

## INTEGRATING EVOLUTION AND BIOGEOGRAPHY: A CASE STUDY INVOLVING DEVONIAN CRUSTACEANS

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**ABSTRACT**—The integration of Geographic Information System (GIS) methodology within a phylogenetic and statistical framework provides a background against which to evaluate the relationship between biogeographic changes and evolution in the fossil record. A case study based on patterns in Middle and Late Devonian phyllocarids (Crustacea) illustrates the usefulness of this integrated approach. Using a combined approach enhances determination of rates of biodiversity change and the relationship between biogeographic and evolutionary changes. Because the interaction between speciation and extinction rates fundamentally determines biodiversity dynamics, and speciation and extinction rates are influenced by the geographic ranges of component taxa, the relationship between biogeography and evolution is important. Furthermore, GIS makes it possible to quantify paleobiogeographic ranges.

Phylogenetic biogeography resolved patterns of both vicariance and geodispersal and revealed that range expansions were more abundant than range contractions in Devonian phyllocarids. In addition, statistical tests on GIS-constrained species ranges and evolutionary-rate data revealed a relationship between increasing species' ranges and increases in both speciation and extinction rates. Extinction rate, however, increased more rapidly than speciation rate in the phyllocarids. The pattern of extinction rate increasing faster than speciation rate in the phyllocarids may illuminate aspects of the Late Devonian biodiversity crisis in particular, and protracted biodiversity crises in general.

### INTRODUCTION

THE ASSOCIATION between environmental changes and biogeographic and macroevolutionary changes is potentially an important area of paleontological research. An understanding of phylogenetic relationships helps constrain the relationship between environmental change, biogeography, and evolution (e.g., Croizat et al., 1974; Platnick and Nelson, 1978; Rosen, 1978; Nelson and Platnick, 1981; Brooks, 1985; Wiley and Mayden, 1985; Wiley, 1988; Page, 1990; Brooks and McLennan, 1991; Lieberman, 2000; Hunn and Upchurch, 2001); it also aids in the calculation of rates of biodiversity change (Lieberman, 2001). In this paper, we analyze phylogenetic biogeographic patterns and also statistical measurements of geographic range obtained from GIS (Geographic Information Systems). The evolutionary and biogeographic patterns of phyllocarid crustaceans during the Middle and Late Devonian are presented as a case study.

The Middle and Late Devonian encompass a time of extensive biogeographic and evolutionary change (Boucot, 1975; Oliver, 1976; Oliver and Pedder, 1994; McGhee, 1996). The transition from the Middle to the Late Devonian is accompanied by an increase in the geographic ranges of species and the loss of endemism. During the Middle Devonian, faunas were differentiated into distinct biogeographic regions; by contrast, the Late Devonian is characterized by the breakdown of geographic barriers resulting in the formation of a cosmopolitan fauna (Oliver, 1976; McGhee, 1981, 1996; Oliver and Pedder, 1994). The expansion of geographic ranges and the transition from an endemic to a cosmopolitan biota during the Late Devonian has been documented in many taxa, including trilobites (Feist, 1991), rugose corals (Oliver, 1976, 1990), brachiopods (Boucot, 1975; McGhee, 1981, 1996), foraminifera (Kalvoda, 1990), fishes (Young, 1987), conodonts (Klapper and Johnson, 1980; Klapper, 1995), and land plants (Raymond and Mertz, 1995). These range expansions are largely attributable to the collapse of climatic and geographic barriers due to tectonic events and sea level oscillations (Oliver, 1976; Oliver and Pedder, 1994; McGhee, 1996). Elevated extinction rates, depressed speciation rates, and an increase in species'

geographic ranges are the hallmarks of the Late Devonian biodiversity crisis (McGhee, 1988, 1990, 1996; Oliver and Pedder, 1994). Therefore, understanding the relationship between biodiversity loss and geographic range increase is an essential part of understanding the dynamics of the Frasnian–Famennian extinction.

The phyllocarids were used to examine the relationship between biogeographic change and biodiversity decline during the Late Devonian. They are a group of arthropods that were diverse during the Middle and Late Devonian, comprising over 50 species in four suborders, and patterns of evolution within this group are well constrained by phylogenetic analysis (Rode and Lieberman, 2002). Although only locally abundant, phyllocarids were a significant macroarthropod group and comprised an important component of marine ecosystems during this time interval (Rolfe, 1969; Hannibal, 1990). The effects of the Frasnian–Famennian extinction are pronounced within the phyllocarids, as they experienced a significant diversity decline during the transition from the Frasnian to the Famennian (Rolfe and Edwards, 1979; Hannibal, 1990; McGhee, 1996). We investigate the relationship between changes in the biogeographic ranges of Middle and Late Devonian phyllocarid species and parameters of biodiversity change, such as speciation and extinction rate.

### PHYLOGENETIC BIOGEOGRAPHIC ANALYSIS

**Methods.**—There are a variety of phylogenetic biogeographic methods (e.g., Platnick and Nelson, 1978; Page, 1990; Brooks and McLennan, 1991; Morrone and Crisci, 1995; Lieberman, 2000; Ebach and Edgecombe, 2001). The method used herein is a modified Brooks Parsimony Analysis (BPA) described in detail in Lieberman and Eldredge (1996) and Lieberman (2000, 2003). We chose this method because it has frequently been applied to the study of biogeographic patterns in the fossil record and also can be used to compare patterns of vicariance and patterns of geodispersal.

Phylogenetic patterns and geographic distributions are from Rode and Lieberman (2002). Six areas were identified for biogeographic analysis: 1) the Appalachian Basin of eastern North America (ENA); 2) the Michigan Basin of ENA; 3) Armorica; 4) western Canada; 5) Bolivia; and 6) South China. The boundaries of these areas of endemism were defined by large-scale geologic features and their existence was established by the presence of

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TABLE 1—Biogeographic character states for the modified BPA data matrix coded for the vicariance analysis. Ancestor refers to the ancestral biogeographic condition for the clades considered; the other biogeographic areas were the areas considered in this analysis. 0 represents absence in a region, the presumed primitive condition. Character states 1 and 2 represent the derived condition of present and present via range restriction, respectively. Characters refer to node and terminal branch position, beginning with the basal part of the cladogram moving upward.

	123456789	1111111111	2222222222	3333333333	4444444444	5555555555	6666666666	7777777777	8
Ancestor	000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0
Appalachian Basin	121211011	1111111011	0111111101	1101110101	1111111111	1111011011	1111011111	1011110000	0
Michigan Basin	000000100	0000000100	0000000010	0000000000	0000000001	0000000000	0000000100	0000001111	1
Armorica	112100000	0000000000	1000000000	0010000011	2100012121	0000000000	0000100000	0000000000	0
Western Canada	000000000	0000000000	0000000000	0000000001	1200011210	0100000100	0000000000	0100000000	0
South China	000000000	0000000000	0000000000	0000000000	0000000000	0000100000	0000000000	0000000000	0
Bolivia	000000000	0000000000	0000000000	0000001000	0000000001	0000000000	0000000000	0000000000	0

large numbers of unique taxa in each region. Further, these regions have been used in several other analyses of Devonian biogeography (e.g., Boucot, 1975; Oliver, 1976; Eldredge and Ormiston, 1979; Feist, 1991; Oliver and Pedder, 1994). There are also two poorly preserved species of phyllocarids, one taxon from Australia and the other from India, that were not included in this biogeographic analysis, because biogeographic regions containing only one species tend to map artifactually as biogeographically basal (Fortey and Cocks, 1992; Lieberman, 1997, 2000).

The vicariance and geodispersal matrices used in the modified version of BPA are derived from the phyllocarids and presented in Tables 1 and 2. The BPA data matrix was coded following the modifications of Lieberman (2000). Under these modifications, different coding schemes are used to produce two matrices, one to capture vicariance patterns and the other to recover geodispersal events. Each data matrix was analyzed using the exhaustive search option on PAUP\* 4.0b10 (Swofford, 2002) with all characters ordered.

**Results.**—Parsimony analysis of the vicariance matrix revealed a singlemost parsimonious tree of length 91 steps (Fig. 1.1). The consistency index is 0.967 and the retention index is 0.864. This value for the consistency index significantly exceeds consistency indices derived from sets of similarly sized matrices constructed from random data at the 0.05 level of significance, following Klassen et al. (1991). The  $g_1$  statistic calculated for a distribution of 10,000 random trees obtained from this data set is  $-0.823$ , which is significant at the  $P = 0.01$  level (Hillis and Huelsenbeck, 1992). The amount of support for specific nodes within the recovered cladogram was further characterized using bootstrap and jackknife analysis, both performed using a full heuristic search with 1,000 replicates, and groups compatible with the 50 percent majority rule consensus tree were retained. The confidence values for the nodes duplicated in the bootstrap and jackknife analyses are presented in Figure 1.1.

Parsimony analysis of the geodispersal matrix produced two most parsimonious trees of length 109 steps. The strict consensus tree is presented in Figure 1.2. The consistency index is 0.881

and the retention index is 0.458. This value for the consistency index significantly exceeds consistency indices derived from sets of similarly sized matrices constructed from random data at the 0.05 level of significance, following Klassen et al. (1991). The  $g_1$  statistic, for a distribution of 10,000 random trees, is  $-0.484$ , which is significant at the  $P = 0.05$  level (Hillis and Huelsenbeck, 1992). Bootstrap and jackknife analysis were also implemented as explained above, and the confidence values for the nodes duplicated in the bootstrap and jackknife analyses are presented in Figure 1.2.

**Discussion.**—The various resolved branches of the vicariance and geodispersal trees both appear moderately to well supported by a variety of measures. They each provide different information about biogeographic relationships. Areas that share a sister relationship on the vicariance tree were recently separated from one another; sister areas on the geodispersal tree were recently joined (Lieberman, 2000).

The vicariance cladogram records a sister area relationship between Armorica and the Appalachian Basin and these areas in turn have a sister-area relationship with western Canada (Fig. 1.1). These biogeographic patterns correspond well to those presented in Oliver (1976) and Eldredge and Ormiston (1979). The rest of the cladogram is unresolved. The lack of resolution between the remaining branches may be indicative of the general lack of vicariance within this group of animals during the Devonian (Rode and Lieberman, 2002).

The geodispersal tree provides evidence for replicated geodispersal events between Armorica and the Appalachian Basin (Fig. 1.2). This result is congruent with paleocontinental reconstructions for the Devonian (e.g., Kent, 1985; Scotese, 1998) in which the Appalachian Basin and Armorica are positioned proximate to one another during the Acadian orogeny, potentially allowing dispersal between these regions. The geodispersal tree also indicates a combined biogeographic relationship between Armorica, the Appalachian Basin, and western Canada. This reiterates biogeographic patterns recovered by Oliver (1976), Eldredge and Ormiston (1979), and Oliver and Pedder (1994). Further, this pattern

TABLE 2—Biogeographic character states for the modified BPA data matrix coded for the geodispersal analysis. Ancestor refers to the ancestral biogeographic condition for the clades considered; the other biogeographic areas were the areas considered in this analysis. 0 represents absence in a region, the presumed primitive condition. Character states 1 and 2 represent the derived condition of present and present via range expansion, respectively. Characters refer to node and terminal branch position, beginning with the basal part of the cladogram moving upward.

	123456789	1111111111	2222222222	3333333333	4444444444	5555555555	6666666666	7777777777	8
Ancestor	000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0
Appalachian Basin	110111111	1111111111	1111111111	1111111111	0011110001	1111111111	1111111111	1111111000	0
Michigan Basin	000000200	0000000200	0000000020	0000000000	0000000002	0000000000	0000000200	0000002111	1
Armorica	101000000	0000000000	2000000000	0020000021	1000021012	0000000000	0000200000	0000000000	0
Western Canada	000000000	0000000000	0000000000	0000000001	0100020100	0200000200	0000000000	0200000000	0
South China	000000000	0000000000	0000000000	0000000000	0000000000	0000200000	0000000000	0000000000	0
Bolivia	000000000	0000000000	0000000000	0000002000	0000000002	0000000000	0000000000	0000000000	0

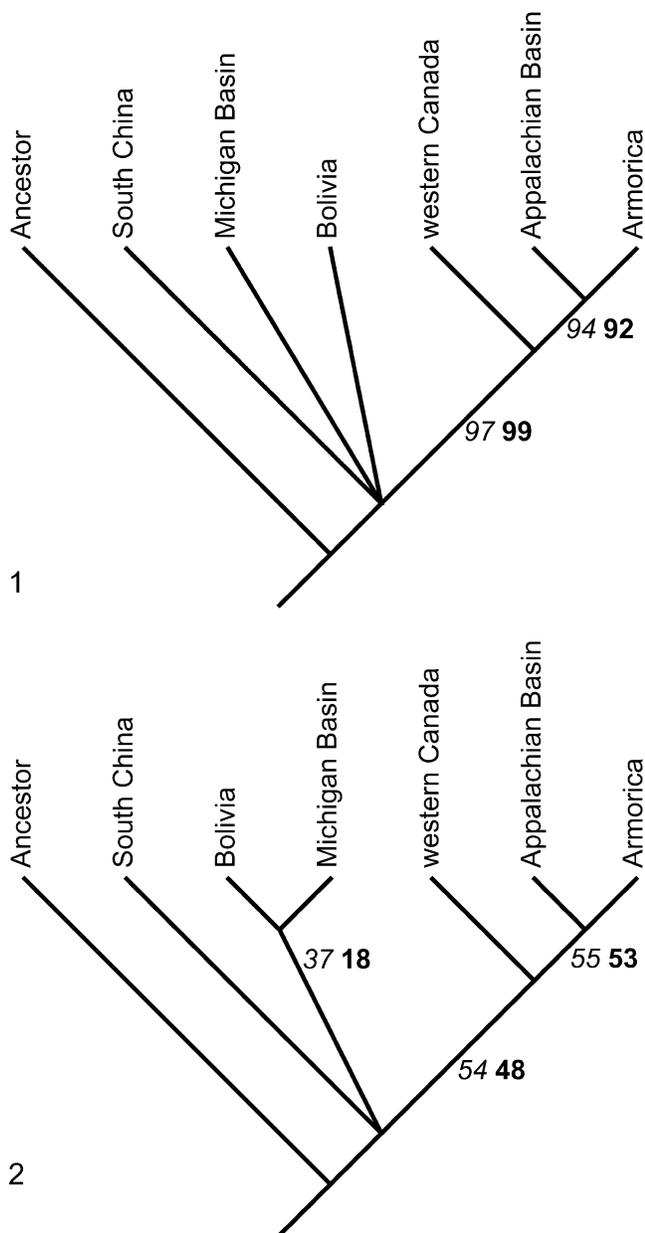


FIGURE 1—Area cladograms derived from modified BPA analysis. 1, Vicariance tree. Tree length is 91 steps; the retention index is 0.864, consistency index is 0.967, and  $g_1$  statistic is  $-0.823$ . Bootstrap values are indicated in italics, jackknife values are indicated in bold. 2, Geodispersal tree. Tree length is 109 steps; the retention index is 0.458, consistency index is 0.881, and  $g_1$  statistic is  $-0.484$ . Bootstrap values are indicated in italics, jackknife values are indicated in bold.

matches the paleogeographic reconstruction of Dineley (1984), which suggests intermittent shallow marine connections between these areas. The sister-area relationship between the Michigan Basin and Bolivia possibly represents jump or traditional dispersal events (*sensu* Humphries and Parenti, 1986), since no Devonian paleocontinental reconstructions support a close position of these areas. The branch support for this clade is considerably weaker than for the other branches, which may pertain to the chance nature of this type of dispersal event. Eldredge and Ormiston (1979) also discussed a pattern of faunal relatedness between Bolivia and ENA.

The vicariance and geodispersal trees show a congruent pattern with respect to the relationships of western Canada, Armorica, and the Appalachian Basin. Congruence between the geodispersal and vicariance trees suggests that cyclical biogeographic processes, especially sea level rise and fall, had an influence on biogeographic patterns (Lieberman, 2000). The tectonic events associated with the Acadian Orogeny as well as cycles of sea level rise and fall have previously been shown to influence Devonian biogeographic patterns (Boucot, 1975; Oliver, 1976; Oliver and Peder, 1994; Lieberman and Eldredge, 1996; Rode, 2002; Rode and Lieberman, 2003).

#### QUANTIFICATION OF GEOGRAPHIC RANGE

Geographic ranges of species can be mapped and quantified using a Geographic Information System (GIS). The use of GIS has many advantages over traditional mapping of species ranges because GIS range maps can be constructed dynamically and can be designed to illustrate both temporal and spatial variability (Berry, 1995; Chou, 1997; Burrough and McDonnell, 1998). GIS methods have been implemented heavily in neocological studies within this context (*i.e.*, Stoms et al., 1993; Iverson and Prasad, 1998; Haltuch et al., 2000), but their use in paleontology has been limited to date. Paleontological extensions of GIS have included the mapping of ranges for Tertiary and Quaternary mammals, such as the FaunMap project (Juliusson and Graham, 1999; Graham, 2000), and other applications in invertebrate paleontology (Rode and Lieberman, 2000, 2001; Ferguson et al., 2001). The GIS approach allows the calculation of the geographic ranges and can also illustrate changes in geographic range by a taxon through time.

*Methods.*—The ranges of archaeostracan phyllocarid species considered in the phylogenetic analysis were determined using maps created with ArcView 3.2 (ESRI, 1999). Each of the 37 species that occurred during the Givetian, Frasnian, or Famennian stages was mapped individually as a separate coverage. Separate coverages were also created for each stage in which the species appears, resulting in 45 total species' range coverages. These coverages were based on data from over 300 museum- and literature-based specimens representing over 150 localities. Species-distribution maps were produced by first creating a point theme which maps known fossil collection localities as individual points with associated data tables. The data tables linked to each shape file include the plate code for use with PaleoGIS (Ross and Scotese, 2000), latitude, longitude, state, and county of occurrence, time of first and last appearance of the species, and geological formation of occurrence. Localities were mapped at the county scale with a single point plotted in the center of each county of occurrence. The distribution coverages and base maps were imported into PaleoGIS (Ross and Scotese, 2000) and rotated onto paleocontinental positions based on the attribute data listed in linked tables. An example of a rotated point coverage of a species geographic range is presented in Figure 2.1. Reconstructions derived from Ross and Scotese (2000) are based on the underlying data from the PaleoMap project of Scotese (1998) and are reconstructed using several data sources including paleomagnetism, paleobiogeography, paleoclimatology, and tectonic and geologic history, which produce maps that are more robust to anomalies that can occur when only a single data source, such as either paleomagnetism or paleoclimatology, provides the entire basis for paleocontinental reconstructions (Scotese and McKerrow, 1990). Since Laurentian species are the primary focus of this analysis, and the position of Laurentia is relatively conserved across different paleogeographic reconstructions of the Devonian (*e.g.*, compare reconstructions of Van der Voo, 1988; Scotese and McKerrow, 1990; Dalziel et al., 1994; Ross and Scotese, 2000),

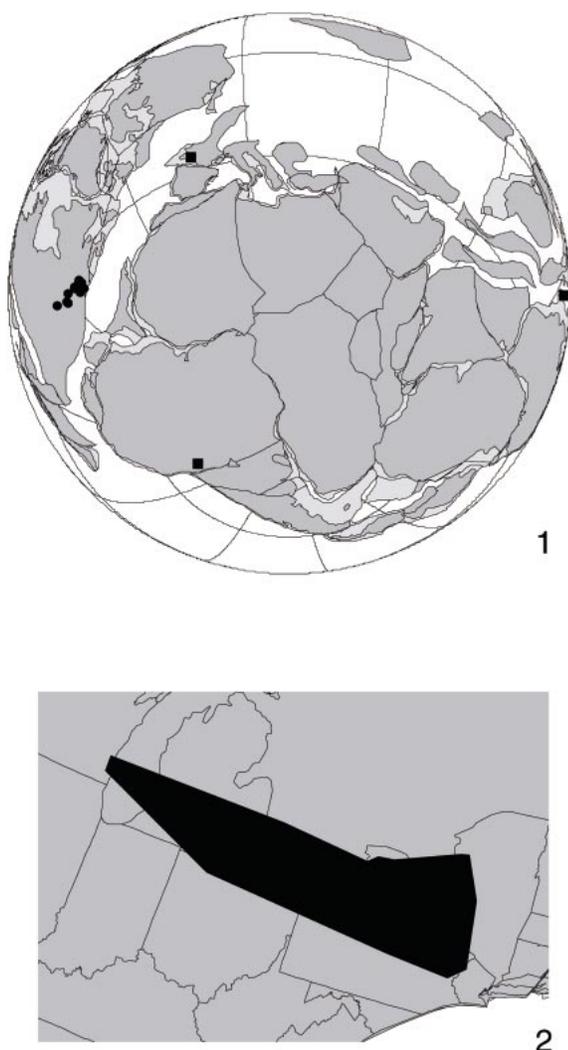


FIGURE 2—1, Rotated point coverage of geographic range of *Paraechinocaris punctata* (Hall, 1863) during the Givetian Stage derived using PaleoGIS (Ross and Scotese, 2000) and method described in the text. Circles represent occurrences of *P. punctata* s.s., and squares represent occurrences of *P. cf. P. punctata*; 2, regional view of interpreted geographic range of the *Paraechinocaris punctata* s.s. during the Givetian Stage.

the reconstructed species' paleogeographic ranges and area calculations are robust to a change in paleogeography.

The reconstructed coverages were then exported to ArcView 3.2 for manipulation. A polygon coverage was digitized to enclose the counties in which the species was shown to occur by the point coverage, and the area of each polygon was then calculated. Where a species range occupied more than one biogeographic region, a narrow band was digitized to connect occurrences in distinct regions across a known Devonian waterway based on the reconstructions of Scotese (1998). Although other methods for reconstructing species ranges could be envisioned, this is a conservative and repeatable method that can be consistently implemented for all taxa. For species that are known only from a single locality outside of the United States, the geographic area was recorded to be the average size of a county included in this study. Range maps were produced for each stage in which a species existed and plotted onto a base map of Devonian paleocontinents. A typical example of a completed range map is shown in Figure

2.2. (Copies of additional range maps can be requested from A. Rode.)

The values for geographic ranges used in the analysis consist of median values for all species extant during each stage (Table 3). Both mean and median values were initially determined for geographic ranges, but the mean values for the Givetian were found to be overly influenced by a single outlier range value, that of *Paraechinocaris punctata* (Hall, 1863), as described below. Mean and median species range for the Givetian were calculated in two ways that incorporated two different definitions of *P. punctata*: *P. punctata* sensu stricto; and *P. punctata* sensu lato (Table 3). *Paraechinocaris punctata* s.s. includes only fossils described as *P. punctata* in the Appalachian Basin, while *P. punctata* s.l. includes fossils described as *Paraechinocaris* sp. cf. *P. punctata* collected from Bolivia, France, and Burma. Although these latter specimens have the diagnostic characters of *Paraechinocaris* Rode and Lieberman, 2002, their state of preservation does not permit specific assignment within that genus. The median species ranges were the same for both calculations,  $1.59 \times 10^3$  km<sup>2</sup> and  $1.60 \times 10^3$  km<sup>2</sup> for the Givetian and Frasnian, respectively. The mean species range for the Givetian, however, increased by a factor of 24 from  $21.0 \times 10^3$  km<sup>2</sup> to  $507 \times 10^3$  km<sup>2</sup> when specimens described as *P. sp. cf. P. punctata* were included within the range of *P. punctata*.

**Results.**—Median species ranges increase from the Givetian to Famennian (Table 3). This pattern is consistent with the Late Devonian decline in endemism described above.

#### ANALYSIS OF BIODIVERSITY CHANGE

To better constrain the influences of biogeographic patterns on biodiversity, information about speciation and extinction rates was obtained so that correlations could be established between changes in these rates and changes in geographic range.

**Methods.**—Numerous recent papers have dealt with the validity of various speciation and extinction metrics (Foote, 1994, 2000a, 2000b; Lieberman, 2001). Simple speciation and extinction metrics, such as the total number of speciation events or extinction events per unit time, were not used because Foote (1994, 2000a, 2000b) has shown the dependence of these metrics on the length of the stratigraphic interval being studied. Speciation rates were derived using the theoretical principles underlying the equation:

$$N_f = N_0 e^{rt}$$

where  $N_0$  is standing diversity at the beginning of the interval,  $N_f$  is the final diversity,  $t$  is the duration of the interval, and  $r$  is the rate of increase of the clade expressed in units per time. Phylogenetic information was also used to help constrain the origin of lineages in the manner of Smith (1994). The recommendations of Foote (2000a, 2000b) were followed and the total rate of diversity change,  $r$ , was calculated by using the  $N_0$  value from the overlying stage as the  $N_f$  value for the stage in question. For example,  $r_{\text{Givetian}} = (\ln N_{0\text{Frasnian}} - \ln N_{0\text{Givetian}}) / t_{\text{Givetian}}$ . This assures continuity within the data set, as the final diversity for one stage must necessarily be the same as the initial diversity for the next stage. In this way, lineages that are known not to persist from one interval to the next are not counted in the final diversity of a stage, since that lineage must have become extinct sometime during the stage in question. Thus, the calculated extinction rates are conservative values (Foote, 2000a, 2000b). Speciation rates for a given interval were calculated similarly; however, the observed  $N_f$  for the given stage was used, as this value includes all speciation events that occurred during the interval in question (Foote, 2000a, 2000b). Thus, for example,  $S_{\text{Givetian}} = (\ln N_{f\text{Givetian}} - \ln N_{0\text{Givetian}}) / t_{\text{Givetian}}$ . The rate of increase,  $r$ , is equal to the speciation rate,  $S$ , minus the extinction rate,  $E$ . Therefore, the extinction rate was calculated by subtracting the speciation rate from the rate of diversity

TABLE 3—Geographic ranges (km<sup>2</sup>) of each species calculated using the method described in the text. Descriptive statistics are calculated considering two definitions of *Paraechinocaris punctata*: w/o *Paraechinocaris* cf. *P. punctata* includes only *P. punctata* sensu stricto as defined in the text; w/ *Paraechinocaris* cf. *P. punctata* includes all occurrences considered to comprise *P. punctata* sensu lato as described in the text.

	Emsian	Eifelian	Givetian	Frasnian	Famennian	Tournaisian
<i>Carinatacaris scaphoptera</i> (Clarke in Hall and Clarke, 1888)			$1.59 \times 10^3$	$1.85 \times 10^3$		
<i>Dithryocaris oceani</i> (Hall and Clarke, 1888)			$35.0 \times 10^3$	$1.00 \times 10^3$		
<i>Dithryocaris oculeus</i> Racheboeuf, 1998			$1.60 \times 10^3$			
<i>Echinocaris auricula</i> Eller, 1935					$16.0 \times 10^3$	
<i>Echinocaris beecheri</i> Copeland, 1960a						$1.60 \times 10^3$
<i>Echinocaris castorensis</i> Copeland, 1960a					$1.60 \times 10^3$	
<i>Echinocaris</i> cf. <i>E. multinodosa</i> Whitfield, 1880				$1.37 \times 10^3$	$3.56 \times 10^3$	
<i>Echinocaris</i> cf. <i>E. sublaevis</i> Whitfield, 1880					$11.5 \times 10^3$	
<i>Echinocaris clarkii</i> Beecher, 1902					$1.84 \times 10^3$	
<i>Echinocaris condylepis</i> Hall and Clarke, 1898					$1.90 \times 10^3$	
<i>Echinocaris consanguinea</i> Eller, 1935					$1.16 \times 10^5$	
<i>Echinocaris crosbyensis</i> Eller, 1937					$2.56 \times 10^3$	
<i>Echinocaris hunanensis</i> Han and Zhou, 1993				$1.60 \times 10^3$	$1.60 \times 10^3$	
<i>Echinocaris multinodosa</i> Whitfield, 1880					$3.56 \times 10^3$	
<i>Echinocaris multispinosus</i> Feldmann and McKenzie, 1981					$2.03 \times 10^3$	
<i>Echinocaris ohioensis</i> Sturgeon, Hlavin, and Kesling, 1964					$2.03 \times 10^3$	
<i>Echinocaris randallii</i> Beecher, 1902					$4.05 \times 10^3$	
<i>Echinocaris socialis</i> Beecher, 1884					$1.61 \times 10^3$	
<i>Echinocaris sublaevis</i> Whitfield, 1880					$2.72 \times 10^3$	
<i>Echinocaris turgida</i> Eller, 1935					$1.90 \times 10^3$	
<i>Echinocaris whidbornei</i> (Jones and Woodward, 1889)					$1.60 \times 10^3$	
<i>Eleutherocaris whitfieldi</i> (Clarke, 1885)				$1.67 \times 10^3$		
<i>Elymocaridopsis capsella</i> Hall and Clarke, 1888			$1.59 \times 10^3$	$1.85 \times 10^3$		
<i>Elymocaridopsis siliqua</i> Beecher, 1884					$1.81 \times 10^3$	
<i>Herbertocaris wideneri</i> Stumm and Chilman, 1969			$8.23 \times 10^2$			
<i>Montecaris lehmannii</i> Jux, 1960					$1.33 \times 10^6$	
<i>Montecaris strunensis</i> Jux, 1959					$1.60 \times 10^3$	
<i>Nahecaris bipennis</i> (Clarke, 1898a)					$1.57 \times 10^3$	
<i>Nahecaris stuerzi</i> Jaekel, 1921	$1.60 \times 10^3$					
<i>Ohioecaris wycoffi</i> Rolfe, 1962					$1.42 \times 10^3$	
<i>Paraechinocaris</i> cf. <i>P. punctata</i> (Hall, 1863)			$4.50 \times 10^6$			
<i>Paraechinocaris punctata</i> (Hall, 1863)			$1.20 \times 10^5$	$16.0 \times 10^3$		
<i>Pephracaris horriplata</i> Clarke, 1898b					$2.14 \times 10^3$	
<i>Ptychocaris novaki</i> Copeland, 1960b		$1.60 \times 10^3$				
<i>Rhinocaris columbina</i> Clarke in Hall and Clarke, 1888			$20.0 \times 10^3$			
<i>Rhinocaris ehlersi</i> Stewart, 1933			$8.23 \times 10^2$			
<i>Rhinocaris veneris</i> (Hall and Clarke, 1888)			$1.32 \times 10^3$			
<i>Tropidocaris alternata</i> Beecher, 1884					$1.81 \times 10^3$	
<i>Tropidocaris bicarinata</i> Beecher, 1884					$1.81 \times 10^3$	
<i>Tropidocaris britannica</i> Morzadec and Rolfe, 1968				$1.60 \times 10^3$		
<i>Tropidocaris interrupta</i> Beecher, 1884					$1.81 \times 10^3$	
<i>Tropidocaris salsiusculus</i> Feldmann, Boswell, and Kammer, 1986					$1.29 \times 10^3$	
Mean species range (w/o <i>Paraechinocaris</i> cf. <i>P. punctata</i> )	$1.60 \times 10^3$	$1.60 \times 10^3$	$20.3 \times 10^3$	$1.24 \times 10^5$	$7.83 \times 10^3$	$1.60 \times 10^3$
Median species range (w/o <i>Paraechinocaris</i> cf. <i>P. punctata</i> )	$1.60 \times 10^3$	$1.60 \times 10^3$	$1.59 \times 10^3$	$1.60 \times 10^3$	$1.90 \times 10^3$	$1.60 \times 10^3$
Mean species range (w/ <i>Paraechinocaris</i> cf. <i>P. punctata</i> )	$1.60 \times 10^3$	$1.60 \times 10^3$	$5.07 \times 10^5$	$1.24 \times 10^5$	$7.83 \times 10^3$	$1.60 \times 10^3$
Median species range (w/ <i>Paraechinocaris</i> cf. <i>P. punctata</i> )	$1.60 \times 10^3$	$1.60 \times 10^3$	$1.59 \times 10^3$	$1.60 \times 10^3$	$1.90 \times 10^3$	$1.60 \times 10^3$

change. For example,  $E_{\text{Givetian}} = S_{\text{Givetian}} - r_{\text{Givetian}}$ . Correlations between speciation and extinction rate were established using linear regression analysis performed with Minitab Release 11 (Minitab Inc., 1996).

Stochastic approaches used in the calculation of probabilities of speciation and extinction such as those described in Lieberman (2001) were not used due to limitations in the data and inadequate available resolution within the Devonian time scale. Finally, the precise age of *Echinocaris hunanensis* Han and Zhou, 1993 was difficult to constrain because of stratigraphic uncertainties in the Chinese sections (Han and Zhou, 1993). Its first appearance was treated as in the Famennian stage since its closest relatives are also Famennian in age. Three different time scales have been advocated for the Devonian, and to constrain our rates each analysis used: Bayer and McGhee (1989) (emended after Oliver and Pedder (1994), McGhee (1996), and McGhee (personal commun., 2002), Tucker et al. (1998), and GSA (1999).

**Results.**—Results of speciation and extinction rate calculations are presented in Table 4. To examine trends in biodiversity change over time, speciation and extinction rates are plotted by stage.

Speciation rates increased during the second half of the Devonian, although a Frasnian decline or plateau is observed (Fig. 3). Discrepancies in speciation rate emerge when different time scales are used. For example, speciation rates calculated using the Tucker et al. (1998) time scale are roughly equivalent for the Givetian and Famennian stages with speciation rate for both stages slightly higher than during the Frasnian. The speciation rates based on the GSA (1999) stage duration values, however, produce a gradual trend of increasing speciation rate from the Eifelian to the Famennian. Meanwhile, calculations using Bayer and McGhee's (1989) [emended after Oliver and Pedder (1994), McGhee (1996), and McGhee (personal commun., 2002)] time scale suggest that speciation rates increased from the Eifelian to Givetian, remained similar during the Givetian and Frasnian, and then increased sharply in the Famennian. Extinction rates increased during the Devonian (Fig. 4). The trajectories for rate calculations based on different time scales are once again divergent but less markedly so than was found with the speciation rates (compare Figs. 3, 4).

Speciation and extinction rates are positively correlated in Devonian phyllocarids (Fig. 5) and correlations are significant at the

TABLE 4—Speciation and extinction rates during Devonian stages incorporating information from stratigraphy and phylogeny. Abbreviations used are  $N_o$  for the standing diversity at the beginning of the stage;  $N_f$  for the final diversity of a stage; #sp and #ext for the number of speciation and extinction events, respectively;  $t$  for time;  $r$  for total rate of biodiversity change;  $S$  for speciation rate; and  $E$  for extinction rate. Devonian time scales used to determine stage lengths were by Bayer and McGhee (1989), Tucker et al. (1998), and GSA (1999), which are abbreviated in the table as B + M, T et al., and GSA, respectively. Since only the GSA (1999) time scale includes Carboniferous dates, it was the only time scale that permitted calculation of speciation rates for the Tournaisian.

	$N_o$	$N_f$	# sp	# ext	Duration			Total rate of diversity change			Rate of speciation			Rate of extinction		
					$t$	$t$	$t$	$r$	$r$	$r$	$S$	$S$	$S$	$E$	$E$	$E$
					(GSA)	(B + M)	(T et al.)	(GSA)	(B + M)	(T et al.)	(GSA)	(B + M)	(T et al.)	(GSA)	(B + M)	(T et al.)
Tournaisian	1	2	1	45	12											
Famennian	5	46	41	10	6	13.6	-0.161	-0.268	-0.118	0.222	0.168	0.163	0.383	0.294	0.282	
Frasnian	10	18	8	13	6	9	-0.116	-0.077	-0.116	0.098	0.065	0.098	0.213	0.142	0.213	
Givetian	11	23	12	13	10	12	-0.010	-0.008	-0.019	0.074	0.061	0.148	0.083	0.069	0.167	
Eifelian	12	13	1	2	11	7	-0.008	-0.012	-0.013	0.007	0.011	0.012	0.015	0.024	0.026	
Emsian	5	14	9	2	9	6	0.097	0.146	0.056	0.114	0.172	0.066	0.017	0.026	0.010	

level of  $P < 0.05$  under all three time scales investigated, with r-squared values ranging from 0.78 to 0.95 (Table 5). Only the results from the emended Bayer and McGhee (1989) time scale are shown in Figure 5 for the purposes of brevity and clarity. Although the Famennian point lies to the right, examination of residuals shows that this point alone is not driving the observed pattern. Residuals for the data points in Figure 5, from left to right, are  $-0.006$ ,  $0.018$ ,  $-0.017$ , and  $0.004$ . When the Famennian point is removed, a similar, but less significant trend can be observed. In addition, the position of the Famennian point is well constrained by the underlying data. Consequently, its position is probably not an artifact but likely represents an accurate representation of speciation and extinction rate values for that stage. Table 6 lists the  $P$ -values retrieved from an analysis of variance (ANOVA) of the data. Both the emended Bayer and McGhee (1989) and GSA (1999) time scales show significant results ( $P < 0.05$ ). The ANOVA results are significant at a lower level ( $P < 0.03$  vs.  $P < 0.01$ ), but this is to be expected given that linear regression recovers continuous variability while ANOVA examines classes (Sokal and Rohlf, 1995), and the data analyzed represent continuous values.

Although clearly it would be desirable to have additional data points in Figure 5 to better help tease these issues apart, it must be recognized that the data points themselves are derived from a large database including several hundred specimens and a phylogeny of more than 40 taxa.

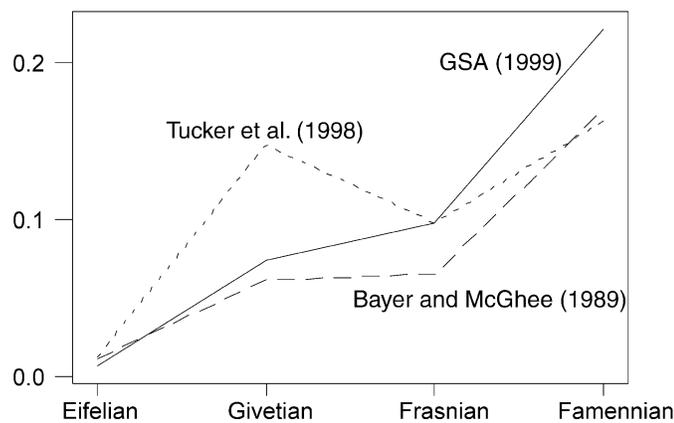


FIGURE 3—Speciation rates derived from Table 4 plotted versus Devonian stage for all phyllocarids calculated using phylogenetic constraints on timing of lineage divergence for the three different time scales: Bayer and McGhee (1989) [as emended by Oliver and Pedder (1994), McGhee (1996), and McGhee (personal commun., 2002)]; Tucker et al. (1998); and GSA (1999); only Eifelian through Famennian values are shown.

*Discussion.*—Different patterns were retrieved using the different time scales, yet determining which time scale to accept is not a simple task. Currently, there is no single accepted absolute timescale for the Devonian, although many have been proposed [for a thorough discussion, see Williams et al. (2000)]. Since each time scale is based on a different set of data and underlying assumptions, it is possible to evaluate which hypothesis of stage duration might be the best fit for the Devonian based on these assumptions. The Bayer and McGhee (1989) time scale [emended after Oliver and Pedder (1994), McGhee (1996), and McGhee (personal commun., 2002)] may be a good estimate of stage duration to use with this analysis because it is based on models of cyclic sediment accumulation. Consequently, this time scale is based on several hundred underlying data points. Radiometric isotopic studies such as those of Tucker et al. (1998) and GSA (1999) are based on less than 15 radiometric ages whose calibrations are based on underlying assumptions about the relative length of conodont zones. The Bayer and McGhee (1989) analysis is not limited by these assumptions and is instead tied to models of sediment accumulation rather than the inferred relative speed of conodont evolution.

Another important factor to consider when examining the extinction rate data in Figures 4 and 5 is potential inflation of the Famennian values due to the edge effect (see Foote, 1994, 2000b). (Because Foote's [2000a, 2000b] method was used, there will be

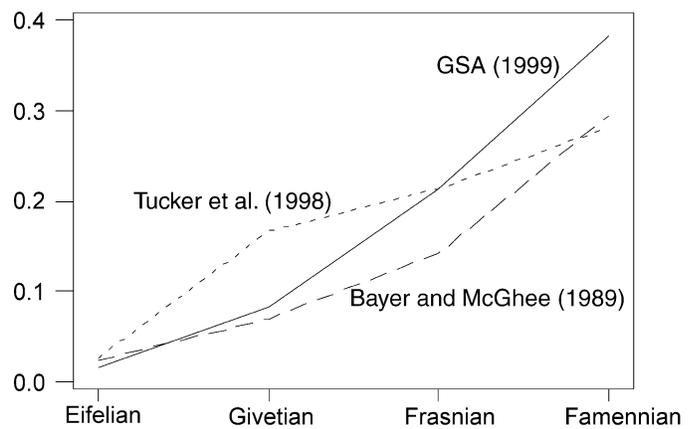


FIGURE 4—Extinction rates derived from Table 4 plotted versus Devonian stage for all phyllocarids calculated using phylogenetic constraints on timing of lineage divergence for the three different time scales: Bayer and McGhee (1989) [as emended by Oliver and Pedder (1994), McGhee (1996), and McGhee (personal commun., 2002)]; Tucker et al. (1998); and GSA (1999); only Eifelian through Famennian values are shown.

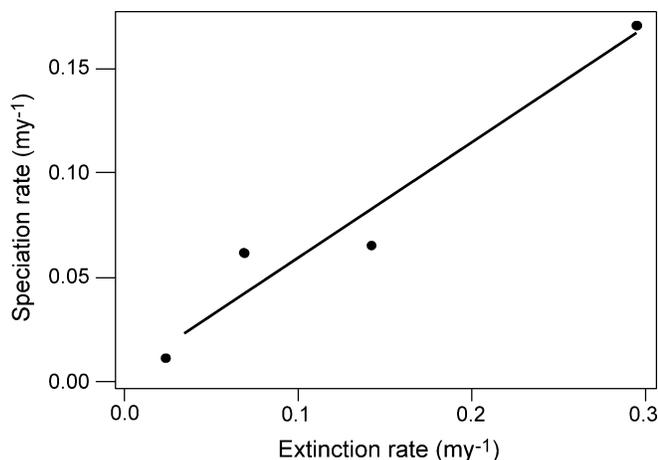


FIGURE 5—Linear regression of speciation rate versus extinction rate based on the Bayer and McGhee (1989) time scale [as emended by Oliver and Pedder (1994), McGhee (1996), and McGhee (personal commun., 2002)]. Regression  $y = 0.550X + 0.004$  and  $r^2 = 0.947$ .

no edge effects for the Famennian speciation rate values in Figure 3.) Since the Bayer and McGhee (1989) and Tucker et al. (1998) time scales only focused on the Devonian period, consideration of species that evolved in the Tournaisian Stage of the Mississippian was impossible, and edge effects may have occurred when these time scales were used. Furthermore, even when Tournaisian age constraints could be included in a calculation, which is possible with the GSA (1999) time scale, insufficient data are available on boundary-crossing phyllocarids from the latest Devonian into the Mississippian to incorporate them in the rate calculations utilized. Thus, something is occurring in the pattern of phyllocarid stratigraphic distribution, perhaps associated with the Late Devonian biodiversity crisis, that makes it impossible to eliminate completely the potential role of edge effects in this database (see Figs. 4, 5). The rise in extinction rates of the phyllocarids in the Frasnian and Famennian, although moderate, may be a manifestation of the more general pattern of increasing extinction rates that has been documented for several other taxa by McGhee (1996) associated with the Late Devonian biodiversity crisis. From the data presented here, there is no general sense that speciation rates declined precipitously at the same time.

The correlation between speciation and extinction rates recovered here has also been recognized in numerous other paleobiological studies (e.g., Eldredge, 1979; Stanley, 1979, 1990; Vrba, 1980). Two features of the regression in Figure 5 warrant discussion, however: the slope and y-intercept values. Regarding the slope, extinction rate increases at a higher rate than speciation rate; the y-intercept is also positive. Therefore, at low rates of speciation and extinction, speciation exceeds extinction and net biodiversity increases. At higher rates of speciation and extinction, however, extinction outstrips speciation, and a biodiversity decline occurs. If these results from the phyllocarids can be generalized, they may have implications for our understanding of macroevolution. Our results suggest it may be important to factor in not only speciation and extinction rates, but also the dynamics between them, in analyses of major evolutionary radiations and mass extinctions.

#### GAUGING THE RELATIONSHIP BETWEEN GEOGRAPHIC RANGE AND RATES OF BIODIVERSITY CHANGE

**Methods.**—The relationships between median geographic range and speciation rate and median geographic range and extinction

TABLE 5—Results of regression analyses that considered the correlation between speciation rate and extinction rate using the three time scales described in the text. † indicates significance at  $P < 0.01$  level. ‡ indicates significance at  $P < 0.05$  level.

Analysis	Time scale	$r^2$ value
Speciation rate vs. extinction rate	Bayer and McGhee (1989)	.947†
	Tucker et al. (1998)	.775‡
	GSA (1999)	.951†

rate were analyzed statistically. Linear regression of both speciation and extinction rate against median geographic range (Table 3) was performed using Minitab Release 11 (Minitab Inc., 1996) and are presented in Table 7. Each analysis was performed using speciation and extinction rates calculated with the Bayer and McGhee (1989) [adjusted after Oliver and Pedder (1994), McGhee (1996), and McGhee (personal commun., 2002)], Tucker et al. (1998), and GSA (1999) time scales, since the choice of time scale may have a significant effect on results, as described previously.

**Results.**—Linear regression of speciation rates versus median geographic range produced a significant correlation, with a slightly positive slope, for the Bayer and McGhee (1989) and GSA (1999) time scales (Table 7). The  $P$ -values retrieved from an analysis of variance (ANOVA) of the regression fit are not significant and are not shown.

Linear regression of extinction rate versus geographic range produced comparable results, though correlation is only significant when the emended Bayer and McGhee (1989) time scale is used (Table 7). Again, the  $P$ -values retrieved from an analysis of variance (ANOVA) of the regression fit are not significant and thus not shown.

**Discussion.**—Speciation rate appears to increase as median geographic range increases, though this is not significant for one of the time scales used. As discussed above, the comparison of Famennian values between time scales suggests that edge effects do not significantly inflate rates of biodiversity change calculated for the Famennian. The recovered pattern of increasing extinction rate with increasing median geographic range is significant, but only for one of the time scales. This association of increased extinction rates at larger geographic ranges is consistent with the modern invasive species theory, in which it is hypothesized that (e.g., Cohen and Carlton, 1998; Eldredge, 1998) a proliferation of invasive species with expanded geographic ranges will reduce total biodiversity. In modern ecosystems, this is frequently due to competitive exclusion of previously established species, though such causal factors cannot be applied to these fossil taxa.

#### CONCLUSIONS

Phylogenetic biogeography provides information on how geographic areas are related in terms of vicariance and geodispersal. Geological and climatic processes, such as the onset of the Acadian Orogeny and cyclical sea level changes, may have produced geodispersal and vicariance between western Canada, Armorica, and the Appalachian Basin, while traditional dispersal events likely controlled the distribution of phyllocarid species within Michigan, Bolivia, and South China. The geodispersal tree is more

TABLE 6—Results of analysis of variance of the regression fit. ‡ indicates significance at  $P < 0.05$  level.

Analysis	Time scale	$P$ -value
Speciation rate vs. extinction rate	Bayer and McGhee (1989)	.027‡
	Tucker et al. (1998)	.120
	GSA (1999)	.025‡

TABLE 7—Results of regression analyses that considered the correlation between speciation rate and median geographic range and extinction rate and median geographic range using the three time scales described in the text. ‡ indicates significance at  $P < 0.05$  level.

Analysis	Time scale	r <sup>2</sup> value
Speciation rate vs. geographic range	Bayer and McGhee (1989)	.855‡
	Tucker et al. (1998)	.301
	GSA (1999)	.810‡
Extinction rate vs. geographic range	Bayer and McGhee (1989)	.833‡
	Tucker et al. (1998)	.447
	GSA (1999)	.746

resolved than the vicariance tree, which is unusual when compared to results of other analyses (e.g., Lieberman and Eldredge, 1996; Lieberman, 1997), suggesting congruent episodes of geodispersal were more common in phyllocarids of this period than episodes of vicariance (Rode and Lieberman, 2001, 2002).

We also uncovered evidence that speciation and extinction rates are correlated and increase in concert, and these may in turn be correlated with increases in species ranges, though the latter result is more equivocal. Further, extinction rate increased faster than speciation rate in the phyllocarids. This may be an effect of the correlation between invasive species and rates of extinction. The pattern of extinction rate increasing faster than speciation rate in the phyllocarids, if corroborated with other taxa, may illuminate aspects of the Late Devonian biodiversity crisis in particular, and protracted biodiversity crises in general. This is because biodiversity is about the interplay between speciation and extinction rates through time (Stanley, 1979; McGhee, 1996). Even a modest increase in speciation rate, if coupled with a greater increase in extinction rate, can result in a severe diversity decline.

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#### REFERENCES

- BAYER, U., AND G. R. MCGHEE JR. 1989. Periodicity of Devonian sedimentary and biological perturbations: implications for the Devonian timescale. *Neues Jahrbuch für Geologie und Paläontologie Monatsheft*, 1989:1–16.
- BEECHER, C. E. 1884. Ceratiocarididae from the Chemung and Waverly Groups of Pennsylvania. Second Geographical Survey of Pennsylvania Report of Progress, PPP:1–22.
- BEECHER, C. E. 1902. Revision of the Phyllocarida from the Chemung and Waverly groups of Pennsylvania. *Quarterly Journal of the Geological Society of London*, 58:441–449.
- BERRY, J. K. 1995. Spatial Reasoning for Effective GIS. GIS World Books, Fort Collins, Colorado, 208 p.
- BOUCOT, A. J. 1975. Evolution and Extinction Rate Controls. Elsevier, Amsterdam, 427 p.
- BROOKS, D. R. 1985. Historical ecology: a new approach to studying evolution of ecological associations. *Annals of the Missouri Botanical Garden*, 72:660–680.
- BROOKS, D. R., AND D. A. MCLENNAN. 1991. Phylogeny, Ecology, and Behavior. University of Chicago Press, Chicago, 434 p.
- BURROUGH, P. A., AND R. A. MCDONNELL. 1998. Principles of Geographic Information Systems. Oxford University Press, Oxford, 193 p.
- CHOU, Y. H. 1997. Exploring Spatial Analysis in Geographic Information Systems. OnWord Press, Sante Fe, New Mexico, 474 p.
- CLARKE, J. M. 1885. On the higher Devonian faunas of Ontario County, New York. United States Geological Survey Bulletin, 16:1–85.
- CLARKE, J. M. 1898a. The stratigraphic and faunal relationships of the Oneonta sandstones and shales, the Ithaca and the Portage Groups in Central New York. New York State Museum, 49<sup>th</sup> Annual Report of the Regents, 1895, 2:69.
- CLARKE, J. M. 1898b. Notes on some crustaceans from the Chemung Group of New York. I. A singularly ornamented phyllocarid genus, *Pephricarid*. New York State Museum, 49<sup>th</sup> Annual Report of the Regents, 1895, 2:731–733.
- COHEN, A. N., AND J. T. CARLTON. 1998. Accelerating invasion rate in a highly invaded estuary. *Science*, 279:555–558.
- COPELAND, M. J. 1960a. The occurrence of *Echinocaris* and *Spathiocaris* (Phyllocarida) in western Canada, p. 1–11, pls. 1–3. In M. J. Copeland and T. E. Bolton (eds.), Canadian fossil Arthropoda, Eurypterida, Phyllocarida, and Decapoda. Geological Survey of Canada Bulletin, 60.
- COPELAND, M. J. 1960b. New occurrences of *Ceratiocarid* and *Ptychocaris* (Phyllocarida) from the Canadian Arctic, p. 49–54, pl. 9. In M. J. Copeland and T. E. Bolton (eds.), Canadian fossil Arthropoda, Eurypterida, Phyllocarida, and Decapoda. Geological Survey of Canada Bulletin, 60.
- CROIZAT, L., G. NELSON, AND D. E. ROSEN. 1974. Centers of origin and related concepts. *Systematic Zoology*, 23:265–287.
- DALZIEL, I. W. D., L. H. DALLA SALDA, AND L. M. GAHAGAN. 1994. Paleozoic Laurentia–Gondwana interaction and the origin of the Appalachian–Andean mountain system. *Geological Society of America Bulletin*, 106:243–252.
- DINELEY, D. L. 1984. Aspects of a Stratigraphic System: The Devonian. Macmillan, London, 223 p.
- EBACH, M. C., AND G. D. EDGEcombe. 2001. Cladistic biogeography: component-based methods and paleontological application, p. 235–289. In J. M. Adrain, G. D. Edgecombe, and B. S. Lieberman (eds.), Fossils, Phylogeny, and Form; An Analytical Approach. Kluwer Academic/Plenum, New York.
- ELDRIDGE, N. 1979. Alternative approaches to evolutionary theory. *Bulletin of the Carnegie Museum of Natural History*, 13:7–19.
- ELDRIDGE, N. 1998. Life in the Balance: Humanity and the Biodiversity Crisis. Princeton University Press, Princeton, New Jersey, 224 p.
- ELDRIDGE, N., AND A. R. ORMISTON. 1979. Biogeography of Silurian and Devonian trilobites of the Malvinokaffric Realm, p. 147–167. In J. Gray and A. J. Boucot (eds.), Historical Biogeography, Plate Tectonics, and the Changing Environment. Oregon State University Press, Corvallis.
- ELLER, E. R. 1935. New species of *Echinocaris* from the Upper Devonian, of Alfred Station, New York. *Annals of the Carnegie Museum*, 24:263–274.
- ELLER, E. R. 1937. *Echinocaris crosbyensis*, a new species from the Upper Devonian of New York. *Annals of the Carnegie Museum*, 25:257–259.
- ENVIRONMENTAL SYSTEMS RESEARCH INSTITUTE, INC. (ESRI). 1999. ArcView GIS 3.2. Redlands, California.
- FEIST, R. 1991. Late Devonian trilobite crises. *Historical Biology*, 5:197–214.
- FELDMANN, R. M., AND S. MCKENZIE. 1981. *Echinocaris multispinosus*, a new echinocarid (Phyllocarida) from the Chagrin Formation (Late Devonian) of Ohio. *Journal of Paleontology*, 55:383–388.
- FELDMANN, R. M., R. M. BOSWELL, AND T. W. KAMMER. 1986. *Tropidocaris salsiusculus*, a new rhinocarid (Crustacea: Phyllocarida) from the Upper Devonian Hampshire Formation of West Virginia. *Journal of Paleontology*, 60:379–383.
- FERGUSON, C. A., B. E. BODENBENDER, J. L. HONES, AND K. AHMED. 2001. Recording the fossil record: a GIS database of Middle Devonian fossils in the Michigan Basin. Geological Society of America Annual Meeting, 2000, Abstracts with Programs, 109:A131.

- FOOTE, M. 1994. Temporal variation in extinction risk and temporal scaling of extinction metrics. *Paleobiology*, 20:424–444.
- FOOTE, M. 2000a. Origination and extinction components of taxonomic diversity: Paleozoic and post-Paleozoic dynamics. *Paleobiology*, 26: 578–605.
- FOOTE, M. 2000b. Origination and extinction components of taxonomic diversity: general problems, p. 578–605. *In* D. H. Erwin and S. L. Wing (eds.), *Deep Time: Paleobiology's Perspective*. *Paleobiology*, 26 (Suppl. to No. 4).
- FORTEY, R. A., AND L. R. M. COCKS. 1992. The early Palaeozoic of the North Atlantic region as a test case for the use of fossils in continental reconstruction. *Tectonophysics*, 206:147–158.
- GEOLOGICAL SOCIETY OF AMERICA (GSA). 1999. 1999 Geologic Time Scale. A. R. Palmer and J. Geissman, compilers.
- GRAHAM, R. W. 2000. FAUNMAP database: filter effects from field to literature to database to analysis to interpretation. Geological Society of America Annual Meeting, 2000, Abstracts with Programs, 109: A131.
- HALL, J. 1863. Contributions to paleontology, no. 6. On the occurrence of crustacean remains of the genera *Ceratiocaris* and *Dithryocaris*, with a notice of some new species from the Hamilton Group and Genesee Slate. 16<sup>th</sup> Report of the New York State Cabinet of Natural History, Appendix D:71–75.
- HALL, J., AND J. M. CLARKE. 1888. Trilobites and other Crustacea of the Oriskany, Upper Helderberg, Hamilton, Portage, Chemung, and Catskill groups. New York State Geological Survey, *Palaeontology*, 7:i–lxiv, 1–236.
- HALTUCH, M. A., P. A. BERKMAN, AND D. W. GARTON. 2000. Geographic information system (GIS) analysis of ecosystem invasion: exotic mussels in Lake Erie. *Limnology and Oceanography*, 45:1778–1787.
- HAN, N., AND Y. ZHOU. 1993. A new species of *Echinocaris* (Phyllocarida) in Late Devonian from Lingling, Hunan. *Acta Palaeontologica Sinica*, 32:228–232.
- HANNIBAL, J. T. 1990. *Echinocaris*: a mid-Paleozoic crustacean. Unpublished Ph.D. dissertation, Kent State University, Kent, Ohio, 362 p.
- HILLIS, D. M., AND J. P. HUELSENBECK. 1992. Signal, noise, and reliability in molecular phylogenetic analyses. *Journal of Heredity*, 83: 189–195.
- HUMPHRIES, C. J., AND L. PARENTI. 1986. Cladistic biogeography. *Oxford Monographs in Biogeography*, 2:1–98.
- HUNN, C. A., AND P. UPCHURCH. 2001. The importance of time/space in diagnosing the causality of phylogenetic events: towards a “chronobiogeographical” paradigm? *Systematic Biology*, 50:391–407.
- IVERSON, L. R., AND A. PRASAD. 1998. Estimating regional plant biodiversity with GIS modeling. *Diversity and Distributions*, 4:49–61.
- JAECKEL, O. 1921. Einen neuen Phyllocariden aus dem Unterdevon der Bundbacher Dachschiefer. *Zeitschrift der deutschen geologischen Gesellschaft, Monatsbericht*, 72:290–292.
- JONES, T. R., AND H. WOODWARD. 1889. I.—On some new Devonian fossils. *Geological Magazine*, n. s., decade 3, 6:384–388.
- JULIUSSON, L., AND R. GRAHAM. 1999. Geographic information systems and vertebrate paleontology. *Journal of Vertebrate Paleontology*, 19(Suppl. to No. 3):56.
- JUX, U. 1959. Phyllocariden-reste aus dem oberen Mitteldevon der Bergisch Gladbach-Paffrather Mulde. *Palaeontologische Zeitschrift*, 33:166–171.
- JUX, U. 1960. *Montecaris lehmanni*, a new crustacean from the Rhenish Devonian and the problem of its systematic position. *Journal of Paleontology*, 34:1129–1152.
- KALVODA, J. 1990. Late Devonian–Early Carboniferous paleobiogeography of benthic foraminifera and climatic oscillations, p. 183–188. *In* E. G. Kauffman and O. H. Walliser (eds.), *Extinction Events in Earth History*. Springer, New York.
- KENT, D. V. 1985. Paleogeographical setting for the Catskill Delta, p. 9–13. *In* D. L. Woodrow and W. D. Sevon (eds.), *The Catskill Delta*. Geological Society of America Special Paper, 201.
- KLAPPER, G. 1995. Preliminary analysis of Frasnian, Late Devonian conodont biogeography. *Historical Biology*, 10:103–117.
- KLAPPER, G., AND J. G. JOHNSON. 1980. Endemism and dispersal of Devonian conodonts. *Journal of Paleontology*, 54:400–455.
- KLASSEN, G. J., R. D. MOOI, AND A. LOCKE. 1991. Consistency indices and random data. *Systematic Zoology*, 40:446–457.
- LIEBERMAN, B. S. 1997. Early Cambrian paleogeography and tectonic history: a biogeographic approach. *Geology*, 25:1039–1042.
- LIEBERMAN, B. S. 2000. *Paleobiogeography: Using Fossils to Study Global Change, Plate Tectonics, and Evolution*. Kluwer Academic Press/Plenum, New York, 208 p.
- LIEBERMAN, B. S. 2001. Analyzing speciation rates in macroevolutionary studies, p. 340–358. *In* J. Adrain, G. D. Edgecombe, and B. S. Lieberman (eds.), *Fossils, Phylogeny and Form: An Analytical Approach*. Kluwer Academic Press/Plenum, New York.
- LIEBERMAN, B. S. 2003. Unifying theory and methodology in biogeography. *Evolutionary Biology*, 33:1–25.
- LIEBERMAN, B. S., AND N. ELDREDGE. 1996. Trilobite biogeography in the Middle Devonian: geological processes and analytical methods. *Paleobiology*, 22:66–79.
- MC GHEE, G. R. JR. 1981. Evolutionary replacement of ecological equivalents in Late Devonian benthic marine communities. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 34:267–283.
- MC GHEE, G. R. JR. 1988. The Late Devonian extinction event: evidence for abrupt ecosystem collapse. *Paleobiology*, 14:250–257.
- MC GHEE, G. R. JR. 1990. The Frasnian-Famennian extinction record in the eastern United States, p. 161–168. *In* O. H. Walliser and E. G. Kauffman (eds.), *Extinction Events in Earth History*. Springer, Berlin.
- MC GHEE, G. R. JR. 1996. *The Late Devonian Mass Extinction: The Frasnian/Famennian Crisis*. Columbia University Press, New York, 303 p.
- MINITAB INC. 1996. Minitab Release 11.21. State College, Pennsylvania.
- MORRONE, J. J., AND J. V. CRISCI. 1995. Historical biogeography: introduction to methods. *Annual Reviews of Ecology and Systematics*, 26: 373–401.
- MORZADEC, P., AND W. D. I. ROLFE. 1968. Découverte d'un nouveau Phyllocaride (Crustacés) dans le Dévonien supérieur de Massif armoricain. *C. R. sommaire Societe Géologique de France*, 6:189–190.
- NELSON, G., AND N. I. PLATNICK. 1981. *Systematics and Biogeography: Cladistics and Vicariance*. Columbia University Press, New York, 567 p.
- OLIVER, W. A. JR. 1976. Biogeography of the Devonian rugose corals. *Journal of Paleontology*, 50:365–373.
- OLIVER, W. A. JR. 1990. Extinctions and migrations of Devonian rugose corals in the Eastern Americas realm. *Lethaia*, 23:167–178.
- OLIVER, W. A. JR., AND A. E. H. PEDDER. 1994. Crises in the Devonian history of rugose corals. *Paleobiology*, 20:178–190.
- PAGE, R. D. M. 1990. Component analysis: a valiant failure? *Cladistics*, 6:119–136.
- PLATNICK, N. I., AND G. NELSON. 1978. A method of analysis for historical biogeography. *Systematic Zoology*, 27:1–16.
- RACHEBOEUF, P. R. 1998. Mid-Devonian phyllocarid crustacea from Bolivia. *Palaeontology*, 41:103–124.
- RAYMOND, A., AND C. MERTZ. 1995. Laurussian land-plant diversity during the Silurian and Devonian: mass extinction, sampling bias, or both? *Paleobiology*, 21:74–91.
- RODE, A. L. 2002. Using GIS to integrate species ranges, evolution, and eustasy during the Late Devonian biodiversity crisis. Geological Society of America Annual Meeting, 2002, Abstracts with Programs, 111: 141–3.
- RODE, A. L., AND B. S. LIEBERMAN. 2000. Using phylogenetics and GIS to investigate the role in invasive species in the Late Devonian mass extinction. Geological Society of America Annual Meeting, 2000, Abstracts with Programs, 109:A368.
- RODE, A. L., AND B. S. LIEBERMAN. 2001. Assessing the role of invasive species in mediating mass extinctions: a case study using Devonian phyllocarids. *PaleoBios*, 21:109.
- RODE, A. L., AND B. S. LIEBERMAN. 2002. Phylogenetic and biogeographic analysis of Devonian phyllocarid crustaceans. *Journal of Paleontology*, 76:271–286.
- RODE, A. L., AND B. S. LIEBERMAN. 2003. GIS and phylogenetics, a combined approach to understanding biogeographic changes in the Late Devonian. Geological Society of America Annual Meeting, 2003, Abstracts with Programs, 112:157–8.
- ROLFE, W. D. I. 1962. A new phyllocarid crustacean from the Upper Devonian of Ohio. *Breviora*, 151:1–7.
- ROLFE, W. D. I. 1969. Phyllocarida, p. R296–R331. *In* R. C. Moore (ed.), *Treatise on Invertebrate Paleontology Part R, Arthropoda 4 (1)*. Geological Society of America and University of Kansas Press, Lawrence.

- ROLFE, W. D. I., AND V. A. EDWARDS. 1979. Devonian Arthropoda (Trilobita and Ostracoda excluded). *Special Papers in Palaeontology*, 23: 325–329.
- ROSEN, D. E. 1978. Vicariant patterns and historical explanation in biogeography. *Systematic Zoology*, 27:159–188.
- ROSS, M. I., AND C. R. SCOTSE. 2000. PaleoGIS/Arcview 3.5. PALEOMAP Project, University of Texas, Arlington.
- SCOTSE, C. R. 1998. PALEOMAP Animations. PALEOMAP Project, University of Texas, Arlington.
- SCOTSE, C. R., AND W. S. MCKERROW. 1990. Revised world maps and introduction, p. 217–277. *In* C. R. Scotese and W. S. McKerrrow (eds.), *Palaeozoic Palaeogeography and Biogeography*. Geological Society of London Memoir, 51.
- SMITH, A. B. 1994. *Systematics and the Fossil Record: Documenting Evolutionary Patterns*. Blackwell Scientific, Cambridge, Massachusetts, 223 p.
- SOKAL, R. R., AND F. J. ROHLF. 1995. *Biometry: The Principles and Practice of Statistics in Biological Research*. W.H. Freeman, New York, 887 p.
- STANLEY, S. M. 1979. *Macroevolution, Pattern and Process*. W. H. Freeman, San Francisco, 332 p.
- STANLEY, S. M. 1990. The general correlation between rate of speciation and rate of extinction: fortuitous causal linkages, p. 103–127. *In* R. M. Ross and W. D. Allmon (eds.), *Causes of Evolution: A Paleontological Perspective*. University of Chicago Press, Chicago.
- STEWART, G. A. 1933. A phyllocarid crustacean from the Devonian rocks of Ohio. *American Midland Naturalist*, 14:363–366.
- STOMS, D. M., F. W. DAVIS, C. B. COGAN, M. O. PAINHO, B. W. DUNCAN, J. SCEPAN, AND S. J. MICHAEL. 1993. Geographic analysis of California condor sighting data. *Conservation Biology*, 7:148–159.
- STUMM, E. C., AND R. B. CHILMAN. 1969. Phyllocarid crustaceans from the Middle Devonian Silica Shale of northwestern Ohio and southeastern Michigan. *Contributions from the Museum of Paleontology, University of Michigan*, 23:53–71.
- STURGEON, M. T., W. J. HLAVIN, AND R. V. KESLING. 1964. Rare crustaceans from the Upper Chagrin Shale in northern Ohio. *Contributions from the Museum of Paleontology, University of Michigan*, 19:47–64.
- SWOFFORD, D. L. 2002. PAUP\*. *Phylogenetic Analysis Using Parsimony (\* and other methods)* [computer program]. Version 4.0b10. Sinauer, Sunderland, Massachusetts.
- TUCKER, R. D., D. C. BRADLEY, C. A. VER STRAETEN, A. G. HARRIS, J. R. EBERT, AND S. R. MCCUTCHEON. 1998. New U-Pb zircon ages and the duration and division of Devonian time. *Earth and Planetary Science Letters*, 158:175–786.
- VAN DER VOO, R. 1988. Paleozoic paleogeography of North America, Gondwana, and intervening displaced terranes: comparisons of paleomagnetism with paleoclimatology and biogeographical patterns. *Geological Society of America Bulletin*, 100:311–324.
- VRBA, E. S. 1980. Evolution, species and fossils: how does life evolve? *South African Journal of Science*, 76:61–84.
- WHITFIELD, R. P. 1880. Notice of new forms of fossil crustaceans from the Upper Devonian rocks of Ohio, with descriptions of new genera and species. *American Journal of Science, third series*, 19:33–42.
- WILEY, E. O. 1988. Vicariance biogeography. *Annual Review of Ecological Systematics*, 19:513–542.
- WILEY, E. O., AND R. L. MAYDEN. 1985. Species and speciation in phylogenetic systematics, with examples from North American fish fauna. *Annals of the Missouri Botanical Garden*, 72:596–635.
- WILLIAMS, E. A., P. F. FRIEND, AND B. P. J. WILLIAMS. 2000. A review of Devonian time scales: databases, construction, and new data, p. 1–21. *In* P. F. Friend and B. P. J. Williams (eds.), *New Perspectives on the Old Red Sandstone*. Geological Society of London Special Publications, 180.
- YOUNG, G. C. 1987. Devonian paleontological data and the Armorica problem. *Palaeogeography, Palaeoclimatology, and Palaeoecology*, 60: 283–304.

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