

*On the Nonprevalence of Competitive
Replacement in the Evolution of Tetrapods*

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The role of competition in evolution has long been debated (Simpson 1953; Stebbins 1974; Stanley 1979; Connell 1980; Schoener 1983; Branch 1984; Strong et al. 1984; Vermeij 1987; Weiner 1995). At one time, most paleontologists assumed that the history of life was progressive, and that most change was mediated by competitive interactions. For example, Stanley (1979, 184) stated that "paleontologists have almost universally accepted the idea that certain body plans have been rendered obsolete during modernization of the world ecosystem. From evidence of adaptive morphology alone, the progressive nature of evolution has long been recognized. . . ." Evolutionists then assumed that progress, change with improvement (Dobzhansky et al. 1977), and hence clade originations were part of a continuous cycle of competitive replacement, in which newly evolved taxa generally possessed competitively superior adaptations and could thereby replace, or drive to extinction, preexisting groups.

Two species are said to be in competition if an increase in abundance by either one harms the other (MacArthur 1972, 21). Such competitive interactions are often viewed as necessary correlates of evolution by natural selection, an idea clearly expressed by Darwin (1859) when he made an analogy between the number of species on the earth and a surface covered with "ten-thousand sharp wedges." In his metaphor, he stated clearly that a new wedge could be driven in only by expelling another; in other words, the origination of a new species can occur only by the displacement of a preexisting one. Extrapolating from this model, diversifications of clades in the past might have resulted largely from competitive replacement of others.

Further consideration of concrete examples and a weighing of the evidence for biotic and abiotic control of evolution have led to a broader view. For example, Jackson (1988) noted that there is evidence for escalation (Vermeij 1987, 1994), or biotically driven changes in morphology and behavior, in the history of life, based on the following points: (1) biological interactions among extant taxa strongly affect their well-being, and hence the distribution and abundance of species; (2) variations in morphology and behavior can affect the success of organisms in finding food or in escaping predation; (3) competition and predation happened in the past; (4) the diversity and effectiveness of burrowing and predatory organisms have increased through time; (5) there are many examples

of increasing resistance to predation through time. However, although such biotically driven evolutionary changes undoubtedly occur, abiotic influences through the agency of extinction and origination events have also constantly affected the course of evolution. This debate over the relative roles of biotic and abiotic influences on evolution is clearly important, but it is sidestepped somewhat when the possibility of expansion is considered.

The older ideas of competitively mediated evolutionary replacement depended on an assumption of plentitude, a pre-Darwinian idea (Rieppel 1984) that there are a fixed number of niches and that life expands to fill those available adaptive slots (Darwin's field of wedges). After the initial filling of ecospace, a dynamic equilibrium state is maintained, with taxa coming and going, but with a constant total species diversity. This kind of view formed a backdrop to many important ideas in ecology (MacArthur and Wilson 1967; Arthur 1980; Rosenzweig 1995), such as the species-area effect, island biogeography models, character replacement, and character release. In paleontology, equilibrium assumptions lie behind the hypothesis of a succession of evolutionary "faunas" (Sepkoski 1984), the Red Queen model of evolution (Van Valen 1973), post-invasion extinctions (Simpson 1953), the community paradigm (Boucot 1975), and many specific examples of evolutionary relays (Simpson 1953) or competitive replacements (e.g., Stanley 1979; Bonaparte 1982).

There is no evidence for any fixed maximum number of species on the earth (Walker and Valentine 1984), nor for the inevitability of post-invasion extinction (Marshall et al. 1982), nor for the assumption of competitive replacement in many particular case studies (Gould and Calloway 1980; Benton 1983a, b, 1987, 1991). There is no evidence for the pre-Darwinian principle of plentitude (Rieppel 1984), but the observation that the diversity of life rebounds explosively after an extinction event (e.g., Miller and Sepkoski 1988; Sepkoski, chapter 9, this volume) suggests that there have been particular patterns of species packing in the past, and that niches emptied by extinction may fill again in a partially predictable manner. Evidently, in normal times, species diversity is damped by competitive interactions, and this control breaks down after drastic species reduction following an extinction event (Jablonski 1986).

The existence of long intervals with fixed numbers of niches has also been proposed by Sepkoski (1984), who discovered that the diversification of marine life during the Phanerozoic followed a logistic pattern, with plateaus in the Cambrian and the later Paleozoic and with a third plateau presumably to be achieved in the future. Courtillot and Gaudemer (1996) also found that the diversification of life followed a logistic pattern, punctuated by mass extinctions in the Late Permian, Late Triassic, and end-Cretaceous. Their best-fit equations indicated plateaus in familial diversity during the Paleozoic, the Triassic, and the Neogene. Benton (1995) found that the diversification of all life, of marine life, and of continental life could fit an exponential model of increase at the familial level, a pattern especially evident in the diversification of tetrapods alone. If this were the case, then there would be no indication even of episodic plentitude. However,

the logistic models, at present, appear to explain the data better than the exponential model.

Expansion in the history of life refers to the fact that, over time, the total number of species on the earth, and the numbers of species in many clades, have increased. This fact is connected with the observation that many radiations have involved new adaptations, such as multicellularity, macroscopic size, skeletons, deep burrowing, tiered filter feeding, terrestrialization, shell boring, and flight. Perhaps most of the diversification of life has been associated with expansion into new habitats and new modes of life (Marshall et al. 1982; Benton 1990; Lidgard, McKinney, and Taylor 1993), and the constraints implied in the double-wedge model, or in the idea of the opportunistic radiation of taxa after mass extinctions, are thereby sidestepped. Such diversifications do not preclude the presence of equilibria in the intervening intervals.

Much of the debate so far about the reality, or otherwise, of competitive replacement has focused on the examination of particular case studies. This focus has been worthwhile in redefining paleontological understanding of individual events and in building a deeper understanding of how major new clades become established, but it does not resolve the broader question of the significance of competition in evolution. A new approach is presented here, in which a quantitative estimate is made of the prevalence of competitive replacement in clade originations. A census of a major clade, the Tetrapoda, is presented, with an assessment of the maximum number of group originations that might have resulted from competitive replacement of a preexisting group or groups. This chapter is based on work begun a number of years ago and presented at the Fifth North American Paleontological Convention in Chicago (Benton and Storrs 1992), but has been substantially revised and updated since then.

Models of Clade Radiations

There are two simple models of clade radiations: pure "competition," involving long-term struggle between clade A and clade B, and pure chance, in which each clade radiates unopposed. This naive polarization of models is unrealistic because there are many other ways in which clades might become established, many of them involving competition at one point or another. Benton (1987, 1991) outlined tests and expectations of patterns of clade replacement and proposed a sequence of five types of clade radiation models (fig. 8.1), which were discussed by Rosenzweig and McCord (1991) and Sepkoski (chapter 9, this volume):

1. Competitive replacement. Members of clade B possess a key adaptation that allows them to compete successfully with, and replace, members of clade A. The clade B organisms demonstrate the competitive superiority conferred upon them by the key adaptation by causing the extinction of all clade A organisms.
2. Post-extinction competitive replacement. There is an extinction event, after which survivors of clade B (with a key adaptation that renders them competi-

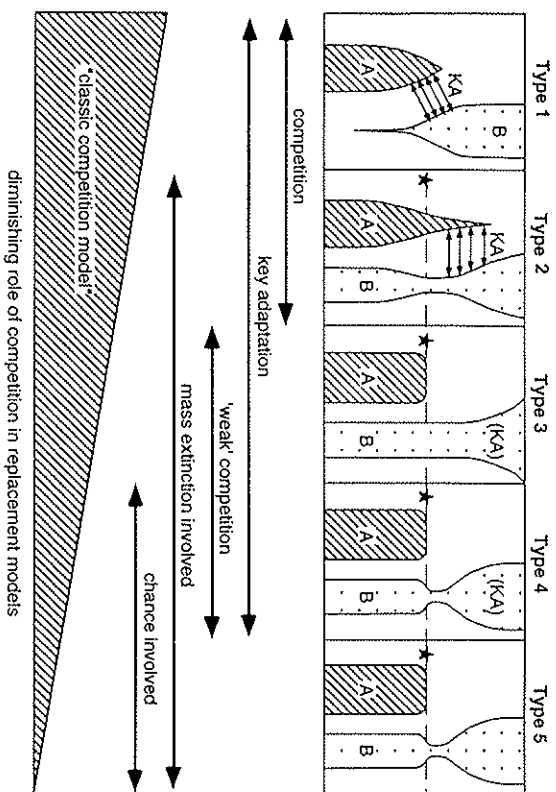


Fig. 8.1. Five models of biotic competition, in which competition and mass extinction play variable roles. The role of competition diminishes from left to right, from fully competitive replacement (type 1) to noncompetitive radiation (type 5), the "stochastic broom" hypothesis. The other models—post-extinction competitive replacement (type 2), extinction resistance (type 3), and noncompetitive adaptive radiation (type 4)—all involve some measure of competition. (After Benton 1991.)

tively superior) compete successfully in the disturbed post-extinction ecosystems with the survivors of clade A (which lack the key adaptation), and clade B prevails. Again, members of clade B demonstrate their competitive superiority, but only after an extinction caused by some other factors. This model was termed "incumbent replacement" by Rosenzweig and McCord (1991) because members of clade B speculate only after the extinction of incumbents, members of clade A.

3. Extinction resistance. Members of clade B resist extinction during a time when other taxa, including members of clade A, are dying out. Clade B organisms demonstrate their ability to resist extinction, but the two groups do not interact in any way. The ability of clade B to survive extinction may or may not be related to any adaptations that enable it to radiate after the extinction event.

4. Noncompetitive adaptive radiation. There is an extinction event during which many A and B organisms die out, and by chance, only a few B organisms survive. The B organisms have an adaptation that ensures a successful radiation. Clade B organisms have not demonstrated their competitive superiority over clade A organisms.

5. Noncompetitive radiation. There is an extinction event during which all or most A organisms, and most B organisms, die out by chance. The survivors of clade B radiate, but there is no particular adaptation that ensures the success of that radiation. This model was termed the "stochastic broom hypothesis" by Rosenzweig and McCord (1991).

In their discussion of these five models, Rosenzweig and McCord (1991) regarded the first as rare and the third, fourth, and fifth as most unlikely. With regard to type 3, these authors rightly asked for some evidence of the kinds of key adaptations that would confer the ability to resist extinctions, but the model was not refuted. However, in their discussion of the stochastic broom hypothesis (type 5), Rosenzweig and McCord (1991) assumed a clear-cut double-wedge pattern, in which a species-rich group dwindles to extinction and a rare group rises to replace it, all by chance. In those terms, the model is unlikely. In real paleontological examples, however, there are many cases of double wedges in which the two taxa in question apparently never interacted, and their relative waxing and waning was unrelated. Rosenzweig and McCord (1991) feel that type 2, incumbent replacement, comes closest to a realistic evolutionary ecological model for clade radiation.

Case Studies

Until 1980, competition was assumed to be the driving force behind many, or most, group originations (Simpson 1953; Stebbins 1974; Stanley 1979; Maynard Smith 1983), and the full-scale competitive replacement model (type 1) was regarded as appropriate. Since then, some of the classic cases have been reexamined (see reviews by Gould and Calloway 1980; Benton 1983a, b, 1987, 1991; table 8.1 herein). Many cases in which there is no evidence that the radiating clade had any effect on other existing groups have been explained in noncompetitive ways. Others have been explained in terms of one or another of the models in which competition plays a lesser role than had been assumed. Debate continues in a number of cases.

The classic example of supposed long-term competitive interaction between brachiopods and bivalves, and the eventual success of the latter, was studied by Gould and Calloway (1980). They argued that bivalves rose to prominence after the end-Permian mass extinction not as a result of competition between the two groups during the Paleozoic, but either by chance or as a result of their superior adaptability and powers of recovery (model types 4 and 5). Miller and Sepkoski (1988) and Sepkoski (chapter 9, this volume), on the other hand, suggest that the rate of diversification of bivalves was damped during much of the Phanerozoic by biotic interactions, and that the end-Permian and end-Cretaceous extinctions released the brake by causing extinction of some of their competitors (perhaps a type 2 model). Donovan and Gale (1990) argued for a type 4 model, in which

TABLE 8.1 Postulated competitive replacements

Replacement	Age	Duration (my)	Replacement type
Peridorsperms vs. progymnosperms	U. Dev.-L. Carb.	20-50	Diff. resp.
Angiosperms vs. gymnosperms	L. Cretaceous	10-50	Diff. resp.
Paleozoic vs. Cambrian marine animals	U. Camb.-L. Ord.	40-80	Exp./type 4
"Modern" vs. Paleozoic marine animals	Permian-Triassic	10-90	Exp./type 4
Bivalves vs. brachiopods	Paleozoic	50-330	Type 2/4
Modern sharks vs. hyodonts	U. Jur.-L. Cret.	40-70	Exp./type 4
Teleost fishes vs. holosteans	Jur.-Cret.	40-140	Exp./type 4
Archosaurs vs. mammal-like reptiles	Triassic	5-40	Type 4
Birds vs. pterosaurs	Cretaceous	50-80	Exp./type 4
Mammals vs. dinosaurs	U. Cretaceous	1-30	Type 5
Cheilosomes vs. cyclostome bryozoans	Cretaceous-Paleogene	30-120	Exp./type 4
Rodents vs. multituberculates	Paleogene	10-45	Exp./type 1
Artiodactyls vs. perissodactyls	Oligocene-Pliocene	5-35	Diff. resp.
North American vs. South American mammals (Great American Interchange)	Pliocene-Pleistocene	1-6	Insulation

Note: Postulated competitive replacements, based on oft-quoted examples from the literature, listing the "winner" first and the "loser" second. The age and duration of the replacement are indicated, together with a classification of the replacement according to the five model types outlined by Benton (1987, 1991; see text for fuller details). Classification of replacement types is based on discussions in Benton (1987, 1991) and D. M. Hitchcock, Phillips, and Olmstead (1987). Several of these supposedly competitive replacements may be outside the five models, being the result of expansion into new adaptive zones, insinuation by invaders into unoccupied adaptive spaces, or the result of differential responses to environmental stresses, but not involving competition or mass extinction. Abbreviations: Camb., Cambrian; Carb., Carboniferous; Cret., Cretaceous; Dev., Devonian; diff. resp., differential response to physical environmental stresses; exp., expansion; Jur., Jurassic; Ord., Ordovician.

brachiopods were selectively preyed upon by starfishes during the early Mesozoic and bivalves were not.

A classic case of major clade replacements among bryozoans has also been cited (Ryland 1970; Jackson and McKinney 1990) as a strong example of competitive replacement (type 1). Today, cheilosome bryozoans regularly out-compete cyclostome bryozoans by overgrowing them, and such overgrowth interactions are well known from the fossil record. During the Jurassic, only cyclostomes existed. Cheilosomes arose during the Late Jurassic and radiated rapidly throughout the Late Cretaceous and Paleogene, rising to their present familial diversity of nearly eighty, compared with eighteen extant families of cyclostomes. A problem for the proponents of competitive replacement is that cyclostomes have not succumbed, even after 150 million years of competition. Further, close scrutiny of the data (Lidgard, McKinney, and Taylor 1993) shows that cyclostomes diversified slowly during the Jurassic and Cretaceous and have maintained a constant familial and specific diversity since then. Cheilosomes have increased in diversity, but not obviously at the expense of the cyclostomes.

The radiation of birds during the Cretaceous has been linked to the decline of the pterosaurs (Uhwin 1988). Superficially, this appears to be the case, since pterosaur diversity worldwide declined from six families at the beginning of the

Cretaceous to only two at the end, both of which then disappeared. During the same time, bird diversity rose from negligible levels at the beginning of the Cretaceous to seventeen families or more at the end (Uhwin 1993). However, most pterosaur families died out before the substantial radiation of birds during the Late Cretaceous; six pterosaur families became extinct at the end of the Jurassic, and a further two during the Early Cretaceous. The four Late Cretaceous pterosaur families (Lonchodectes, Azhdarhidae, Nyctosauridae, Pteranodontidae) consisted of large or very large flying animals, and it is likely that they did not interact with the small birds of the time. The only large birds at that time, the hesperornithiforms, were flightless divers.

Rodents are said to have replaced the multituberculata mammals competitively during the Paleogene (Krause 1986). Both clades include several families of small to medium-sized gnawing animals, and their temporal and geographic distributions overlap. Four families of multituberculates died out at the end of the Paleocene, another at the end of the Early Eocene, and a sixth at the end of the Eocene. Two families of rodents originated in the Late Paleocene, three more in the Early Eocene, three in the Middle Eocene, five in the Late Eocene, four in the Oligocene, and a further ten in the Miocene. A similar pattern of apparently correlated waxing of rodents and waning of multituberculates is seen for generic data. This case seems to be a possible example of type 1 competitive replacement, although there is almost certainly an element of expansion in that rodents occupy a wider array of niches than the multituberculates ever did.

In a debate of this sort, the state of the argument may be assessed from time to time by adding up the numbers of supporting case studies on each side. Connell (1983) carried out such a tally in trying to resolve some questions about the frequency and role of competitive interactions among extant organisms. A census of case studies does not provide an absolute answer, however, since it may reflect partly the reality of nature and partly the skill and energy of the protagonists on either side of the debate. A more useful approach may be to carry out a comprehensive scrutiny of all data within a defined part of the history of life. Here, an attempt is made to assess the relative roles of competition and expansion in macroevolution by determining the likely mode of origination of each family within a single large clade.

The Database

Many postulated competitive replacements involve the clade Tetrapoda. This group is well suited for analysis because it contains a large number of families (1,034 families that have a fossil record of some kind; Benton 1993b), the taxa are mainly monophyletic (as a result of numerous cladistic analyses), and their broad ecological attributes can be assessed by comparison with modern forms. In this study, marine and nonmarine tetrapods were considered, and the family and the stratigraphic stage were selected as the focus for analysis. The data on stratigraphic distributions and on family contents were taken from the relevant

chapters in *The Fossil Record 2* (Milner 1993; Benton 1993a; Unwin 1993; Stucky and McKenna 1993).

Families were used as proxies for lower-level taxa, even though, for any major group, patterns at the species, genus, and family levels may not be congruent (Valentine 1968; Lidgard, McKinney, and Taylor 1993). The family level was selected in this analysis for three main reasons: First, among tetrapods, thousands of species and genera have been described, but their validity is unclear since many (if not most) have been based on single specimens or limited samples, and their taxonomy has not been comprehensively revised. Tetrapod families, on the other hand, have been subject to revision, and they show some measure of stability when databases are compared through research time, possibly because most are monophyletic, being defined by one or more apomorphies. Second, at generic and specific levels, the data are incomplete because of the sporadic nature of the fossil record, while the familial-level data are probably more comprehensive. Finally, tetrapod families are generally homogeneous in terms of the ecologies and functional attributes of their constituent members, and hence may be regarded as ecological entities.

The key drawbacks of the tetrapod fossil record are questions about the precision of dating of fossils and problems of incompleteness. However, these geological problems are not unique to tetrapods, and they are probably not critical. Indeed, the intensity of collection and study of fossil tetrapods over the past 200 years has been greater than the effort invested in other groups, and this effort probably largely offsets any perceived inadequacies in the representation of higher taxa in the fossil record when compared with marine invertebrates, for example (Benton and Simms 1995).

The quality of the tetrapod fossil record has been tested stringently in a number of ways, and these tests have tended to confirm its adequacy for studies of macroevolution. First, macroevolutionary patterns derived from fossil record data have not been substantially altered by recent major changes in knowledge (Maxwell and Benton 1990; Sepkoski 1993). Second, the stratigraphic order of appearance of fossils matches the order of branching in cladograms (Norell and Novacek 1992). Third, new collecting and systematic revision have filled clastically predicted gaps in the fossil record, leading to a 5% improvement in knowledge over the past 26 years (Benton and Storrs 1994, 1996). Finally, the continental tetrapod fossil record is as complete, at the family level, as is that of (marine) echinoderms (Benton and Simms 1995) and fishes (Benton and Hitchin 1996). The last finding shows that field observations of the relative abundance of specimens in particular localities cannot necessarily predict the overall completeness of knowledge of a group over long spans of geological time: local abundance does not automatically correlate with global diversity.

In this study, the origins of 840 tetrapod families, out of the total of 1,034, were investigated. The remaining 194 families were excluded because they were singletons—that is, families represented by a single species from a single locality. Families represented by multiple species from a single locality and

families represented by a single species from several localities were not treated as singletons. Singletons represent point occurrences and, with present knowledge, cannot seriously be considered as potential competitors with established families.

Before analysis, the 840 tetrapod families in the database were assigned to a number of ecological and geographic groupings, as follows:

1. Body size, defined as snout-vent lengths of < 150 mm (small), 150 mm–1.5 m (medium-sized), or > 1.5 m (large)
2. Diet, defined as carnivory (insect eaters, fish eaters, predators on tetrapods, mollusc eaters, egg eaters), omnivory, or herbivory (browsers, grazers, grain eaters, fruit eaters, nectar drinkers, gnawers)
3. Habitat, defined as predominantly terrestrial, freshwater, marine, arboreal, aerial, or subterranean
4. Geographic zone occupied by the family during its entire history, defined as North America, Central America (and the Caribbean), South America, Europe, Asia, Africa, Australasia, Antarctic, Pacific Islands, Indian Ocean islands, or cosmopolitan (if represented in five or more of the geographic zones)

Data for the category assignments of families were taken from the primary literature, and geographic ranges were largely based on the lists of vertebrate genera in Carroll (1987), supplemented by more recent literature when possible. In cases in which there was no clear evidence for assignment of a poorly known family, it was placed in all possible habitat and ecological categories. In other cases in which a family included taxa of highly variable sizes, or variable ecologies, the family was also assigned to the maximum number of categories possible. Finally, in cases in which the date of origin of a family was uncertain because of poorly known early taxa, the maximum date was selected.

The Census Method

The census method was simply a search for overlaps of family ranges. Such overlaps are designated here as candidate competitive replacements (CCRs), which require further case-by-case investigation in order to establish whether they are correctly interpreted as such. Two guiding principles operated throughout the construction of the database, and its analysis: First, it was necessary to show that postulated competitors shared some major aspect of their modes of life (as a proxy for a more precise demonstration that they shared a limiting resource or a common enemy), and that they could have met each other in at least some part of their ranges (hence evidence for shared geographic distributions was sought). Sepkoski (Chapter 9, this volume) notes that replacement of one group by another in the past can be postulated only if there is evidence for appropriate diversity changes through time, as well as evidence for a shared limiting resource or enemy, and at least some overlap of geographic ranges. Second, I attempted to maximize the potential for discovery of CCRs, chiefly by retaining

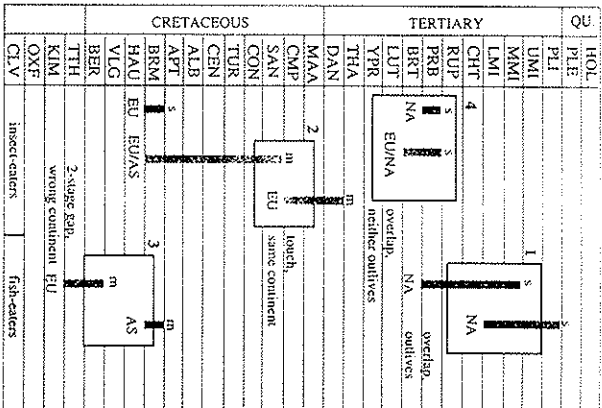


Fig. 8.2. The search window technique used in censusing candidate competitive replacements (CCRs) from the fossil record of tetrapods: CCRs were identified only where there was genuine overlap of two families in terms of broad geographic area occupied, body size, and preferred diet. The best-case CCRs involved temporal overlap, but maximum numbers of CCRs were assessed by relaxing this criterion and allowing for gaps of zero, one, or two stratigraphic stages between the apparent extinction and the apparent origination of supposed competitor families. Case 1 is a clear overlap of two families that share all attributes, and it is thus a CCR. Case 2 might have involved competitive overlap, and may also be a CCR. In case 3, however, members of the two families probably never met, and in case 4 neither family outlived the other, so competitive replacement cannot be considered.

very crude category definitions for habitats, diets, and geographic distributions. In the future, many, or most, of these CCRs may be excluded from consideration after case-by-case studies.

Family ranges were plotted on stratigraphic charts similar to those in *The Fossil Record 2*, and separate charts were plotted for each broad habitat and ecological grouping. The points of origin of each of the 840 families were then inspected in an attempt to determine how many could be regarded as CCRs. The definition of a CCR was based on the assumption that the new family must overlap in geographic range and in ecology with its supposed vanquished competitor family. In addition, the stratigraphic ranges of the two families had to overlap, or at least exist in proximity, allowing for some possible missing fossils.

The search strategy (fig. 8.2) consisted of moving an imaginary viewing win-

dow over the stratigraphic charts and seeking adequate concordance in all dimensions of the data that characterized each family. CCRs were defined as those cases in which (1) both families shared the same habitat, body size, and diet; (2) both families shared at least part of their geographic range; (3) the stratigraphic ranges of both families overlapped; and (4) the "successful" family survived the "unsuccessful" one. The third criterion was relaxed in order to allow for the fact that the oldest members of the replacing family, or the youngest members of the replaced family, might not be known as fossils. Hence, counts of CCRs were made for overlapping stratigraphic ranges and for those separated by a gap of zero, one, and two stratigraphic stages. A two-stage gap between the extinction of one family and the origination of its supposed competitive replacement represents missing fossils during a time span of 5–22 million years (my; mean ca. 12 my), and a one-stage gap represents a missing time span of 2–19 million years (mean ca. 6 my).

Geographic and ecological categories were deliberately made broad in order to maximize the CCR values. Hence, only three size categories were employed, which allows for potential wide size variations among species within a family, and for size changes during growth. Geographic categories were at the level of modern continents, even though at times in the past many of these were not coherent land masses. Hence, assignment of two families to "Asia" means that they may be judged as CCRs, although in reality Siberia, India, and parts of China were long separate, and many contemporaneous "Asian" families never met. This broad view of geography, however, allows the best chance of finding all CCRs, even if most of them are later excluded after close study.

Counts of CCRs are presented as percentages of the total number of origins for all of the span of tetrapod existence (table 8.2). In addition, stage-by-stage data are presented in graphical form (see figs. 8.3–8.10). The measures

TABLE 8.2. Candidate competitive replacements (CCRs) among nonsingleton tetrapod families, listed according to broad habitat type

Habitat	Total		One-stage		Two-stage		Maximum CCRs
	origina- tions	Stages overlap	Stages touch	gap	gap		
Terrestrial	405	77 (19 ± 3.8%)	67 (17 ± 3.7%)	48 (12 ± 3.2%)	37 (9 ± 2.8%)	146 (36 ± 4.7%)	
Freshwater	120	3 (2 ± 2.5%)	4 (3 ± 3.1%)	3 (2 ± 2.5%)	4 (3 ± 3.1%)	13 (11 ± 5.6%)	
Marine	60	9 (15 ± 9.0%)	6 (10 ± 7.6%)	2 (3 ± 4.3%)	2 (3 ± 4.3%)	13 (22 ± 10.5%)	
Subterranean	27	2 (7 ± 9.6%)	2 (7 ± 9.6%)	0	1 (4 ± 7.4%)	3 (11 ± 11.8%)	
Arboreal	32	0	0	0	0	0	
Aerial	196	15 (8 ± 3.8%)	12 (6 ± 3.3%)	12 (6 ± 3.3%)	9 (5 ± 3.1%)	45 (23 ± 5.9%)	
Total	840	106 (13 ± 2.3%)	91 (11 ± 2.1%)	65 (8 ± 1.8%)	53 (6 ± 1.6%)	220 (26 ± 3.0%)	

Note: The criteria for the selection of families in each column are described in the text. The maximum number of CCRs in the last column does not equal the sum of the preceding four columns, since some families fall into more than one of the categories. In each case, the numbers of candidates and their proportions of the total number of origins (in parentheses) are given. 95% confidence limits are calculated according to the approximation formula for errors based on a binomial probability distribution, given by Raup (1991: 213).

(raw data and percentages) are given for stratigraphic overlaps, touching stratigraphic stages, one-stage gaps, and two-stage gaps, and for the sum of these as a measure of maximum CCRs. Family originations were not considered CCRs when pairs of families arose at the same time, or when the "unsuccessful" competitor survived for more than two stratigraphic stages after the minimum date of origin of its supposed "successful" competitor.

Results

The majority of family originations cannot be considered CCRs (see table 8.2, appendix 8.1). The proportion of stratigraphic stage overlaps to total originations ranges from 0% to 19% for different broad habitat types, and the proportion of all CCRs to total originations ranges from 0% to 36%. Values are highest for terrestrial organisms (19%, 36%), perhaps because this habitat category includes the largest number of families (405 of the total of 840), and hence the potential for overlaps is much greater than for habitats occupied by few families.

For terrestrial organisms (fig. 8.3), the numbers of CCRs vary through time, broadly in line with the total number of originations. Numbers of CCRs are low

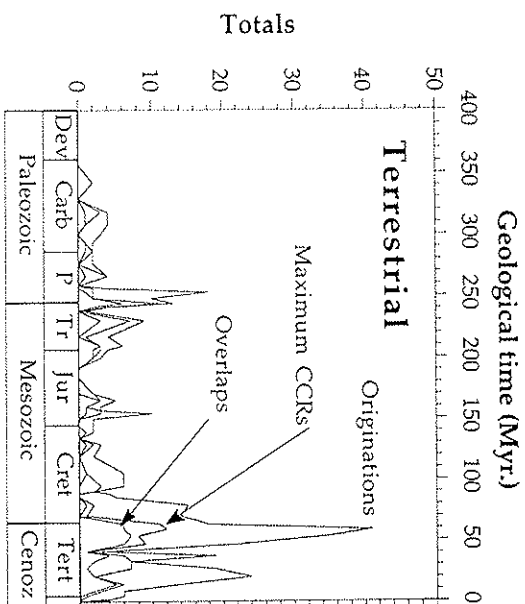


Fig. 8.3. Distribution in time of originations of terrestrial tetrapods, the occurrences of overlaps (strong candidate competitive replacements, or CCRs), and the occurrences of maximum potential CCRs (including temporal gaps of zero, one, and two stages). Abbreviations: Carb, Carboniferous; Cenoz, Cenozoic; Cret, Cretaceous; Dev, Devonian; Jur, Jurassic; P, Permian; Tert, Tertiary; Tr, Triassic.

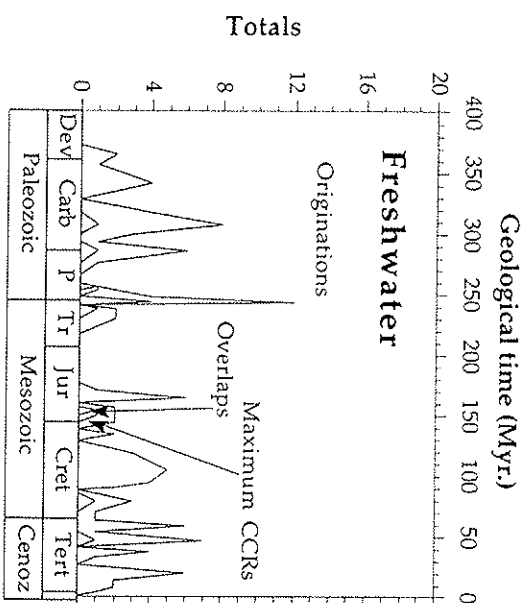


Fig. 8.4. Distribution in time of originations of freshwater tetrapods, the occurrences of overlaps, and the occurrences of maximum potential CCRs. Abbreviations and conventions are as in figure 8.3.

during certain phases of major expansion (e.g., Late Permian, Late Cretaceous), but high during others (i.e., Early to Middle Triassic, Paleogene). In these latter cases, the CCRs include apparent replacements of families that arose early during a radiation event by a second wave of family originations. In both of these cases, the maximum numbers of CCRs are much elevated, probably artificially, because the stratigraphic gaps of zero, one, or two stages encompass major mass extinctions. Families originating in the Paleocene (Danian, Thanetian) or Early Eocene (Ypresian) are unlikely to have arisen by competitive interaction with taxa that died out at the end of the Cretaceous (Maastrichtian), but such families are retained as CCRs by the census method employed here.

Similar patterns were found in the temporal analyses of data on originations of freshwater (fig. 8.4), marine (fig. 8.5), subterranean (fig. 8.6), arboreal (fig. 8.7), and aerial (fig. 8.8) families. Overall, proportions of CCRs are low (see table 8.2), and bursts of CCRs occur only some time after tetrapods have expanded into the habitat in question.

The combined data for all tetrapods (fig. 8.9) show relatively few CCRs in the Paleozoic, despite several bursts of family radiation. During this time, most families were expanding unrestrained into new habitats, new ecological modes, or new geographic areas. Bursts of CCRs in the Early and Middle Triassic and in the Paleogene may include artifacts (families that supposedly might have

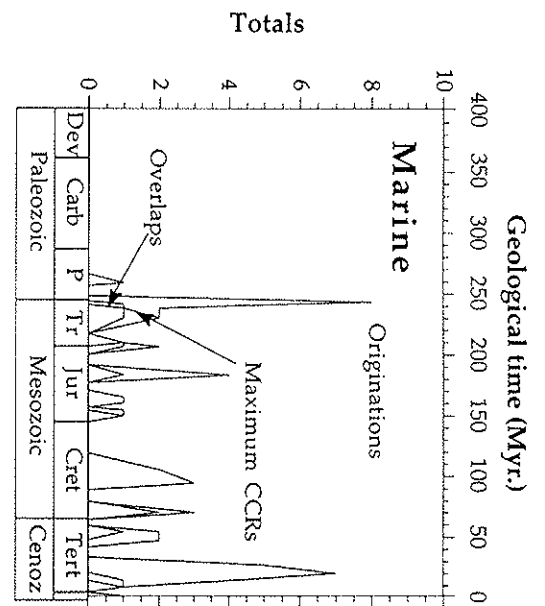


Fig. 8.5. Distribution in time of originations of marine tetrapods, the occurrences of overlaps, and the occurrences of maximum potential CCRs. Abbreviations and conventions are as in figure 8.3.

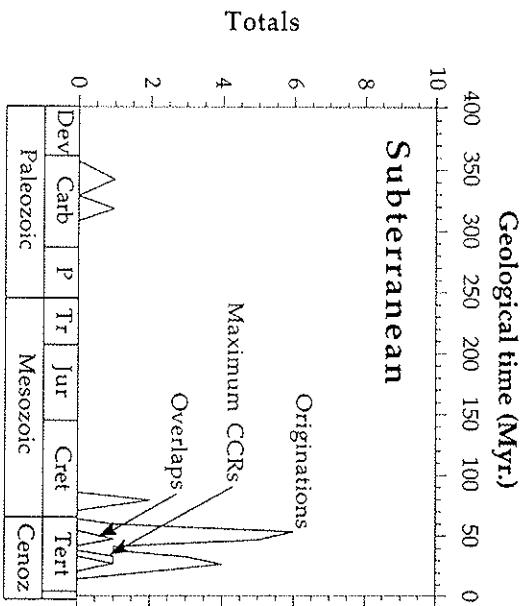


Fig. 8.6. Distribution in time of originations of subterranean tetrapods, the occurrences of overlaps, and the occurrences of maximum potential CCRs. Abbreviations and conventions are as in figure 8.3.

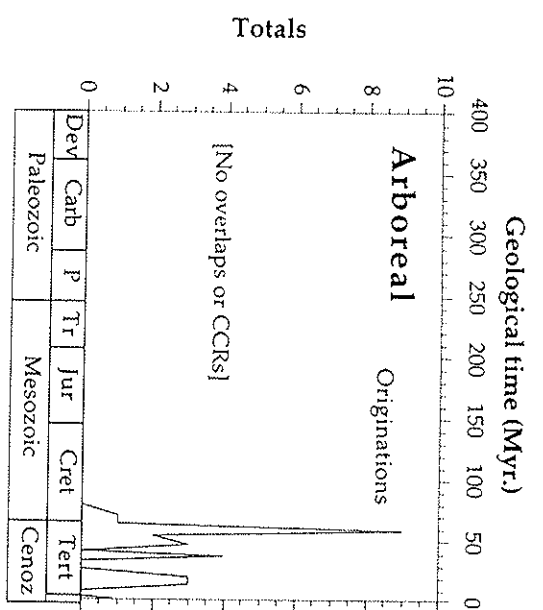


Fig. 8.7. Distribution in time of originations of arboreal tetrapods. There were no overlaps or CCRs in this case. Abbreviations and conventions are as in figure 8.3.

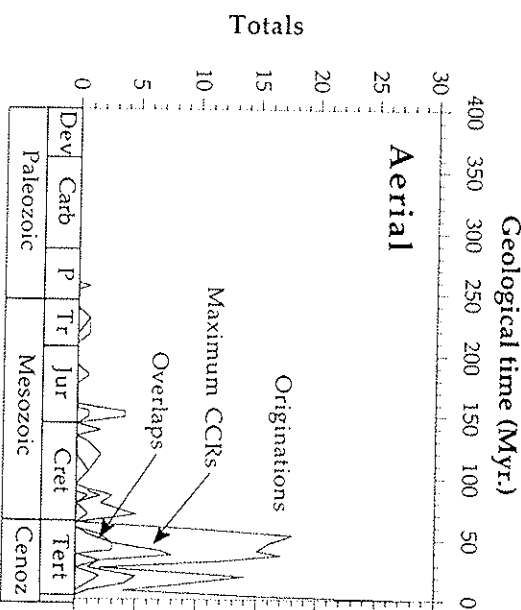


Fig. 8.8. Distribution in time of originations of aerial tetrapods, the occurrences of overlaps, and the occurrences of maximum potential CCRs. Abbreviations and conventions are as in figure 8.3.

competed with families that actually died out at the end of the Permian or at the end of the Cretaceous, respectively). The Paleogene period, however, contains particularly high levels of overlap CCRs, many of which may turn out to be second-wave families truly competitively replacing families that arose during the first wave of radiation in the Late Cretaceous and Paleocene.

The numbers of CCRs, assessed as a proportion of all families originating during each time interval (fig. 8.10), show considerable fluctuations. Relative numbers of overlap CCRs were highest during the latest Triassic and earliest Jurassic, during a time of low family origination rates, so the figures may not be particularly meaningful. Other peaks of relatively high overlap CCRs, in the middle and late Carboniferous, the middle Permian, the Middle Jurassic, and early to middle Cretaceous all similarly represent times of low family origination. The Late Permian to Middle Triassic, Late Jurassic, and Late Cretaceous through Tertiary peaks in proportions of overlap CCRs may, however, be more realistic, since family origination rates were high at those times (9–64 new families per stage; mean ca. 30). The fall in overlap CCRs from Late Miocene times onward (figs. 8.9, 8.10) probably represents in part the “pull of the Recent” (Raup 1978): CCRs can be identified only when the replaced family dies out before the replacing family, and yet most families that originated during, or after, the Late Miocene are still with us.

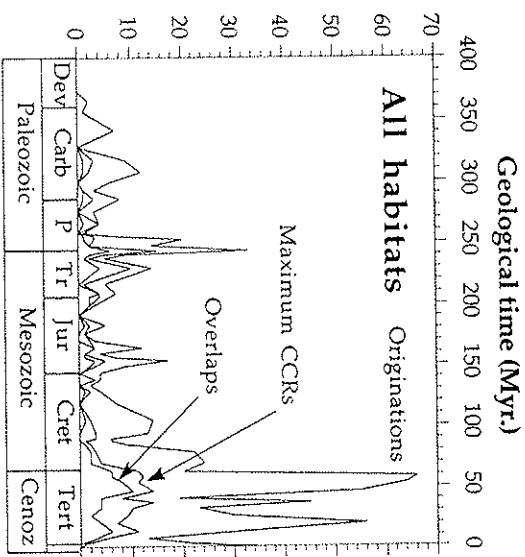


Fig. 8.9. Distribution in time of originations of tetrapods from all habitats, the occurrences of overlaps, and the occurrences of maximum potential CCRs. Abbreviations and conventions are as in figure 8.3.

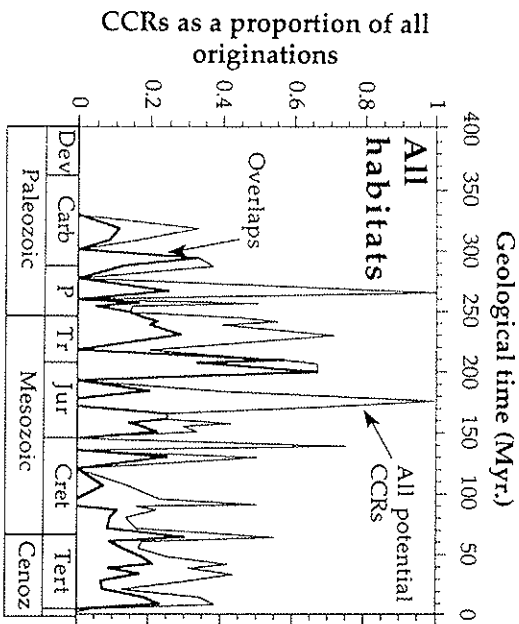


Fig. 8.10. Relative importance of CCRs for tetrapods from all habitats, measured as the ratio of overlaps and of occurrences of maximum potential CCRs to total originations during each stratigraphic stage. Abbreviations and conventions are as in figure 8.3.

Discussion

Refining the List of CCRs

The test carried out here is admittedly very crude. It ignores the possibility of complex interactions involving more than two families, or involving only certain species within particular families. The possible involvement of non-tetrapods in some cases is also ignored. However, the method used here does not assume that competitive replacements can occur only close to the origination of a family. There may be cases in which biotic replacements occurred long after the origination of the replacing family. A CCR is recorded here for such situations provided that the successful family arose at the same time as, or after, the family it replaced, and provided that the successful family outlived the unsuccessful one by at least one stratigraphic stage.

The discovery that 13% (or 26%, at most) of tetrapod family originations could have involved competitive replacement of a preexisting family is the first quantitative indication of the prevalence of competition in macroevolution. It is likely that the figures of 13% and 26% represent maximum values. New discoveries may add further CCRs to those considered here, but new work, on the whole, will tend to diminish these values.

New fossil discoveries may add to the roster of CCRs in the following ways: First, dates of first occurrence of some families may be moved downward, bring-

ing the family origination into overlap with a preexisting family with shared ecological and geographic attributes. Second, dates of extinction of some families may be moved upward, with the same effects. Third, new finds may enlarge the recorded geographic ranges of some families, bringing them into overlap with others. In all three cases, however, the stratigraphic and geographic range expansions will frequently involve rare marginal species, which in reality were not effective competitors.

New work will tend to cut radically into the list of CCRs considered here in the following ways: First, detailed study of the ecological attributes of families will lead to refinement of the categories, and this can only show that many of the CCRs identified here actually involve no overlap. Second, refinement of the rather crude geographic divisions used here will show that many families currently considered CCRs actually never met. Third, reexamination of supposed oldest members of families may indicate that they have been wrongly assigned taxonomically.

The maximum figure of 26% given here for family originations by competitive replacement is likely, then, to be a considerable overestimate, and the lower figure of 13% may be a more realistic estimate of CCRs. When all 106 CCRs (see appendix 8.1) have been inspected closely by experts in the respective groups, it will be interesting to see how many survive the scrutiny and retain some likelihood of being genuine competitive replacements.

Equilibrium or Expansion?

Assumptions of equilibrium are prevalent in many types of modeling in ecology and paleontology. The classic work of MacArthur and Wilson (1967) and MacArthur (1972) laid the foundations for a continuing school of thought in evolutionary ecology in which the relationships between species diversity and area, latitude, habitat numbers, disturbance, productivity, body size, position in the food chain, and so on are explored and modeled; these topics are presented eloquently by Rosenzweig (1995). Such models assume that there are fixed carrying capacities for islands and other patches of territory, and that these species diversity levels will be achieved in time and will be maintained as a dynamic equilibrium. Hence, as Darwin supposed, in normal equilibrium situations, new species can originate or establish themselves only by causing the extinction of a preexisting species. This modeling program has been extended explicitly to large-scale patterns in the diversification of life over geological time, especially by Sepkoski (1984; chapter 9, this volume), who argues for equilibrium diversities of individual clades, of assemblages of clades (the "evolutionary faunas"), and of all life. These fixed diversity levels may be permanent, or they may be reset after the passage of tens or hundreds of millions of years.

My question is: What happens to all this elegant theory if there is no equilibrium cap on species diversity? There is no evidence for equilibria, or for fixed carrying capacities, at the clade level, at the regional level, or on a global scale

(Marshall 1982; Rieppel 1984; Walker and Valentine 1984). There is no reason why the species diversity of an island, or of any other patch of territory, should not go on increasing forever. With enough time, and with normal rates of origination (or immigration) and extinction, new species can surely insinuate—that is, find new things to do—and thereby increase species diversity with almost no limit. Granted, the early stages of species addition and juggling between niches, as a barren island is colonized or during a radiation event into empty ecospace, must involve classic competitive interactions leading to species extinction, character displacement, and the like. Also, obviously, large patches can hold more species than small ones, and the reasons are rooted in species interactions, as Rosenzweig (1995) argues. But why should there be a limit that can never be exceeded?

The Great American Interchange (GAI) is an excellent test case for distinguishing between equilibrium and expansion. The GAI involved the exchange of mammal species between South America and Central and North America 3 million years ago, after the formation of the Isthmus of Panama. Older work suggested that there was a major extinction of South American mammal species when they encountered the North American invaders—a fine example of straight competition at the regional level, in which the equilibrium number of mammalian species in South America was apparently maintained. However, more recent analyses (Marshall et al. 1982) dispose of the equilibrium view once and for all. The North American mammals did invade South America, but equal numbers went the other way, into Central and North America. A great number of South American mammals, such as giant ground sloths, glyptodonts, litopterns, notoungulates, and marsupial carnivores, died out, but this happened 3 million years later, at the end of the Pleistocene, at the same time most of the large North American mammals, such as horses, camels, mastodons, and mammoths, also died out. North American mammals entered South America in large numbers, but they insinuated, and raised total generic diversity from 77 to 120 genera. Almost nothing was directly killed by competitive interactions during the GAI, but total regional diversity increased. Perhaps expansion is the normal circumstance in nature, not equilibrium carrying capacities.

A further telling assertion of equilibrium modelers is that the diversity of life rose rapidly to modern levels—the long-term global equilibrium—and that these levels have been maintained throughout the Phanerozoic at least, if not for most of the time since the origin of life. Rosenzweig (1995) follows Sepkoski (1984) in admitting that global diversity has passed through two or three equilibrium levels, but probably no more. Rosenzweig (1995) admits that there have been times when life invaded major new sets of habitats and thereby increased in overall diversity, but he mentions only a few such occasions: the colonization of muddy sea floors in the Ordovician, the move of plants and animals onto land in the Silurian and Devonian, marine community diversification in the Cretaceous, and the radiation of angiosperms in the Cretaceous. But why stop at those

few? It is not clear that these expansion phases are any different from countless others, such as the invention of tiering among burrowers in scabed sediments, the invention of tiering in the benthic organisms that filter-feed in bottom waters, the invention of trees and tiering of trophic levels on land, flight, endothermy, shell piercing and crunching in marine predators, lignin digestion, large size, internal skeletons, tree climbing, tool use, and many more. Each of these represents the conquest of previously unoccupied ecospace, and each is associated with a jump in total global diversity, without any major depression of diversity in other ecological settings. Why admit to only a small number of such opportunistic leaps in global species diversity when there appear to have been dozens of such events?

All the plots of global diversification through time show evidence for a continuing increase in diversity through time, punctuated by plateaus here and there (interpreted by some as temporary global equilibrium levels, but perhaps indicating nothing at all) and sudden declines at times of mass extinctions. However, the post-Paleozoic portions of all such plots, whether for marine invertebrates, plants, or tetrapods, seem to show continuing rapid rates of diversity increase, with no sign of a levelling off. Rosenzweig (1995) has argued that these plots of diversification patterns are largely meaningless, since they simply show the poor quality of the fossil record and the fact that it becomes worse with time. This criticism presents paleontologists with the fundamental challenge of testing whether the Paleozoic fossil record is strikingly worse than that of the post-Paleozoic. If both halves of the Phanerozoic fossil record are of comparable quality in terms of how well they represent reality, then expansion has dominated competitive replacement, both in terms of numbers of new taxa and in terms of the amount of time involved.

Summary and Conclusions

The role of competition in shaping large-scale biotic patterns has often been assumed, but is difficult to test in the fossil record. In this chapter, tests were carried out on the fossil record of tetrapods (amphibians, reptiles, birds, mammals), both marine and continental, to discover how many family-level origins might potentially relate to biotic interaction between clades. An attempt was made to maximize the number of candidate competitive replacements (CCRs), which required that clades overlap geographically (at the continental scale), temporally (at the scale of the geologic stage), and ecologically (using broad habitat and habit categories). In this survey of 840 nonsingleton families of tetrapods, the maximum prevalence of CCRs was 13% of family origins. The highest value of CCRs (19%) occurred among terrestrial tetrapods, with lower values for freshwater (2%), marine (15%), subterranean (7%), arboreal (0%), and aerial (8%) forms. Thus, competitive replacement was apparently rare in the evolution of tetrapod families, and family origins were most often associated with expansion into new niches.

Acknowledgments

It is a pleasure to present this chapter in honor of Jim Valentine, a founding father of the quantitative paleontological study of macroevolution (Valentine 1968) and a longtime advocate of the role of abiotic factors in controlling clade histories (Valentine 1990). I thank the Leverhulme Trust for continued support of this work, and Anne Blacker for compilation of the habitat and ecological data on tetrapods. I thank Doug Erwin, David Jablonski, and Jere Lipps for inviting a transatlantic person to contribute. I also thank Scott Lidgard, David Jablonski, and an anonymous reviewer for their very helpful comments.

Appendix 8.1

Families of Tetrapods that May Have Radiated by Competitively Replacing a Preexisting Family

This list includes all 106 families that show overlaps of one or two stages duration with a preexisting family. The "successful" family is given first, its "unsuccessful" competitor second. Families are listed in stratigraphic order of origination, and total number of candidate competitive replacements is indicated for each stratigraphic stage. The geographic area in which the overlap occurs is noted: AF, Africa; AS, Asia; EU, Europe; NA, North America; SA, South America.

CARBONIFEROUS

BASHKIRIAN (1): Limnoscelidae vs. Dendrotritonidae (NA)

MOSCOWIAN (1): Dissorophidae vs. Dendrotritonidae (NA/EU)

GZELIAN (1): Pantylidae vs. Tuditanidae (NA)

PERMIAN

ASSELIAN (1): Brachystelechidae vs. Scincosauridae (EU)

ARTINSKIAN (1): Gascidae vs. Edaphosauridae (NA)

URMIAN (1): Leptorophidae vs. Intasuchidae (EU)

KAZANSKIAN (1): Procolophonidae vs. Captorhinidae (NA/EU)

TAVRIAN (2): Proterosuchidae vs. Pithinosuchidae (EU); Kingorriidae vs. Robertiidae/Pristerodontidae/Dicynodontidae/Auliacephalodontidae/Cryprodontidae/Fendohiodontidae (AF)

TRIASSIC

SCYTHIAN (6): Prolaetidae/Tirachodontidae vs. Ictidosuchidae/Scaloposauridae/Galesauridae (AF); Cenosauriscidae vs. Eochambersiidae (EU); Euparkeriidae/Cynognathidae vs. Eochambersiidae (AF); Bauriidae vs. Emydopidae (AF)

ANISIAN (3): Rautiusuchidae vs. Erythrosuchidae (AF); Poposauridae vs. Euparkeriidae/Ctenosauriscidae/Protosuchidae (AF/EU); Placochelyidae vs. Placodontidae (EU)

LADINIAN (1): Simosauridae vs. Pachypleurosauridae (EU/NA)

CARNIAN (4): Stagonolepididae vs. Rhynchosauridae (NA/EU/SA); Trilophosauridae vs. Rhynchosauridae (NA); Podokesauridae vs. Poposauridae (NA); Shonisauridae vs. Shastasauridae (EU/NA)

RHAETIAN (4): Tritylodontidae vs. Traversodontidae (SA); Protosuchidae vs. Sphenosuchidae (AF); Megalosauridae vs. Podokesauridae/Sphenosuchidae/Rausisuchidae (EU); Leptopterygiidae vs. Shonisauridae (EU/NA)

JURASSIC

HETTANGIAN (2): Vulcanodontidae/Massospondylidae vs. Melanorosauridae (AF)
SINEMURIAN (2): Ceratosauridae vs. Podokesauridae (NA); Amphilestidae vs. Simondontidae (AS)

TOARGIAN (1): Elasmosauridae vs. Plesiosauridae (EU)
BATHONIAN (3): Stegosauridae vs. Huayangosauridae (AS); Dryolestidae/Peramuridae vs. Morganucodontidae (EU)

CALLOVIAN (1): Nodosauridae vs. Scelidosauridae (EU)/Huayangosauridae (AS)
OXFORDIAN (1): Camarasauridae vs. Cetiosauridae (NA/AS)

KIMMERIDGIAN (3): Titanosauridae vs. Cetiosauridae (SA); Pleurosternidae vs. Platycheilyidae (EU); *Dermodactylus* vs. Rhamphorhynchidae/Pterodactylidae (NA)

TITHONIAN (2): Aigialosauridae vs. Ichthyosauridae (EU); Azhdarichidae vs. Rhamphorhynchidae/Pterodactylidae (EU)

CRETACEOUS

BARREMIAN (1): Pachycephalosauridae vs. Dryosauridae/Carnptosauridae (EU/AS)

ALBIAN (1): Abelisauridae vs. Megalosauridae/Allosauridae/Baryonychidae (SA)

SANTONIAN (1): Bapornithidae vs. Ichthyornithidae (NA)

CAMPANIAN (2): Pedionymidae vs. Spalacotheriidae (NA); Alligatoridae vs. Goniopholididae (NA)

MAASTRICHTIAN (2): Chelonitidae/Osteopygidae vs. Desmatocheilyidae/Protostegidae (NA)

TERTIARY

DANIAN (6): Bemalambidae/Harpodidae/Pastoralodontidae vs. Wangliidae (AS); Nyctitheriidae/Microptermodontidae/Anagalidae vs. Gypsonictopidae (NA)

THANETIAN (6): Baryambidae/Stylinodontidae vs. Miclaenidae/Hypodontidae (NA); Panlambodontidae vs. Bemalambidae/Harpodidae/Pastoralodontidae (AS); Polydolopidae vs. Sudamericidae/Carloameghinidae (SA); Oxyaenidae/Pristichampsidea vs. Taeniolabidae/Arctocyoniidae/Peripychidae/Mesonychia (NA)

YPRESIAN (8): Cylindrodontidae vs. Eucosmodontidae (AS); Myoxidae vs. Cimolodontidae/Cimolomyidae (EU); Eurygomidae vs. Pitlodontidae/Cimolodontidae/Cimolomyidae (NA); Homacodontidae vs. Stylinodontidae (NA); Bromotheriidae vs. Umatheriidae (NA); Pellephnidae vs. Caroloameghinidae (SA); Plesiosoricidae vs. Palaeorycidae (NA/AS); Diatrymidae vs. Gastornithidae (NA)

LUETETIAN (10): Agrochoeridae/Leptomerycidae/Oromerycidae/Protocezaridae vs. Stylinodontidae (NA); Soricidae vs. Palaeorycidae (NA); Nimravidae vs. Oxyaenidae

(EU/NA); Dipodidae vs. Coomyidae (NA); Aegialornithidae vs. Sandcolifidae (NA); Emballonuridae/Rhinolophidae vs. Icaronycteridae/Palaeochoiropterygiidae (EU/NA)

BARTONIAN (4): Anoplotheriidae vs. Lophodontidae (EU); Vespertilionidae vs. Palaeochoiropterygiidae (EU); Ardeidae/Halcyonidae vs. Sylphornithidae (EU)

PRIVABONIAN (4): Cainotheriidae/Geocidae/Hyperragulidae vs. Amphimerycidae (EU)/Cabochoeridae (EU)/Mixitheriidae (EU)/Homacodontidae (NA)/Oromerycidae (NA); Mesotheriidae vs. Olfideltomasiidae (SA)

RUPPELLIAN (4): Moschidae vs. Dichobunidae/Diacodexidae (AS/EU); Tapiridae vs. Palaeoheriidae/Lepertellidae/Helalidae (EU/AS); Sagitariidae vs. Hornsornithidae (EU); Trogonidae vs. Archaeotrogonidae/Jugonithidae (EU)

CHATTIAN (2): Cervidae vs. Anoplotheriidae/Dacrytheriidae/Diacodexidae/Dichobunidae (EU/AS); Distyliomyidae vs. Chapattimyidae (AS)

LOWER MIOCENE (4): Antilocapridae/Dromomerycidae vs. Hyperragulidae/Leptomerycidae/Agrochoeridae (NA); Cracidae vs. Gallinuloididae (NA); Columbigidae vs. Gallinuloididae/Quercymegapodidae (EU)

MIDDLE MIOCENE (6): Vombatidae vs. Wynyardiidae (AU); Caviidae/Hydrochoeridae/Chinchillidae/Capromyidae vs. Eocardiidae (SA); Phaeothontidae vs. Plotopieridae (NA)

UPPER MIOCENE (3): Abrocomidae vs. Neophiblemidae/Eocardiidae (SA); Elephantidae vs. Amebelodontidae (NA/EU/AF); Phocoenidae vs. Kentriodontidae (NA)

References

- Arthur, W. 1980. The evolutionary consequences of interspecific competition. *Advances in Ecological Research* 12: 127–87.
- Benton, M. J. 1983a. Dinosaur success in the Triassic: A noncompetitive ecological model. *Quarterly Review of Biology* 58: 29–55.
- _____. 1983b. Large-scale replacements in the history of life. *Nature* 302: 16–17.
- _____. 1987. Progress and competition in macroevolution. *Biological Reviews* 62: 305–38.
- _____. 1990. The diversification of life. In *Major evolutionary radiations*, ed. P. D. Taylor and G. Larwood, 409–30. Systematics Association Special Volume 42. Oxford: Clarendon Press.
- _____. 1991. Extinction, biotic replacements, and clade interactions. In *The unity of evolutionary biology*, ed. E. C. Dudley, 89–102. Portland, Oregon: Dioscorides Press.
- _____. ed. 1993a. *The fossil record 2*. London: Chapman and Hall.
- _____. 1993b. Reptilia. In *The fossil record 2*, ed. M. J. Benton, 681–715. London: Chapman and Hall.
- _____. 1995. Diversity and extinction in the history of life. *Science* 268: 52–58.

- Benton, M. J., and R. Hitchin. 1996. Testing the quality of the fossil record by groups and by major habitats. *Historical Biology*. In press.
- Benton, M. J., and M. J. Simms. 1995. Testing the marine and continental fossil records. *Geology* 23:601-4.
- Benton, M. J., and G. W. Storrs. 1992. Replacement events among tetrapods: Expansion or competition? In *Fifth North American Paleontological Convention, abstracts and program*, ed. S. Lidgard and P. R. Crane, 25. Paleontological Society Special Publication no. 6. Knoxville, Tenn.: The Paleontological Society.
- _____. 1994. Testing the quality of the fossil record: Paleontological knowledge is improving. *Geology* 22:111-14.
- _____. 1996. Diversity in the past: Comparing cladistic phylogenies and stratigraphy. In *Aspects of the genesis and maintenance of biological diversity*, ed. M. E. Hochberg, J. Clobert, and R. Barbault, 19-40. Oxford: Clarendon Press.
- Bonaparte, J. F. 1982. Faunal replacement in the Triassic of South America. *Journal of Vertebrate Paleontology* 21:362-71.
- Boucot, A. J. 1975. *Evolution and extinction rate controls*. Amsterdam: Elsevier.
- Branch, G. M. 1984. Competition between marine organisms: Ecological and evolutionary implications. *Oceanography and Marine Biology Annual Review* 22:429-593.
- Carroll, R. L. 1987. *Vertebrate paleontology and evolution*. San Francisco: W. H. Freeman.
- Connell, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35:131-38.
- _____. 1983. On the prevalence and relative importance of interspecific competition: Evidence from field experiments. *American Naturalist* 122:661-96.
- Curtillot, V., and Gaudemer, Y. 1996. Effects of mass extinctions on biodiversity. *Nature* 381:146-48.
- Darwin, C. 1859. *On the origin of species by means of natural selection*. London: John Murray.
- DiMichele, W. A., T. L. Phillips, and R. G. Olmstead. 1987. Opportunistic evolution: Abiotic environmental stress and the fossil record of plants. *Review of Paleobotany and Palynology* 50:151-78.
- Dobzhansky, T., F. J. Ayala, G. L. Stebbins, and J. W. Valentine. 1977. *Evolution*. San Francisco: W. H. Freeman.
- Donovan, S. K., and A. S. Gale. 1990. Predatory asteroids and the decline of the articulate brachiopods. *Lethaia* 23:77-86.
- Gould, S. J., and C. B. Calloway. 1980. Clams and brachiopods: Ships that pass in the night. *Paleobiology* 6:383-96.
- Jablonski, D. 1986. Background and mass extinctions: The alternation of macroevolutionary regimes. *Science* 231:129-33.
- Jackson, J. B. C. 1988. Does ecology matter? *Paleobiology* 14:307-12.
- Jackson, J. B. C., and F. K. McKinney. 1990. Ecological processes and progressive macroevolution of marine clonal benthos. In *Causes of evolution: A paleontological perspective*, ed. R. M. Ross and W. D. Allmon, 173-209. Chicago: University of Chicago Press.
- Krause, D. W. 1986. Competitive exclusion and taxonomic replacement in the fossil record: The case of rodents and multituberculates in North America. In *Vertebrates: phylogeny and philosophy*, ed. K. M. Flanagan and J. A. Lillegraven, 95-117. Contributions to Geology Special Publication no. 3. Laramie: University of Wyoming.
- Lidgard, S., F. K. McKinney, and P. D. Taylor. 1993. Competition, clade replacement, and a history of cyclostome and cheilosstome bryozoan diversity. *Paleobiology* 19:352-71.
- MacArthur, R. H. 1972. *Geographical ecology*. New York: Harper & Row.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton, N.J.: Princeton University Press.
- Marshall, L. G., S. D. Webb, J. J. Sepkoski, Jr., and D. M. Raup. 1982. Mammalian evolution and the Great American Interchange. *Science* 215:1351-57.
- Maxwell, W. D., and M. J. Benton. 1990. Historical tests of the absolute completeness of the fossil record of tetrapods. *Paleobiology* 16:322-35.
- Maynard Smith, J. 1983. Current controversies in evolutionary biology. In *Dimensions of Darwinism*, ed. M. Grene, 273-86. Cambridge: Cambridge University Press.
- Miller, A. I., and J. J. Sepkoski, Jr. 1988. Modeling bivalve diversification: The effect of interaction on a macroevolutionary system. *Paleobiology* 14:364-69.
- Milner, A. R. 1993. Amphibian-grade Tetrapoda. In *The fossil record 2*, ed. M. J. Benton, 665-79. London: Chapman and Hall.
- Norell, M. A., and M. J. Novacek. 1992. The fossil record and evolution: Comparing cladistic and paleontologic evidence for vertebrate history. *Science* 255:1690-93.
- Raup, D. M. 1978. Cohort analysis of generic survivorship. *Paleobiology* 4:1-15.
- _____. 1991. The future of analytical paleobiology. In *Analytical paleobiology*, ed. N. L. Gilinsky and P. W. Signor, 207-16. Short Courses in Paleontology no. 4. Knoxville, Tenn.: The Paleontological Society.
- Rieppel, O. 1984. The problem of extinction. *Zeitschrift für zoologische Systematik und Evolutionsforschung* 22:81-85.
- Rosenzweig, M. L. 1995. *Species diversity in space and time*. Cambridge: Cambridge University Press.
- Rosenzweig, M. L., and R. D. McCord. 1991. Incumbent replacement: Evidence for long-term evolutionary progress. *Paleobiology* 17:202-13.
- Ryland, J. S. 1970. *Bryozoans*. London: Hutchinson.

- Schoener, T. W. 1983. Field experiments on interspecific competition. *American Naturalist* 122:240–85.
- Sepkoski, J. J. Jr. 1984. A kinetic model of Phanerozoic taxonomic diversity. III. Post-Paleozoic families and mass extinctions. *Paleobiology* 10:246–67.
- . 1993. Ten years in the library: How changes in taxonomic data bases affect perception of macroevolutionary pattern. *Paleobiology* 19:43–51.
- Simpson, G. G. 1953. *The major features of evolution*. New York: Columbia University Press.
- Stanley, S. M. 1979. *Macroevolution*. San Francisco: W. H. Freeman.
- Stebbins, G. L. 1974. Adaptive shifts and evolutionary novelty: A compositionist approach. In *Studies in the philosophy of biology*, ed. F. J. Ayala and T. Dobzhansky, 285–306. Berkeley: University of California Press.
- Strong, D. R. Jr., D. Simberloff, L. G. Abele, and A. B. Thistle. 1984. *Ecological communities: Conceptual issues and the evidence*. Princeton, N.J.: Princeton University Press.
- Stucky, R. K., and M. C. McKenna. 1993. Mammalia. In *The fossil record 2*, ed. M. J. Benton, 739–71. London: Chapman and Hall.
- Unwin, D. M. 1988. Extinction and survival in birds. In *Extinction and survival in the fossil record*, ed. G. P. Larwood, 295–318. Oxford: Clarendon Press.
- . 1993. Aves. In *The fossil record 2*, ed. M. J. Benton, 717–37. London: Chapman and Hall.
- Valentine, J. W. 1968. The evolution of ecological units above the population level. *Palaeontology* 42:253–67.
- . 1990. The macroevolution of clade shape. In *Causes of evolution: A paleontological perspective*, ed. R. M. Ross and W. D. Allmon, 128–50. Chicago: University of Chicago Press.
- Van Valen, L. M. 1973. A new evolutionary law. *Evolutionary Theory* 1:1–30.
- Verniej, G. J. 1987. *Evolution and escalation*. Princeton, N.J.: Princeton University Press.
- . 1994. Selection, escalation, and coevolution. *Annual Review of Ecology and Systematics* 25:219–36.
- Walker, T. D., and J. W. Valentine. 1984. Equilibrium models of evolutionary species diversity and the number of empty niches. *American Naturalist* 124:887–99.
- Weiner, J. 1995. Evolution made visible. *Science* 267:30–33.