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EVOLUTION OF HERBIVORY IN TERRESTRIAL VERTEBRATES: PERSPECTIVES FROM THE FOSSIL RECORD, edited by Hans-Dieter Sues. 2000. Cambridge University Press, Cambridge, 256 pp., hardcover $89.00.

When we look across fields of grazing cattle or sheep, or contemplate the huge diversity of hoofed mammals on the Serengeti Plain, it seems normal and natural that there have always been large numbers of herbivores on the landscape. In ecology classes, we are taught that the terrestrial food pyramid has much more bio-mass of herbivores than of the predators that feed upon them, and that a large standing crop of herbivores is essential in any trophic system to convey the energy of plant matter to other animals in the food web.

It comes as a complete surprise to most people, then, to find out that not only has it not always been this way, but that large areas of rapidly growing plants (such as grasses) and herbivores feeding upon them are a relatively recent innovation in the history of life. Like many other ecological concepts founded strictly on the modern biota, the concept of food pyramids and food webs needs drastic rethinking the further back we go in time. For most of life's history (from 3.5 to 0.5 billion years ago), there was no "food pyramid" or "food web"—just an uncropped layer of cyanobacteria and later eukaryotic algae forming a "Planet of the Scum." When the first grazing invertebrates arose in the latest Proterozoic, the landscape was changed forever, but as Bambach and others have shown, even in the Cambrian and Early Ordovician, the levels of ecological complexity did not yet match the food webs of present, and many guilds still had no occupants.

This is true not only of the marine realm, but also of terrestrial ecosystems as well. Simple vascular land plants and arthropods that fed upon them arose the Late Ordovician and Early Silurian, but the first land vertebrates did not appear until the Late Devonian, more than 70 million years later (a time lag longer than the entire Cenozoic). For most of the early history of vertebrates, all these terrestrial tetrapods were predators. The first likely herbivorous vertebrates do not appear until the Late Carboniferous, and they were rare. Clearly, the "food web" we take for granted was very different than the one we have today. Vertebrates fed on other vertebrates, or on insects and other arthropods, which were their only means of obtaining nutrition derived from plants.

Why did the evolution of herbivory take so long? Surely, the abundance of plant resources suggests that some sort of early tetrapod should have mastered the trick of eating this untapped reservoir of energy, and flourished in great numbers. But as Sues and also Reisz and Sues point out, herbivory takes many specialized adaptations that do not arise easily; they formed adaptive thresholds to eating plants directly. First of all, vertebrates do not have the natural enzymes to break down many plant materials, so they need specialized gut bacteria to digest cellulose and obtain nutrition from plants. This, in turn, demands a much longer digestive tract to allow bacterial fermentation, and a barrel-shaped rib cage for this huge gut. Most early tetrapods had simple peg-like teeth for grabbing prey, so herbivores needed to develop teeth for cropping and grinding plants, and eventually some even evolved jaws that can move back and forth in a chewing motion. Reisz and Sues discuss the appearance of these features in tetrapods, and discuss how herbivory might be recognized in an extinct taxon. The surprising conclusion is how late herbivory appeared, but it did nevertheless arise at least 12 times independently. Even more surprising, herbivores did not become common until the Late Permian with the appearance of several groups of herbivorous synapsids (especially dinocephalians and dicynodonts), the huge pareiasaur reptiles, and eventually herbivorous archosaurs (such as the rhynchosaurs and aetosaurs) in the Triassic.

Barrett and also Upchurch and Barrett discuss some of the paradoxes of Mesozoic herbivores, especially the huge sauropod dinosaurs, the largest terrestrial animals that ever lived. Despite their huge body size, sauropods did not have complicated dental batteries (such as those found in duckbill dinosaurs or horned dinosaurs), but simple peglike or spatulate teeth. Upchurch and Barrett speculate that the differences in neck length, head shape, and tooth shape may have allowed sauropods to feed at different levels of the tree canopy, and on different parts of plants, so that a high diversity of taxa (up to 14 genera in the Morrison Formation, with as many as six from one locality) could live in the same place. Still, their study does not address the fundamental problem that most of the plants that fueled sauropods (such as slow-growing conifers, ginkgoes, and cycads) do not recover from animal damage well, and do not grow as rapidly as angiosperms. Tiffney has speculated that ferns provided the rapid-growing "fodder" in the Jurassic before angiosperms arose, but clearly not all the pieces of this puzzle have been discovered.

Weishampel and Jianu use the method of ghost lineages to show that the apparent diversity of herbivores at any given time in the Mesozoic is a gross underestimate, and that many more lineages must have been present, making a totally different picture of how diversity changed through time.

Rensberger analyzes patterns of dental wear and cusp shape to discuss how herbivory first arose in mammals. Janis looks at the diversity patterns of different feeding groups of mammals (as defined by tooth morphology, and by body size) through the Paleogene. Her methods capture the well-known increase in diversity in the Paleocene, and the increase in body size of the larger herbivores by the Eocene, as well as the eventual replacement of ungulates with simple rounded ("bunodont") cusps for omnivorous diets by those with different configurations of crests ("lophs") and higher-crowned teeth. Her data also reveal paradoxes as well. For example, despite the prevalence of dense forests in the Paleocene and early Eocene, few ungulates were specialized leaf-eaters until the middle Eocene. Then there is a significant diversity increase in taxa (especially leaf eaters) continuing through the late Eocene and Oligocene, even though climate was cooling and changing, and the dense forests were largely gone by the early Oligocene. Janis provides additional analyses (such as plotting climates in a "dry-wet" axis as well as the simple temperature axis) to address the complexities of the real data, although some puzzles still have no good explanation.

Finally, MacFadden provides a review of the recent literature on the development of grasslands and grazers in the Neogene. The simplistic story that mammals evolved high-crowned teeth ("hypsodonty") for eating gritty grasses is now complicated by the fact that such teeth appeared in many lineages at 15-16 Ma, but the isotopic signal for abundant C4 grasslands (the dominant type found in temperate and tropical latitudes) did not appear until 7 Ma. Why did hypsodonty appear 8 million years before abundant grasslands? Were there C3 grasslands, as some suggest? If so, we have no modern analogues for such vegetation, since C3 grasslands occur today only in high latitudes or high altitudes. Were conditions drier so that the plants had more gritty dust on them? Clearly, the isotopic data have demolished the simplistic stories that we still tell our undergraduates, and leave as many questions to be answered as they have solved.

This volume was based on a symposium at NAPC-96 in Washington, D.C, but not published until more than four years later. Consequently, some of the papers have suffered because of new developments that have occurred in the four years from presentation to publication. Nonetheless, it is nicely produced, and yields many provocative papers that are of interest to anyone who has though about terrestrial paleoecology.

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