

The hypocone as a key innovation in mammalian evolution

(adaptive zone/convergent evolution/dentition/diversity/Theria)

JOHN P. HUNTER* AND JUKKA JERNVALL†

*Department of Anatomical Sciences, State University of New York, Stony Brook, NY 11794-8081; and †Department of Ecology and Systematics and Institute of Biotechnology, University of Helsinki, P.O. Box 17, FIN-00014, Finland

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ABSTRACT The hypocone, a cusp added to the primitively triangular upper molar teeth of therian mammals, has evolved convergently >20 times among mammals during the Cenozoic. Acquisition of the hypocone itself involves little phenotypic change, but subsequent diversification of groups possessing the hypocone may be greatly enhanced. Our analysis of the Cenozoic mammalian radiations, including the Recent fauna, shows that high species diversity of mammals with hypocones and association of the hypocone with herbivory strongly support recognition of the hypocone as a key innovation that has allowed invasion of, and diversification within, herbivorous adaptive zones. In contrast, mammals lacking hypocones show no marked increase in species diversity during the Cenozoic.

A key innovation, as defined by Mayr (1), is “any newly acquired structure or property that permits the performance of a new function, which, in turn, will open a new adaptive zone.” Because invasion of adaptive zones has been considered a prelude to the origin of higher taxa (1–3), studies of key innovations have focused on characters that define higher taxa, and workers have sought causal relationships between particular characters and diversification (4–8). When hypothesized key innovations are unique to a single clade, associations between innovation and diversification rate are not easily testable (9, 10). Although key innovations are also usually thought to involve large changes in structure or function (9), magnitude of phenotypic change is not necessary to a key innovation. Rather, a key innovation, whether large or small, must be demonstrated to be important, or even essential, to the crossing of an adaptive threshold and subsequent diversification of a group (1–3). In addition, characters that have evolved multiple times convergently are more easily testable as key innovations because they provide many examples for study (11). One such possible key innovation is the hypocone, a character that has appeared at the base of numerous radiations of mammals.

While all therian mammals are descended from an ancestor with tribosphenic (12) molars (upper molars with three major cusps), most mammals also derive from ancestors with quadritubercular (13) molars—i.e., molars with a hypocone. Acquisition of a hypocone involves little initial modification of the tribosphenic molar (Fig. 1), and this cusp has evolved repeatedly among mammalian lineages and in various ways (Table 1). Acquiring a hypocone initially increases occlusal area, effectively doubling the area devoted to crushing food; the hypocone fills in the space between upper molars, the interdental embrasure, eventually squaring off these molars (14, 15) (Fig. 1). In derived forms, the hypocone becomes an essential part of occlusal morphology—e.g., in the specialized bladed systems of advanced herbivores (Fig. 1) (13, 14). The hypocone is incompatible with carnassiform upper molars, as it disrupts

occlusal contact between metacrista and paracristid (16), crests that are well developed in carnivorous mammals. Thus, possession of a hypocone is generally thought to be associated with herbivory.

We investigated the evolutionary potential of the hypocone in two ways. First, we compared taxonomic diversity of living, terrestrial, nonvolant mammals with different molar types across dietary groups to determine whether the hypocone is indeed associated with herbivorous habits and whether mammals with hypocones are more diverse today than those lacking hypocones. Second, we compared the taxonomic diversity of fossil mammals with different molar types across geologic time to determine whether the presence of a hypocone has been associated with higher standing diversity and radiations on each continent.

METHODS

Foods (invertebrates, meat, fish, fruit, nectar, and fibrous vegetation) (17, 18) used as primary resources by members of each extant family were tabulated. Families with three or more primary diets were classified as generalists. Other families were classified as specialized faunivores or herbivores accordingly. Bats, most of which possess hypocone shelves (see below), were excluded because, although diverse today, bats are rare and species poor in the fossil record.

All Cenozoic therian, terrestrial mammals with unreduced teeth were classified morphologically as forms with hypocones, without hypocones, or with hypocone shelves. This last group is morphologically heterogeneous, and members may possess moderately expanded cingula, greatly expanded shelves, or diminutive hypocones. These morphological categories cut across phylogenetic boundaries and are used here to measure taxonomic diversity within ecomorphological groupings (19). These morphological data are from observations on fossil and extant mammalian teeth, including casts, largely in the American Museum of Natural History (New York), and from the primary and secondary literature.

Taxonomic classification for Recent therians largely follows the guidelines presented in ref. 20. Faunal data are from ref. 21 at the resolution of land mammal age (North America, Europe, Africa, and South America) or early, middle, and late intervals of epochs (Asia and Australasia) by using an updated timescale (22). Both fossil and extant data bases incorporate morphological information on families and, where the hypocone evolved within families, at lower taxonomic levels. Results were tabulated with and without rodents to assess the impact of this diverse and highly morphologically specialized—e.g., gnawing incisors—order on observed patterns.

RESULTS

Familial and species-level diversity of living mammals within the morphological classes across dietary groups is presented in Fig. 2. Herbivores with hypocones have high familial diversity, whereas generalists with hypocones have moderate familial diversity (Fig. 2A). High species-level diversity among generalists with hypo-

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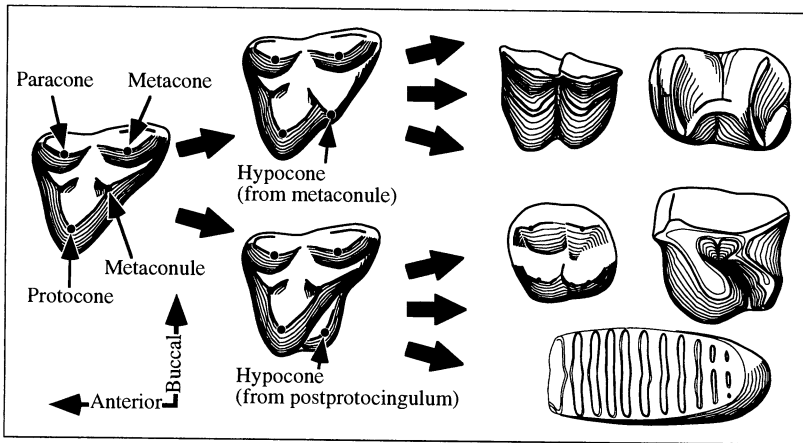


FIG. 1. The two most common ways of evolving a hypocone (Left) and some examples of the diversity of molars with hypocones (Right). (Top) Selenodont molar of a deer (Artiodactyla) and bilophodont molar of a kangaroo (Diprotodontia). (Middle) Bunodont molar of a human (Primates) and trilophodont molar of a rhinoceros (Perissodactyla). (Bottom) Lamellar molar of a mammoth (Proboscidea). Many of the different tooth types have evolved convergently, regardless of the mode of the hypocone origin. Examples are left upper molars, not to the same scale.

cones (Fig. 2B) is due largely to the rodent family Muridae. When rodents are excluded, the number of dietary generalist species with hypocones is reduced drastically (Fig. 2B). All herbivores possess either hypocones or, in a few cases, hypocone shelves.

Species-level diversity of fossil mammals within each morphological class was calculated for each continent (Figs. 3 and 4). Trends in diversity (Figs. 3 and 4) indicate that nearly all mammalian radiations throughout the Cenozoic have occurred

Table 1. Mammalian taxa with hypocones and the probable origin of the hypocone in each group

Taxon	Source		
	Postprotocingulum	Metaconule	Other
Mammalia, <i>incertae sedis</i>			
<i>Florentinoameghinia</i>		?	
Metatheria			
Paucituberculata	X		
Polydolopoidea		X	
Caroloameghinoidea		X	
Peramelina			
Peramelidae, Peroryctidae		X	
Thylacomyidae			Metacone*
Diprotodontia		X	
Eutheria			
Mixodonta	X		
Insectivora			
Erinaceidae	X		
Pantodonta			
Coryphodontidae			Metacone
Dinocerata			Protocone†
Embrithopoda	X		
Carnivora			
Procyonidae, Ursidae	X	X‡	
Condylartha			
Periptychidae, Meniscotheridae,	X		
Phenacodontidae, Didolodontidae			
Pleuraspidotheridae		X	
Artiodactyla		X	
Other ungulates (Perissodactyla,	X		
Hyracoidea, Proboscidea,			
Notoungulata, Xenungulata,			
Pyrotheria, Litopterna)			
Macroscelidea	X		
Primates	X§		
Chiroptera			
Mystacinidae, Pteropodidae¶,	X		
Phyllostomidae¶			
Rodentia	X		
Lagomorpha	X		

Each listing does not necessarily represent a single origin.

*Metaconule-derived "hypocone" reduced.

†True hypocone reduced.

‡Possibly metaconule in Procyon.

§Includes nannopithec fold (notharctines) and lingual cingulum.

¶Hypocone well developed in only a few genera.

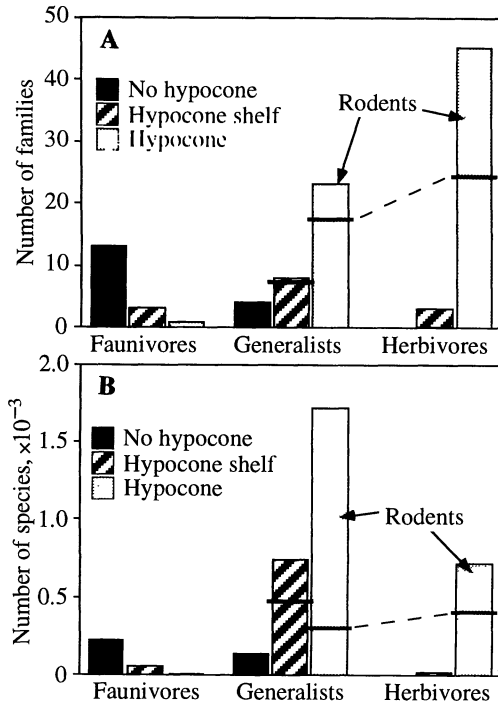


FIG. 2. Familial (A) and species-level (B) diversity of living terrestrial, nonvolant mammals with hypocones, without hypocones, or with hypocone shelves. See text for explanation of dietary groupings and methods. Note the absence of specialized herbivores without hypocones and the paucity of specialized faunivores with well-developed hypocones.

among forms with hypocones. This pattern holds for all continents, including Australasia, where the major contributors to diversity are the Diprotodontia. A total of 54% of orders with hypocones possessed a maximal standing diversity of 10 or more species, and 11% have peaked at 30 or more species. The values for orders without hypocones are 29% (≥ 10) and 0% (≥ 30), respectively, and for orders with hypocone shelves, the values are 44% (≥ 10) and 6% (≥ 30), respectively.

The high diversity observed among mammals with hypocones is not an artifact of primitive-character retention because numerous unrelated lineages have evolved the hypocone convergently (Table 1) and subsequently radiated. Nor is this observation an artifact of biased representation of mammals with hypocones in the available taxonomic pool because many higher mammalian taxa lack hypocones.

DISCUSSION

High diversity of mammals with hypocones, both today and in the geologic past, requires explanation. To a first approximation, species diversity can be used to estimate the amount of niche space occupied by a group (23), and diversity is also related to the quantity of available energy in Recent ecosystems (24–27). An energy-rich environment can sustain larger populations and, thus, may result in high diversity because of a lowered extinction rate, the probability increases that these taxa will be sampled in the fossil record. One way to increase available energy is to exploit directly primary producers because available energy increases at lower trophic levels (24).

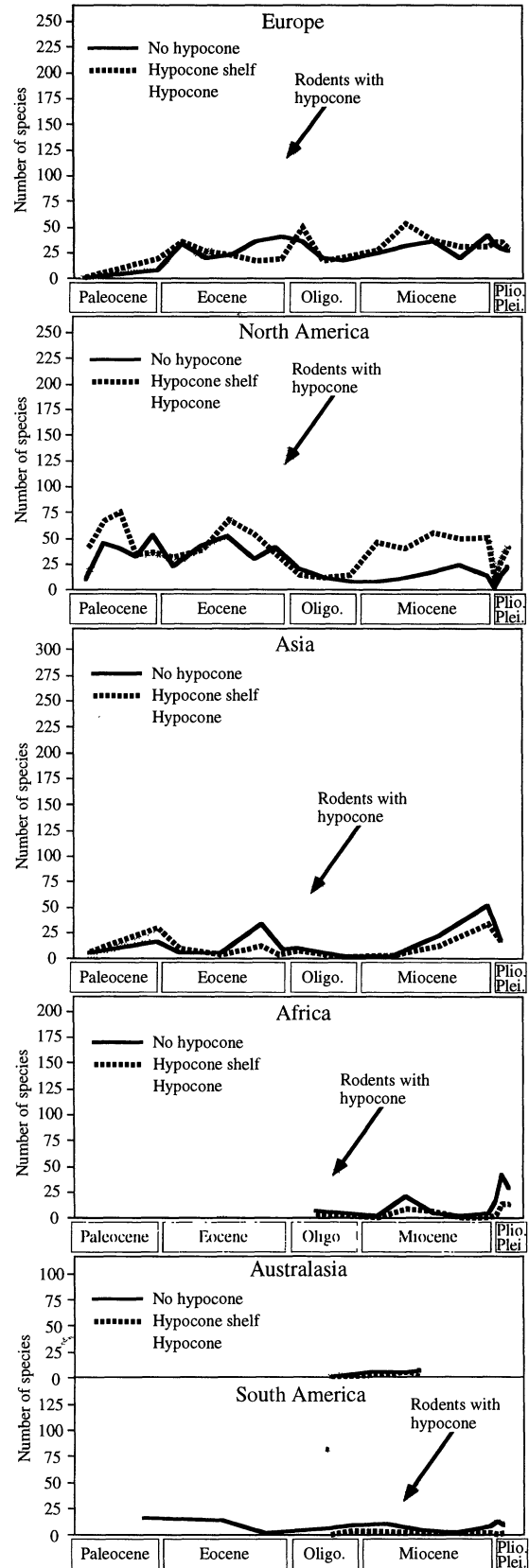


FIG. 3. Continental species-level diversity through time of fossil mammals with hypocones, without hypocones, or with hypocone shelves. Note the apparent limit to diversity of mammals without hypocones or with hypocone shelves on each continent. Radiations of mammals with hypocones begin across the middle/late Eocene boundary and continue through the rest of the Cenozoic. Excluding rodents does not change the overall patterns. See text for methods.

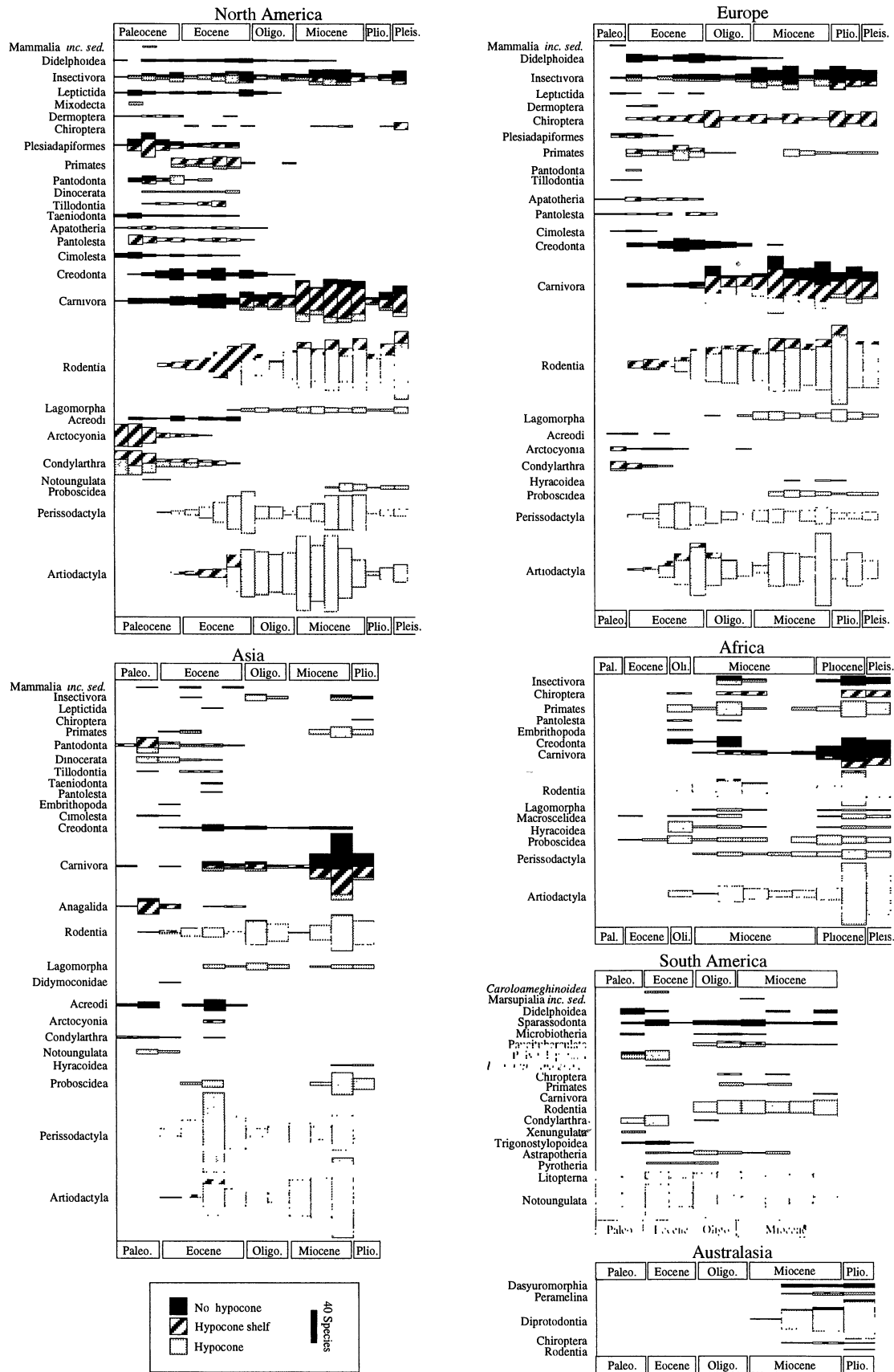


FIG. 4. Species-level diversity through time of fossil mammalian orders with hypocones, without hypocones, or with hypocone shelves on each continent. The major mammalian radiations on each continent have been among forms with hypocones, although possession of a hypocone does not ensure that diversification will occur. No single order is responsible, although Rodentia, Perissodactyla, and Artiodactyla each contribute highly. The radiation of Carnivora largely involves forms with hypocone shelves with the exception of the Pliocene and Pleistocene of Africa and the late Miocene of Asia. Data for Asia exclude Turkey.

This allows higher diversity among herbivores than among faunivores.

High diversity among living and fossil mammals with hypocones implies that abundant available trophic energy supports this diversity. Radiation of mammals with hypocones on all continents approximately synchronously (possibly later in Australasia) suggests the utilization of primary producers, perhaps made possible by a floral turnover with cooling and drying trends starting in the middle Eocene (22, 28). Change toward more open-forest environments (28) may have increased the available fibrous plant parts—e.g., leaves and stems—as food for terrestrial mammals. Also, as our analysis of the Recent fauna shows, mammals with hypocones or with hypocone shelves may have been preadapted, or exapted, for utilization of fibrous plant parts. This tough, fibrous food required dental specialization, such as lophodonty and selenodonty (Fig. 1), before mammals could efficiently process and exploit these new resources. Mammals that had evolved a hypocone were preadapted for evolving these specializations because they already possessed a posterolingual cusp, the hypocone, on the upper molars, perhaps originally evolved for the purpose of increasing occlusal area, that could be incorporated into new morphologies. Mammals without hypocones would have to evolve a cusp in that position *de novo*. Our analysis of the fossil record supports this hypothesis by showing that hypocones evolved early in lineages of mammals that diversified only later. Increases in diversity rarely precede the acquisition of the hypocone, as in Carnivora. However, only Carnivorans that had previously evolved hypocone shelves diversified greatly in the Oligocene and Miocene, after major herbivorous radiations.

In a strong contrast, nearly constant diversity of mammals without hypocones and with hypocone shelves during this interval implies that their resource base did not expand in response to climatic change. Because insects already had evolved to eat fibrous plants long before the Cenozoic (19), insectivorous mammals (mammals lacking hypocones) did not experience the same appearance of new diet choices as did herbivorous mammals. Bats could be an exception, but their fossil record is far too fragmentary to pinpoint the time of their diversification.

The moderate proportion of generalists with hypocones, the very high proportion of herbivores with hypocones, the hypothesized dietary succession from faunivory to herbivory in mammals—e.g., see ref. 29 for Primates—and the convergent incorporation of the hypocone into the dentitions of specialized herbivores suggest that the hypocone evolved under generalized dietary regimes but is a prerequisite for specialized herbivory. Because only herbivores can directly exploit primary producers, only herbivores possess a sufficient resource base to generate very high diversity. Thus, the hypocone is a key innovation in that it allows descent on the food chain given the ecological opportunity.

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