

The Nature of Evolutionary Radiations: A Case Study Involving Devonian Trilobites

Francine R. Abe · Bruce S. Lieberman

Received: 5 February 2009 / Accepted: 16 April 2009 / Published online: 6 May 2009
© Springer Science+Business Media, LLC 2009

Abstract Evolutionary radiations, times of profound diversification of species against a broader background of more muted evolutionary change, have long been considered one of the fundamental patterns in the fossil record. Further, given the important role geological, environmental, and climatic processes play in causing speciation, analyzing the biogeographic context of radiations can yield important insight into their evolutionary mechanisms. In this study we examine biogeographic patterns and quantify rates of speciation in a diverse group of Devonian trilobites, the calmoniids, that has been hailed as a classic paleontological example of an evolutionary radiation. In particular, a phylogenetic biogeographic analysis—modified Brooks Parsimony Analysis—was used to examine the processes and geographic setting of speciation within the group. Results indicate that the Malvinokaffric Realm was a geographically complex area, and this geographic complexity created various opportunities for speciation via geodispersal and vicariance that created the fuel that fed the speciation in these taxa. Part of the geographic complexity was created not only by the inherent geologic backdrop of the region, but the overlying changes of sea level rise and fall. Rates of speciation were highest when sea level was lowest. Low sea level encouraged isolation of faunas in different tectonic basins. By contrast, sea level

rise facilitated range expansion and geodispersal to other distinct tectonic basins, and speciation rates concomitantly fell; however, the taxa with the expanded ranges were later fodder for diversification when sea level fell again. Here we present a view of evolutionary radiations driven fundamentally by external abiotic factors—geology and climate—that cause range expansion and opportunities for geographic isolation with resultant rapid speciation.

Keywords Evolutionary radiations · Macroevolution · Trilobites · Biogeography · Speciation rates · Devonian

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; Vogler and Goldstein 1997; Schluter 2000). While it is important to

F. R. Abe (✉)
Department of Ecology and Evolutionary Biology, University of
Kansas, 1345 Jayhawk Blvd., Lawrence, KS 66045, USA
e-mail: fabe@ku.edu

B. S. Lieberman
Department of Geology and Natural History Museum and
Biodiversity Research Center, University of Kansas, 1475
Jayhawk Blvd., 120 Lindley Hall, Lawrence, KS 66045, USA
e-mail: blieber@ku.edu

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 (Mayr 1942; Cracraft 1982). 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 (Stanley 1979; Gilinsky and Bambach 1987; Vrba 1987; Sepkoski 1998; Rode and Lieberman 2005). 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; Lieberman et al. 1991; Hulbert 1993; Lieberman 2001).

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 acaetid trilobites endemic solely to the Malvinokaffric Realm (Fig. 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 et al. 1991; Lieberman 1993).

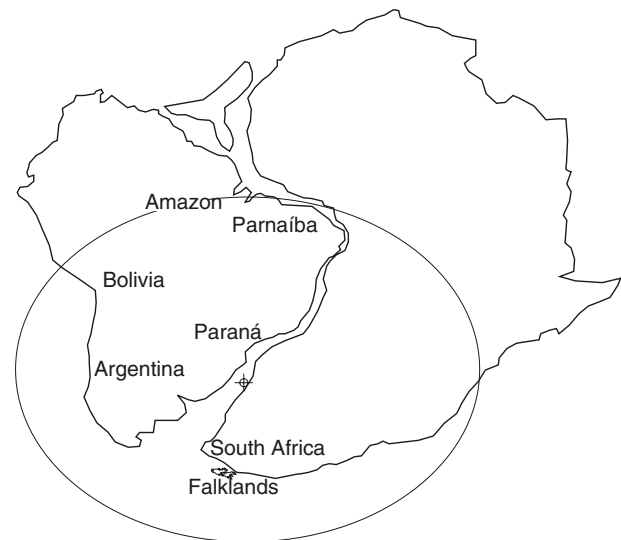


Fig. 1 Map of the Malvinokaffric Realm ca. 400 Ma (modified from Cocks and Torsvik 2002) with the position of the South Pole indicated by a cross. Position of areas used in the biogeographic analysis of Devonian trilobites also shown

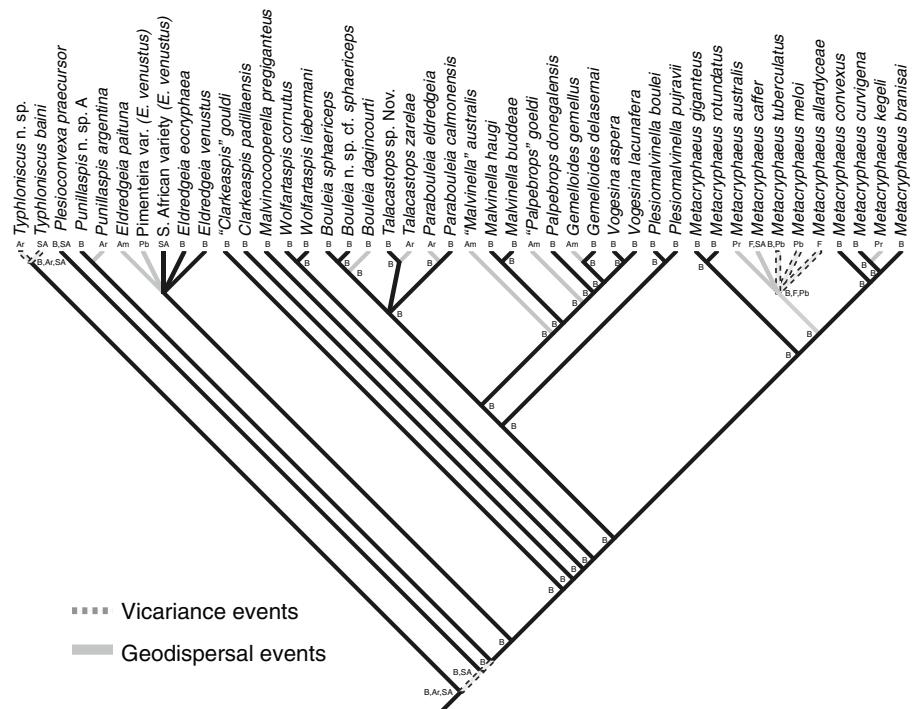
Here, we characterize the dynamics of speciation and extinction rates in this clade of calmoniids during its evolutionary radiation. Further, we determine the role biogeographic and geologic factors played in motivating its diversification. The calmoniid radiation appears to follow a pattern of explosion 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.

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 kegeli* 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. 2).

Fig. 2 Phylogenetic relationships of the *Metacryphaeus* group calmoniids modified from Lieberman et al. (1991) and Lieberman (1993) with new taxa added in as described in the text. Abbreviations indicate biogeographic areas of occurrence (Am, Ar, B, F, Pb, Pr, SA for Amazon, Argentina, Bolivia, Falklands, Parnaíba, Paraná, and South Africa, respectively)



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 and Eldredge 1996; Lieberman 2000). 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) and geodispersal (Table 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). 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 3) using a standard birth-death exponential growth model; (Stanley 1979) was an early advocate for the applicability of the

Table 1 Matrix used to evaluate biogeographic patterns of geodispersal employing a modified Brooks Parsimony analysis and the area cladogram in Fig. 2

	10	20	30	40	50	60	70	80	
Ancestor	000000000	000000000	000000000	000000000	000000000	000000000	000000000	000000000	0
Bolivia	110011111	111111111	111111111	111111111	111111111	111111111	111111111	110011111	1
Argentina	111000000	200000000	000000000	000000002	020000000	000000000	000000000	000000000	0
Falklands	000000000	000000000	000000000	000000000	000000000	000000000	000000021	100100000	0
S. Africa	110111000	000020000	000000000	000000000	000000000	000000000	000000000	200000000	0
Paraná	000000000	000000000	000000000	000000000	000000000	000000000	000000002	000000000	0
Parnaíba	000000000	000020000	000000000	000000000	000000000	000000000	000000021	011000002	0
Amazon	000000000	000200000	000000000	000000000	000200000	200020000	000000000	000000000	0

The ancestor denotes the ancestral biogeographic condition and serves as the outgroup. The other locations used in the biogeographic analysis are discrete areas in the Malvinokaffric Realm. Character state “0” is primitive; character states “1” and “2” are derived states. Results from analysis of matrix presented in Fig. 4

Table 2 Matrix used to evaluate the biogeographic patterns of vicariance employing a modified Brooks Parsimony Analysis and the area cladogram in Fig. 2

	10	20	30	40	50	60	70	80	
Ancestor	000000000	000000000	000000000	000000000	000000000	000000000	000000000	000000000	0
Bolivia	111121211	0110001111	111111111	1111111110	1011011111	0111101111	1111111110	0211111110	1
Argentina	112110000	100000000	000000000	000000001	010000000	000000000	000000000	000000000	0
Falklands	000000000	000000000	000000000	000000000	000000000	000000000	000000010	111200000	0
S. Africa	111221100	0000010000	000000000	000000000	000000000	000000000	000000000	100000000	0
Paraná	000000000	000000000	000000000	000000000	000000000	000000000	000000001	000000000	0
Parnaíba	000000000	0000100000	000000000	000000000	000000000	000000000	000000010	022100001	0
Amazon	000000000	0001000000	000000000	000000000	0000100000	1000010000	000000000	000000000	0

The ancestor denotes the ancestral biogeographic condition and serves as the outgroup. The other locations used in the biogeographic analysis are discrete areas in the Malvinokaffric Realm. Character state “0” is primitive; character states “1” and “2” are derived states. Results from analysis of matrix presented in Fig. 4

exponential model and it has been used extensively with fossil data to study speciation and extinction rates (Lieberman 2001; Nee 2006). In our study the methods of taxonomic rate calculations proposed by Foote (2000a, b) 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.

The number of first and last appearances was tabulated using the stratigraphic occurrence data for each species (Fig. 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 Gradstein (2004); Tucker et al. (1998); and Kaufmann (2006).

Results

Biogeographic Analysis

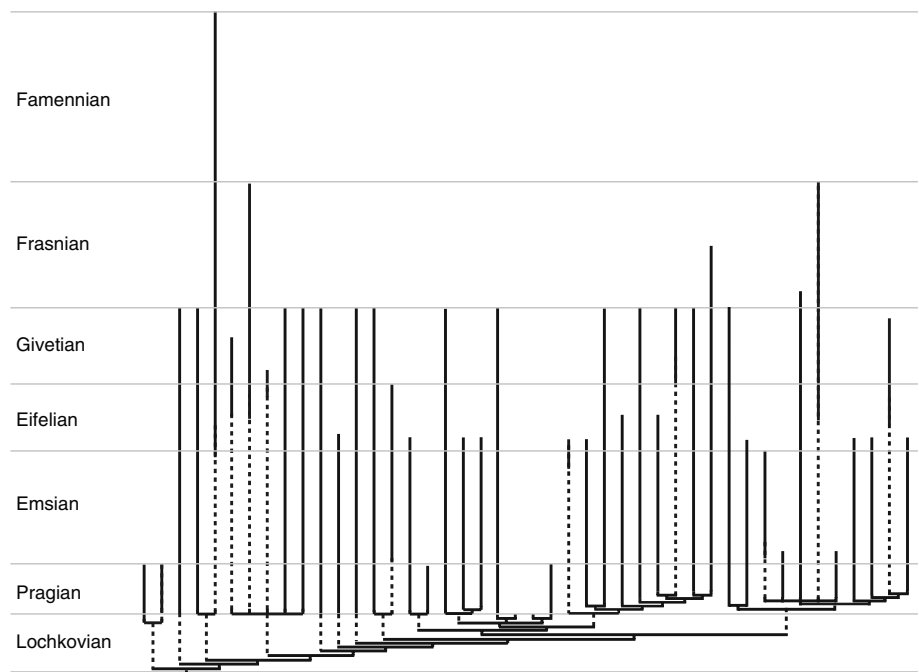
The phylogeny with biogeographic states mapped to terminals and nodes indicated most speciation events in calmoniids transpired within individual areas of endemism. Many of the transitions between nodes on the tree are associated with no major changes in geographic range (Fig. 2), at least not at the scale of major tectonic barriers and areas of endemism. Whether this actually represents sympatric differentiation, or smaller scale within-region

Table 3 Speciation and extinction rates calculated using a standard birth–death exponential growth model

	N_0	N_f	#sp	#ex	Duration of interval (t)			Total rate of diversity Δ (r)			Rate of speciation (S)			Rate of extinction (E)		
					T et al.	H & G	K	T et al.	H & G	K	T et al.	H & G	K	T et al.	H & G	K
					Famennian	2	2	0	2	14.5	15.3	15.4	–	–	–	–
Frasnian	5	5	0	3	6	10.8	7.6	–0.153	–0.085	–0.121	0.000	0.000	0.000	0.268	0.085	0.121
Givetian	22	22	0	17	5	6.5	4.4	–0.277	–0.228	–0.337	0.000	0.000	0.000	0.296	0.228	0.337
Eifelian	35	35	0	13	6.5	5.7	3.8	–0.077	–0.081	–0.122	0.000	0.000	0.000	0.071	0.081	0.122
Emsian	36	36	0	1	15.5	9.5	17.2	–0.002	–0.003	–0.002	0.000	0.000	0.000	0.002	0.003	0.002
Pragian	8	56	48	20	4	4.2	3.2	0.708	0.358	0.470	0.486	0.463	0.608	0.110	0.105	0.138
Lochkovian	1	32	31	24	4.5	4.8	5.8	0.433	–0.153	0.359	0.722	0.770	0.598	0.289	0.308	0.239

Abbreviations include N_0 for standing diversity at the beginning of the stage, N_f for the diversity at the end of a stage, #sp and #ex for number of speciation and extinction events during a stage. Calculations were performed using three different Devonian time scales: Tucker et al. (1998); House and Gradstein (2004); and Kaufmann (2006), abbreviated as T et al., H & G, and K, respectively

Fig. 3 Phylogeny of the *Metacryphaeus* group calmonioid 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 1992; Smith 1994) of sister taxa divergence. Devonian time calibrations were obtained through radiometric dating (Tucker et al. 1998; House and Gradstein 2004; Kaufmann 2006) and stratigraphic correlations were based on analysis of palynomorph and event stratigraphy (Cooper 1986; Grahn 2005)

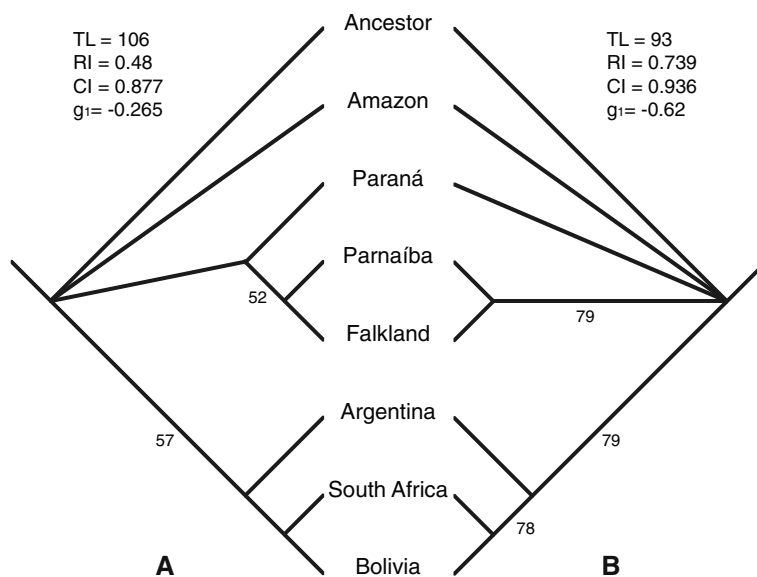


vicariance, could not be determined at this time. However, there is some evidence for vicariance and geodispersal (see Fig. 2) as indicated by contractions and expansions (respectively) of the geographic regions occupied by ancestors and their descendants.

Application of mBPA to the data matrix in Table 1 yielded a single best vicariance tree with a number of well-resolved branches (Fig. 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 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 and Eldredge

Fig. 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



1996; Lieberman 2000, 2003). This typically implicates cyclical processes that may at times cause vicariance and other times geodispersal. In the case of marine invertebrates like trilobites, those cyclical processes likely involved repeated episodes of sea level rise and fall (Lieberman and Eldredge 1996; Lieberman 2000, 2003, 2005).

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. 5).

The different timescales show very similar patterns in extinction rate (Fig. 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.

Fig. 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)

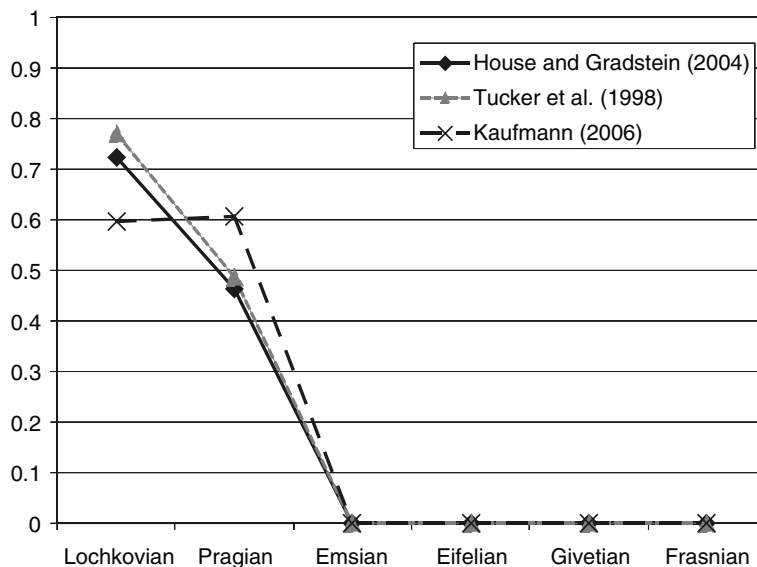
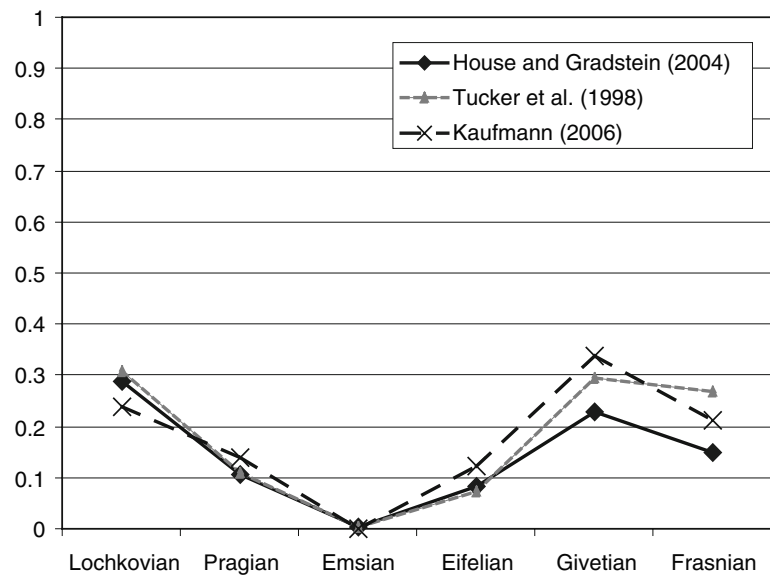


Fig. 6 Extinction rates in calmonioid trilobites plotted against stages of the Devonian. Rates were calculated based on a birth–death model and the inferred appearance of fossil taxa as shown in Fig. 3. Calculations were performed using three different Devonian time scales: Tucker et al. (1998); House 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 calmonioid radiation. As such, the radiation seems to represent an excellent example of species sorting mediated by Vrba's (1984) effect hypothesis. 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. 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. 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. 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 (Johnson et al. 1985; Cooper 1986).

A breakdown of the taxonomic rates during the diversification of the *Metacryphaeus* group shows high initial speciation rates for the first nine myrs, followed by no speciation events (Fig. 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. 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.

Notably, a pattern of initial peak in rates of evolution, with subsequent decline, was recognized previously in the calmonioids (Eldredge and Cracraft 1980) and has been

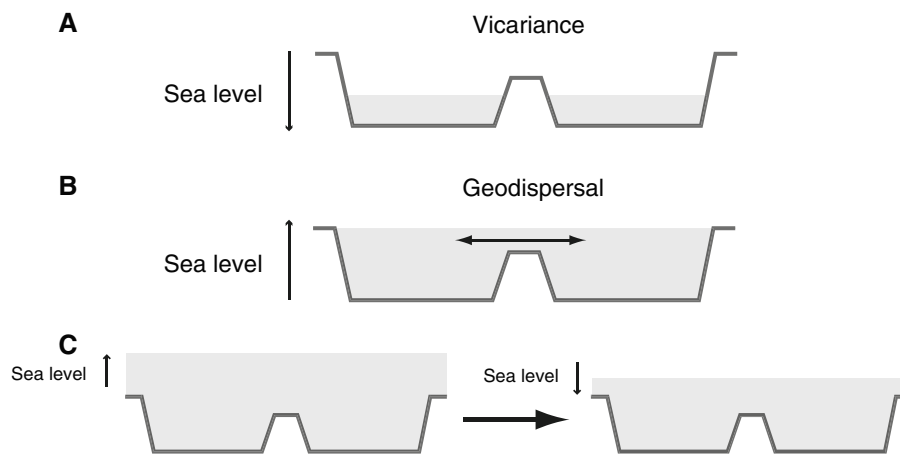


Fig. 7 A model showing how sea-level changes might affect biogeographic patterns and episodes of speciation in species such as trilobites inhabiting different marine basins. Regression allows for physical separation of the basins leading to vicariance (a).

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)

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 (Simpson 1953; Phillimore and Price 2008). 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. 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 (e.g., Stanley 1979; Vrba 1987; Lieberman 2001). 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 1996; 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 (Vrba 1980; Eldredge 1989; Lieberman 2000). Often, the adaptive character of evolutionary radiations is stressed (though not always, e.g., Eldredge and Cracraft 1980; Vrba 1980; Cracraft 1982; Platnick 1992; Lieberman 1993) 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.

Acknowledgments We thank the Panorama Society of the Natural History Museum and Biodiversity Research Center (to FRA) and NSF DEB 0716162 (to BSL) for funding and Ed Wiley, Benedikt Hallgrímsson, and one anonymous reviewer for comments.

References

- Boucot, A. J. (1988). Devonian biogeography; an update. In N. J. McMillan, A. F. Embry, & D. J. Glass (Eds.), *Devonian of the World* (pp. 211–227). Canadian Society of Petroleum Geologists, Calgary.

- Carvalho, M. G. P. (2006). Devonian trilobites from the Falkland Islands. *Palaeontology*, 49(1), 21–34. doi:10.1111/j.1475-4983.2005.00529.x.
- Carvalho, M. G. P., & Edgecombe, G. D. (1991). Lower-early middle Devonian calmonioid trilobites from Mato Grosso, Brazil, and related species from Paraná. *American Museum Novitates*, 3022, 1–13.
- Carvalho, M. G. P., Edgecombe, G., & Lieberman, B. S. (1997). Devonian calmonioid trilobites from the Parnaíba Basin, Piauí State, Brazil. *American Museum Novitates*, 3192, 1–11.
- Carvalho, M. G. P., Edgecombe, G. D., & Smith, L. (2003). New calmonioid trilobites (Phacopina, Acostoidea) from the Devonian of Bolivia. *American Museum Novitates*, 3407, 1–17. doi:10.1206/0003-0082(2003)407<0001:NCTPAF>2.0.CO;2.
- Cocks, L. R. M., & Torsvik, T. H. (2002). Earth geography from 500 to 400 million years ago: A faunal and palaeomagnetic review. *Journal of the Geological Society*, 159(6), 631–644. doi:10.1144/0016-764901-118.
- Cooper, M. R. (1986). Facies shifts, sea-level changes and event stratigraphy in the Devonian of South Africa. *South African Journal of Science*, 82(5), 255–258.
- Copper, P. (1977). Paleolatitudes in the Devonian of Brazil and the Frasnian-Famennian mass extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 21(3), 165–207. doi:10.1016/0031-0182(77)90020-7.
- Cracraft, J. (1982). Geographic differentiation, cladistics, and vicariance biogeography: Reconstructing the tempo and mode of evolution. *American Zoologist*, 22(2), 411–424.
- Edgecombe, G. D. (1992). Trilobite phylogeny and the Cambrian-Ordovician “Event”: Cladistic reappraisal. In M. J. Novacek & Q. Wheeler (Eds.), *Extinction and phylogeny* (pp. 144–177). New York: Columbia University Press.
- Edgecombe, G. D., Vaccari, N. E., & Waisfeld, B. G. (1994). Lower Devonian calmonioid trilobites from the Argentine Precordillera; new taxa of the *Bouleia* group, and remarks on the tempo of calmonioid radiation. *Geological Magazine*, 131(4), 449–464.
- Eldredge, N. (1979). Alternative approaches to evolutionary theory. *Bulletin of Carnegie Museum of Natural History*, 13, 7–19.
- Eldredge, N. (1989). *Macroevolutionary dynamics: Species niches, and adaptive peaks*. Columbus: McGraw-Hill.
- Eldredge, N., & Cracraft, J. (1980). *Phylogenetic patterns and the evolutionary process: method and theory in comparative biology*. New York: Columbia University Press.
- Eldredge, N., & Ormiston, A. R. (1979). Biogeography of Silurian and Devonian trilobites of the Malvinokaffric realm. In J. Gray, & A. J. Boucot (Eds.), *Historical biogeography, plate tectonics, and the changing environment* (pp. 147–167).
- Engelmann, G. F., & Wiley, E. O. (1977). The place of ancestor-descendant relationships in phylogeny reconstruction. *Systematic Zoology*, 26(1), 1–11. doi:10.2307/2412861.
- Erwin, T. L. (1979). Thoughts on the evolutionary history of ground beetles: Hypotheses generated from comparative faunal analyses of lowland forest sites in temperate and tropical regions. In T. L. Erwin, G. E. Ball, & D. R. Whitehead (Eds.), *Carabid beetles, their evolution, natural history, and classification* (pp. 539–592). The Hague: W. Junk.
- Foote, M. (2000a). Origination and extinction components of taxonomic diversity: General problems. *Paleobiology*, 26(sp 4), 74–102. doi:10.1666/0094-8373(2000)26[74:OAECOT]2.0.CO;2.
- Foote, M. (2000b). Origination and extinction components of taxonomic diversity: Paleozoic and post-Paleozoic dynamics. *Paleobiology*, 26(4), 578–605. doi:10.1666/0094-8373(2000)026<0578:OAECOT>2.0.CO;2.
- Gilinsky, N. L., & Bambach, R. K. (1987). Asymmetrical patterns of origination and extinction in higher taxa. *Paleobiology*, 13(4), 427–445.
- Givnish, T. J., & Sytsma, K. J. (1997). *Molecular evolution and adaptive radiation* (p. 621). New York: Cambridge University Press. xvii.
- Grahn, Y. (2005). Devonian chitinozoan biozones of Western Gondwana. *Acta Geologica Polonica*, 55(3), 211–227.
- Hillis, D. M., & Huelsenbeck, J. P. (1992). Signal, noise, and reliability in molecular phylogenetic analyses. *The Journal of Heredity*, 83(3), 189.
- House, M. R., & Gradstein, F. M. (2004). The Devonian period. In F. M. Gradstein, J. G. Ogg, & A. G. Smith (Eds.), *A geologic time scale* (pp. 202–221). Cambridge: Cambridge University Press.
- Hulbert, R. C., Jr. (1993). Taxonomic evolution in North American Neogene horses (Subfamily Equinae): The rise and fall of an adaptive radiation. *Paleobiology*, 19(2), 216–234.
- Isaacson, P. A., & Sablock, P. E. (1988). Devonian system in Bolivia, Peru, and northern Chile. In: N. J. McMillan, A. F. Embry, & D. J. Glass (Eds.), *Devonian of the World* (pp. 719–728). Canadian Society of Petroleum Geologists, Calgary.
- Johnson, J. G., Klapper, G., & Sandberg, C. A. (1985). Devonian eustatic fluctuations in Euramerica. *Bulletin of the Geological Society of America*, 96(5), 567–587. doi:10.1130/0016-7606(1985)96<567:DEFIE>2.0.CO;2.
- Kaufmann, B. (2006). Calibrating the Devonian time scale: A synthesis of U–Pb ID–TIMS ages and conodont stratigraphy. *Earth-Science Reviews*, 76(3–4), 175–190. doi:10.1016/j.earscirev.2006.01.001.
- Lieberman, B. S. (1993). Systematics and biogeography of the “*Metacryphaeus* Group” Calmoniidae (Trilobita, Devonian) with comments on adaptive radiations and the geological history of the Malvinokaffric realm. *Journal of Paleontology*, 67(4), 549–570.
- Lieberman, B. S. (2000). *Paleobiogeography*. New York: Kluwer Academic Publishers.
- Lieberman, B. S. (2001). A test of whether rates of speciation were unusually high during the Cambrian radiation. *Proceedings: Biological Sciences*, 268(1477), 1707–1714. doi:10.1098/rspb.2001.1712.
- Lieberman, B. S. (2003). Paleobiogeography: The relevance of fossils to biogeography. *Annual Review of Ecology Evolution and Systematics*, 34(1), 51–69. doi:10.1146/annurev.ecolsys.34.121101.153549.
- Lieberman, B. S. (2005). Geobiology and paleobiogeography: Tracking the coevolution of the earth and its biota. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 219(1–2), 23–33. doi:10.1016/j.palaeo.2004.10.012.
- Lieberman, B. S., Edgecombe, G. D., & Eldredge, N. (1991). Systematics and biogeography of the “Malvinella Group”, Calmoniidae (Trilobita, Devonian). *Journal of Paleontology*, 65(5), 824–843.
- Lieberman, B. S., & Eldredge, N. (1996). Trilobite biogeography in the Middle Devonian; geological processes and analytical methods. *Paleobiology*, 22(1), 66–79.
- Maguire, K. C., & Stigall, A. L. (2008). Paleobiogeography of Miocene Equinae of North America: A phylogenetic biogeographic analysis of the relative roles of climate, vicariance, and dispersal. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 267(3–4), 175–184. doi:10.1016/j.palaeo.2008.06.014.
- Mayr, E. (1942). *Systematics and the origin of species from the viewpoint of a zoologist*. New York: Columbia University Press.
- McGhee, G. R. (1996). *The Late Devonian mass extinction: The Frasnian/Famennian crisis*. New York: Columbia University Press.
- Nee, S. (2006). Birth-death models in macroevolution. *Annual Review of Ecology Evolution and Systematics*, 37, 1–17. doi:10.1146/annurev.ecolsys.37.091305.110035.

- Phillimore, A. B., & Price, T. D. (2008). Density-dependent cladogenesis in birds. *PLoS Biology*, 6(3), e71. doi:[10.1371/journal.pbio.0060071](https://doi.org/10.1371/journal.pbio.0060071).
- Platnick, N. I. (1992). Patterns of biodiversity. In N. Eldredge (Ed.), *Systematics, ecology, and the biodiversity crisis* (p. 220). New York: Columbia University Press.
- Rode, A. L., & Lieberman, B. S. (2004). Using GIS to unlock the interactions between biogeography, environment, and evolution in Middle and Late Devonian brachiopods and bivalves. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 211(3–4), 345–359. doi:[10.1016/j.palaeo.2004.05.013](https://doi.org/10.1016/j.palaeo.2004.05.013).
- Rode, A. L., & Lieberman, B. S. (2005). Integrating evolution and biogeography: A case study involving Devonian crustaceans. *Journal of Paleontology*, 79(2), 267–276. doi:[10.1666/0022-3360\(2005\)079<0267:IEABAC>2.0.CO;2](https://doi.org/10.1666/0022-3360(2005)079<0267:IEABAC>2.0.CO;2).
- Schluter, D. (2000). *The ecology of adaptive radiation*. Oxford: Oxford University Press.
- Sepkoski, J. J. (1998). Rates of speciation in the fossil record. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 353(1366), 315–326. doi:[10.1098/rstb.1998.0212](https://doi.org/10.1098/rstb.1998.0212).
- Simpson, G. G. (1953). *The major features of evolution*. New York: Columbia University Press.
- Smith, A. B. (1994). *Systematics and the fossil record: Documenting evolutionary patterns*. Oxford: Blackwell Publishing.
- Stanley, S. M. (1979). *Macroevolution, pattern and process*. San Francisco: W. H. Freeman.
- Swofford, D. L. (2002). PAUP*: Phylogenetic analysis using parsimony (* and other methods). Version 4.0*.
- Torsvik, T. H., & Cocks, L. R. M. (2004). Earth geography from 400 to 250 Ma: A palaeomagnetic, faunal and facies review. *Journal of the Geological Society*, 161(4), 555–572. doi:[10.1144/0016-764903-098](https://doi.org/10.1144/0016-764903-098).
- Tucker, R. D., Bradley, D. C., Ver Straeten, C. A., Harris, A. G., Ebert, J. R., & McCutcheon, S. R. (1998). New U–Pb zircon ages and the duration and division of Devonian time. *Earth and Planetary Science Letters*, 158(3–4), 175–186. doi:[10.1016/S0012-821X\(98\)00050-8](https://doi.org/10.1016/S0012-821X(98)00050-8).
- Vogler, A., & Goldstein, P. (1997). Adaptive radiation and taxon cycles in North American tiger beetles: A cladistic perspective. In T. J. Givnish & K. J. Sytsma (Eds.), *Molecular evolution and adaptive radiation* (pp. 353–373). Cambridge: Cambridge University Press.
- Vrba, E. S. (1980). Evolution, species and fossils: How does life evolve? *South African Journal of Science*, 76, 61–84.
- Vrba, E. S. (1984). What is species selection? *Systematic Zoology*, 33, 318–328. doi:[10.2307/2413077](https://doi.org/10.2307/2413077).
- Vrba, E. S. (1987). Ecology in relation to speciation rates: Some case histories of Miocene–Recent mammal clades. *Evolutionary Ecology*, 1(4), 283–300. doi:[10.1007/BF02071554](https://doi.org/10.1007/BF02071554).