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DINOSAURS, MAMMALS, AND MESOZOIC TAPHONOMY

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Predation is an important mode by which animals enter the fossil record. Reptilian and amphibian digestive systems decalcify prey, whereas those of small mammalian predators do not. The origin of endothermy in the fossil record should be marked by abundant, undecalcified coprocoenoses. If predacious dinosaurs were endothermic, microvertebrate coprocoenoses produced by them should reflect this. Ectothermic warm-bloodedness in dinosaurs could have resulted from high ambient temperatures, at least during the Cretaceous. An elevated body temperature in reptiles may be more important for digestion than for levels of activity. A short-term lowering of temperatures at the end of the Cretaceous could have induced digestive failure in reptiles, without affecting other physiological activities. A trend toward giantism in herbivores may be a means of processing forage high in cellulose.

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PREDATION AND SCATOLOGY

Predation appears to be an important means by which animals are introduced into the fossil record (Mellett 1974; Mayhew 1977). Recent work has indicated that the nature of the predator will have an important influence on the final fossil assemblage. Fisher (1981) has demonstrated that crocodylians will decalcify the bones and teeth of their prey, whereas this does not appear to happen in the case of small mammalian predators (Mellett 1974) or in owls (Dodson and Wexlar 1979). I have no information on what large mammalian predators (body weights > 50 kg) do to the skeletal remains of their prey, but I would predict that a modest amount of decalcification does occur, but not to the extent seen in crocodylians.

Other reptiles appear to macerate and decalcify their prey (Skoczylas 1970), and decalcification also appears to occur in the gut of large amphi-

bians. At the New York University herpetology laboratory, mice (*Mus musculus*) fed to an African bullfrog (*Pyxicephalus adspersus*) were completely digested, except for small amounts of hair and claws, which are keratin derivatives.

The major difference between what reptiles and mammals do to their prey appears to involve residence time of food in the gut, more specifically, in the stomach. Bone is rapidly denatured in a low pH environment, and the pH in the stomach of predatory reptiles can be as low as 1.2 (Skoczylas 1970). Once the food has passed from the stomach to the small intestine, pH rapidly rises toward neutrality or alkalinity, and further digestion of bone and tooth enamel ceases.

In general, the passage of food through the gut of predacious reptiles is measured in days, whereas carnivorous mammals of equivalent body mass will process food in a matter of hours (Skoczylas 1978; Stephens 1977). Again, the time difference is critical: the longer the prey remains in the stomach, the more likely it will become decalcified.

MESOZOIC TAPHONOMY

Now, what has this to do with taphonomic events in the Mesozoic? Basically, there should be a qualitative change in the vertebrate fossil record at the time endothermy arose, because endothermy cannot exist without rapid digestion of food. Coprocoenoses (Mellett 1974) prior to the advent of endothermic carnivores would have consisted of decalcified bone and teeth, and the record should be very sparse. Where Late Paleozoic or Early Mesozoic fossil remains are abundant, they would represent catastrophic mass deaths, or isolated deaths from natural causes.

Abundant, undecalcified microvertebrate accumulations would mark the development of a digestive physiology that was of a mammalian grade. The earliest coprocoenosis that fits this criterion was described by Kühne (1956), who examined fragmentary remains of *Oligokyphus*, a Rhaeto-Liassic tritylodont. There was no indication in the fossil deposit of what animal was feeding on *Oligokyphus*, but whatever it was clearly had a mammalian grade digestive system; the bones of *Oligokyphus* bear numerous tooth marks, and the tooth enamel is intact. The genera *Microconodon* and *Morganucodon* were contemporaries, and may have been the predatory forms.

Thus, the presence of a comminuted, undecalcified microvertebrate coprocoenosis would provide evidence that endothermy in some predator existed at the time of that accumulation. If such deposits can be found in Late Paleozoic or Early Mesozoic rocks, they could help settle the argument of whether some mammal-like reptiles were endothermic or not.

DINOSAUR ENDOTHERMY

If carnivorous dinosaurs were endothermic (Thomas *et al.* 1980), then coprocoenoses produced by them should reveal evidence of short gastric residence times. Relating a deposit exclusively to dinosaurs will not be an easy task, but if one were to find large amounts of decalcified fossil material of small vertebrates in a dinosaur community where there was no evidence of crocodylians or other reptiles, it would suggest that the carnivorous dinosaurs had a reptilian grade digestive system. On the other hand, discovery of a more typical coprocoenosis where no carnivorous mammals were found would imply an endothermic mammalian grade digestive system existed in the dinosaurs.

Mammalian remains throughout most of the Mesozoic are quite sparse indeed. Might that sparseness suggest not so much that mammals were not abundant, but that their remains were completely digested by large reptiles, and that no traces of them remain?

DINOSAUR ENDOTHERMY AND DIGESTIVE RATES

I cannot close without adding my thoughts on the "hot-blooded dinosaur" controversy. As it became clear that some degree of temperature control exists in many tetrapods, a variety of terms were proposed to attempt to clarify concepts of endothermy and ectothermy (Ostrom 1980). One significant concept advanced by McNab (1978) is that a large animal can be an "inertial homeotherm" because it cannot scale down its metabolic rate low enough to prevent heat from accumulating in its body. An inertial homeotherm is thus an endotherm by default, and the condition probably characterized most large dinosaurs. Whether all dinosaurs, including the smallest ones were endothermic is still speculative. Warmbloodedness by default may have arisen by another route. During the Cretaceous at least, where paleoclimatic data are abundant, mean surface temperatures were much warmer than today, averaging 31°C at the equator, 15°C at the poles, and 25°C in mid-latitudes (Barron *et al.* 1981). In such an environment, a terrestrial animal might be nominally ectothermic, but would in fact be warm-blooded because it was living in sauna-like ambient temperatures.

My second suggestion follows a line opened up by Skocyzylas (1970) and has to do with why endothermy is adaptive. It is clear that enzyme systems function better at elevated temperatures, and many workers have focussed on activity levels and muscular contraction as the important reasons for endothermy (Heinrich 1977). Skocyzylas has emphasized that rates of digestion in reptiles are temperature sensitive. I suggest that

digestion of food is far more important than activity levels in assessing the adaptiveness of endothermy.

Herndon G. Dowling (pers. comm.) reported that the New York Zoological Society had a large number of cobras (*Naja naja*) in captivity in late 1965. The snakes were active enough to consume laboratory rats (*Rattus rattus*) which were fed to them weekly. In spite of the fact that the ambient temperature was between 21–24°C and the snakes were moving about, within six weeks the cobras began regurgitating completely intact and undigested rats. Because modern predacious reptiles (and presumably carnivorous dinosaurs) swallow large boluses of food which take very long times to digest, any reduction in digestive rates would be critical.

This observation of course entitles me to propose yet another dinosaur extinction model. In this case, we suggest that if all dinosaurs were meteorologically warm-blooded ectotherms, a brief (< 1 year) period of climatic cooling sufficient to halt or seriously restrict digestion without affecting activity levels would give us a world of dinosaurs with full bellies, slowly starving to death.

FOOD QUALITY AND GIANTISM

Evolution of large size has occurred in many lineages of terrestrial animals, and the reasons proposed to account for giant size are just as numerous. I wish to propose yet another. To simplify matters, I concentrate on herbivorous forms, and assume that giantism in carnivores occurs as a result of increases in the size of their prey. Basically, I see giantism as a condition that can arise when food quality is poor, that is when the food consists of a high proportion of cellulose, as opposed to more soluble carbohydrates and protein. My assumption is based on the observation that among large ruminants, the introduction of small amounts of grain (rich food, high in soluble carbohydrates) to the normal high cellulose diet has a devastating effect on the digestive systems of the animals and radically alters the composition of the gastric bacterial flora (Stephens 1977). At the other end of the scale, it is essential for small animals to consume rich, highly soluble food because they cannot afford the time lag inherent in the digestion of a cellulose-rich diet.

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