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EVOLUTIONARY RATES AND TRENDS IN RHINOCEROSES

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THE rhinoceroses are not merely one more example of an evolutionary case history. Like the horses, they belong to the order Perissodactyla; but, having a sharply contrasted phylogenetic development, they can counterbalance the frequent tendency to overgeneralize from the horse record.

The general impression that horses evolved far more rapidly than rhinoceroses is broadly true, yet there are many exceptions and qualifications to this summary statement. Rates of rhinoceros evolution may be conveniently measured in "horse-units," using the familiar main horse line as the standard of comparison. The plural form, rates, is used advisedly, since different lines of rhinoceroses evolved at very different rates. Different parts of the body—the skull, teeth and feet, in particular—have also evolved at very different rates in any given line, in contrast with the roughly parallel evolutionary rates of horse teeth and feet. Except for the head and feet, the skeleton remained very stable. For example, the white rhinoceros of Africa and the Pleistocene woolly rhinoceros of Eurasia reached a stage comparable to Pliocene horses in crown height of the cheek teeth; in weight distribution their tridactyl feet are most comparable with Oligocene horses. The Indian and Javan rhinoceroses still barely survive, in the Oriental Region; comparative anatomy and paleontology indicate that of the two the Javan rhinoceros is much less modified from their Pliocene common ancestry. Compared with horses, their teeth and feet have reached only Miocene stages.

The extraordinary elasmotherine rhinoceroses can be traced from the Pleistocene back to the Late Miocene, and, less certainly, farther back into the more generalized aceratheres of the Late Oligocene. While always remaining rhinoceroses, they out-horsed the horses in developing high-crowned cheek teeth with crenellated enamel buried in cement to form an efficient grinding mill. From the Late Miocene until their extinction before the end of the Pleistocene, the elasmothere cheek teeth evolved in the same direction as, but definitely farther than, the horses evolved from the Middle Miocene to the present. Over the same time, their feet elongated slightly, with some emphasis on the middle digit, thus also

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paralleling the horses, but making only the progress made by the horses from Early to Middle Miocene.

The baluchitheres were by a wide margin the largest of all land mammals. By the time of their extinction in the Early Miocene they had developed gigantism farther, and I believe more rapidly, than any other mammalian line, during the Oligocene epoch. Their legs had elongated and their feet had emphasized the middle toe rather more than the contemporaneous Early Miocene horses. Their teeth, at the same time, compare more nearly with latest Eocene than with any Oligocene horse teeth in molarization of the premolars and in the retention of low crowns; in comparison with other rhinos their teeth represent an Early Oligocene stage.

In the same way, tapir evolutionary achievement can be summarized as follows: from the Early Eocene to the present day, tapir cheek teeth have made roughly the progress that horses made by the Early Oligocene; in size and skull, tapirs compare best with Miocene horses; during all this time, their feet have remained in an Eocene stage, compared with perissodactyls in general, or with horses in particular.

If Goldschmidt had kept to his saltatory concept of "macroevolution" as a possible occasional *deus ex machina*, it would be impossible to disprove it by paleontological evidence; but for its universalized form such refutatory evidence is readily available. There are many such evolutionary series as the European dicerorhine rhinoceroses, where one closely-knit species succeeds another from a primitive Late Oligocene form to the highly specialized woolly rhinoceros of the Pleistocene. The curves of variation of the populations of some succeeding levels overlap, but the total amount of evolutionary change from beginning to end is more than "macroevolutionary" by Goldschmidt's standard. There is, however, no single level at which his postulated evolutionary jump could have occurred. The familiar horse series from *Mesohippus* to *Equus* covers an even longer time, produced a greater morphological change, and shows still more closely-knit successive populations.

So far as evolutionary trends are concerned, the rhinoceroses are perhaps more instructive than the horses, since they show as diverse trends as the messenger who jumped on his horse and galloped off in all directions. They have run to larger size than the horses, and have specialized in brawn rather than brain, but even in brain they show some progress, although at a slower rate than their rivals. Their well-publicized stupidity is only relative; even a pretty stupid rhinoceros is more intelligent than a brilliant alligator. Both horses and rhinoceroses developed distinct browsing and grazing trends; in the horses, the grazers predominated and alone survive to the present. Both types occur in living and fossil rhinoceroses. The browsers, the predominant type, had low (or, at most, medium) crowned teeth, represented by the living Sumatran and black rhinoceroses and most fossil forms. The white rhinoceros, the only living grazing form, has high crowned teeth. *Elasmotherium*, presumably a grazer, surpassed any horse in height of crown, being rivalled only by a few rodents. A few lines of rhinoceroses have even gone in for speed: *Diceratherium* and *Hyracodon*, or, as the extreme form, *Triplopus*, with its gazelle-like figure. The development of bulk has been much more typical, with the elasmotheres and the baluchitheres as the most striking examples. A semiaquatic fluviatile habitat like that of the hippos has been adopted twice independently, in the amynodonts and in *Teleoceras*; the former developed hippo-like canine tusks, and the latter, a more extreme barrel-like torso than the hippo.

The rhinoceros horn, which may be described as a high cone of appressed fibers (like hair without follicles), is unique in the animal kingdom. Besides this original invention, rhinoceroses have shown their individuality in the number and placement of their horns. The following patterns occur: a single median horn on the nasals, as in the Indian and Javan rhinoceroses, or on the frontals as in *Elasmotherium,* or on both, in a file, as in the Sumatran rhinoceros, the woolly rhinoceros, and the African rhinoceroses, or paired horns on the nasals as in *Diceratherium.* Most of these fashions evolved more than once from the diversified primitive stock of hornless rhinoceroses.

It is customary, though not very accurate, to cite the horses as a prime example of monophyletic evolution. The rhinoceroses have the opposite extreme, a "bushy" family tree, with no definite main stem but all side-branches, as illustrated either by the thirteen or so "main" lines of rhinoceros evolution (whether they are assigned family, subfamily, or supergeneric rank), or by the equally bushy development of the relatively primitive subfamily Caenopinae in both hemispheres.

One of the most striking convergences in parallel evolution (if the mathematicians will condone the solecism) is that between the woolly rhinoceros and the living white rhinoceros of Africa. The resemblance, especially in skull and teeth, is so close that it long seemed incontrovertible that they were extremely closely related. This now appears not to be the case. The white rhinoceros seems to be derived, with its relatively primitive cousin, the more abundant black rhinoceros, from a different Miocene-Pliocene ancestry, whereas the woolly rhinoceros is descended from a long known line of dicerorhine rhinoceroses related to the living Sumatran rhinoceros.

In the past, paleontologists have been among the worst offenders in offering orthogenetic interpretations of what appear to be more or less straight-line sequences. The rhinoceroses furnish a striking illustration of this type of phylogeny together with the evidence to act as antidote for this interpretation. The accompanying table shows the distribution in time and space of all known American amynodonts. No actual intergradation has yet been established in this sequence except between *Amynodon advenus* and *A. intermedius*, where there is either stratigraphic or morphologic intergradation, according to one's concept of species in paleontology. If species are defined strictly by their morphology,

DISTRIBUTION OF AMERICAN AMYNODONT RHINOCEROSES

		California		Rocky Mountain basins and Great Plains	
Oligocene	Whitneyan		No amynodonts are known from this age.	Orella	Upper *Metamynodon* sp., cf. *planifrons* but more advanced
	Orellan				Lower *Metamynodon planifrons*
	Chadronian			Chadron	*Metamynodon chadronensis*
Eocene	Duchesnean	Sespe	*Amynodontopsis bodei*	Duchesne River	*Megalamynodon regalis*
	Uintan		*Amynodon* sp.	Uinta	C *Amynodon intermedius* intergradation B *Amynodon advenus* and *A. reedi* A *Amynodon advenus*
	Uintan or Bridgerian or transitional	Poway	*Amynodon reedi*		
	Bridgerian Wasatchian	No amynodonts yet found			

one specimen of *A. intermedius* is known from Uinta B and several members of *A. advenus* have been collected from a quarry in Uinta C. On the other hand, if species are defined partly in terms of their geologic levels and (purely theoretical[2]) opportunities to interbreed, then the two species can be separated stratigraphically but overlap somewhat in structure. There is a virtually unitary succession of progressively more specialized types at each ascending geologic level. Except for the occurrence of *Amynodon reedi* (the most primitive species) in Uinta B as well as in the probably earlier Poway conglomerate of California, and the somewhat aberrant Californian *Amynodontopsis*, this series is a made-to-order example of so-called orthogenetic evolution. I know no other authentic case so devoid of side lines in which an "internal perfecting principle" seems so clearly to drive the organism through the predestined stages of racial youth, maturity, and old age to the inevitable doom of racial senescence and extinction. Such a plausibly mystical interpretation of the American amynodonts is rendered slightly ludicrous when the Mongolian amynodonts are examined; preliminary study shows that they include forms closely related to the American stock, by direct migration, as well as a group of autochthonous forms, diverging in multiple directions, in typical rhinoceros fashion. If the "orthogenetic" evolution of the North American amynodonts is attributed to some kind of purely internal control, it is difficult to see why this control should have disappeared at what was later to become the International Date Line.

Some amynodont evolutionary trends are remarkable illustrations of "relative growth." The progressive atrophy of the incisors and premolars contrasts sharply with the hypertrophy of the canines and molars. The molars seem to suffer plastic deformation; the lower molars are pulled out antero-posteriorly, with some shear, and pinched in transversely, and the buccal sides of the upper molars become progressively more hypsodont than their lingual sides, as if trying to grow over them in an arc. Altogether this is a remarkable evolutionary development, toward which the South American astrapotheres converge remarkably, as the only really similar combination. In all lines of amynodonts the skull tends toward achondroplasia. In both America (*Amynodontopsis*) and in Mongolia a wedge-shaped front of the skull evolved.

[2] Obviously, it is pure fiction that individuals from, say, the top and bottom of Uinta B belonged to a single interbreeding population, whereas those from the top of B and the bottom of C belonged to different populations.