models must therefore accurately reproduce these processes to correctly simulate ENSO.

With the eastern edge of the warm pool moved back and forth along the equator by zonal currents during La Niña and El Niño, the variation of zonal currents in the equatorial central Pacific controls the basic time scale of the ENSO cycle. In the central equatorial Pacific, these zonal currents are generated by local wind forcing, equatorial Kelvin and first meridional mode Rossby waves, and their reflections on the eastern and western ocean basin boundaries (*8*, *15*, *32*, *33*). Eastern boundary reflections and resulting first meridional mode Rossby waves (enhanced along their propagation by wind forcing further west) were observed to shift the 1986–87 El Niño into the 1988–89 La Niña through zonal advection of the eastern edge of the warm pool (*15*). Therefore, we propose for the oscillatory nature of ENSO an extension of the original delayed-action oscillator theory (*34*, *35*). In this extension, the predominant ocean-atmosphere coupling is situated in the central equatorial Pacific, as observed (*36*). In addition, reflections of equatorial waves at both eastern and western boundaries are important in shifting the phase of ENSO (*33*). In this scenario, zonal advective processes, as determined by us, are fundamental in establishing the ENSO time scale.

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Molar Tooth Diversity, Disparity, and Ecology in Cenozoic Ungulate Radiations

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A classic example of adaptive radiation is the diversification of Cenozoic ungulates into herbivore adaptive zones. Their taxonomic diversification has been associated with changes in molar tooth morphology. Analysis of molar crown types of the Artiodactyla, Perissodactyla, and archaic ungulates ("Condylarthra") shows that the diversity of genera and crown types was high in the Eocene. Post-Eocene molars of intermediate crown types are rare, and thus the ungulate fauna contained more taxa having fewer but more disparate crown types. Taxonomic diversity trends alone give incomplete descriptions of adaptive radiations.

Mammals are today the dominant terrestrial vertebrate group using plants as food (*1*). Mammalian herbivory has evolved independently numerous times during the past 65 million years (*2*). Along with rodents, ungulates are the most taxonomically diverse group of herbivorous mammals, both today and in the geologic past (*1*). The taxonomic diversification of ungulates, starting in the Paleocene, was associated with distinct changes in dental morphology (*1*–*3*), but the evolution of morphologies associated with herbivory is only incidentally correlated with phylogenetic groupings (*4*). Ecomorphological groupings that cut across phylogenetic boundaries should be used to study the rise of herbivory (*2*, *5*). Teeth offer good opportunities to link morphology to ecology through diet. Here we develop criteria to classify mammalian molar shapes and thus connect taxonomic and morphological diversity in ungulates through the Cenozoic.

We tabulated each morphological type of upper second molar as a discrete crown type (*6*). The crown type classification is a phylogenetically neutral scheme in which cusp shape, number, and location as well as

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loph (shearing blade) number and orientation are recorded (*7*), allowing measures of morphological diversity and disparity. Morphological disparity, which is different conceptually from simple number of morphological types, is understood as "range of anatomical design" (*8*) and is usually approached as the distance among samples in morphospace (*9*). We applied the crown type scheme to the North American, European, and Asian members of the ungulate orders Artiodactyla and Perissodactyla, as well as to the archaic ungulates, the "Condylarthra" (*10*).

We identified 28 upper molar crown types (Fig. 1). Only seven crown types (25%) are found among extant members of Artiodactyla and Perissodactyla (Fig. 1). In each region, crown type diversity increased from the Early Eocene to a maximum in the Late Eocene and crashed in the Oligocene to pre-Eocene levels (Fig. 2A), roughly paralleling changes in ungulate taxonomic diversity (Fig. 2B). The smallest number of genera for each crown type occurred in the early Eocene, and only an average of two (with a maximum of five) genera shared the same crown type (Fig. 2). A low number of genera per crown type could indicate that morphological diversification outstripped taxonomic diversification. It has been argued that this pattern characterizes the beginning of some adaptive radiations (*11*). In contrast, taxonomic diversification in the Miocene did not result in a similar increase in diversity of crown types (Fig. 2, A and B). Thus, in the Miocene, ungulate crown type diversity does not appear to be a simple function of taxonomic diversity.

To study the causes behind this discordance between morphological and taxonomic diversity, we tabulated the morphological distance between each crown type (disparity) within a land mammal age (a biochronological unit). Morphological distance is calculated as the sum of the absolute values of the differences in each variable (*12*). A single disparity value is the number of changes needed to make two crown types the same. Even a difference of one is morphologically quite large (addition or loss of one cusp or loph or a change in cusp shape).

The data show that maximum disparity (maximum distance between any pair of crown types) rose quickly in the Early Eocene (Fig. 3), which is in keeping with this being a time of expansion in morphological diversity (Fig. 2). Maximum disparity rose to the modern levels in the Late Eocene (except in Europe), and, after a slight decline in the Late Oligocene–Early Miocene, the values reached a maximum of seven on each continent in the Pliocene. We also tabulated the frequency distribution of individual disparities within each land mammal age to illustrate the packing of morphospace (Fig. 3). For the Paleocene fossils (data for which are largely limited to North America), most crown type pairs had disparity values of one or two (epochal average, 2.3 for North America). This analysis implies that disparity was higher in the Eocene and remained high in the Oligocene despite a drop in crown type diversity (epochal averages, 2.9 to 3.2). For the Miocene fossils, disparity values between crown types are mostly high (epochal averages, 3.2 to 3.6), and disparity increases further in the Pliocene (Fig. 3). The increasing disparity implies that the packing of ungulate molar morphospace decreased in the Cenozoic.

Adaptive shifts in ungulate resource use may have been responsible for the observed increase in disparity. Adaptive shifts can be analyzed by measures of ecological specialization. Informative structures in ungulate molars that can be directly related to resource use are lophs. Lophs are best developed in herbivores consuming fibrous plant foods (for example, leaves and grass) and less developed in consumers of less fibrous plant foods (for example, fruit). Among extant mammals, 89% of families having a diet of only fibrous vegetation have two or more lophs on their upper molars. Only 64% of less specialized herbivorous families (also eating fruits, nectar, or seeds) and 45% of generalist families have two or more lophs (*13*). It can be hypothesized that loph number correlates with specialized herbivory in fossil taxa as well.

We tabulated the total number of lophs among the crown types and divided this by the number of crown types for each land mammal age. The resultant statistic—aver-

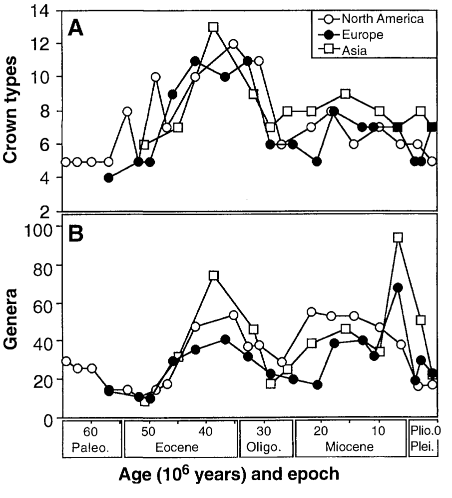

Fig. 2. Crown type (**A**) and generic (**B**) diversity trends over time. Note the concordant peaks in crown type and genus diversity in the Eocene and the peak in genus diversity at low crown type diversity in the Miocene. Spearman rank correlations (r_s) between genus and crown type diversity are as follows: in North America, $r_s = 0.44$ [not significant (NS)]; in Europe, $r_s = 0.77$ ($P < 0.005$); and in Asia, $r_s = 0.61$ ($P < 0.05$). For the Paleogene the corresponding values are as follows: r_s = 0.58, 0.89, and 0.90 (all are $P < 0.05$); and for the Neogene, r_s = 0.66, 0.69, and 0.06 (all are NS). Paleo., Paleocene; Oligo., Oligocene; Plio., Pliocene; and Plei., Pleistocene.

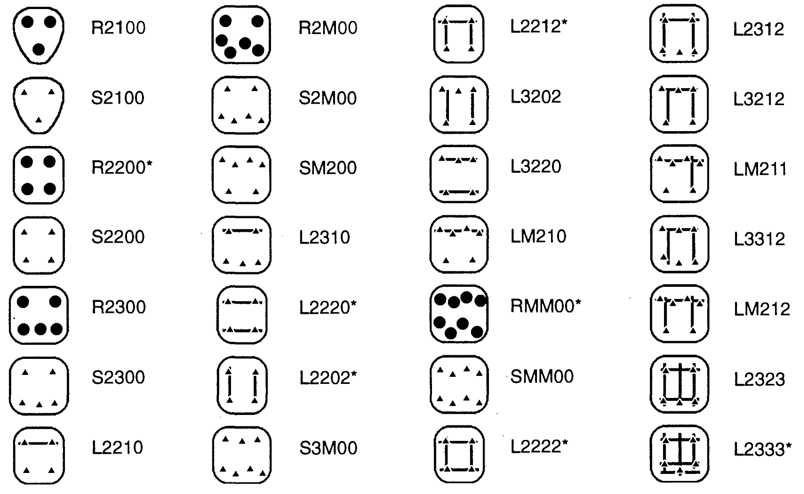

Fig. 1. The 28 upper molar crown types encountered in this study. The simplified drawings represent occlusal views of each crown type, buccal side toward the top, with no mesiodistal polarity. Note that, for example, three lingual cusps can be any combination of prominent protocone, hypocone, metaconule, paraconule, or protostyle (epicone). A crown type consists of five variables: (i) cusp shape (R, round, S, sharp, and L, loph); the number of (ii) buccal and (iii) lingual cusps; and the number of (iv) longitudinal and (v) transverse lophs. M ("many") equals ≥4 buccal or lingual cusps. The crown types of recent Artiodactyla and Perissodactyla are marked with an asterisk (R2200 and RMM00 represent suids; L2220 represents camels and pecoran artiodactyls; L2202 represents tapirs; L2212 and L2222 represent rhinoceroses; and L2333 represents horses).

age lophedness—increases over time in North America, Europe, and Asia (Fig. 4). This pattern is accounted for by the loss of nonlophodont crown types and the radiation of forms with many lophs in the latter part of the Cenozoic. However, the similar trends on each continent are not composed of the same crown types. Only between 44% (in the Oligocene) and 54% (in the Miocene) of crown types are shared among the regions. Thus, similar average lophedness among fossils reflects ecological similarity rather than morphological resemblance per se. This suggests that parallel and convergent evolution have occurred frequently in the evolution of ungulate molar shape and stresses the importance of ecological factors in shaping ungulate communities (*1*, *2*). In contrast to the rise in average lophedness in the Paleocene and Early Eocene fossils, average lophedness remains at around one loph per crown type in the Late Eocene and Oligocene fossils, despite fluctuations in taxonomic and crown type diversity (Fig. 2). During the Miocene, the data imply that average lophedness gradually increased to the modern ungulate value (2.4 lophs per crown type; Fig. 4). The increase in average lophedness in the Miocene is concomitant with the evolution of high-crowned molars (*14*) and indicates that dietary specializations gradually shifted toward more fibrous food.

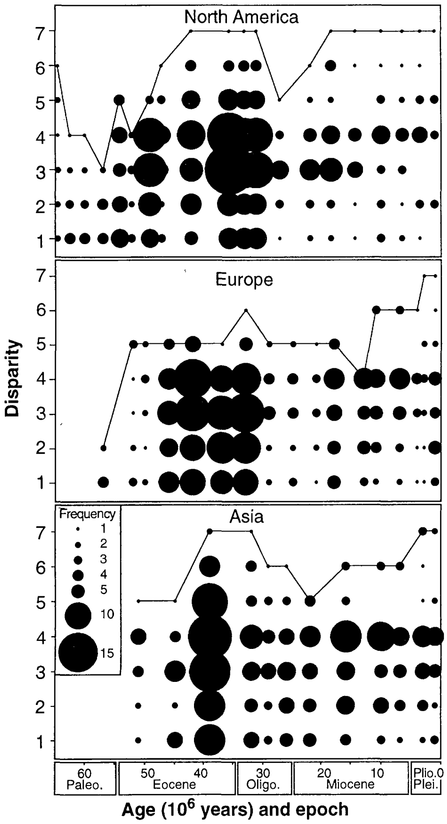

Fig. 3. Crown type disparity through the Cenozoic. The size of each dot represents the frequency of a particular disparity value within a land mammal age (*12*). The line indicates maximum disparity. Note the low maximum disparity for North America and Europe in the Paleocene (data for Asia are missing). The large dots in the Eocene are the result of high crown type diversity. After the Eocene, crown type diversity declines but disparity increases, with low values gradually disappearing. Epochal averages for North America are as follows: Paleocene = 2.3, Eocene = 3.1, Oligocene = 3.2, Miocene = 3.6, and Plio-Pleistocene = 4.0. Corresponding values for Europe are 1.3, 2.9, 3.0, 3.2, and 3.5; and for Asia, starting in the Eocene, they are 3.1, 3.2, 3.3, and 3.6. Average land mammal age disparity is not significantly correlated with crown type or generic diversity ($-0.28 \leq r_s \leq 0.50$; $P = 0.86$ to 0.06).

The association of crown type and taxonomic diversification in the Eocene indicates an Eocene "bloom phase" (*15*) of adaptive radiation. With simultaneous increases in crown type diversity (Fig. 2) and disparity (Fig. 3), as well as evolution of new dietary specializations (Fig. 4), the Eocene was the time of the greatest number of ways for an ungulate to make a living (*16*). In recent ecosystems, taxonomic diversity generally correlates positively with available energy (*17*). Eocene diversification began during the inferred temperature maximum for the Cenozoic (*18*). As evidenced by plant leaf size and morphology, tropical-like forests were found in the higher latitudes during this time (*19*). Also, plant diversity in the Eocene was comparatively high (*20*), which could indicate high local productivity and environmental patchiness that allowed relatively high packing of crown types (dietary similarity) as compared with that in later epochs.

Whereas Paleocene and Eocene morphological and taxonomic trends are generally concordant, the post-Eocene patterns are not. Steep climatic cooling in the Late Eocene was probably responsible for the drop in taxonomic diversity (*16*, *21*). Although we observe a similar decline in crown type diversity, the other two measures of ecomorphology, average lophedness and disparity, do not appear to change in pre-Miocene fossils. This may indicate that environmental disturbances [such as a shift toward more open forest environments and increased seasonality (*19*)] first affected all ungulates equally. Later, starting in the Oligocene, the adaptive response (which may have included competitive displacement) produced the observed changes in average lophedness and disparity.

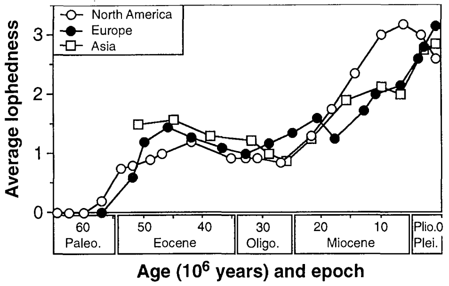

Fig. 4. The average lophedness (number of lophs per crown type) through the Cenozoic.

The trends imply that the Miocene ungulates evolved increasingly disparate crown types together with dietary specialization in more fibrous vegetation. Continued climatic cooling beginning in the Middle Miocene (*18*) may have promoted the further loss of intermediate crown types and, presumably, intermediate niches. In addition, the high taxonomic diversity of ungulates in the Miocene could be a result of increased provinciality, which has been documented for North America (*22*). An alternative hypothesis is that these ungulates evolved new ways to subdivide resources. These evolutionary changes could, for example, have been physiological adaptations or an increase in range of body size that enabled several species to share similar (but different-sized) crown types.

We have shown that the Eocene and Miocene radiations produced two different ungulate communities. The Eocene ungulate radiations involved adaptations to narrow but high-quality niches, which is reflected in the diverse and less disparate crown types. The Miocene radiations created communities of ungulates with dental adaptations to deal with vegetation of low primary productivity, correlated with the loss of intermediate crown types. The analysis of morphological trends describes the ecological aspect of ungulate radiations better than taxonomically based analyses alone.

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R2M00). Sharp cusps are pointy and most of their slopes are straight or concave, whereas the slopes of round cusps are convex. A loph can consist of a single cusp or of several cusps. Structures that had a tip and were equal in height to or exceeded two-thirds of the total crown height were counted as cusps. A similar cutoff point was used for lophs. The crown type scheme is conservative in the recognition of morphological features and underestimates the origin of these features in the phylogeny. For information on crown types in recent mammals, see (6).

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Ecological Controls on the Evolutionary Recovery of Post-Paleozoic Crinoids

Mike Foote

Analysis of morphological characters of a global sample of post-Paleozoic crinoid echinoderms shows that this group underwent a rapid diversification after the extinction at the end of the Permian to reach maximal morphological disparity by the Late Triassic, which is essentially the same evolutionary pattern seen during the group's early Paleozoic radiation. The accelerated morphological diversification of a single class implies that, even if clades surviving from the Paleozoic represented ecological incumbents that hindered the origin of new higher taxa, species within individual higher taxa rapidly exploited available ecological opportunities in the Mesozoic.

After the late Paleozoic (Late Permian) mass extinction, the origination of higher taxa (phyla and classes) of marine animals was more subdued than in the early Paleozoic (*1*, *2*). Even though most marine species became extinct in the Late Permian (*3*), most of the major adaptive zones occupied during the Paleozoic were not completely evacuated (*2*, *4*). Thus, Mesozoic taxa may have experienced greater competition than their early Paleozoic counterparts that were diversifying into unoccupied adaptive zones (*4*). Therefore, given a correlation between morphological and ecological diversification (*2*, *5*, *6*), Mesozoic taxa might be expected to have reached peak morphological diversity (disparity) (*7*, *8*) more gradually than did many early Paleozoic clades that rapidly attained maximal disparity (*8*–*10*). Crinoids, a large marine clade, reached a plateau of disparity in the early Paleozoic (*10*) but suffered a great reduction in diversity in the late Paleozoic, apparently to a single lineage (*11*). They then diversified ecologically and morphologically (*12*–*15*). The fossil record of crinoids can thus be used to compare macroevolutionary patterns within the same clade under significantly different ecological circumstances.

The post-Paleozoic radiation of marine animals has been documented mainly with taxonomic data [(*1*, *2*, *5*) but see (*6*)]. Because the correspondence between taxonomic origination and morphological innovation is unclear, it is important to document morphological diversification directly. On the basis of the primary systematic literature, I used data on 69 discrete characters to quantify the major anatomical features (*16*) for a global sample of 355 crinoid species from the Triassic through the Eocene. This sample represents 121 of the ~156 genera known for this ~200-million-year (*17*) period (*18*). This span of time was divided into 11 time intervals (mean duration, 19 million years; SD, 7.1 million years), reflecting a balance between temporal resolution and sample size. Within each interval, species were aggregated into a single statistical sample. Although genealogy is essential in a clade's evolutionary history, disparity concerns net morphological differences rather than branching sequence [(*7*, *8*, *10*) but see (*19*)]. Therefore, disparity was measured as the mean pairwise character difference between species (*9*, *10*, *20*). I compared disparity to genus- and family-level taxonomic diversity [based on several data compilations (*10*, *12*, *15*, *21*, *22*)]. The number of species sampled for each interval is generally proportional to the number of known genera and families.

Disparity among post-Paleozoic crinoids peaked early in the radiation (in the Late Triassic, less than 40 million years into the Mesozoic), well before the time of maximal taxonomic diversity (Fig. 1, A through H) (*23*). This period is similar to the 40 million to 50 million years between the appearance of unquestionable crinoids in the Early Ordovician and the Paleozoic peak of disparity in the Caradocian (*10*, *24*). Disparity declined from the Late Triassic to the Early Jurassic, in part reflecting the extinction of encrinids, holocrinids, and other taxa (*12*, *13*, *15*). Disparity again increased early in the Cretaceous (Neocomian). Much of this increase is attributable to origination within the order Cyrtocrinida, which displays many unusual forms and habits, such as reduced, bilaterally

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