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Herbivory in terrestrial vertebrates: an introduction

Introduction

Understanding the ecological attributes of extinct organisms has long been a major research topic in paleobiology, dating back to the pioneering work of the French paleontologist Georges Cuvier in the early nineteenth century. Inferences concerning the ecology of an extinct organism can be based on functional interpretation of its structure, by analogy with present-day relatives, or from the sedimentary context and distribution of fossil remains referable to this taxon (Wing *et al.* 1992). Traditionally, functional morphology has been the most widely used of these approaches. It basically relies on the analysis of organisms as simple machines with functional attributes that can be inferred from the physical properties of their bodies as well as from their shape and size. Chemical analyses of hard tissues (such as extraction of preserved stable carbon isotopes) increasingly are providing significant new data for inferring diet in extinct animals. In recent years, researchers have developed various procedures for linking inferences concerning function in fossils to phylogenetic analyses, increasing confidence in the robustness of these reconstructions (see various papers in Thomason [1995]).

Herbivory, the consumption of plant tissues, is a widespread phenomenon among terrestrial vertebrates. It has frequently and independently evolved in many lineages of amniotes during the last 300 million years or so. Some major groups of herbivorous tetrapods, such as ungulate mammals and ornithischian dinosaurs, attained great abundance and taxonomic diversity. Indeed, the advent of herbivory among land-dwelling tetrapods was one of the key events in the history of life on land. It led to the establishment of 'modern' continental ecosystems, with vast

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numbers of herbivores supporting a relatively small number of carnivores, during the Permian period (Olson 1966; Hotton *et al.* 1997; Sues and Reisz 1998).

Feeding on plants requires many morphological and physiological modifications to facilitate the efficient reduction and digestion of plant tissues. Plant fodder contains less caloric energy per volume unit than do animal foods (Southwood 1973). Furthermore, in most instances, much of that energy is tied up in substances that are difficult to digest for vertebrates. The contents of plant cells are enclosed by walls that are primarily composed of cellulose, hemicellulose, and lignin. Cellulose is a polymer of glucose, but its glucose units are linked together in such a fashion that it cannot be readily broken down. This makes plant tissues, to varying degrees, more difficult to digest than animal tissues, which are devoid of resistant cell walls. Extant vertebrates lack any endogenous enzymes to hydrolyze the compounds forming the cell walls of plant tissues, but many micro-organisms (bacteria, protists) can produce them. Thus many plant-eating tetrapods have entered into endosymbiotic relationships with such organisms to facilitate cellulysis in their digestive tracts, resulting in the production of sugars and volatile fatty acids that can be absorbed by the vertebrate host. Not only are the walls of the plant cells themselves resistant to unaided digestion by vertebrates but they often protect the digestible cellular contents such as lipids, sugars, organic acids and proteins. Initial breakdown of the cell walls by mechanical or chemical action is thus required.

Plant tissues are highly variable in terms of their nutritional value to vertebrate consumers. Certain plant parts, such as fruits, seeds, and immature vegetative tissues, contain much digestible matter that is only protected by relatively delicate cell walls and often require only little processing to make the enclosed nutrients available to the consumer. However, these are seasonally available resources, and most herbivores subsist on the tougher, more cellulose-rich vegetative structures, such as leaves, roots, shoots and stems that form the bulk of available plant material. The effective utilization of such fodder by the vertebrate consumer requires two steps. First, the plant material must be mechanically broken up by oral processing or by comminution in a muscular foregut or gizzard using ingested grit and pebbles. Grinding the plant fodder more finely clearly increases the rate at which herbivores can process it (Bjornedal *et al.* 1990). Second, symbiotic micro-organisms in the gut must convert the cellulose into volatile fatty acids (especially acetic, butyric,

and proprionic acid) that can be readily absorbed by the vertebrate host. Not all extant herbivorous vertebrates employ microbial endosymbionts. Some animals such as the giant panda *Ailuropoda melanoleuca* (Schaller *et al.* 1985) apparently compensate for this lack by consuming large amounts of plant fodder as well as maintaining relatively low activity and growth rates (see McNab 1986).

Most studies of herbivory in present-day vertebrates have focused on the digestive performance of plant-eating mammals, particularly ungulates, due to the commercial importance of the latter (McBee 1977; Chivers and Langer 1994). The adaptations for feeding on plants in non-mammalian tetrapods are much less well studied. Relatively few taxa of present-day reptiles are obligate herbivores, and the range of structural features of the skull and dentition for feeding on plants is limited compared with that in mammals (Throckmorton 1976). However, more recent work has demonstrated that plant-eating iguanid lizards can degrade cellulose and hemicellulose almost as efficiently as herbivorous mammals (Troyer 1984).

Herbivory in extinct vertebrates

Unequivocal evidence for trophic interactions between extinct animals and plants is only rarely found. Therefore, inferences concerning herbivory in extinct vertebrates must rely almost entirely on circumstantial evidence. Starting with Cuvier's pioneering work, paleontologists have correlated broadly defined feeding categories with specific morphological attributes, primarily of the skull and dentition, in tetrapods. Such correlations are based either on analogy to present-day animals with known dietary habits or on biomechanical assessment of the suitability of tooth structure for processing potential food items (e.g., Rensberger 1973; Lucas 1979). In a few instances, fossilized gut contents provide a more direct line of evidence, but it is important to rule out postmortem introduction of material into the abdominal cavity. Furthermore, some food stuffs may have already been digested prior to the death and fossilization of the consumer.

Mammals are distinguished from most other tetrapods by extensive oral processing of food or mastication. Thus their masticatory apparatus provides an excellent model for correlating tooth structure with diet. The specific relationships between gross occlusal structures and mechanical performance can be modeled (Rensberger 1973; Lucas 1979; Lucas and

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Luke 1984) and, in many instances, can be tested experimentally in extant forms (Kay and Sheine 1979; Teaford and Oyen 1989). Wear on tooth enamel at the microscopic level can be related to diet and the masticatory system (Walker *et al.* 1978; Rensberger 1986), and complex functional associations exist between enamel microstructure, gross occlusal features, and chewing direction (Koenigswald 1980; Rensberger and Koenigswald 1980). As teeth are the most commonly preserved part of the mammalian skeleton, they thus become a valuable resource for paleontologists and physical anthropologists concerned with paleoecological questions.

In non-mammalian vertebrates, the correlation between diet and dentition is much more difficult because oral processing of food and thus tooth occlusion are uncommon. Furthermore, in some groups (especially birds) with herbivorous taxa, teeth are absent altogether. However, based on biomechanical considerations and comparison with extant forms, it is still possible in many cases to interpret craniodental attributes in general terms of their biomechanical suitability for feeding on a particular type of material.

Dental features suggestive or indicative of high-fiber herbivory include dentitions adapted for crushing and grinding, or marginal teeth with labiolingually compressed, leaf-shaped, and cuspidate crowns suitable for puncturing and shredding plant fodder. Features of the skull and mandible variously associated with feeding on plants, especially in mammals, include short tooth rows (along with foreshortening of the snout and mandible), elevation/depression of the jaw joint relative to the occlusal plane for increased mechanical advantage of the adductor jaw muscles, enlargement of the adductor chambers and temporal openings as well as deepening of the zygomatic arches and mandibular rami for the origin and insertion of substantial adductor jaw muscles, and jaw joints suitable for complex mandibular motion (Maynard Smith and Savage 1959; Turnbull 1970; Rensberger 1986; Janis 1995). Finally, plant-eating tetrapods typically have longer and/or bulkier digestive tracts, and a longer and/or broader trunk region, than related faunivorous forms (Schiek and Millar 1985; Dearing 1993) because part of the gut is modified to form a reservoir housing and creating suitable pH conditions for the endosymbiotic micro-organisms involved in the fermentative breakdown of the cellulose from the ingested plant fodder. Passage of food through longer intestinal tracts also allows for longer periods of time for processing of resistant materials. Thus the rib cages of many herbivorous tetrapods are either much wider and more capacious ('barrel-shaped')

than those of their closest faunivorous relatives, or the trunk region is elongated to accommodate a longer digestive tract. This is reflected in overall body proportions as well as in the structure of the vertebral column.

In this volume, nine contributors examine the structural correlates of herbivory in various taxa of herbivorous tetrapods and discuss them in relation to the evolutionary diversification of these groups.

Reisz and Sues (Chapter 2) review the earliest occurrences of herbivory in amniote tetrapods. They use the craniodental and, to a lesser extent, postcranial features discussed above to identify probably herbivorous taxa among late Paleozoic and Triassic amniotes. The oldest known putative herbivores, of Late Pennsylvanian age, are the Diadectidae, a group of tetrapods very closely related to the Amniota, and the basal synapsid *Edaphosaurus*. Surprisingly, feeding on plants only became common among tetrapods during the Late Permian. At that point in time, vertebrate herbivores first became a key component of the terrestrial food web, leading to the establishment of the basic trophic structure of modern terrestrial ecosystems (Olson 1961, 1966). Phylogenetic analysis indicates that herbivory was repeatedly and independently acquired in various lineages of amniotes during the Late Carboniferous and Permian (Sues and Reisz 1998).

In his discussion of possible diets for prosauropod dinosaurs, Barrett (Chapter 3) injects a cautionary note concerning the identification of herbivory in non-mammalian tetrapods based primarily on dental features. Citing anecdotal evidence, he argues that present-day iguanid lizards, which have teeth with leaf-shaped, serrated crowns, have long provided a model for inferring herbivory in certain dinosaurs with similar teeth, but are actually omnivorous rather than strictly herbivorous. However, few extant vertebrates are exclusively herbivorous, and many herbivores supplement their diet by the intake of animal protein.

Upchurch and Barrett (Chapter 4) review the craniodental and postcranial features of the constituent clades of sauropod dinosaurs in relation to possible feeding strategies. They marshal evidence ranging from patterns to dental microwear to browsing height inferred from skeletal proportions to demonstrate a diversity of possible feeding styles among sauropods. Sauropodomorph dinosaurs (prosauropods and sauropods) are noteworthy because they represented the first diverse radiation of mega-herbivores (*sensu* Owen-Smith [1988], with body weights exceeding one metric ton) and were capable of foraging at greater heights (i.e., more

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than one or two meters above the ground) than other plant-eating tetrapods at that time.

Weishampel and Jianu (Chapter 5) present a detailed phylogenetic analysis of the various major taxa of dinosaurian herbivores. They emphasize the importance of taking into consideration the unrecorded segments of lineages ('ghost lineages') that can be inferred based on phylogenetic hypotheses in estimating overall diversity. The authors find little evidence to support the currently popular coevolutionary scenario linking the onset of the evolutionary diversification of flowering plants (angiosperms) to the radiations of large ornithomimid and ceratopsian dinosaurs.

Rensberger (Chapter 6) provides an elegant analysis of the biomechanical factors dictating tooth configuration in herbivorous placental mammals from the early Cenozoic. In the two most common groups of early Paleocene ungulates in North America, the shearing component of mastication was greatly reduced relative to the condition in more primitive mammals and compression became the dominant component. Rensberger demonstrates that the stresses in the tooth enamel induced by chewing are lower in low, wide cusps than in tall, sharp cusps. Prism decussation (where zones of prisms with a common orientation alternate with zones of prisms with a different orientation) in the enamel increases resistance to fracturing. It appears in most ungulates as body size increases later during the Paleogene. With the acquisition of stronger enamel, the earlier trend toward more blunt cusps is reversed, and shearing crests reappear.

Based on a recent compendium of Tertiary mammals from North America, Janis (Chapter 7) reviews the diversification of the different types of feeding strategies (as deduced from tooth shape) in herbivorous mammals from the Paleogene (Paleocene–Oligocene) of North America. She relates the relative abundance of the different kinds of tooth shape to climatic changes during the Early Tertiary inferred from other lines of evidence. The early 'condylarths' were presumably omnivorous rather than strictly herbivorous. Feeding on foliage (folivory) apparently did not occur until the latest Paleocene. The earliest artiodactyls and perissodactyls appear in the early Eocene, but they had dentitions more typical of omnivores/frugivores, and folivory in these groups was not common until the late Eocene. Although ungulates with relatively high-crowned teeth are known from the Paleogene, there is no evidence of true grazers in the fossil record until the Neogene.

MacFadden (Chapter 8) presents an overview of recent work by him and various colleagues, including the application of isotopic analyses, on the origin and early evolution of the grazing guild among Neogene mammals from the Americas. Grazing first developed as a major feeding strategy during the Miocene. The acquisition of high-crowned teeth, which appears to be an adaptation to the pervasive occurrence of highly abrasive silica particles in grasses, is interpreted as a coevolutionary response to the advent of widespread grassland communities at that time. Grazing was independently acquired in various North American groups (artiodactyls, perissodactyls, proboscideans, rodents) and in the South American notoungulates prior to the formation of the Panamanian land bridge. Based on MacFadden's work, grasslands and grazing mammals may have originated slightly earlier in South America than in North America. Data for stable carbon isotopes indicate that the earliest grasslands were formed by C₃ grasses. The change to the grasslands dominated by C₄ grasses (which comprise most grasslands today) occurred after the late Miocene and may explain the observed decline in grazing diversity after the late Miocene.

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ROBERT R. REISZ AND HANS-DIETER SUES

2

Herbivory in late Paleozoic and Triassic terrestrial vertebrates

Introduction

The exploitation of land plants as a major food resource by amniote tetrapods led to profound changes in the pattern of trophic interactions in terrestrial ecosystems during the late Paleozoic (Olson 1961, 1966; King 1996; Hotton *et al.* 1997; Sues and Reisz 1998). Prior to the appearance of various forms specialized for feeding on plants, tetrapods could access the plentiful vegetal resources only indirectly through detritivory and consumption of invertebrates that fed on plants and/or plant detritus (Olson 1961, 1966). The oldest plant-eating tetrapods are known from the Late Pennsylvanian (Late Carboniferous) of North America and Europe. However, herbivores did not form a major component of the known terrestrial tetrapod assemblages from the Early Permian. Only during the Late Permian, some 40 million years after their first appearance, did plant-eating tetrapods become abundant and much diversified in the fossil record. At that time, a 'modern' pattern of trophic interactions was established, with a vast standing crop of herbivores sustaining a relatively small number of top carnivores. Communities of this type are first documented by diverse assemblages of tetrapods from the Late Permian portion of the Beaufort Group of South Africa (Kitching 1977) and, to a lesser extent, from more or less coeval continental strata in other regions of the world.

Morphological and physiological correlates of herbivory

The effective utilization of high-fiber plant material by vertebrates requires two steps. First, the plant material must be mechanically broken

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up by oral processing or by comminution in a muscular gizzard using ingested grit and pebbles. Present-day herbivorous lizards do not chew their food (Throckmorton 1976), and leaves often pass through the gastrointestinal tract virtually intact (Bjorndal 1979; Iverson 1982). Grinding the plant fodder more finely clearly increases the rate at which herbivores can process it (Bjorndal *et al.* 1990). Second, symbiotic micro-organisms in the gut must convert the cellulose into volatile fatty acids (especially acetic, butyric, and propionic acid) that can be readily absorbed by the vertebrate host.

In this chapter, we review the possible exploitation of high-fiber plant material by various groups of late Paleozoic and Triassic terrestrial tetrapods. We discuss the earliest stages in the evolution of herbivory among terrestrial tetrapods and the possible impact of this feeding strategy on the evolution of continental vertebrate communities. It is important to stress here that relatively few extant reptiles are obligate herbivores (see also Barrett, this volume), and most feed on a variety of dietary items (see below). By analogy, we expect similar dietary versatility among late Paleozoic and early Mesozoic amniotes. However, we should note that the skeletal modifications observed in certain extinct forms are, among extant vertebrates, most commonly associated with diets that include high-fiber plant material as the primary component.

In most cases, inferences concerning the dietary habits of extinct vertebrates rely on circumstantial evidence. Dental features suggestive or indicative of high-fiber herbivory include dentitions adapted for crushing and grinding, or marginal teeth with labiolingually compressed, leaf-shaped, and cuspidate crowns suitable for puncturing and shredding plant fodder. Cranial features variously associated with feeding on plants, especially in mammals, include short tooth rows (and related foreshortening of the snout and mandible), elevation or depression of the jaw joint relative to the occlusal plane for increased mechanical advantage of the adductor jaw muscles during biting, enlargement of the adductor chambers and temporal openings as well as deepening of the zygomatic arches and mandibular rami to accommodate powerful adductor jaw muscles, and jaw joints suitable for complex mandibular movements (Maynard Smith and Savage 1959; Turnbull 1970; Rensberger 1986; Janis 1995). Herbivorous tetrapods typically have longer and/or bulkier digestive tracts, and a longer and/or broader trunk region, than related faunivorous forms (Schiek and Millar 1985; Dearing 1993) because part of the gut is modified to form a reservoir housing and creating suitable pH conditions for endo-