PATTERNS OF EVOLUTION AMONG THE ARTIODACTYLA AND PERISSODACTYLA (MAMMALIA)

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Diversity changes through time of the mammalian ungulate orders Artiodactyla and Perissodactyla have been touted long and widely as exemplifying ordinal level taxonomic (and presumably ecologic) displacement (Simpson, 1953; Stanley, 1974) since, as Van Valen (1971) has pointed out, they have a nearly identical "way of life" (=adaptive zone, Simpson, 1953; plus competitive interactions, Van Valen, 1971). The controversial assumption that herbivores are food limited (cf. Hairston et al., 1960; Murdoch, 1966; Ehrlich and Birch, 1967; Slobodkin et al., 1967) is implicit to this generalization. Both orders presumably appeared in the late Paleocene, as they are well differentiated by the early Eocene (Figs. 1 and 2). While perissodactyls seem to have undergone taxonomic diversification at both generic and familial levels somewhat earlier than artiodactyls, the difference is much less than most authors suggest. Perissodactyls declined in importance after the middle Eocene, while the artiodactyls maintained a stable "dominance" from the early Oligocene until their apparently enormous Plio-Pleistocene radiation. Various deterministic hypotheses have been forwarded in explanation of this pattern. Such hypotheses usually invoke the acquisition of one or more characters (double trochleated astragalus, selenodont molars, ruminant digestion) by the artiodactyls as giving that group a relative adaptive advantage. Here I review the evolutionary histories of these two orders in search of evidence supporting these hypotheses. Further, I analyze overall patterns to detect possible correspondence to or support for the various "empirical" (Valentine, 1973) and "equilibrium" (Mark and Flessa, 1977) models of Phanerozoic diversity. All data

have been compiled from Romer (1966). Current revisions might alter the data somewhat, but it is doubtful that the differences would be systematic or great. Question-marked taxa or those not designated chronostratigraphically to subepoch were ignored. The time scale used is from Harland et al. (1964).

DOMINANCE AND DISPLACEMENT

Competitive interactions leading to the relative dominance of the artiodactyls are expected to be reflected in changes of diversity and turnover rates through time. Generic and familial diversity of the two orders are shown in Figures 1 and 2. Here, as elsewhere, I have systematically overestimated chronologic ranges for genera—and therefore calculated standing diversity at any given point in time—by considering originations to have occurred at the beginning of the subepoch of first appearance and extinctions at the end of the subepoch of last known occurrence. Although it would be desirable to conduct the analysis at the species level, the fossil record is inadequate to the task, and genera are used. While sampling of families is doubtless better than of genera, the latter are more appropriate in the present context, since they reflect more accurately events which ultimately must occur at the species level. Whereas biases in the fossil record (preservation, relative exposures of fossiliferous strata, "monographic" effects; Raup, 1972) hamper comparison through time, I assume that relative diversities of the two orders at any given point in time are unaffected by such biases. The possibility of differences in geographic distribution is discussed below.

The adaptive advantage conferred by the acquisition of a double trochleated as-
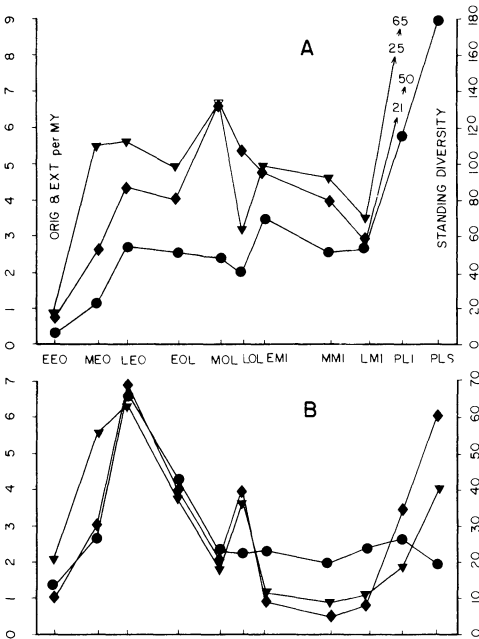
FIG. 1. Generic diversity (dots) and rates of origination (triangles) and extinction (diamonds) of perissodactyls (A) and artiodactyls (B). Abbreviations: EEO; early Eocene, MEO; middle Eocene, LEO; late Eocene, EOL; early Oligocene, MOL; middle Oligocene, LOL; late Oligocene, EMI; early miocene, MMI; middle Miocene, LMI; late Miocene, PLI; Pliocene, PLS; Pleistocene.
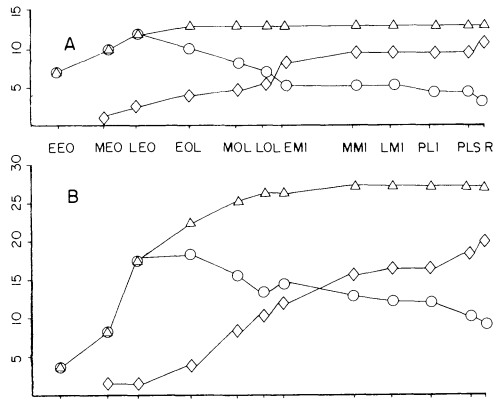

FIG. 2. Familial diversity (circles), originations (triangles), and extinctions (diamonds) of perissodactyls (A) and artiodactyls (B). Originations and extinctions are cumulative. R; Recent; other abbreviations as in Fig. 1.

tragalus (Schaeffer, 1947) cannot be evaluated in the present context, since it appears as a basic ordinal character of the earliest (basal Eocene) artiodactyls. There is no discernible change in pattern during the late Eocene, when the highly efficient selenodont dentitions arose, although this might have been expected to have stimulated an artiodactyl radiation. The increase in artiodactyl diversity in the early Miocene corresponds roughly to the evolution of the fully ruminating stomach (as projected by Janis, 1976), which is hypothesized to have conferred great adaptive advantage ("eat and run") upon its bearers (see, for instance, Young, 1962). However, the Miocene artiodactyl radiation is comprised in large part by the non-ruminating Merycoidodontidae (Janis, 1976; see Table 1). Here, the problem of differences in relative duration of subep-

ochs (Raup, 1972) must be confronted: while vertical corrections to absolute time have been made in the figures, relative diversity is biased. This is because, all other conditions being equal, a long interval is expected to show greater diversity than a short one. In the present case, high diversity in the early Miocene (duration = 9 million years) follows low diversity in the late Oligocene (duration = 3 million years). Estimates of standing diversity may be made by subtracting cumulative extinctions from cumulative originations at any given point in time. Figure 3 shows that the late Oligocene constriction and the early Miocene expansion are real, although the magnitude of difference is not great. This is further supported by changes in familial diversity (Fig. 2b).

The great Plio-Pleistocene artiodactyl radiation (comprised mainly of bovids and cervids; Table 1) apparently had no noticeable effect on perissodactyl diversity, which seems to have increased over this time period (although this may be a sampling bias, as the Plio-Pleistocene mammal record is particularly good).

If, as Newell (1952) suggests for Mesozoic nautiloid-ammonoid diversities, competitive advantage of one group is indicated by its diversification occurring concomitantly with the decline of its com-

TABLE 1. *Generic diversity of perissodactyl and artiodactyl families by subepoch, early Eocene to Pleistocene. Abbreviations: E; early, M; middle, L; late.*

	Eocene			Oligocene			Miocene			Plio.	Pleis.
	E	M	L	E	M	L	E	M	L		
A. Perissodactyl families											
Equidae	3	5	5	3	2	1	4	5	6	8	6
Palaeotheriidae		1	2	2							
Brontotheriidae	3	7	22	13	3	1					
Eomoropidae	1	1	4								
Chalicotheriidae			1	2	1	3	4	3	2	5	4
Isectolophidae	1	1	1	1							
Helaletidae	2	6	4	1	1	1					
Lophialetidae		1	2								
Deperetellidae		1	2	1							
Lophiodontidae	3	2	2								
Tapiridae				1	1	2	4	2	2	2	1
Hyracodontidae		2	4	3	1	1	1				
Amynodontidae			7	3	2	1	1				
Rhinocerotidae		1	10	13	10	14	7	9	10	13	7
B. Artiodactyl families											
Diacodectidae	3										
Leptochoeridae				1	1	1					
Homacodontidae	1	3	4								
Dichobunidae	1	9	4	3	1						
Achaenodontidae		1	2								
Choeropotamidae			3	2	1						
Cebochoeridae		2	2	2							
Entelodontidae			2	3	3	1	1				
Suidae			1	1	1	2	6	6	7	12	12
Tayassuidae				1	2	1	3	2	4	5	6
Anthracotheriidae		4	9	6	7	8	9	5	5	7	1
Hippopotamidae										1	2
Cainotheriidae			2	2	3	2	1	1			
Anoplotheriidae		3	6	3	2						
Xiphodontidae		2	3	2							
Amphimerycidae		1	2	2							
Agriochoeridae			1	1	1	1	1				
Merycoidodontidae				7	9	8	15	7	3	2	
Oromerycidae		2	1								
Camelidae			1		2	3	5	3	3	12	12
Hypertragulidae			5	4	5	3	5				
Protoceratidae				2	1	1	2	1	1	2	
Gelocidae			3	4	3	1					
Tragulidae								1	1	3	3
Palaeomerycidae				1	1	3	10	10	7	5	1
Cervidae							3	5	5	24	33
Giraffidae							3		5	15	5
Antilocapridae								1	2	9	6
Bovidae					1		3	6	8	67	105

petitor(s), the record of odd- and even-toed ungulates gives no such indications; nor is there any apparent negative correlation between generic diversities of the two orders as would be predicted (Fig. 4). An analysis by zoogeographic province might be more meaningful, but here, again, the evidence is not supportive of displace-ment (Fig. 5). Although increase in artiodactyl diversity corresponds roughly to perissodactyl decline in North America, "clades" on all other continents resemble those of the combined data; in fact, periods of increased diversity of artiodactyls and perissodactyls seem to coincide, suggesting that both are either dependent on
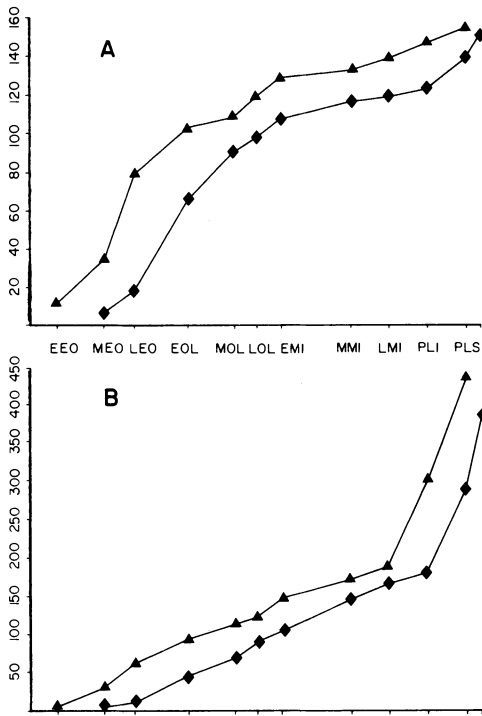
FIG. 3. Cumulative generic originations (triangles) and extinctions (diamonds) of perissodactyls (A) and artiodactyls (B). Abbreviations as in Fig. 1.

FIG. 4. Correlation of perissodactyl and artiodactyl generic diversities.

some outside factor, such as climate, or are the subjects of some systematic bias(es) which has (have) not been recognized. Africa appears to have been depauperate
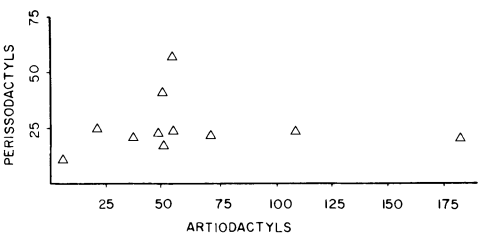
during the middle and early late Tertiary, but this is probably due to an inadequate fossil record.

Changes in turnover rates, which may not be indicated by generalized diversity trends, must also be considered. If selective advantage of one group causes an increase in turnover rates of a competitor, an increase in perissodactyl extinction rate should accompany an artiodactyl radiation. Taxonomic survivorship curves, which indicate extinction rates, have been plotted for six perissodactyl cohorts (Fig. 6; vertical scale is log percent of surviving genera per lineage million years). The cohorts are those genera originating in the early, middle, and late Eocene; early and middle/late Oligocene; and the Miocene, respectively. Subepochs of the Oligocene and Miocene were pooled so as to improve sampling. Increase in rate of extinction,
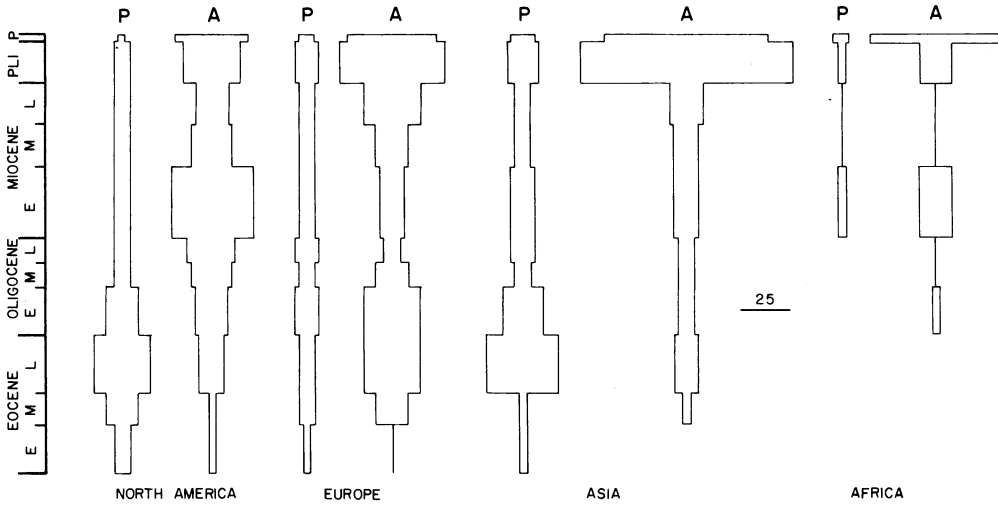

FIG. 5. Distribution of generic diversities by continent, exclusive of South America. Abbreviations: P; Perissodactyla, A; Artiodactyla.
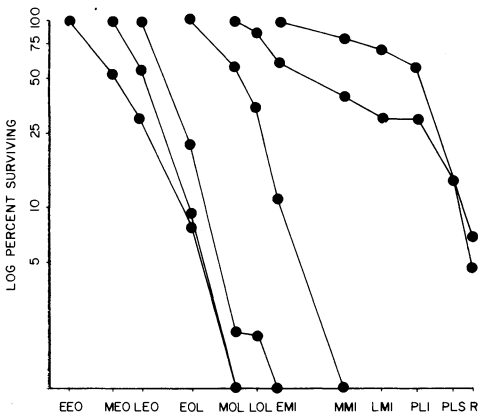
FIG. 6.   Taxonomic survivorship of six perissodactyl generic cohorts. Abbreviations as in Fig. 1.

FIG. 7.   Correlation of origination and extinction rates of odd- and even-toed ungulates.

represented by a sharp drop in the curve, should affect overlapping cohorts coincidentally, since extrinsic extinction causes affect genera without respect to their age. No such trends are evident in these data. Cohort survivorship appears to increase in the later cohorts, undoubtedly due to the fact that the two youngest cohorts represent pooled samples.

Van Valen (1973) has calculated perissodactyl origination and extinction rates. He found extinction rates to be approximately equal through time, and therefore concluded that observed perissodactyl diversity patterns resulted from differences in origination rates. Diversity and generic origination/extinction rates for perissodactyls and artiodactyls are plotted in Figure 1. Little correspondence between artiodactyl diversity and perissodactyl origination/extinction rates, or between perissodactyl diversity and artiodactyl origination/extinction rates, is evident (see below).

PATTERNS OF TAXONOMIC DIVERSITY

Various models have been proposed to account for Phanerozoic diversity patterns, and may be broadly categorized as "continuous diversification" (Valentine, 1969, 1973) or "equilibrium" (Mark and Flessa, 1977) approaches. The former, which is more nearly empirical and which perhaps has historical priority, predicts an early diversification of higher taxa. Major
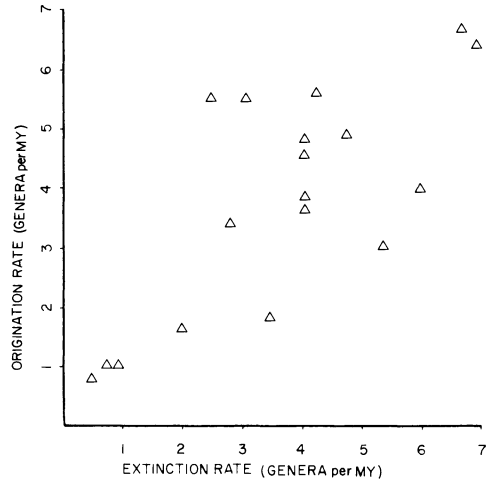
adaptive zones, to which higher taxa generally correspond, are filled early and originations taper off as the amount of change necessary to produce a new taxon becomes increasingly difficult to attain (Valentine, 1969). At lower levels, however, diversification continues through progressive partitioning of ecological niches into smaller functional units: average niche size of species decreases as specialization increases. Extrinsic environmental factors (i.e., abiotic or diversity independent) produce periodic extinctions, opening up previously occupied niches (Newell, 1952; Valentine, 1969).

Diversity and originations/extinctions are depicted for genera and families in Figures 1 and 2, respectively. While perissodactyl families follow the predicted pattern (all originated by the late Eocene), genera do not become increasingly abundant. Generic diversity closely mirrors that of families through time. The patterns afforded by artiodactyl diversity appear to support the continuous diversification hypothesis more cogently. The Plio-Pleistocene radiation, which constitutes the "trend" for genera, is largely the result of expansion of two families, the Bovidae and Cervidae. These families originated in the late Oligocene and early Miocene, respectively, and therefore may represent the invasion of new adaptive zones rather

than increased canalization of previously occupied niches. Except for the fact that rates of speciation must exceed those of extinction, the continuous diversification hypothesis further proposes that any correspondence between the two rates is fortuitous. Flessa and Levinton, who argue for unbounded diversity, present a graph (Flessa and Levinton, 1975, Fig. 3) which shows no correlation between origination and extinction rates of Phanerozoic marine taxa (but see Mark and Flessa, 1977). Flessa and Levinton's pooling of ecologically disparate taxa may not be justifiable. My Figure 7 indicates a relationship between the two rates for artiodactyls and perissodactyls. The evidence, therefore, does not lend credence to the continuous diversification hypothesis. The effects of such biases as the "taxonomic hindsight" effect (Raup et al., 1973)—the inability of taxonomists to recognize "incipient" taxa (particularly at higher taxonomic levels)— and the relatively better representation of lower taxa as the Recent is approached (Raup, 1972) are unknown.

Newell (1952) proposed that periodicity in invertebrate evolution resulted from rapid evolution (=increased speciation or rate of origination) into niches vacated by previous extinctions. Diversity eventually reaches a stabilization point, which is followed by a more or less abrupt extinction event (environmentally controlled) which opens niches and therefore paves the way to another diversification peak. Implied, therefore, is an alternation of periods of increased originations and extinctions. This is not evident in Figure 1, which suggests that the situation is somewhat more complex. Increased rates of extinction (in genera per million years) accompany increased originations and diversity, and similarly decrease with them as well; they do not alternate. Diversity trends, as Webb (1969) has pointed out, may result from "original pull," "extinction push," or (most likely) an interaction between the two rates.

The equilibrium model, an extension of insular biogeographic theory (MacArthur and Wilson, 1963; see also Simberloff,

1972) to the fossil record and an evolutionary scale, assumes that diversity in any given adaptive zone or zoogeographic area rises until a saturation point is reached, after which it will fluctuate about some stable mean. Implied is that origination and extinction rates are diversity dependent and will be approximately equal at equilibrium, which corresponds to environmental carrying capacity. Mark and Flessa (1977) present somewhat equivocal data supporting evolutionary equilibria in brachiopods and mammals. As Figure 1 shows, origination and extinction rates of artiodactyls and perissodactyls parallel each other rather closely with, however, some important divergences. Originations markedly outstrip extinctions through most of the Eocene for both artiodactyls and perissodactyls. This may represent the rise to an equilibrium level of diversity. Although numerous archaic subungulate types were present in the early Tertiary, the Eocene radiation of artiodactyls and perissodactyls represents the first important diversification of large, specialized herbivorous mammals. The equilibrium model predicts such a pattern of diversification: initially high diversification rates should decrease and stabilize as the limiting boundary (environmental carrying capacity) is reached. In this case, this effect may be partially an artifact of method, since originations were plotted at the beginning of each subepoch and extinctions at the end. The rates for the early Eocene were therefore omitted from the correlation plotted in Figure 7, which shows a fairly close relationship between origination and extinction rates. The rates diverge rather drastically in the Plio-Pleistocene. Perhaps this is in part due to the proximity of the Recent, yet the relationships are not the same for both orders (originations exceed extinctions for artiodactyls, while the reverse is true of perissodactyls). The equilibrium hypothesis predicts not only a close correspondence of turnover rates during periods of stability, but also that these vary with diversity. This is broadly true (Fig. 6), but turnover peaks in the

middle Oligocene for artiodactyls and late Oligocene for perissodactyls are not reflected in diversity trends; moreover, these peaks correspond to decreases in diversity of the other order, the opposite of what would be expected given the assumption of nearly identical adaptive zones. Webb (1969) suggests that the pattern of evolution for North American Plio-Pleistocene mammals represents diversity dependent equilibrium shifts, and it is possible that the noise in this system is due to a similar shifting of equilibria throughout Cenozoic time. Such equilibrium shifts, in turn, may be related to long term climatic change and consequent change in the extent of open country "savanna" habitats (see review by Webb, 1977).

SUMMARY

A qualitative analysis of generic and familial diversity trends and changes in turnover rates in the mammalian orders Artiodactyla and Perissodactyla shows no evidence of competition and ordinal displacement. On the contrary, available evidence suggests that the two orders evolved independently, despite the ecological similarity of the groups. Evolution of these two mammalian orders does not fit patterns predicted by the continuous diversification or periodicity models of taxonomic diversification. Application of equilibrium or periodicity explanations to terrestrial evolution may be inappropriate if, as Raup (1972) notes, exploitation of the environment is not yet fully developed. Stanley (1974) proposed that degree of interspecific competition results in two fundamentally different modes of taxonomic diversification, here termed continuous diversification and equilibrium. It is conceivable that continuous diversification, a model based on data from benthic marine organisms such as brachiopods and bivalves, is inapplicable to mammals. This is because mammals differ drastically from these invertebrates in feeding habits, food supply, mobility, and behavior (Stanley, 1974). Some support is lent to the application of biogeographic equilibrium theory to mammalian evolution, for

a positive correlation exists between origination and extinction rates of artiodactyls and perissodactyls. The broad correspondence of turnover rates to diversity may well represent equilibrium shifts, but the significance of this pattern and its generality among other mammalian groups are unknown.

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