009). Different lines shown are based on calculations using different Devonian time scales.

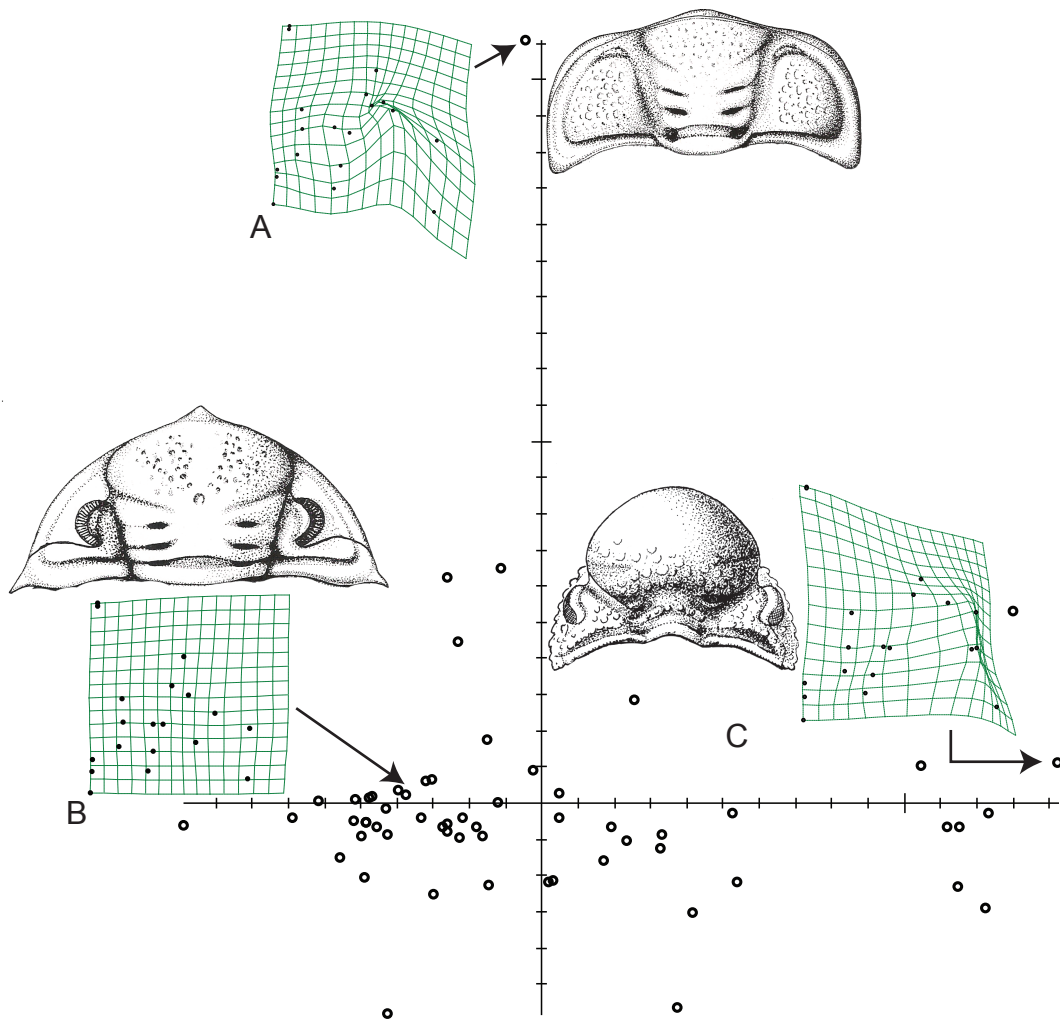


FIGURE 3.4. Graphical representation of morphospace from geometric morphometric analysis, using principal components plot of the first and second relative warp scores of calmoniid cephala. Deformation grid and associated specimen are shown for A) *Typhloniscus baini* (basal-most taxon) B) *Metacryphaeus caffer* and C) *Bouleia dagincourti* (drawings from Moore 1959 and Cooper 1982).

indicating that *Typhloniscus*' distinctive anterior-facing eyes are an apomorphy of the genus.

Regarding morphology and biogeography, there are no significant differences in morphological transition distance between cladogenetic events that involved vicariance, range expansion, or *in situ* differentiation (Table 3.1; Fig. 3.5). In particular, allopatric versus sympatric (at least at the scale that could be determined) differentiation does not correlate with the amount of morphological change. Moreover, morphological transition distance does not change through time (Table 3.2; Fig. 3.6). Finally, results of correlation analyses of morphological change with cladistic rank were not significant (Kendall's coefficient of rank correlation; $\tau = 0.078$; $p = 0.44$; $n = 51$) (Fig. 3.7), indicating that there was no apparent trend toward decreasing (e.g., Fig. 1A) or increasing (e.g., Fig. 3.1C) morphological change throughout the evolutionary history of the radiation.

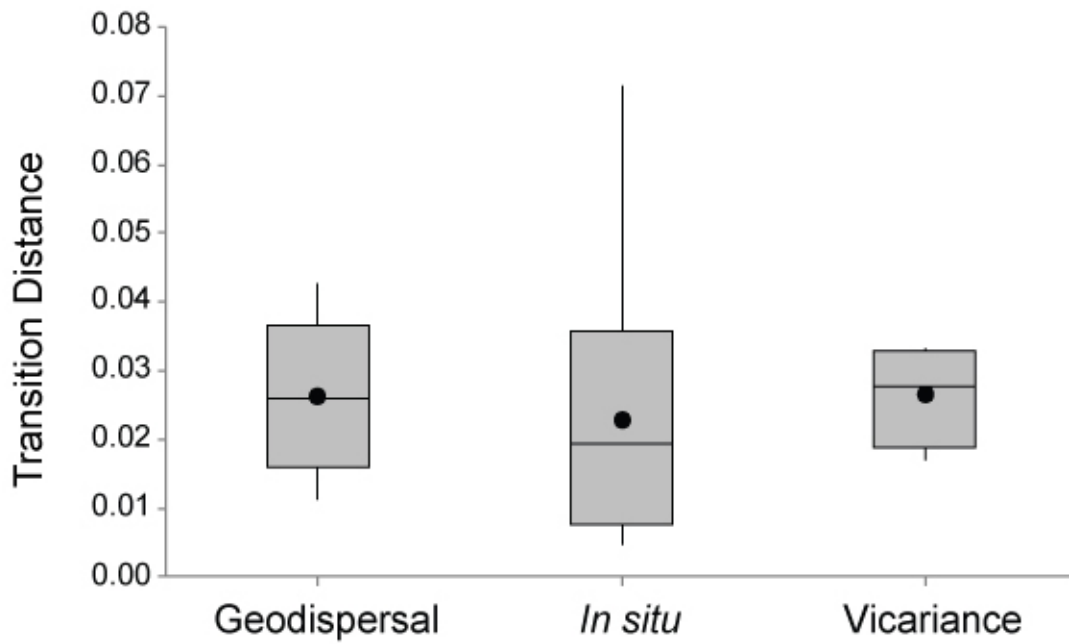


FIGURE 3.5. Comparison of morphologic transition distance between ancestors and descendants at speciation events involving range expansion (geodispersal), range contraction (vicariance), and *in situ* differentiation (sympatry). Boxes represent 25th to 75th percentile; solid circles are the mean for each group.

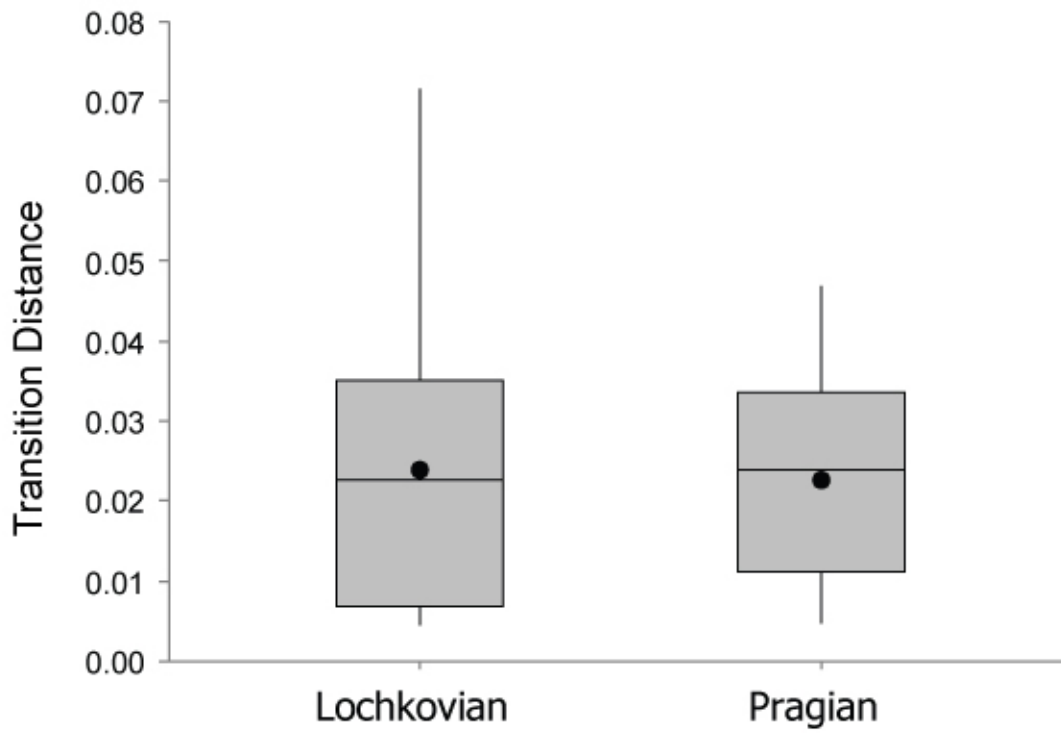


FIGURE 3.6. Morphologic transition distance between ancestors and descendants during the different Devonian stages when diversification occurred. Box represents 25th to 75th percentile; solid circles are the mean for each group.

TABLE 3.1. Analysis using a non-parametric Kruskal-Wallis to test differences between morphological transitions depending on geographic change at cladogenesis. These involved two possible allopatric modes: range expansion (geodispersal), range contraction (vicariance), and *in situ* speciation (sympatry). Phylogeny from Abe and Lieberman (2009).

	N	Median	Av. Rank	Z
Geodispersal	5	0.02591	30.6	0.73
Vicariance	4	0.02765	31.0	0.70
Sympatric	42	0.01922	25.0	-1.06
Overall	51		26.0	
H = 1.13 DF = 2 p = 0.568				

TABLE 3.2. Analysis of differences between morphological transitions for the first two stages of the Devonian using a non-parametric Mann-Whitney U test. Speciation was highest during the Lochkovian and declined slightly and ended by the end of the Pragian. Phylogeny and speciation rates from Abe and Lieberman (2009).

Lochkovian	$n = 25$	Median = 0.02275
Pragian	$n = 26$	Median = 0.02406
Point estimate for Lochkovian-Pragian is -0.00135		
95.1% CI for Lochkovian-Pragian is $(-0.00895, 0.00773)$		
Test of Lochkovian = Pragian vs Lochkovian \neq Pragian is not significant $p = \mathbf{0.6993}$		

DISCUSSION

Calmonioid trilobites of the *Metacryphaeus* Group have been held up as a classic example of adaptive radiation in the fossil record (Eldredge and Cracraft 1980, Fortey and Owens 1990), and phylogenetic and biogeographic patterns and rates of speciation within the group have been characterized in detail (Abe and Lieberman 2009, Eldredge and Cracraft 1980, Lieberman 1993, Lieberman et al. 1991). Analyses of patterns of morphological change within the context of this radiation allow us to characterize the nature of the evolutionary patterns and processes that occurred in greater detail. To this end, a geometric morphometric analysis quantified morphological change during the radiation using landmark data. One crucial aspect of adaptive radiations that has been repeatedly identified in the literature is their ecological and competitive character, including the production of ecologically diverse species through numerous speciation events (e.g., Grant and Grant 2007, Schluter 2000). If the *Metacryphaeus* Group radiation was fundamentally about ecologically mediated speciation, one would predict that there should be greater morphological changes when speciation involved ancestors and descendants living within the same general area, where there should be greater opportunities for competitive overlap and interaction, than when it involved ancestors and descendants living in different areas. However, the recovered patterns of morphological divergence that occurred at speciation in the *Metacryphaeus* Group are not necessarily compatible with the notion of an ecologically driven adaptive radiation. In particular, there were no significant differences between the amount of changes that occurred at speciation events involving ancestors and descendants in the same general area as opposed to

ancestors and descendants living in different areas (Table 3.1; Fig. 3.5). Of course, important caveats do need to be raised. For instance, we cannot verify that speciation events that occurred in the same area actually involved sympatry; instead, they may involve smaller-scale allopatry beneath our limits of resolution to assess. This is perhaps most likely to involve Devonian intra-cratonic basins in Bolivia and Peru that served as the calmoniid biodiversity hot spot (Abe and Lieberman 2009, Eldredge and Ormiston 1979, Isaacson and Sablock 1988). However, certainly organisms that live in the same general area are more likely to be able to interact competitively than those that occur in completely disjunct areas. It is also conceivable that the measures of morphology we used imply little if anything about species ecology. Our landmark data did capture information about the trilobite cephalon, which contains anatomically and functionally important structures. Changes of the cephalic shape provide some information about changing ecology, but the nature of these is certainly unspecified; still, this is essentially what we are limited to by the very nature of the fossil record. It is also possible that patterns of speciation that appear to occur sympatrically, or allopatrically, or the temporal patterns of speciation themselves simply may be artifacts of an incomplete fossil record from which we have little access to actual paleobiogeographic or stratigraphic distributions. However, trilobites do seem to have among the very best preservation probabilities for fossil invertebrates (Foote and Raup 1996). Finally, the phylogenetic patterns and the methods of reconstructing biogeographic patterns and ancestral morphology could be inaccurate.

Even considering these caveats, alternative hypotheses of abiotically mediated radiations must be considered since a prominent signature of an ecologically mediated radiation is lacking. Instead, the more prominent aspect of the calmoniid radiation is that it appears to

have been influenced by the geographic complexity of the Malvinokaffric Realm during the Devonian. Geographic complexity is shown by the heterogeneous areas that are broken up into several distinct tectonic basins, which served as areas of endemism (Abe and Lieberman 2009). Allopatrically mediated radiations (termed non-adaptive radiations) have been documented in extant taxa (e.g., Cameron et al. 1996, Gittenberger 1991, Kozak et al. 2006) and even classic examples of adaptive radiations (particularly the insular radiations) confer important roles to allopatric mechanisms (Genner et al. 2010, Gillespie 2005, Grant and Grant 2007). Moreover, in addition to this geographic heterogeneity during the Devonian, there were several major episodes of sea-level rise and fall (Eldredge and Ormiston 1979, Hallam 1992, Isaacson and Sablock 1988, Johnson et al. 1985) that would have repeatedly isolated and then joined these basins, allowing for numerous opportunities for range expansion and allopatric speciation (Abe and Lieberman 2009). The importance of these abiotic factors in generating multiple instances of geographic isolation is being examined in the cichlid radiation (Genner et al. 2010, Rueber et al. 1998, Sturmbauer et al. 2001) and the anoles (Glor et al. 2004). Notably, what appears to have led to the reduction of speciation in the calmoniids is that the sea level rose such that by the later part of the Middle Devonian, all of the tectonic basins in the Malvinokaffric realm may have been joined by marine connections. The increase in sea level was sufficiently great that subsequent oscillations in sea level no longer caused repeated episodes of geographic isolation and range expansion (Abe and Lieberman 2009).

Still, we are not implying that ecological factors played no role in the radiation of these trilobites. Many factors including population size and structure, mating systems, changes in predator-prey dynamics, and other ecological aspects could well have had an important

role in the morphological diversification. In addition, the divergence that occurred in allopatry may be related to adaptations to distinctive environments. It is just the absence of differences between morphological divergence occurring *in situ*, as opposed to in other areas, that indicates sympatrically driven, ecologically mediated speciation has not left its stamp on this taxonomically impressive radiation.

The relationship between taxonomic and morphologic diversity has been of broad interest to the paleontological community for some time (Foote 1993, Gould 1990, Wagner 1995, Wills et al. 1994); thus, it is worth considering in the context of adaptive radiations in general and this evolutionary radiation in particular. In the literature on evolutionary radiation, both early, rapid diversification and high initial disparity are sometimes interpreted as indicating the filling-in of empty and available ecological niches. Once the ecological opportunities have been taken, speciation rates should decline and morphological diversity would become constrained (Fig. 3.1A). Speciation rates for the calmoniids are high early and then decline (Fig. 3.3)—a pattern found in other evolutionary radiations (Harmon et al. 2003, Hulbert 1993a, Phillimore and Price 2008). Measures of disparity through time have shown similar results with the greatest morphological change occurring early in the radiation (see Foote 1997 for review). However, when the diversity of the calmoniids declined as a result of attrition caused by extinction, diversification did not begin anew. This suggests that it was not merely empty niche space that was serving to attract new diversity; instead, speciation rate in the calmoniids is correlated with relative sea level and episodes of sea-level change (Abe and Lieberman 2009). In addition, the magnitude of morphological change does not significantly increase through time (Table 3.2; Fig. 3.6) (although there are only a limited

number of temporal events to consider), nor does it change significantly with cladistic rank across the phylogeny (Fig.3.7). However, the morphological change considered here, although a metric related to disparity, is not the same thing as disparity (Smith and Lieberman 1999). Still, in the case of diversity patterns and morphological change, the calmoniid radiation seems to best match the idealized pattern shown in Figure 1B. This could indicate that diversification was occurring in the absence of ecological constraints, but other mechanisms might be indicated, including aspects of organismal development, and we are hesitant to ascribe a specific cause to explain this pattern. Notably, Mahler et al. (2010) found that during the evolutionary radiation of Greater Antillean anoles, the amount of morphological change decreases as ecological opportunities decline and endorsed the notion that patterns of change in overall morphology could be used to consider these issues.

Ultimately, the roles that different sorts of ecological, environmental and geological factors play in mediating evolutionary radiations will continue to be debated (Cameron et al. 1996, Eldredge and Cracraft 1980, Erwin 1992, Esselstyn et al. 2009, Gillespie 2005, Grant and Grant 2007, Losos et al. 1998, Petren et al. 2005, Rueber et al. 1998, Rundell and Price 2009, Schluter 2000, Simpson 1944, Vrba 1992). However, in this case, the calmoniids of the *Metacryphaeus* Group were diversifying in a heterogenous environment comprised of several geological areas in conjunction with episodes of climatic change stimulated opportunities for speciation (Abe and Lieberman 2009); these episodes of speciation were associated with consistent morphological change. Undoubtedly new neontological data will continue to be gathered to inform our understanding of what causes dramatic blooms of taxa to occur. Nonetheless, we hope that data from paleontology,

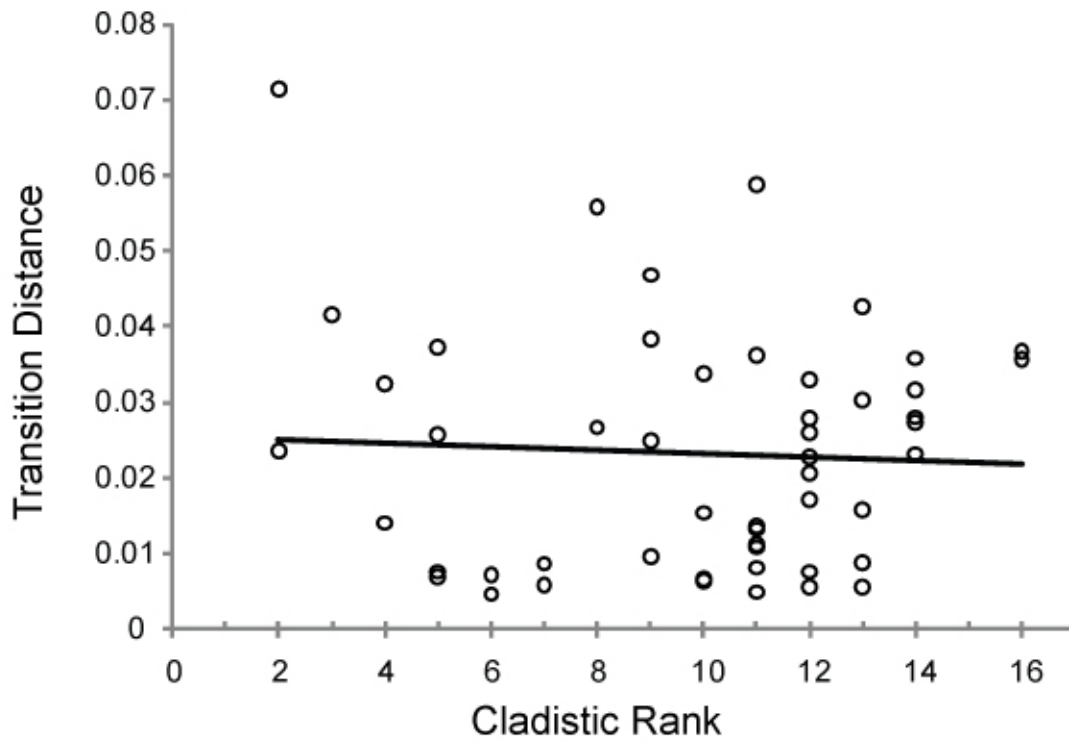


FIGURE 3.7. Morphologic transition distance versus cladistic rank across the phylogeny of the *Metacryphaeus* Group. Root of the tree was assigned a cladistic rank of one. Kendall's coefficient of rank correlation; $\tau = 0.078$; $p = 0.44$; $n = 51$.

which played the earliest role in the genesis of theories on evolutionary radiations (e.g., Osborn 1902, Simpson 1944), will continue to be integrated with studies from extant taxa to yield a more synthetic picture of the nature of evolutionary patterns and processes.

CHAPTER 4

PALEONTOLOGY, GEOGRAPHY, AND AN EXPANDED VIEW OF ADAPTIVE RADIATIONS

INTRODUCTION

At first glance, one might anticipate that the phenomenon of adaptive radiations, seemingly so important to evolutionary theory, should be well constrained and characterized. Instead, there has been considerable debate about what precisely constitutes an adaptive radiation and more importantly, what processes are behind such radiations and speciation in general. To some, adaptive radiations are seen as a major evolutionary paradigm, uniting micro- and macroevolution (Givnish 1997); further, it has been posited that radiations are the process by which most of life's diversity has speciated (e.g., Givnish 1997, Schluter 2000, Simpson 1953). By contrast, Olson and Arroyo-Santos (2009) suggested that adaptive radiations are only one extreme type of diversification pattern that does not represent a special phenomenon. Moreover, the concept of adaptive radiations was first developed by paleontologists but is now heartily endorsed by neontologists; yet, neontological and paleontological interpretation of the concept have diverged throughout the years. Here, the focus will be on developing a theoretically consistent view of adaptive

radiations that considers both paleontological and neontological perspectives and views the concept from both pattern- and process-based frameworks.

Adaptive radiation has been an important theoretical concept for many years. Therefore, it is not surprising that definitions abound (Givnish 1997) and that they have changed in focus (Erwin 1992), ensuring an extensive associated literature. In addition, the fact that the adaptive radiation paradigm was originally developed in the early and mid 20th century, when speciation theory was different and fewer scientific methodologies were available augurs well for the notion that this concept needs to be revisited. For instance, developments in the fields of phylogenetics, molecular systematics, biogeography, developmental biology, ecology, and paleontology have shed new light on ideas first presented by Osborn (1902) and Simpson (1944, 1953).

The study of the fossil record has been an important source for ideas on macroevolution in general and evolutionary radiations in particular (e.g., Eldredge and Gould 1972; Eldredge 1979, 1985, 1989, 1995; Gould 1980, 1985, 1991, 2002; Vrba 1980, 1985; Eldredge and Salthe 1984; Allmon and Ross 1990; Lieberman 1995; Jablonski 2007; Lieberman et al. 2007; etc.). Paleontology's relevance for understanding adaptive radiations will be a focus herein. In particular, study of the fossil record indicates that macroevolutionary patterns usually are produced by the complex interaction of both biotic and abiotic processes working in a complex, hierarchical framework. Another topical focus of this paper relates to problematic fact that the theoretical interpretation of "adaptive radiations" is constrained by the use of the term "adaptive" in the couplet. For instance, what if a combination of seemingly non-adaptive mechanisms, such as climatic or geological change, is responsible for triggering an evolutionary radiation? Allopatric

differentiation might involve a combination of adaptive and non-adaptive mechanisms (including drift). Is such a radiation still “adaptive”? Is it better viewed as partially “adaptive”? Such questions are not hypothetical because sometimes, evolutionary radiations of taxa seem to be triggered by their occurrence in a geographically complex setting (e.g., Abe and Lieberman 2009). The components of these mechanisms of evolutionary radiations (allopatry, geographic complexity, abiotic factors) will be considered based on examples of currently denominated “adaptive radiations.”

The evolution of the adaptive radiation concept

Osborn (1902) developed the term “adaptive radiation” to explain the evolution of ecologically diverse mammalian clades in the fossil record. He distinguished two types of adaptive radiations—*general* and *local*. *General adaptive radiations* were held to span many clades that were geographically widespread and that were characterized by convergence in form and ecological function. In contrast, *local adaptive radiations* were held to be much smaller in phylogenetic and geographic scope; moreover, the taxa in question were supposed to have developed distinctive adaptations, and there was much less emphasis on convergence. Subsuming two different types of macroevolutionary patterns under the heading “adaptive radiation” and also linking the issues of pattern and process clouded the definition of “adaptive radiation” at the outset. Moreover, his distinction between large-scale (“general”) and small-scale (“local”) radiations seems to have been largely dismissed in the subsequent literature.

As one of the pioneers of what today is referred to as the Modern Synthesis, G. G. Simpson embraced the concept of adaptive radiation and tied it to his “explosive” evolutionary tempo and mode (Simpson 1944, p. 213). Further, he attempted to modernize the concept by synthesizing fossil data with emerging concepts from population genetics. Simpson (1953) implemented Sewall-Wright’s fitness landscape to the concept of an adaptive landscape formed of adaptive zones through which groups could radiate via divergent speciation. This view established ecologically mediated phenomena to explain the processes driving adaptive radiations, which might be “minor” (e.g., Galápagos finches) or “major” (e.g., placental mammals) radiations. In particular, he popularized the idea of the empty and open adaptive landscape that could be populated quickly. One way to open an adaptive landscape, according to Simpson (1953, p. 355), is by acquiring a particular trait or key innovation.

Ernst Mayr’s initial (Mayr 1942) treatment of adaptive radiations was far more perfunctory. He seems to have deliberately avoided the term, given that he cited Lack’s (1942) work on Galápagos finches. (See quote from Mayr 1942, p. 85 below.) Mayr (1942) also discussed the “explosive sympatric speciation” of the African lake cichlids (today, considered a classic example of an adaptive radiation) and the Hawaiian tree snails; he instead treated them largely as involving allopatric speciation (Mayr 1942, p. 214; Mayr 1984). Later, Mayr (1960) did embrace the term more fully and treated them as invasions of open adaptive zones and endorsed the concept of key innovations. After the inception of the Modern Synthesis, the concept of adaptive radiations continued to be popular. Perhaps this can be attributed to the fact that, at least by some characterizations (e.g.,

Gould and Lewontin 1979; Cracraft 1982) during the 1950's and 60's, ideas on adaptation and selection were ascendant in evolutionary theory.

Many contemporary evolutionary biologists, especially paleontologists, began to avoid the term “adaptive radiation” owing to the theoretical baggage associated with the word “adaptive” (Eldredge and Gould 1972; Stanley 1979; Eldredge and Cracraft 1980; Cracraft 1982; Erwin 1982; Gould 1991; Lieberman 1993); instead the more theoretically neutral “taxic” or “evolutionary” radiation was used. Further, the term “adaptive radiation” is most frequently invoked to explain smaller-scale radiations (similar, though not exactly equivalent, to the “local” type that Osborn [1902] specified). Interestingly, many of these “evolutionary radiations,” despite their more neutral name, still assumed the existence the same ecological processes as those that drove “adaptive radiations” (e.g., Foote 1996), thereby suggesting that the same theoretical baggage is there.

Understanding the terminological confusion: pattern versus process

The term *adaptive radiation* has led to considerable confusion because it has been used primarily as a pattern-based definition with implied—though not always examined—processes. Both the modifier “adaptive” and the noun “radiation” are difficult to interpret because they can be viewed and used as either patterns or processes. Of the term “adaptation” Mayr (1942) wrote (p. 85):

The word adaptation has, unfortunately, somewhat of a double meaning, according to whether one sees in adaptation a process or the result of a process, in other words whether one considers adaptation as something active or passive. Whenever the

words adaptive or adaptation occur in the following discussion, they are used in a descriptive sense to indicate the results of a selective process.

In an evolutionary context, *radiation* can also denote either a pattern (diversification or divergence from a central lineage or form) or a process (speciation). Thus, the combination of the terms is doubly confusing; some definitions seem to imply a process on an observed pattern, whereas others specify only pattern. This terminological duality was noted previously (e.g., Eldredge and Cracraft 1980; Vogler and Goldstein 1997). The pattern- and process-based aspects of the definition must be decoupled to determine when the patterns can be used to test the processes involved. This isolation of patterns from processes is particularly relevant because non-adaptive processes mediated by abiotic factors potentially can generate some of the same patterns attributed to adaptive radiations, as will be discussed more fully below.

Givnish's (1997) review and critique of commonly used definitions of adaptive radiation is a useful heuristic to clarify the focus on adaptive radiations. A summary based on his analysis parses definitions of radiations with respect to whether they presume monophyletic groups and particularly rapid speciation, and whether they are associated with ecological diversification is presented in Table 4.1. A consideration of these three elements is critical to the development of a more precise and synthetic understanding of the concept of "adaptive radiation."

Must adaptive radiations be monophyletic?—Eldredge and Cracraft (1980) argued that adaptive radiations should occur in monophyletic clades, which seems eminently

reasonable. However, as mentioned above, Osborn (1902) did not make this requirement. (See also Schluter 2000). Furthermore, by restricting the definition to single clades, certain types of radiations would be excluded. For instance, many of the large-scale radiations that generated spectacular diversity (e.g., the Cambrian, the Cenozoic mammal, and the Ordovician radiations) involved several different lineages within larger clades that were diversifying independently and simultaneously (Fig. 4.1). This is especially true considering that some of the phylogenetic proliferation associated with these radiations likely occurred some time before the first appearance of the fossils, as part of a low-diversity “phylogenetic fuse” (Fortey et al. 1996; Cooper and Fortey 1998; Archibald and Deutschman 2001; Meert and Lieberman 2004; Lieberman et al. 2007). Absence of monophyly need not be limited to large radiations. The African lake cichlids seem to have undergone (monophyletically) radiations within several lakes; if the entire African region or the entire cichlid clade is considered, then the radiation is not monophyletic (Kocher 2004; Seehausen 2006).

Thus, it is important to ask whether determining the monophyly of a radiating group is important for understanding underlying evolutionary processes. The answer is clearly yes, because if scientists are testing whether group-level properties (e.g., easily interrupted sexual recognitions system; tendency to hybridize; sustained key innovations) of a clade are driving the radiations, it is important to document monophyly (Lieberman 1995; Lieberman and Vrba 1995). In contrast, if extrinsic (relative to the organisms themselves) factors such as climate change, geological change, and availability of ecological opportunity are driving the radiation, then one might predict extensive diversification of only parts of the clade in the regions affected (documenting non-monophyly of

diversifying parts of the clade). For example, consider one of many hypothesized mechanisms facilitating the adaptive radiation of Galápagos Finches—viz., the propensity of these particular finches to utilize different seed-types and diversify in

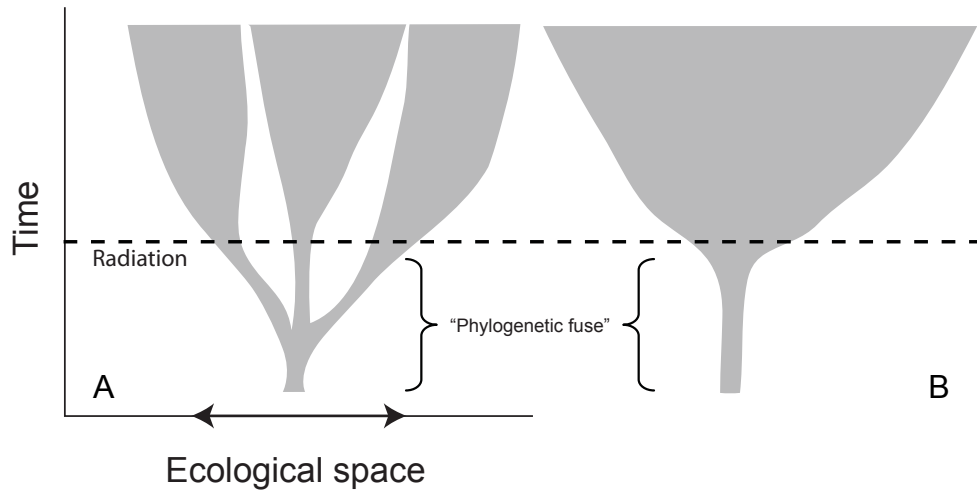


FIGURE 4.1. Two representations of adaptive radiations in the literature. A) Non-monophyletic radiation composed of several different clades. Examples of these radiations tend to be large scale (Cambrian, Ordovician, mammalian radiations). B) Evolutionary radiation within a clade, or stemming from a common ancestor (*sensu* Schluter 2000). Key innovations and exploration of empty landscape by a single ancestor will generate this monophyletic pattern.

their trophic structure. (See Grant and Grant 2007 for an excellent summary of research findings on these organisms.) Galápagos finches are not a monophyletic clade. A single species phylogenetically nested within the group resides in Cocos Island, some 800 km northeast of the Galápagos Island chain (Werner and Sherry 1987). This species is a generalist with diverse feeding behaviors, but it has not radiated as its Galápagos relatives have. This suggests that the force driving radiation in these finches is not solely intrinsic to the group; it may be partly dependent on extrinsic factors affecting the Galápagos members of the clade, but not their brethren on Cocos Island.

TABLE 4.1. Several definitions of “adaptive radiation” taken from the literature. These are characterized as to which three components of the radiation the authors focused on in their definitions—viz., Ancestry (the mono- or polyphyly of the radiation); Tempo (the association of the radiation with elevated tempos of speciation); and Ecology (the association of the radiation with the generation of ecologically diverse forms).

Author	Definition	Primary Components of Definition		
		Ancestry	Tempo	Ecology
Osborn (1902)	Differentiation of habit in several directions from a primitive type	✓		✓
Huxley (1942)	Invasion of different regions of the environment by different phylogenetic lines, which secondarily exploit different modes of life, within a group	✓		✓
Simpson (1944, 1953)	Approximately simultaneous divergence of numerous lines from the same ancestral adaptive type into different adaptive zones	✓	✓	✓
Mayr (1970)	Evolutionary divergence of members of a single phyletic line into a series of different niches or adaptive zones	✓		✓
Stanley (1979)	Rapid proliferation of new taxa from a single ancestral group	✓	✓	
Futuyma (1986)	Diversification into different ecological niches by species derived from a common ancestor	✓		✓
Erwin (1992)	Rapid bursts of taxonomic proliferation within a single clade triggered by extinction, the opening of an unoccupied geographic region, or key adaptations that allow a clade access to a new area of ecological space.	✓	✓	✓
Guyer and Slowinski (1993)	some organisms have features that allow them to speciate prolifically or if there is adaptive divergence cued by the appearance of some ecological stimulus		✓	✓
Skelton (1993)	An episode of significantly sustained excess of cladogenesis, as opposed to extinction, with adaptive divergence cued by the appearance of some form of ecological stimulus		✓	
Givnish (1997)	Origin of a diversity of ecological roles and attendant adaptations in different species within a lineage	✓		✓
Schluter (2000)	Evolution of ecological and phenotypic diversity within a rapidly multiplying lineage	✓	✓	✓
Losos and Miles (2002)	Clades that exhibit unusually profound phenotypic divergence into a variety of adaptive forms	✓		✓
Losos (2009)	Evolutionary divergence of members of a clade involving adaptation to the environment in a variety of different ways	✓		✓

How much diversity and what increases in tempo of speciation are necessary to invoke the term "adaptive radiation?"— Interestingly, not all scientists have focused on increasing tempo in their discussions of adaptive radiations (Table 4.1). For instance, Givnish (1997) stressed that the uniqueness of adaptive radiations lay in adaptive divergence rather than taxonomic diversification. Still, the requirement that the pace of taxonomic diversification increases during an adaptive radiation is central to the definitions of Simpson (1953), Stanley (1979), Eldredge and Cracraft (1980), Futuyma (1986), Gould (1991), Guyer and Slowinski (1993), Skelton (1993), and Schluter (2000). In the context of diversification patterns, it should be recognized that there are two indices of taxonomic diversification—total diversity and rate of diversification. Regarding the former, there is no consensus on how much diversity justifies use of the term adaptive radiation. Indeed, there is a considerable range in species numbers among cited examples of adaptive radiations. Consider that the Galápagos finches comprise 14 species and Hawaiian silverswords 28 species, whereas African cichlids comprise about 2000 species and the angiosperms approximately 350,000 species (Olson and Arroyo-Santos 2009). These disparities are problematic because the same ecological processes are being applied to radiations involving single species complexes and extrapolated to clades containing hundreds of thousands of species.

Although the size of radiation is not a relevant component of most definitions, rates of diversification (specifically, high speciation rates) are thought by some (Table 4.1) to result from ecological processes that allow rapid invasion into novel, open ecological opportunities. With respect to the notion that increasing evolutionary tempo is an important indicator of adaptive radiation, there has been some contention of what

constitutes “high” rates of diversification (Olson and Arroyo-Santos 2009). The study of evolutionary tempo has held an important place in paleontological studies of radiations (Simpson 1944). Moreover, diversification models provide a rigorous way to test for high speciation rates against a null hypothesis (Sanderson and Donoghue 1996; Lieberman 2001; Nee 2006). These approaches have been applied in paleontological studies, as well as in analyses of molecular datasets.

In the identification of adaptive radiations, one cannot focus solely on increasing diversification rate. Patterns must be identified in both molecular phylogenetic (Harmon et al. 1993; Baldwin and Sanderson 1998; Agrawal 2000; Rüber et al. 2003; Phillimore and Price 2008) and paleontological studies (Hulbert 1993; Foote 2000; Abe and Lieberman 2009 and others), because high initial rates of speciation subsequently decline. The discovery of such a pattern often entails differing opinions about the processes that might cause it.

What is the role for ecology?—Often, the high speciation rates mentioned above are ascribed to a rapid invasion of organisms into a geographic region or ecological lifestyle that facilitates numerous novel ecological opportunities, whereas declining rates of speciation suggest that the finite number of available niches are being filled (Simpson 1953). Such density-dependent cladogenesis has been invoked for both small and large-scale radiations (Cracraft 1982; Erwin 1982; Rabosky 2009). Nevertheless, one should be careful about invoking an adaptive radiation every the time the pattern of high initial and later declining speciation rates is recovered. For instance, such a pattern might be an artifact because molecular phylogenies cannot sample extinction directly (Crisp and Cook 2009; Rabosky 2009). Even if the pattern is real, phylogenetic biogeographic studies of

fossil taxa indicate they might be caused by changing environmental conditions that first encouraged, but later reduced, opportunities for allopatric speciation (e.g., Abe and Lieberman 2009). Phylogenetic biogeographic perspectives, when coupled with molecular data, may allow these issues to be considered with the extant biota (e.g., Phillimore and Price 2008; Esselstyn et al. 2009).

Several scientists have argued that ecological information is critical to the identification of adaptive radiations. As mentioned above, Givnish (1997) argued that recovery of a pattern of morphological/ecological divergence is fundamental to identifying an adaptive radiation, regardless of the amount of taxonomic diversification. Schluter (2000) suggested that to label a radiation as "adaptive," the taxonomic group must be ecologically diverse; further, a particular phenotype must be associated with the use of particular resources or the occupation of a particular environment. Extensive tests of phenotype-environment correlation have been applied. Beak size is correlated with choice of seed type in Darwin's finches (Grant 1986), Leg lengths leg lengths and coloration of lizards of the genus *Anolis* are associated with habitat (Irschick and Losos 1998; Losos et al. 1998; 2006), and cichlid jaw morphology matches trophic groups (Clabaut et al. 2007).

There is also an entire field, ecomorphology (Ricklefs and Miles 1994), dedicated to associating—via function— morphology to ecology. This enables the use of morphological diversification as a proxy for ecological diversification in studies of adaptive radiations. A pattern frequently used as evidence of an adaptive radiation is clades in which there are several independent acquisitions of purportedly ecologically relevant morphological traits (Losos et al. 1998; Young et al. 2009). In fact, the original formulation of adaptive radiation theory grew from the observation that convergent

ecological types had evolved within placental and marsupial clades (Osborn 1902). Important modern exemplars of such a pattern include *Tetragnatha* spiders from the Hawaiian Islands (Gillepsie 2005) and *Anolis* lizards from the Caribbean (Losos 2009). The proponents of ecology as a driver of adaptive radiations sometimes have used convergence as evidence that selective pressures are causing the radiation (Schluter 2000).

The advancement of ecomorphology signifies an important role for morphometric methods in the study of adaptive radiations. Because many aspects of behavior and ecology are indeterminate for extinct species, paleontologists often must rely on preserved morphology to make such inferences (Van Valkenburgh 1994); it is in the fossil record where morphometric approaches contribute greatly to the study of evolutionary radiations. Morphometric approaches have been applied frequently in paleontological studies that focus on the meaning of disparity and its changes through time (Gould 1989; Briggs et al. 1992; Foote 1993; 1997; Erwin 2007).

As described already, some scientists have focused on identifying a particular signature of adaptive radiations in relation to diversification rates—viz., high initial rates that decline subsequently. Sometimes they have ascribed a particular process to explain that pattern. Some paleontologists have formulated similar approaches to studying disparity and identifying the patterns and processes of evolutionary radiations. For example, a pattern of high initial disparity followed by constant or decreasing disparity, especially relative to species diversity, often has been explained by either invoking open ecological opportunities that subsequently close or increasing developmental constraints (e.g., Gould 1989; Ciampaglio 2002). (This is not the only process that might explain such a pattern, and below changing opportunities for allopatric differentiation are discussed).

An early peak in disparity that subsequently declines, and then stays constant typifies many paleontological studies—e.g., Paleozoic gastropods (Wagner 1995), blastozoans (Foote 1992), crustaceans (Wills 1998), and angiosperms (Lupia 1999). However, not all analyses have found this pattern—e.g., Briggs et al. 1992, 1994 with arthropods; Harmon et al. 1993 with various lizard groups; Young et al. 2009 with cichlids. Ecology has been used to explain patterns characterized by concurrent disparity and exponential taxonomic increase without saturation without exploring alternate hypotheses (e.g., Jernvall et al. 1996).

Many earlier paleontological studies of disparity lack a phylogenetic framework; further, disparity is not typically thought of in a context that considers monophyly to be important. However, as more phylogenies become available, this is likely to change, and some authors have tried to view disparity in a phylogenetic context (e.g., Wagner 1995; Smith and Lieberman 1999; Harmon et al. 2003; Stone 2003; Clabaut et al. 2007; Sidlauskas 2008; Abe and Lieberman 2009). Determination of the amount of morphological change that occurs at speciation events has the potential to be informative about the role of ecological processes in motivating diversification.

Using Adaptive Radiations as a Model for Integrating Ecological processes with Macroevolutionary Theory

“Nature abhors an empty niche.” Schluter (2000, p. 69)

Although other (non-adaptive) processes for adaptive radiations have been proposed—e.g., rampant hybridization (Seehausen 2004), developmental release (Gould

1989), and sexual selection-driven speciation (Galis 1998)—ecological explanations have dominated the evolutionary radiation literature. For instance, Schluter's (2000) ecological theory forms the most complete framework for studying adaptive radiations in recent times (1360 times, Google Scholar 2010); this theory is so prominent in the field that it merits additional detailed discussion. Schluter's (2000) ecological theory of adaptive radiation considered several aspects of ecology—viz., ecological divergence; competition and ecological opportunity; and ecological speciation. Ecological opportunity is the overarching concept joining both small and large radiations (Cracraft 1982; Erwin 1982) and is considered first, followed by a discussion of ecological divergence and ecological speciation.

Ecological opportunity—. Ecological opportunity applied to adaptive radiations posits expansion first and subsequent saturation of ecological space. Expansion occurs upon: (1) invasion of a new, unoccupied area; (2) acquiring a key innovation that opens previously unavailable ecological space; or (3) modification/expansion of ecological space (Simpson 1953; Schluter 2000). Saturation is achieved when competitive interactions for resources in a finite ecological space become extensive (Benton 1996).

Island radiations frequently are cited as examples in which new ecological space becomes available (Simpson 1953; Grant 1998; Harmon et al. 2008; Losos and Ricklefs 2009). The extraordinary morphological diversity and endemism seen in islands has been attributed to a lack of predators and competitors, allowing for diversification and specialization of new arrivals (Darwin 1859). One mechanism considered relevant here is the generalist-to-specialist hypothesis. (See Schluter 2000 for references and criticism.) In this view, generalist species can colonize new areas more easily and can be partitioned

ecologically into specialized niches. In the adaptive landscape metaphor, a generalist would cover a much wider adaptive area, and thus, would be exposed to more adaptive (specialized) peaks (Simpson 1944). A pattern of morphological change that might be expected in such a transition is as follows. First, a generalist species faced with open ecological opportunities would rapidly diversify morphologically and ecologically. Second, as several species come to occupy the different adaptive peaks, there should be a decrease in the amount of morphological and ecological change.

The idea of key innovations was advanced by Simpson (1953) to explain rapid diversification patterns during adaptive radiations, but see also Hunter (1998) and Heard and Hauser (1995). A key innovation is a trait that allows an organism to invade a new ecological space. (These should not be confused with species-level properties that might incite speciation —e.g., limited dispersal ability that subsequently affects population structure [Lieberman and Vrba 1995]; these are likely to be very important in explaining aspects of evolutionary radiations, but are not what authors typically intended when they invoked key innovations.) One way key innovations have been identified is through phylogenetic studies, in which it is possible to study the distribution of characters in diverse and depauperate clades (e.g., Berenbaum et al. 1996; Bond and Opell 1998; Hunter 1998; Hulsey et al. 2006; but see Alfaro et al. 2009). However, because phylogenies are based on synapomorphies, *a posteriori* identification of any of these synapomorphies as “key innovations” could be tautological (Guyer and Slowinski 1993; Donoghue 2005). Another problem is finding a causal relationship between the acquisition of a trait and increased speciation rates. For example, Hunter and Jernvall (1995) hypothesized that independently acquired hypocone cusp attachment on molars of several mammal groups

allowed them to radiate into other trophic ecologies and speciate. Although this trait is associated with herbivory, trophic success is not likely only dependent on one attachment on the molars. Moreover, acquiring a trait that allows access to a new adaptive zone does not necessarily translate to higher speciation rates (Vrba 1987; Cracraft 1990; Allmon 1992); adaptive success is not the same as speciation potential.

It is also important to recognize that expansion and modification of ecological space is a complex phenomenon that can involve changes in physical and biotic factors. An example of modification of current ecological space is the classic idea that mammals were only able to radiate after the disappearance (mass extinction) of the incumbent dinosaurs (Simpson 1953; Stanley 1993). These radiations following mass extinctions are attributed to invasion facilitated by newly open ecological opportunities (e.g., Sepkoski and Miller 1985; Erwin 2001). To complicate this issue further, other authors have suggested that the creation of increasing ecological complexity might trigger expanding opportunities for diversification through positive feedback loops (Vermeij 1977; Erwin 1994; Bambach 2007; Erwin 2008; but see Cornette and Lieberman 2004 and Novack-Gottshall 2007). The Mesozoic Marine Revolution is hypothesized to exemplify this. In response to increased predation pressure, the marine shelly fauna greatly diversified and there was increased ecological structuring (Vermeij 1977). Co-evolutionary interactions could also be important in this regard (Odling-Smee et al. 2003).

Another potential hallmark signature of an adaptive radiation is the saturation of ecological space. In particular, saturation of taxonomic and morphological diversification has been used to validate the notion that ecospace is finite (e.g., Rabosky 2008). Some have suggested that logistic growth curves characterize small and large-scale radiations

(Rieppel 1984; Erwin 1992; Benton 1997; Benton and Emerson 2007) which prompted the use of such equilibrium models; these have been applied at hierarchical levels as small as bacteria in a petri dish (Brockhurst et al. 2007) and as large as the evolution of all animal life (e.g., Sepkoski's 1984 evolutionary faunas). In the case of the latter, however, it is important to recognize that overall diversification cannot be distinguished from a random walk, except for the last 75 MY (Cornette and Lieberman 2004).

Juxtaposing the arguments relating open ecological opportunities and saturation, there has been considerable discussion as to whether ecospace is finite and whether the laws of competition should even be viewed to operate in such a manner (Rieppel 1984; Benton 1996). Some have also argued that adaptive zones are not ontologically relevant and, instead, are simply an intellectual remnant of the Neo-Darwinian synthesis (Cracraft 1982). In this regard, it is useful to revisit the difference between large- and small-scale radiations. The metaphor that Simpson (1944, 1953) developed for adaptive zones and higher taxa originally was developed for populations and species (Eldredge 1985, 1989). In addition, the ecological theory associated with niches—incumbency, competition, predator-prey interactions, resource limitation, saturation, etc.—also focused on the population and at times the species level. Extrapolating what happens at these lower levels to higher levels such as clades is neither well justified by data nor theory (Eldredge 1979, 1985, 1989; Gould 1980, 1982; Vrba 1980, 1985; Lieberman and Dudgeon 1996). A classic example focusing on competition was the idea that the decline of brachiopods was caused by the competitive superiority of mollusks; Gould and Calloway (1980) remarked that whole diverse clades are not the entities competing, and the diversification patterns in the two groups were much like “ships that pass in the night.” Perhaps similarly the notion

that ecospace saturation explains the dynamics of large-scale evolutionary radiations may be problematic. Moreover, ecosystem structure has changed significantly through time (detailed summary in Bambach et al. 2007) and also produced increasing environmental and geographic complexity. An expanding and fluctuating ecospace suggests that saturation is not real. More research is required, along with an understanding the dynamics of taxonomic diversification with ecospace occupation (e.g., Pie and Weitz 2005).

ABIOTIC FACTORS AND ADAPTIVE RADIATIONS

Above, we discussed particular patterns and the ways in which studies of adaptive radiations interpreted them with ecological processes. However, a number of these patterns that have been attributed to ecologically mediated diversification can be explained by allopatric mechanisms. In the following section, a process by which climate-driven allopatric speciation in geographically complex areas generates patterns of ecologically diverse prolific clades is proposed. This view of radiations further supports the importance of abiotic factors driving evolution and calls for a re-interpretation of the adaptive radiation paradigm.

Speciation

Speciation is central to any adaptive radiation. Therefore, an examination of speciation theory could be crucial to understanding the core of adaptive radiation. In the minds of most contemporary biologists, speciation centers on a sequence of geographic isolation, divergence, and the development of reproductive isolation (Dobzhansky 1937;

Mayr 1942; Coyne and Orr 2004). A key aspect of this view of speciation is that it is a sequential process. Isolation occurs when populations are separated by a geographical barrier that interrupts gene flow. The disparate populations diverge (natural selection, drift, etc.), and given enough divergence, the populations become reproductively isolated such that if they were to meet, they could not interbreed successfully (Mayr 1942).

Divergence and reproductive isolation are viewed as by-products of isolation (discussed in detail by Baker 2005). These fundamental steps of speciation are the backbone of many evolutionary studies. There is much debate on this sequence of steps; supporters of non-allopatric speciation emphasize mechanisms that cause genetic divergence and reproductive isolation given occurring gene flow (Baker 2005), but the allopatry vs. sympatry debate will not be focus here.

The importance of geographic isolation in the speciation process is clearly outlined by Mayr (1942, p. 187):

The primary factor is thus geographic segregation and isolation, and the secondary factor is the gradual accumulation of genetic differences leading to morphological, physiological, ecological and ethological differences.

This is reiterated (and preceded) by Dobzhansky (1937, p. 229), “Species formation without isolation is impossible.” Perhaps more of the focus on what causes an adaptive radiation should be on geographic isolation because finding that there are ecological differences between closely related species does not mean they have undergone sympatric speciation. Mayr (1942) stated, “There is no geographic speciation that is not at the same

time ecological and genetic speciation.” The difference between selective forces as divergence mechanism and speciation mechanism is recognized (e.g., Losos and Glor 2003); however, adaptive patterns are seldom interpreted as the product of isolation mechanisms through allopatric means.

Allopatry and adaptive radiations.—The same is true of the theory of adaptive radiations. Ecological causes for adaptive radiations include natural selection as the result of environmental change, competitive displacement, sexual selection, coevolution, predator-prey dynamics, and introgression. However, the occurrence of such divergence mechanisms does not preclude isolation from being the primary mechanism that initiates speciation. This is crucial to our understanding of the process of adaptive radiation. Thus, a radiation could be mediated by factors promoting geographic isolation, but because the subsequent mechanism causes ecological divergence, the latter process is considered as the sole mechanism. Even an allopatrically driven radiation with subsequent ecological divergence can produce a phenotypically diverse group. The exceptional character of prolific speciation seen in some radiations could be explained by allopatry if there were multiple opportunities for isolation. Such opportunities can occur in geographically complex regions, and these can be amplified when the taxa in such region are exposed to environmental change that allows for additional and simultaneous opportunities for isolation.

Consider what might be involved an allopatrically mediated adaptive radiation—(1) invasion into a geographically complex area with multiple areas of endemism; (2) expansion into all areas, facilitated by climate change, followed by subsequent isolation, again caused by climate change; (3) action of one or more divergence mechanisms that

results in reproductive isolation; and (4) repetition of the process with cycling climatic changes.

The simplest way for populations to become isolated and have their gene flow interrupted is physical separation (Dobzhansky 1937; Mayr 1942; see Coyne and Orr 2004), and this is why there is a high frequency of sister-species separated by geographic barriers (Cracraft 1982; Wiley and Mayden 1985; Bolnick and Fitzpatrick 2007). Such allopatric differentiation can be caused either by the formation of a barrier (vicariance) or movement across a barrier (dispersal), and there abiotic factors, such as geological and climatic changes, are important in mediating allopatric patterns (Lieberman 2000). Further, a changing and dynamic earth is replete with phenomena that promote vicariance and range expansion. In turn, such range expansion could be mediated by abiotic and biotic factors (Lieberman 2000).

Because abiotic factors that cause allopatry can have profound consequences for evolution, it is worth considering the geologic and climatic setting of adaptive radiations. A tabulation of some adaptive radiations in the recent literature reveals a variety of different settings (Table 2); a number have occurred on islands, which allow for multiple opportunities for allopatry. The importance of allopatry for driving radiations is best exemplified by cases of so-called “non-adaptive” radiations (*sensu* Gittenberger et al. 1991). There are examples involving *Albinaria* snails in Greece and Crete, Porto Santo Island snails, and North American woodland salamanders (Gittenberger 1991; Cameron et al 1996; Kozak et al. 2005). The signature of a non-adaptive radiation is a rapidly speciating clade that contains geographically discrete taxa that show little morphological/ecological diversity. Allopatric speciation supposedly would not likely

have to be accompanied by niche expansion (Gitternberger 2004). This is especially true given that speciation involving allopatry is a sequential process, and following geographic isolation divergence could cause only small phenotypic change, particularly if not mediated by selective forces, perhaps genetic drift.

TABLE 4.2. Some recent studies since 2004 that identified a particular diversification pattern as an “adaptive radiation.”

Citation	Organism	Location	General type	# of species
(Austin et al. 2004)	Geckos	Mascarene Islands	Insular	5
(Chinn and Gemmell 2004)	cockroach <i>Celatoblatta</i>	New Zealand	Local	10
(Crisp and Cook 2009b)	Legumes	Australia and Africa	Worldwide	300
(Davis et al. 2005)	Malpighiales plants	Tropics	Worldwide	124
(Dunbar-Co et al. 2008)	<i>Plantago</i> plant	Hawaii	Insular	42
(Gillespie 2005)	<i>Tetragnatha</i> spiders	Hawaii	Insular	5
(Glaubrecht and von Rintelen 2008)	<i>Tylomenia</i> gastropods	Sulawesi lakes	Lake	34
(Goldblatt et al. 2009)	Iris <i>Ferraria</i>	Sub-Saharan Africa	Wide-ranging	17
(Guzman et al. 2009)	<i>Cistus</i> plant	Mediterranean	Wide-ranging	12
(Hughes and Eastwood 2006)	<i>Lupinus</i> plant	Andes	Insular	85
(Irestedt et al. 2009)	Ovenbirds	Neotropical	Wide-ranging	105
(Kassen et al. 2004)	<i>Pseudomas fluorescens</i>	Laboratory	Laboratory	1
(Kocher 2004)	Cichlids	African Rift Lakes	Lake	>1000
(Koepfli et al. 2008)	Mustelidae	Worldwide	Worldwide	59
(Lopez-Fernandez et al. 2005)	Geophagine cichlids	South America	Wide-ranging	>30
(Lukoschek and Keogh 2006)	Hydrophiine sea snakes	Indo pacific	Wide-ranging	40
(Mangel et al. 2007)	Rockfishes	Northeast Pacific	Wide-ranging	100
(Meimberg et al. 2006)	<i>Micromeria</i> plant	Canary Islands	Insular	16
(Parent and Crespi 2009)	Land snails	Galápagos	Insular	30
(Pinto et al. 2008)	<i>Anolis</i>	Mainland	Wide-ranging	197
(Price 2010)	Leaf warblers	Eurasian	Wide-ranging	80
(Sakai et al. 2006)	<i>Schiedea</i> plant	Hawaii	Insular	34
(Steeman et al. 2009)	Cetaceans	Worldwide	Worldwide	87
(Wirta et al. 2008)	Dung beetles	Madagascar	Local	>60

Given the importance of allopatric speciation, it stands to reason that multiple opportunities for isolation can cause higher speciation rates. Cracraft (1982) proposed that rate of speciation should be directly proportional to the evolutionary history of lithospheric complexity for a given interval of space and time, and it is worthwhile to expand on his framework. In particular, an area can be characterized as geographically complex if it contains multiple, habitable and isolated areas. Moreover, complexity increases given the number of possible connections between the areas, and the frequency and duration of the connections. Consider an idealized example in which an abiotic change such as climate change causes every area to become connected to every other area and all taxa subsequently move between the no longer isolated areas. Posit a subsequent climate change that then isolates the areas to a sufficient degree and for enough time to allow speciation. Assuming speciation always follows this discontinuity and that this is the primary factor causing speciation and this would lead to an exponential increase in the number of species (S) where $S = n^i$ with n the number of areas, and i the number of events that connect and later disconnect the areas. As an example, consider a region with three distinct areas of endemism, and starting with a single species in one of the area, and one cycle of climate change that first connected and then disconnected the areas, allowing range expansion with subsequent vicariance. First there would be three new species. $S = 3^1 = 3$; upon another cycle of climate change quickly there would be 9 species with additional cycles producing 27, etc. This is of course a model, but the circumstances are not entirely farfetched (e.g., Abe and Lieberman 2009). This illustrates how increasing geographic complexity can dramatically raise speciation rates.

Areas of obvious geographic complexity include islands for which there are many cases of adaptive radiations, but this model is possible for any isolation-forming heterogeneous environment (e.g, river systems, mountain tops, refugia, etc.). Because isolation depends upon the species in question, an area of geographic complexity for one species may not be so for another. For example, a benthic marine population might be separated from another conspecific population by a complex sea-floor, but the complexity of the seafloor would not affect the pelagic species swimming above it. Geographically complex places that have been targeted in the adaptive radiation literature include marine basins separated by relatively elevated arches (e.g., Abe and Lieberman 2009), lake systems connected by rivers (e.g., the East African Lake system [Johnson et al. 1996]; lakes in Sulawesi [Glaubrecht 2008]) and heterogenous habitat (e.g., Appalachian *Desmognathus* salamanders [Kozak et al. 2005]). It is worth mentioning that these are tectonically active systems, and both climatic and plate-tectonic changes could play a role in isolating and joining regions in all of these places. Geographic complexity has been implicated as the reason for higher diversity in a number of cases; for example, Cocos Island comprises a single area that contains only one species of Darwin's finches (Grant and Grant 2007).

The importance of climate change as a trigger for adaptive radiation

Climate change can have a profound impact on diversification patterns (Vrba 1980; 1993; 1995a,b; Benton et al. 2009). Because the history of the Earth shows dynamic shifts of climate, speciation mediated by climate change is relevant to the study of radiations

(Benton and Emerson 2007). Climate change triggers vicariant speciation by promoting geographic isolation with the formation of physical barriers and the fragmentation of continuous habitat. In the marine realm, climate change often involves changes in sea level that connect or separate areas; this can also have important effects on the terrestrial realm, and there, climate change will also alter river and lake systems (e.g., Wiley and Mayden 1985; Rueber et al. 2009). The Milankovitch cycles—caused by precession, obliquity, and eccentricity in the Earth’s orbit—are important climatic factors and today produce oscillations in climate of roughly 20k, 40k, and 100k years (Bennett 2001; Jansson and Dynesius 2002). These cycles have been implicated in causing speciation and species turnover as part of the turnover-pulse hypothesis (Vrba 1980; 1995a,b). These climate-driven diversification pulses have left their signature in the fossil record (Vrba 1980; 1995b; Janis 1993; Raia et al. 2005; but see Barnosky 2001). A related concept of formation of multiple isolates in refugia (see reviews in Hewitt 2001; Bennett and Provan 2008) has potential for high speciation in fragmented areas (Tainaka 2006).

Adaptive radiations are produced by a complex interplay of geographic complexity, climate change and biotic factors

However, the simple combination of geographic complexity and climate change is not a guarantee that a radiation will happen. Great changes in climate occurred during the Quaternary, including multiple ice-ages (Webb and Bartlein 1992), but this was not accompanied by unusually high diversification rates (Barnosky 2005; reviewed in Bennett 2008). This may be because the climatic cycles were too short to produce barriers of

sufficient duration to allow speciation to occur (Vrba 1996; Bennett 1997; Barnovsky 2005). Furthermore, geographic complexity alone does not seem to always produce an adaptive radiation (e.g., Ricklefs and Bermingham 2007); in particular, some taxa in geographically complex regions may radiate whereas others do not (e.g., mockingbirds in the Galápagos, Grant and Grant 2007). Thus, any model of adaptive radiation must consider not only abiotic factors but biotic factors as well; the abiotic factors may set the stage for the allopatric speciation that allows the biotic factors to come to the fore.

An important biotic factor may be differences in the potential for speciation among groups. For instance, consider emergent, species-level properties of clades that directly affect the propensity to become geographically isolated. Examples of these are considered in Vrba (1988) and include the limited dispersal ability of cichlids (Sturmbauer and Meyer 1992), the wide dispersal ability of white-eyed birds (Moyle et al. 2009), host switches to wider-ranging prey (Wirta et al. 2008), and colonization of insular habitats of silverswords and tarweeds (Baldwin 2007). Understanding these emergent properties in a hierarchical framework may transform Simpson's (1953) original understanding of key innovations; he focused solely on organismic adaptations as key to opening ecological opportunities.

Re-evaluating classic examples of adaptive radiation in light of these new views.

Below, the African lake cichlids and calmoniid trilobites from the Devonian Malvinkaffric Realm (Eldredge and Cracraft 1980) are considered under the allopatric-mediated model of radiation.

African lake cichlids are one of the most enduring examples of adaptive radiation owing to their spectacular diversity and rapid diversification (Galis 1998; Kocher 2004;

Seehausen 2006). Comprising about 2000 species, these fish account for about 7% of the total number of fish species, all contained in rift-formed lakes in East Africa. Each major lake has its own independent monophyletic radiation. Some processes invoked to explain this radiation include trophic differentiation (Clabaut et al. 2007), key innovations of the pharyngeal jaw (Liem 1973), sexual selection (Galis 2008), generalist-to-specialist transitions (Salzburger et al. 2005), and hybridization (Seehausen 2006). However, the geographic history of the area is complex. Substantial tectonic and climatic changes caused major oscillations in lake level (Johnson et al. 1996; Sturmbauer 2001; Salzburger et al. 2005). Congruence in patterns of radiation among all lakes suggests that single climatic events (refilling of lakes 10,000 years ago) could have caused the rapid speciation in different African lakes (Sturmbauer 2001). A study of lake-level fluctuations of African cichlids in Lake Tanganyika found correlations between radiations and Pleistocene glaciations, which split the lake into three parts (Ruber et al. 1998). The complete desiccation of Lake Victoria about 15Ka did not match the age of the cichlid radiation based on molecular divergence estimates; this suggests that the fish used isolated riverine and lacustrine refugia (Elmer 2009). A study on reconstruction of habitat shifts based on phylogeny of haplochromine cichlids documented multiple movements from riverine to lacustrine habitats (Salzburger et al. 2005), although lake stocks remained monophyletic. Thus, there is ample evidence for the importance of allopatry in the lakes, suggesting that the divergence mechanisms producing high ecological diversity might be less important than allopatry. However, how does one explain why these particular cichlids speciated in the lakes, and not other species? Two possible explanations are (1) the limited dispersal ability that lead to high degrees of microallopatry in these cichlids (Givnish 1997), and (2)

their sexual-recognition systems, which are easily modified (Seehausen et al 1997; Smith and Kornfield 2002). These biotic properties are not inherently adaptive and are better viewed as emergent, species-level properties. Given that climate-driven isolation may have been the initiating factor of the radiation, it might be more appropriate to view this example as an allopatric -mediated adaptive radiation.

The calmoniid trilobites were an endemic monophyletic group consisting of more than 40 species of morphologically diverse trilobites that diversified in the Malvinokaffric Realm of the Devonian (Eldredge and Cracraft 1980; Eldredge and Ormiston 1981). This diverse group has been hailed as a classic example of adaptive radiation in the fossil record and also displays high morphological diversity. Abe and Lieberman (2009) examined patterns of diversification and found high initial rates of speciation, followed by decreasing rates. Biogeographic analysis of the Malvinokaffric Realm indicated an area of high geographic complexity with multiple intracratonic basins affected by cyclical sea-level regressive and transgressive events that would have allowed expansion and contraction of taxon ranges. Ultimately, speciation rates were correlated with sea-level changes and associated geographic complexity. A geometric morphometric approach was used to quantify morphological change during the evolutionary radiation in order to test the hypothesis that ecological divergence would show patterns of increased morphological diversification. Morphological change was not found to show any ecologically- mediated trends within the clade. This indicated abiotic factors were initiating the mechanisms of speciation.

CONCLUSION

In this chapter, the term “adaptive radiation” was reviewed both in terms of patterns and processes. The traditional view was that radiations were caused by ecological processes driving speciation, namely, the equilibrium model due to filling and saturation of ecological space. This model has been applied to radiations of small clades (e.g., insular radiations), and large, non-monophyletic diversification over geological time (e.g., the metazoan radiation). Invoking a process such as ecological saturation is problematic because there is little support for the existence of fixed, finite ecospace; it seems inaccurate to suggest these played a role in larger radiations. Instead of simply focusing on biotic processes, abiotic factors, especially those that promote allopatry, must play a role in adaptive radiations. This does not mean there is no role for adaptation in such radiations, but the important initiating role of geographic and climatic complexity must be considered. Studies of the classic examples of adaptive radiations agree with this new framework. Given the major role of abiotic and allopatric processes, the term “adaptive radiation” as it is currently used is therefore misleading, as the process causing most of them are not confined to ecological divergence alone. A new understanding of radiations is emerging that abandons the single, deterministic process of ecological divergence as the main driver of evolution and speciation.

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APPENDIX 1

Specimens used in the geometric morphometrics. Most specimens did not have accession numbers, so identification may not be databased.

Location	Identification	Species
AMNH	044238	<i>Punillaspis</i> sp.
AMNH	Pujravi z. M. venustus	<i>Eldredgeia venustus</i>
AMNH	047147	<i>Eldredgeia eocryphaea</i>
AMNH	044260	<i>Malvinocooperella pregiganteus</i>
AMNH	044249	<i>Malvinocooperella pregiganteus</i>
AMNH	044257	" <i>Clarkeaspis</i> " <i>gouldi</i>
AMNH	044268	<i>Metacryphaeus rotundatus</i>
AMNH	044269	<i>Metacryphaeus rotundatus</i>
AMNH	044263	<i>Metacryphaeus giganteus</i>
AMNH	044243	<i>Plesioconvexa praecursor</i>
AMNH	044240	<i>Eldredgeia venustus</i>
AMNH	044274	<i>Metacryphaeus conexus</i>
AMNH	17923	<i>Vogesina lacunafera</i>
AMNH	17953	<i>Vogesina lacunafera</i>
AMNH	n/a	<i>Eldredgeia venustus</i>
AMNH	Chacoma 49	<i>Metacryphaeus giganteus</i>
AMNH	Pujravi-z.Fb-9	<i>Metacryphaeus giganteus</i>
AMNH	Chacoma- 11	<i>Metacryphaeus giganteus</i>
AMNH	26336:3	<i>Vogesina devonica</i>
AMNH	26360-3	<i>Plesiomalvinella boulei</i>
AMNH	26360-9	<i>Malvinocooperella pregiganteus</i>
AMNH	branisa "15"	<i>Metacryphaeus branisai</i>
AMNH	Limba-140	<i>Metacryphaeus curvigena</i>
AMNH	n/a	<i>Eldredgeia venustus</i>
AMNH	Chacoma-184	<i>Eldredgeia venustus</i>
AMNH	z.Patacayama-115	<i>Eldredgeia venustus</i>
AMNH	136	<i>Metacryphaeus curvigena</i>
AMNH	n/a	<i>Plesioconvexa praecursor</i>
AMNH	36745	<i>Parabouleia calmonensis</i>
AMNH	36722	<i>Bouleia dagincourti</i>
AMNH	44139	<i>Plesiomalvinella boulei</i>
AMNH	44143	<i>Malvinella buddae</i>
AMNH	44147	<i>Palpebrops donegalensis</i>

AMNH	44144	<i>Palpebrops donegalensis</i>
AMNH	44141	<i>Malvinella buddae</i>
AMNH	44130	<i>Metacryphaeus tuberculatus</i>
AMNH	044137	<i>Plesiomalvinella pujravii</i>
AMNH	44142	<i>Malvinella haugi</i>
AMNH	46441	<i>Eldredgeia venustus</i>
AMNH	29104	<i>Bouleia dagincourti</i>
Cooper 1982		<i>Metacryphaeus caffer</i>
Cooper 1982		<i>Metacryphaeus caffer</i>
Cooper 1982		<i>Metacryphaeus caffer</i>
Cooper 1982		<i>Metacryphaeus caffer</i>
Carvalho et al. 1997		<i>Metacryphaeus kegesi</i>
Carvalho et al. 1997		<i>Metacryphaeus kegesi</i>
Carvalho et al. 1997		<i>Metacryphaeus meloi</i>
Carvalho 2003		<i>Wolfartaspis liebermanii</i>
Cooper 1982		<i>Typhloniscus baini</i>
Cooper 1982		<i>Typhloniscus baini</i>
Cooper 1982		<i>Typhloniscus baini</i>
Cooper 1982		<i>Metacryphaeus caffer</i>
Edgecombe et al. 1994		<i>Talacastops</i> sp.
Edgecombe et al. 1994		<i>Talacastops zarelae</i>
Edgecombe et al. 1994		<i>Talacastops zarelae</i>
Edgecombe et al. 1994		<i>Bouleia</i> cf. <i>sphaericeps</i>
Wolfart 1968		<i>Plesioconvexa praecursor</i>
Lieberman et al. 1991		<i>Metacryphaeus australis</i>
Lieberman et al. 1991		<i>Malvinella haugi</i>
Baldis and Longobucco 1977		<i>Punillaspis argentina</i>
Baldis and Longobucco 1977		<i>Punillaspis argentina</i>
MNRJ	33	<i>Metacryphaeus australis</i>
MNRJ	35	<i>Metacryphaeus australis</i>
MNRJ	n/a	<i>Metacryphaeus australis</i>
NHNM	23815	<i>Eldredgeia venustus</i>
NHNM	76-3	<i>Malvinella buddae</i>
NHNM	C-6	<i>Plesiomalvinella boulei</i>
NHNM	Pjd-2	<i>Vogesina aspera</i>
NHNM	Pjd-2	<i>Malvinella buddae</i>
NHNM	Purjavi	<i>Malvinella buddae</i>
NHNM	i	<i>Metacryphaeus branisai</i>
NHNM	287920	<i>Bouleia dagincourti</i>
NHNM	O1-9188	<i>Metacryphaeus conexus</i>
NHNM	9230	<i>Malvinocooperella pregiganteus</i>
NHNM	O1	<i>Metacryphaeus curvigena</i>

NHNM	O1-5822-9479	<i>Plesiomalvinella pujravii</i>
NHNM	O1	<i>Metacryphaeus curvigena</i>
NHNM	O1	<i>Plesiomalvinella pujravii</i>
NHNM	457044	<i>Metacryphaeus curvigena</i>
NHNM	468743	<i>Metacryphaeus branisai</i>
NHNM	468746	<i>Metacryphaeus curvigena</i>
NHNM	468741	<i>Clarkeaspis padillaensis</i>
NHNM	468742	<i>Clarkeaspis padillaensis</i>
NHNM	468744	<i>Metacryphaeus branisai</i>
NHNM	C.9	<i>Vogesina aspera</i>
NHNM	9203	<i>Malvinocooperella pregiganteus</i>
NHNM	A-24	<i>Metacryphaeus giganteus</i>
NHNM	7.2	<i>Metacryphaeus giganteus</i>
NHNM	7.2-5820	<i>Plesiomalvinella boulei</i>
NHNM	7.2	<i>Plesiomalvinella boulei</i>
NHNM	7.2	<i>Plesiomalvinella boulei</i>
NHNM	Patacamaya	<i>Plesiomalvinella boulei</i>
NHNM	Branisa-8.3	<i>Eldredgeia venustus</i>
NHNM	Branisa-8.3	<i>Metacryphaeus tuberculatus</i>
NHNM	Branisa-Belen-7.9	<i>Wolfartaspis cornutus</i>
NHNM	Branisa-Belen-7.9	<i>Wolfartaspis cornutus</i>
NHNM	Branisa-Belen-7.9	<i>Wolfartaspis cornutus</i>
NHNM	Eremopyge-7-9	<i>Wolfartaspis cornutus</i>
NHNM	Branisa-Belen	<i>Malvinocooperella pregiganteus</i>
NHNM	Branisa-Belen-7.9-X69-M-196	<i>Wolfartaspis cornutus</i>
NHNM	Branisa-Belen-7.9	<i>Wolfartaspis cornutus</i>
NHNM	Branisa-Belen-7.9	<i>Vogesina aspera</i>
NHNM	Branisa-Belen-7.9	<i>Vogesina aspera</i>
NHNM	Branisa-Belen-7.9-M210	<i>Vogesina aspera</i>
NHNM	Branisa-7.3	<i>Metacryphaeus conexus</i>
NHNM	Branisa-7.7	<i>Eldredgeia venustus</i>
NHNM	Branisa-7.7	<i>Eldredgeia venustus</i>
NHNM	Branisa-7.7	<i>Metacryphaeus tuberculatus</i>
NHNM	Branisa-7.5	<i>Malvinella buddae</i>
NHNM	Branisa-7.10	<i>Vogesina lacunifera</i>
NHNM	Branisa-C6	<i>Vogesina aspera</i>

APPENDIX 2

Description of landmark locations used in the geometric morphometric analyses on trilobite cephalata.

1. Antermost point on cephalon located on anterior margin (may be same as 2 if no anterior border present)
2. Antermost point of glabella
3. Midpoint of posterior margin of S0
4. Midpoint of anterior margin of L0
5. Midpoint of posterior margin of L0 ; landmark placed at base if occipital spine or node present
6. Anterolateral contact of axial furrow with cephalic margin
7. Posterior distal end of S3 contact with axial furrow
8. Posterior proximal end of S3
9. Contact of axial furrow with transverse line to proximal end of S2
10. Posterior distal end of S2
11. Posterior proximal end of S2
12. Contact of axial furrow with distal S1
13. Proximal end of S1
14. Contact of axial furrow with posterolateral of L1
15. Antermost point at base of eye
16. Postermost point at base of eye
17. Contact of lateral cephalic margin directly transverse of proximal end of S2
18. Anterodistal end of posterior border furrow
19. Midpoint on eye curvature