Fossil Horses

Systematics, Paleobiology, and Evolution of the Family Equidae

BRUCE J. MACFADDEN
Florida Museum of Natural History
University of Florida

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(positive allometry of the nasal horn relative to nose-to-ear lenght
for a hypothetical rhinoceros lineage through time)

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Haldane (1949) calculated rates of linear-dimension evolution between 0.002 and 0.060 d for dinosaurs, and much higher rates between 0.3 and 0.6 d for hominids. In a modern context, as Gingerich (1983) noted, these rate differences may be artifacts of the divergent time intervals (Δt's) used for dinosaurs (tens of millions of years) versus hominids (about 1 myr). Kurtén (1960) calculated evolutionary rates for lower molar lengths between 0.4 and 3.2 d for Pleistocene bears (*Ursus*) of Europe. Gingerich has long been interested in quantification of morphological rates of evolution. He has even introduced a "darwinometer," which depicts the rate of stratophenetic evolution (e.g., Figure 8.3), into many of his illustrations. Gingerich (e.g., 1982, 1983, 1987b) found relatively high rates of molar evolution (0.1–1.0 d) for early Tertiary mammals of North America. Relative to fossil horses, Gingerich's results could reflect the artifact of a shorter time duration (Δt) of about 1–2 myr. However, his data could equally as well indicate more rapid mammalian evolution during radiations into new adaptive zones. For all fossil vertebrates, Gingerich (1983) found a geometric mean of 0.08 d. Thus, for fossil horses, the mean evolutionary rates, between 0.113 and 0.046 d (Table 9.2) for the four linear dental dimensions lie within the midrange of those observed for other taxa.

Almost half a century ago Haldane provided a means for quantifying evolution with the introduction of the darwin. Although this currently seems to be the best system for comparing evolutionary rates in such widely divergent taxa as mice and elephants, or invertebrates and vertebrates, Gingerich's important paper (1983) highlights the limitations of this technique. Thus, whether it be different levels within the Linnean hierarchy, or different time scales for fossil taxa, the scale of observation affects our perception of evolutionary phenomena.

As a final note, the results presented here further underscore the principle of mosaic evolution as it was originally proposed by de Beer (1954). All organisms are complex mixtures of primitive and derived characters evolving at different rates. For horses, this can even be seen on a fine scale, where characters within a functionally interrelated complex, such as the dentition, evolve at significantly different rates.

Allometry and scaling of horse evolution: Does ontogeny recapitulate phylogeny?

In addition to examination of rates of evolution of single characters, another popular line of inquiry has been the application of allometry. Allometry is the study of the relative proportions that occur during ontogenetic growth, or size changes within clades. Two kinds of allometry are relevant here. In positive allometry, as size changes, one dimension (usually a linear di-

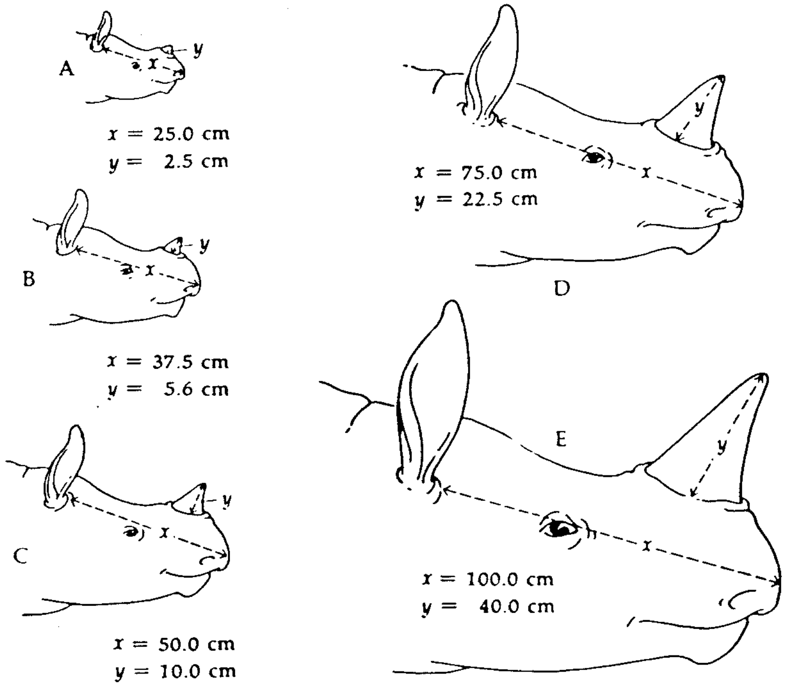

Figure 9.5. *Positive allometry of the nasal horn (y) relative to nose-to-ear length (x) for a hypothetical rhinoceros lineage through time. From Moody (1970),* Introduction to Evolution, *original copyright 1953 by Harper & Row, Publishers, Inc. Reprinted by permission of HarperCollins Publishers.*

mension) grows more than another (Figure 9.5). In static allometry there is isometric growth, where all dimensions under study grow by the same proportion. In the hypothetical rhinoceros lineage shown in Figure 9.5, if isometric growth had occurred, then for the youngest species depicted in part E, the horn length (y) would be 10 cm.

Many workers have made the distinction between ontogenetic allometry and evolutionary allometry, that is, respectively, the relative changes in proportions that occur during an individual's lifetime, and those that occur within the phylogenetic history of a clade. This obviously leads to a question that was first asked by Ernst Haeckel during the nineteenth century, as well as by many other natural historians since that time: To what extent does ontogeny recapitulate phylogeny? Related to this, some classic studies of fossil horse cranial proportions and their evolutionary interpretations will be examined here.

Osborn (1902, 1912b) studied the changes in the skull proportions of many fossil mammals, including horses, and coined the term "dolichocephaly" for any type of cranial elongation. He noticed two principal kinds of dolichocephaly, in which, relative to the total skull length, either (1) the preorbital length (i.e., the cheek and muzzle) is enlarged (proopic) or (2) the postorbital length (i.e., the braincase and basicranial region) is enlarged (opisthopic).