

Review

## Prey processing in amniotes: biomechanical and behavioral patterns of food reduction

S.M. Reilly<sup>a,\*</sup>, L.D. McBrayer<sup>a</sup>, T.D. White<sup>b</sup>

<sup>a</sup>*Department of Biological Sciences, Ohio University, Athens, OH 45701, USA*

<sup>b</sup>*Biology Department, Buffalo State College, Buffalo, NY 14222, USA*

Received 1 April 2000; received in revised form 14 August 2000; accepted 4 October 2000

---

### Abstract

In this paper we examine the biomechanics of prey processing behavior in the amniotes. Whether amniotes swallow prey items whole or swallow highly processed slurries or boluses of food, they share a common biomechanical system where hard surfaces (teeth or beaks) are brought together on articulated jaws by the actions of adductor muscles to grasp and process food. How have amniotes modified this basic system to increase the chewing efficiency of the system? To address this question we first examine the primitive condition for prey processing representative of many of the past and present predatory amniotes. Because herbivory is expected to be related to improved prey processing in the jaws we review patterns of food processing mechanics in past and present herbivores. Herbivory has appeared numerous times in amniotes and several solutions to the task of chewing plant matter have appeared. Birds have abandoned jaw chewing in favor of a new way to chew — with the gut — so we will detour from the jaws to examine the appearance of gut chewing in the archosaurs. We will then fill in the gaps among amniote taxa with a look at some new data on patterns of prey processing behavior and jaw mechanics in lizards. Finally, we examine evolutionary patterns of amniote feeding mechanism and how correlates of chewing relate to the need to increase the efficiency of prey processing in order to facilitate increased metabolic rate and activity. © 2000 Elsevier Science Inc. All rights reserved.

**Keywords:** Chewing; Feeding; Functional morphology; Mastication; Prey transport; Prey processing

---

\* Corresponding author. Tel.: +1-740-593-0424; fax: +1-740-593-0300.

E-mail address: reilly@ohiou.edu (S.M. Reilly).

## 1. Introduction

Feeding is of fundamental importance in the process of energy acquisition because it is the feeding mechanism that delivers food to the digestive system where nutrients required for energy, maintenance, growth, and reproduction are assimilated. In terrestrial vertebrates feeding involves prey capture or ingestion followed by varying amounts of processing before the prey item (or what is left of it) is transported to the esophagus for swallowing. Feeding mechanisms exhibit a myriad of anatomical features related to getting food into the mouth and optimal foraging strategies are often used to select the highest quality foods. However, once food is in the mouth, the processing stage can have a major influence on the nature of the food passed on to the gut and subsequent digestive efficiency. In fact, elaborations of food processing mechanisms and the resultant increases in the mechanical reduction of food being digested were critical in the evolution of both herbivory and endothermy in amniotes. In this paper we examine the biomechanics of prey processing behavior in the amniotes. Whether amniotes swallow prey items whole (e.g. lizards) or swallow highly processed slurries or boluses of food (e.g. mammals), they share a common biomechanical system where hard surfaces (teeth or beaks) are brought together on articulated jaws by the actions of adductor muscles to grasp and process food. How have amniotes modified this basic system to increase the processing efficiency of the system? We will begin with a review of the prey processing in mammals because by definition they are the only amniote that 'chews'. We have to understand the unique transverse chewing system in mammals and its terminology before we can examine the nature of prey processing behaviors in other taxa. We will then examine the primitive condition for prey processing representative of many of the past and present predatory amniotes. Because herbivory is expected to be related to improved prey processing in the jaws we will review patterns of food processing mechanics in past and present herbivores. Herbivory has appeared numerous times in tetrapods and it occasionally has involved changes in the primitive scissors-like jaw closing system to allow propalinal (longitudinal) movements of the lower jaw to effect grinding of plant matter. Birds have abandoned jaw chewing in favor of a new

way to chew — with the gut — so we will detour from the jaws to examine the appearance of gut chewing in the archosaurs. We will then fill in the gaps among amniote taxa with a look at some new data on patterns of prey processing behavior and jaw mechanics in lizards. Finally, we will examine correlates of chewing and how they relate to the need to increase the efficiency of prey processing in order to facilitate increased metabolic rate and activity. We emphasize that this review is a first look at some of the issues herein and based on an incomplete comparative literature available to date from which to base our synthesis.

## 2. Mammals: the definitive chewers

Approximately 180 million years ago in the synapsid lineage that was to become the mammals, three unique features arose in the feeding system: (1) The jaw joint and relative shapes of the upper and lower jaws changed so that the jaws could be brought together to breakdown food *unilaterally* — that is with only one side of the jaw at a time; (2) changes in the jaw joint and adductor muscles allowed *transverse* (lateromedial) *movements* of the lower jaw against the upper jaw; and (3) upper and lower molars developed into what are called *tribosphenic molars* which have complex surfaces and cusps that fit together in a dynamic way during occlusion (Turnbull, 1970; Crompton, 1971; Crompton and Hylander, 1986; Bown and Kraus, 1979; Herring 1993). When these three features operate together it produces the tribosphenic chewing stroke (Crompton and Hiiemae, 1970; Hiiemae, 1976), unique to therian mammals, where individual cutting edges on the lower molars shear lateromedially against one or more matching facets on the upper molars before certain cusps settle into their final matching basins on the opposing teeth (Fig. 1). These repetitive shearing and mortar and pestle-like movements of occluding tooth cusps reduce food material to a fine particle size that expedites the rate of chemical breakdown after bolus formation and swallowing. Earlier cycles in which high points of tooth crowns break and crush larger particles of food without the teeth coming into contact are termed 'puncture crushes' (Hiiemae, 1976). In puncture crushing the predominant direction of movement is vertical and the jaw begins to open well before the full latero-

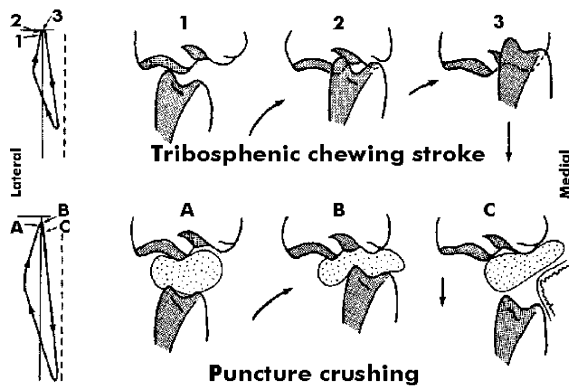


Fig. 1. Chewing and puncture crushing in mammals. In the tribosphenic chewing cycle chewing occurs on one side of the jaw as the lower molars are ground lateromedially across the upper molars. Puncture crushing involves mostly vertical movements where the teeth crush the food item without occlusion. Head on kinematics of the lower jaw are shown on the left relative to the midline of the oral cavity (vertical dashed line). Numbers and letters indicate the point in the kinematic profile that each of the drawings occurs. Adapted from Hiiemae (1976).

medial translation seen in the tribosphenic chewing stroke occurs (Fig. 1). Various therians also use blade-shaped teeth (such as carnassials), blades on the sides of molars, and serial arrays of low-profile blades on molars (as in ungulates) to cut, tear, and grind food by 'shearing' these blades past each other. Prey items or food particles are also moved from side to side or repositioned using the tongue for another reduction cycle and this is referred to as 'manipulation.' Thus, in generalized therian mammals, prey processing (the activities between ingestion and transportation to begin swallowing) involves shearing bites, puncture crushing bites, and tribosphenic chewing strokes interspersed with manipulation movements with the tongue.

The extensive three-dimensional mechanical reduction of food produced by this system is unique to mammals (Turnbull, 1970; Crompton, 1971; Herring, 1993). It has been variably defined as 'chewing', 'mastication', and 'trituration' by mammalian workers, and thus, by this definition mammals are not only the definitive chewers, they are the only chewers. In understanding the evolution of prey processing in terrestrial vertebrates we are left with the paradox that 'chewing', being defined on the basis of the derived mammalian system, is limited to mammals. To gain some

generality about prey processing one must consider the functions of food reduction in mammals. Mammalian chewing or mastication is proposed to serve two functions: first, to reduce material to a condition suitable for swallowing; and second, to facilitate for the penetration of digestive enzymes and so to expedite chemical breakdown (Hiiemae and Crompton, 1985). We will show in the following sections that prey processing systems in a variety of amniotes carry out these functions with a variety of prey reduction mechanisms and that chewing in the functional sense, though not done with unilateral, transverse occlusion of tribosphenic molars, is widespread.

### 3. Biomechanical solutions to processing plant matter

To exploit plant resources animals have to break down the structural polymers of cell walls to gain access to the easily digestible contents of plant cells. Because vertebrates lack the enzymes to chemically break down cell walls most herbivores utilize a set of symbiotic micro-organisms to break down structural polymers chemically into volatile fatty acids which can be absorbed along with the cell contents. Any mechanical reduction that can be accomplished with the jaws or by muscular churning in the stomach increases the efficiency of fermentation and decreases the adaptive cost of herbivory as a foraging strategy. Comparisons of biomechanical patterns found in herbivores are thus heuristic in understanding the evolution of amniote chewing. A review of the jaw mechanics of food processing patterns associated with herbivory in amniotes (excluding mammals) reveals two basic strategies used to process plant foods. In one, which is essentially similar to the primitive jaw mechanism of all non-mammalian predatory tetrapods, the lower jaw articulates tightly with the upper jaw and the jaws close like a hinge, shearing the lower teeth inside the upper teeth as the jaws close. As we will see this system is the predominant system employed in both herbivorous and predatory forms. In the second pattern, the jaw articulation surfaces are shaped such that the lower jaw moves longitudinally relative to the upper jaw in a propalinal fashion, grinding plant matter between molariform teeth or keratinized surfaces on both jaws.

### 3.1. Arcilineal jaws: the default prey processing system in tetrapods

Although there is great variety in skull size, form, and feeding adaptations the basic amniote skull has a long rostrum with a row of simple pointed teeth along the upper and lower jaws. The jaw joint is near the back of the skull and at about the level of the tooth rows when the mouth is closed. Non-mammalian amniote skulls have isognathous jaws where the lower jaw is about the same size as the upper jaw. When these jaws close, the teeth slide past one another or sometimes occlude simultaneously on both sides of the jaw (unilateral occlusion seen in the anisognathous jaws of mammals is not possible). Because matching articulating surfaces on the quadrate and articular bones of the jaw joint do not allow longitudinal or transverse movements of the lower jaw, the joint acts like a hinge. Thus, the lower jaw can only rotate down and up as it opens and closes. Because the teeth can only swing dorsoventrally in an arc relative to the upper jaw we term this an *arcilineal* jaw (a term to contrast with the propalineal jaw described below). This jaw system is the present in amphibians and thus, is the basal condition for amniotes (Olson, 1961; Hotton et al., 1997).

The adductor muscles are divided into external and internal groups (Olson, 1961; Turnbull, 1970; King, 1996). The internal group (primarily the pterygoideus muscles) run from the palate anterior to the jaw joint to the back of the lower jaw. They are oriented perpendicular to the jaw when it is open and thus are positioned to act primarily in producing rapid and forceful jaw closing during the bite (Fig. 2a, kinetic bite). The external adductors extend from the side of the skull down to the rear third of the lower jaw where there is often a coronoid eminence or process to which some muscle bundles attach. These muscles are more perpendicular to the jaw when it is closed, and thus, are positioned to primarily apply static pressure on prey or food already in the jaws as would be needed for prey processing (Fig. 2b). Electromyographical data from a number of taxa have verified that the external adductors function more or less continuously during feeding with greater activity during prey processing while the internal adductors are used primarily to increase biting forces during wide open bites (Robinson, 1976; Dalrymple, 1979; Reilly and Lauder, 1990;

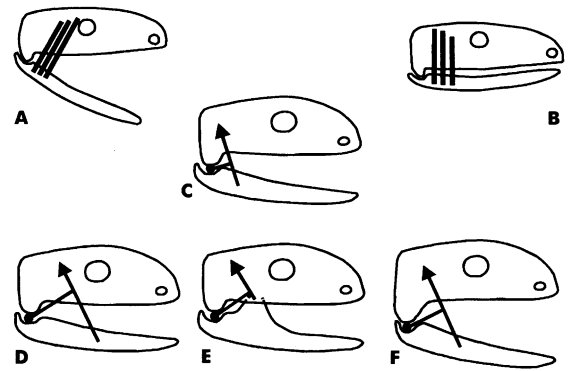


Fig. 2. Simplified biomechanics of amniote jaws. In general, based on muscle alignments relative to the jaw, muscle groups are designed for either inertial biting (a) when the jaws are open, or static chewing (b) when the jaws are nearly closed (Olson, 1961). From this basic combination of muscle groups the jaw lever system in amniotes (c) there are three primary ways to increase the lever arm of jaw muscles acting on the jaw joint to increase chewing forces: (d) moving muscle insertions further out on the lower jaw; (e) moving the muscle insertions higher onto the coronoid process; (f) moving the position of the jaw joint to increase the lever arm [adapted from King (1996)].

Herring, 1993; McBrayer and White, unpublished data). This basic biomechanical system (with biting and chewing muscles) occurs widely among predatory and omnivorous amniotes; prey processing is produced by arcilineal bites that bring the array of simple, pointed teeth together (Fig. 3a–e) to grasp, puncture, shear, crop, and crush prey items that are being captured and swallowed more or less whole. Beyond the function of grasping prey items for capture and transport, the remaining functions act to condition the prey item for swallowing and in crushing and puncturing the prey item they expedite chemical breakdown by increasing the surface area available to digestive enzymes. The arcilineal jaw system thus serves the functions of prey processing defined for mammals (Hiimeae and Crompton, 1985). Details of the functioning of arcilineal jaws in lizards are presented below (Section 5).

### 3.2. Arcilineal herbivory

Surprisingly, many amniote taxa have become successful herbivores with only slight modifications of the arcilineal jaw system (Fig. 4: open circles and triangles). These modifications involve changes in the jaw mechanics to facilitate greater static pressure between the jaws during interme-

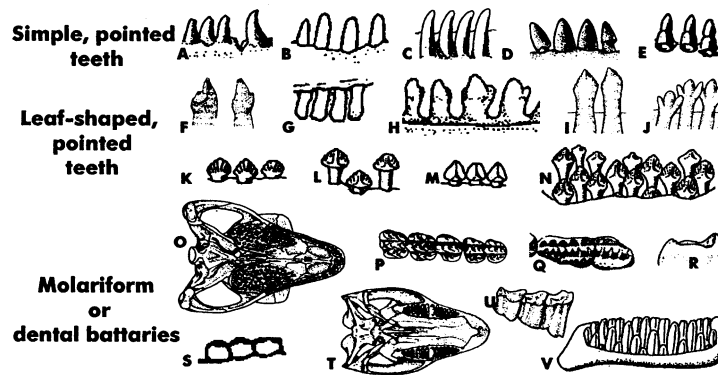


Fig. 3. Representative amniote teeth (excluding therians). The top row illustrates the generalized teeth of many amniotes that are simple and pointed. These are common to most omnivorous and many herbivorous forms. The second two rows illustrate the leaf-shaped or blade-like teeth common in herbivores. The last two rows illustrate molariform teeth and dental batteries exhibited by herbivorous amniotes. Individual taxa (discussed in text) are: (a) an early synapsid, *Ophiacodon retroversus*; (b) a procolophonian anapsid, *Procolophon*; (c) a lizard, *Gerrhonotus liocephalus*; (d) a crocodilian, *Alligator allegheniensis*; (e) a bird, *Archeopteryx lithographica*; (f) a dinocephalian synapsid, *Tapinocephalus*; (g) a caseid synapsid, *Casea*; (h) a bolosaurid anapsid, *Bolosaurus*; (i) a lizard, *Iguana iguana*; (j) a lizard, *Amblyrhynchus cristatus*; (k) a stegosaur, *Stegosaurus*; (l) an ankylosaur, *Edmontia*; (m) a pachycephalosaurid, *Stegoceras*; (n) a ceratopsian, *Protoceratops*; (o) an Edaphosaurid synapsid, *Edaphosaurus*; (p) a tritylodontid synapsid, *Kayentatherium*; (q) a multituberculate synapsid, *Cimolodon nitidus*; (r) a therocephalian synapsid, *Bauria*; (s) a diademodontid synapsid, *Diademodon*; (t) a trilophosaurid, *Trilophosaurus*; (u) a dinosaur, *Heterodontosaurus*; and (v) an euornithopod, *Bactrosaurus*. Adapted from Edmond, 1960 (a,c,e,i–n,v); Smith, 1960 (d); King, 1996 (b,f–h,o,p,r–u); and Clemens and Kielan-Jaworowska, 1979 (q).

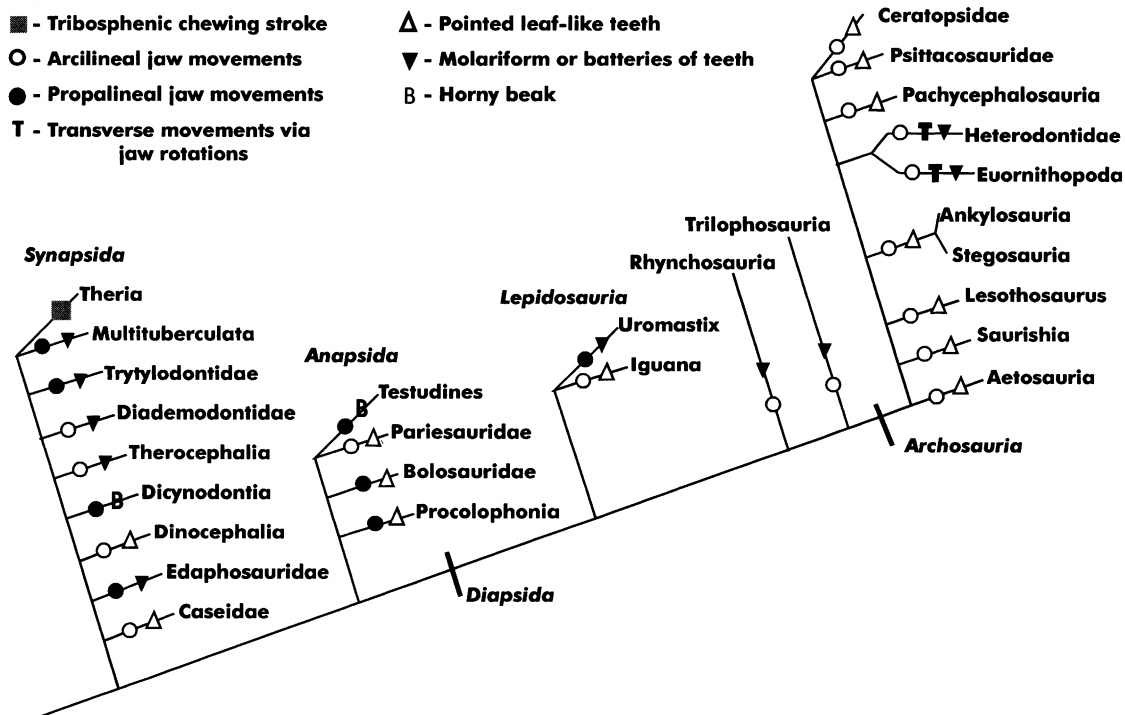


Fig. 4. General patterns of jaw mechanics and tooth shape in representative herbivorous amniotes. Note the prevalence of arcilineal jaws with pointed leaf-like teeth and the rarity of propalinal jaws and molariform teeth outside the synapsids. Determinations of herbivory, jaw mechanics and tooth morphology are based on Olson (1961), Sokol (1967), Carroll (1991), King (1996), and Hotton et al. (1997). Phylogenetic framework based on Gauthier et al. (1988) with lepidosaur pattern from Estes and Pregill (1988), and archosaurian pattern from Witmer (1997).

diate to small gape angles used in prey processing. Although variability is widespread and multiple changes can occur, three basic biomechanical changes are observed in the relationship between the adductor muscles and the jaw joint (Fig. 2). Each of these increases the moment arm of the jaw joint (the perpendicular distance between the line of adductor action and the jaw joint) which results in greater jaw closing forces during prey processing. From the basic arcilneal jaw (Fig. 2c) the moment arm is increased by: (1) moving the external adductors anteriorly on the lower jaw (Fig. 2d); (2) shifting the adductors dorsally with a longer coronoid process on the lower jaw (Fig. 2e); or (3) moving the jaw joint farther away from the adductors (Fig. 2f). In addition, forces used in prey processing can be increased by shortening the lengths of the jaws by shortening the snout. Some arcilneal herbivores retain the basic shearing, scissors-like jaw closing movements while in others the upper and lower tooth rows have become parallel allowing all the teeth to shear at once (sometimes described as an orthal movement). Among arcilneal herbivores one or more of these changes may be observed to improve prey processing mechanics at the expense of forceful kinetic bites. However, several herbivorous taxa have retained the primitive adductor muscles observed in carnivorous relatives and ancestors. For example, the caseids, dinocephalians and therocephalians (synapsids), modern iguanian lizards, and several dinosaur lineages (ankylosaurs, stegosaurs, and pachycephalosaurs) have the primitive generalized adductor pattern (King, 1996). Another obvious change that would increase the efficiency of reducing plant matter would be to develop chewing teeth better shaped to increase food reduction as the jaws come together.

What is surprising about arcilneal herbivores is that the predominant shift in tooth form is a minor one in which primitive, pointed teeth (Fig. 3a–e) simply become blade-like (Fig. 3f–n). These teeth are broader anteroposteriorly, usually still pointed, but either serrated or triradiate on the cutting edge. They form rows of blades along each jaw that would shear across the teeth of the opposing jaw to cut and shred plant matter. This herbivorous strategy, which is similar to predatory and omnivorous amniotes except for the serrated blade-like teeth, has appeared in two synapsid lineages, three anapsid lineages, in several lepidosau-

saurians, and in many dinosaur lineages (Fig. 4, open circles, open triangles). Except for the lizards, these were not rare forms but represent significant radiations, some of which were dominant forms of their times. They show that successful herbivory is possible with the comparatively little mechanical reduction afforded by arcilneal jaw mechanism with simple blade-like teeth whether the jaw mechanics remain unchanged (as in the taxa listed in the previous paragraph) or change to increase jaw closing forces.

Arcilneal herbivores with molariform teeth (Fig. 4, open circles, closed triangles) are rare and some exhibit fairly extreme features to enable the teeth to occlude. The diademodontids and therocephalian synapsids and the trilophosaurians (an outgroup to the Archosauria) had broadened molariform teeth worn down into grinding surfaces. The Rhynchosauria (a more distant outgroup to the Archosauria) had two rows of broad molariform teeth on each jaw that occluded with opposing tooth rows or fit into bony grooves in the opposite jaw. The Psittacosaurus cropped food with their sharp beaks and chewed with a single row of cheek teeth with broad planar wear surfaces bordered by self-sharpening lateral cutting surfaces. The Ceratopsidae also cropped with a beak but chewed with extensive dental batteries of closely packed leaf-shaped cheek teeth (Fig. 3n) stacked low on the inside and high on the outside that would cut on the outside but grind on the inside as the jaw closed (Dodson, 1997).

The euornithopod dinosaurs maintained the arcilneal jaw joint but incorporated movable jaw bones to get the opposing teeth (Fig. 3u,v) to grind together transversely. The heterodontosaurids rotated the lower jaws medially to allow the lower tooth rows to shear medially across the stationary upper tooth rows while the euornithopods (including *Iguanodon* and hadrosaurs) had a pleurokinetic hinge (Norman and Weishampel, 1985) that allowed the maxillary teeth to rotate laterally across the stationary lower jaw teeth. The transverse grinding movements of these dinosaurs are the only other cases of transverse chewing known outside the mammals. The size of the tooth batteries in these dinosaurs relative to their body sizes seems small but as we will see below dinosaurs also had another way of chewing. Given the relative rarity of molariform teeth in arcilneal forms and the extreme features needed for their use it appears that the con-

straints of isognathous jaws and multiple tooth replacement have limited the development and success of accurately occluding teeth in arcilneal forms. Interestingly, the arcilneal forms with molariform teeth usually exhibit specialized tooth eruption patterns and fewer cycles of replacement (Edmond, 1960; King, 1996). Thus, it is not necessarily the development of molariform teeth that is so difficult — it is getting the teeth to grind across one another in occlusion that is the primary constraint of arcilneal system. In Section 3.3 we will discuss one solution to this problem that has arisen in several amniote groups.

### 3.3. Propalinal jaws: using longitudinal movements to increase food reduction

An interesting observation from the jaw mechanics in arcilneal forms is that the shifts in adductor positions to increase vertical jaw closing forces to facilitate prey processing would also increase the ability to move the lower jaw anteriorly and posteriorly if the jaw joint would permit it. Adductors in the arcilneal jaw are essentially preadapted to pull anteriorly (with the internal group) and posteriorly (with the external group). All that is needed to effect propalinal jaw movements is for the jaw articulation surfaces to allow the lower jaw to slide anteriorly from the hinge socket during prey processing. This has happened several times in several herbivorous amniote clades (Fig. 4: solid circles). In every case where propaliny is found (based on jaw articulating surfaces that permit propalinal jaw movements and the presence of longitudinal tooth wear) there is also a shift to either molariform teeth or a cornified jaw covering with which to grind food (Fig. 4, filled triangles). Propalinal chewing is not only associated with expanded chewing surfaces in the cheek region but is usually accompanied by additional changes in the adductor complex, jaw joint position, and/or coronoid process to facilitate the forward and backward movements used during prey processing (King, 1996). In addition, in each of the groups that has developed propaliny, not only have more molariform grinding surfaces appeared, but tooth replacement has either been lost (one set of teeth or a beak), reduced, or modified to produce dental batteries where normal replacements of individual teeth are inconsequential to the overall grinding surface (Edmond, 1960; King, 1996).

Propalinal chewing (Fig. 4) was present in the earliest synapsids (edaphosaurids), in the dicynodonts (who lost teeth in favor of a beak and a horn covered palate and jaws) and in several later synapsid taxa appearing before the advent of anisognathous jaws in the Mammalia (tritylodontids, which includes the Traversodontidae). Among the anapsids, propalinal jaw movements are used in the Procolophonia, bolosaurs and the modern herbivorous Testudinates (turtles) to process food. Although studies of jaw function in carnivorous turtles are lacking it is clear that tortoises (Bramble, 1974) and several herbivorous side-necked turtles (Schumacher, 1973) use propalinal jaw movements to grind plant matter between specially ridged masticatory surfaces on their horny beaks. Among the lepidosaurians one species has adopted propaliny with herbivory and one species has developed propaliny with carnivory. The genus *Uromastix* (Agamidae) is unique in using propalinal jaw movements to grind plant matter with precisely occluding molariform teeth and highly modified adductor muscles (Throckmorton, 1978). It has only one set of teeth and these often are worn completely down in older individuals where chewing and even cropping is done with the jaw itself forming the cutting edge (Throckmorton, 1976, 1978, 1980). The basal lepidosaur group, Rhynchocephalia, contains one extant genus (*Sphenodon*) that has developed propaliny that must be a formidable chewing system. The upper jaw has two rows of carnassial-like teeth that straddle the single row on the dentary on closing. Propalinal movements of this system produces perhaps one of the best shearing jaws known in amniotes (Gorniak et al., 1982) and it is the only form we know that uses propaliny and blade-like teeth.

Biomechanically, the combination of propaliny with molariform teeth (or keratinized jaws) seems like it would increase grinding efficiency over arciliny (or even the tribosphenic chewing system as evidenced by approximately half the mammals (most rodents and a few others) and the extinct multituberculates that have secondarily acquired propalinal chewing). The propalinal system would clearly appear to reduce food material to a finer condition for swallowing and chemical breakdown. Thus, it might be expected to be more prevalent among herbivores. Our review, however, reveals that propalinal chewing is rare outside the synapsids (Fig. 4). Basically, it is

observed in five herbivore radiations — four among the synapsids and in the Testudines. The first terrestrial herbivores, the edaphosaurs (Fig. 3), had propaliny as did the dicynodonts (with a beak). Multiple variations of propaliny with molars arose in the cynodonts (diademodontids, multituberculates, Fig. 3s,q). Turtles have settled on propaliny as a successful feeding system even without teeth. Surprisingly, except for two Lepidosaurians (*Uromastix* and *Sphenodon*), propaliny is not found in the diapsids (Fig. 4). Among archosaurs, herbivory was rare in the crocodile side of the group (the Crurotarsi) being found only in the aetosaurs but was common on the dinosaur side of the group. The herbivorous archosaurs with their arcilineal jaws, were among the most successful herbivores in history and were certainly the largest. Why they did not experiment with propaliny is an interesting question. The answer may have had something to do with their development of a different way to chew, with the gut.

#### 4. Archosaurs: chewing with your gut

The jaws in birds are widely known to be specialized for prey gathering. The complex cracking and winnowing performed by jaws and tongues of seed eaters is the only semblance of chewing in birds and some groups, like the parrots, have taken it to an extreme level. Most birds, however, use their jaws to gather, strip, and manipulate pieces of food that are then thrown down the throat (Cloudley-Thompson, 1972; Kear, 1972). Observing a heron eating a fish, a pigeon gathering grain, a hawk stripping off pieces of flesh, or an insectivore feeding shows there is little prey processing occurring once the food enters the mouth. Biomechanically birds have effectively lost the chewing component of the amniote jaw mechanism (Smith, 1993; Zusi, 1993). The design of the bird jaw, although still arcilineal, shows an obliteration of the cheek region, the loss of teeth, and expansion of the anterior portion of the jaw. In fact, most of the upper 'beak' of birds is the premaxillary bone and the major tooth-bearing upper jaw bone involved in chewing in amniotes (the maxilla) is reduced, often to the point of nearly being lost (Bock and Kummer, 1968; Buhler, 1981). In addition, the great increases in the size of the orbits and braincase have nearly overrun the postorbital bar and arch between the

temporal fenestrae characteristic of diapsids (Zusi, 1993). Accordingly, the external adductors, usually large and prominent in this area of the tetrapod skull, are small and simple. The entire area where the upper jaws, palate, and lower jaws meet the brain case has changed drastically, is highly kinetic, and bones are much reduced in size (Simonetta, 1960). The lower jaw articulates through several bones to the lower brain case, the upper jaw hinges with the skull roof and palate. The upper and lower jaws can be moved independently but their movements are often coupled so that both jaws move during opening (Bock, 1964; Zusi, 1967; Buhler, 1981). Many biological roles have been suggested for the independent and coupled jaws systems in birds (Bock, 1964) but it is clear that the fundamental advantage for the highly kinetic skull in birds is in the versatility of the jaws as manipulative tools not only in feeding but in preening, nest building and defense (Beecher, 1962; Zusi, 1967; Smith, 1993). In fact, the tight relationship of avian trophic morphology with the *location* of the food rather than the properties of the food has made them the model group for relating bill morphology to resource use (Lederer, 1975; Grant and Grant, 1989; Smith, 1993). In addition, skull kineticism allows for the production of larger gapes in the distal part of the jaws with a relatively smaller jaw depressor muscle (Bock, 1966; Zusi, 1967). In a sense, birds are left with only the anterior cropping part of the amniote jaw. This is reflected in the use of the jaws only in prey gathering and as a way to hold the esophagus open during feeding to deliver food to the gut. Birds have a distensible crop off of the esophagus that stores food essentially as swallowed until it can be fed to the stomach for processing — another indication that that jaws are primarily a gathering device. In birds, all of the time spent 'feeding' is dedicated to gathering and chewing is done later.

Birds chew with a specialized portion of their stomachs — the gizzard. The gizzard, or ventriculus, is a muscular organ in which large opposing muscles surround the central lumen where food is ground. The lumen is lined with a horny layer that is periodically molted as it wears down. Contraction of the huge smooth muscles generates forces that grind the food between the horny sides of the lumen. The gizzard muscles are asymmetrical so they generate translational forces grinding the two sides of the lumen together as



indicated by the wear patterns on the horny lining (Moore, 1998a,b). The muscularity of the gizzards is related to prey hardness (Richardson and Wooller, 1990). The parallels to grinding food with mammalian jaws are striking. Rhythmic contractions are used (Duke et al., 1972) and rocks, pebbles and grit often are ingested to add even harder grinding surfaces for chewing. These 'gastroliths' remain in the gizzard (Browne, 1922), are worn smooth by the chewing action, and birds pick the roughest stones they can find to replace them. Gizzard stones increase both the efficiency and perhaps more importantly the speed of grinding in the gizzard (Titus, 1955). As might be expected, gizzard force production varies with diet with the greatest force development in the grazers which can produce intraluminal pressures of 180–280 mmHg, compared to 100–150 mmHg in granivores, and 8–26 mmHg in carnivores (Sturkie, 1976). Adding to the chewing efficiency of the gizzard is the fact that it secretes its own pepsinogen, maintains a low pH of 2–3.5, and receives food pre-soaked in a variety of gastric secretions from the proventriculus (Ziswiler and Farner, 1972; Sturkie, 1976). In addition, there are mechanisms operating in the gizzard that wring out and filter larger as yet undigested parts of food (such as separating seeds from fruit) and pump out the digested slurry much as the tongue would during swallowing in the mouth. In a sense, the gizzard functions in 'swallowing' as well. Undigested boluses are either ground further or regurgitated as in owls, flycatchers and birds of prey. So, the addition of the gizzard to the bird stomach creates a stomach that functions like the jaws plus the stomach in other vertebrates. Coefficients of digestibility in birds are comparable to those of mammals (Titus, 1955; Nakahiro, 1966), and thus, the gizzard works at least as well as tribosphenic chewing in mammals eating similar foods. In fact, given the limitations on the size of the bird gut owing to the limitations of flight, they may actually 'chew' more efficiently than mammals and they do it with less body mass devoted to prey processing.

Modern crocodilians also have a two part stomach that works essentially exactly like that of birds including the extensive use of gizzard stones (Corbet, 1960). Although gastroliths have been suggested to function as ballast in these secondarily aquatic archosaurs, the fact that they are held in the gizzard and ground smooth, and that cro-

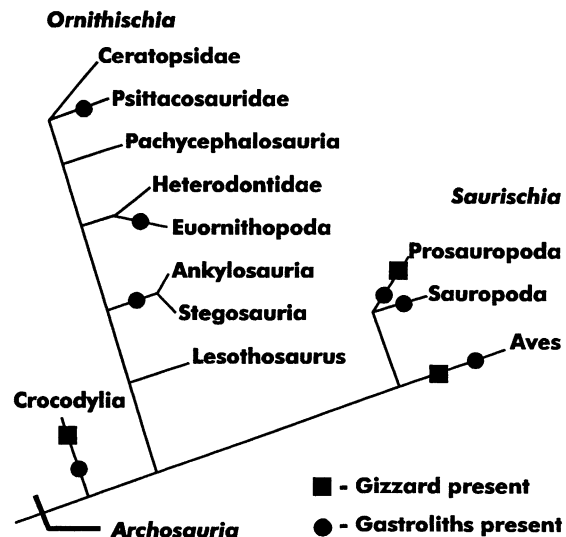


Fig. 5. Evidence of a gastric mill in the Archosauria. Phylogenetic topology from Witmer (1997). Evidence of gastroliths from Corbet (1960), Currie and Padian (1997), Glut (1997), Gillette (1994), Brown (1907), Manley (1991), Raath (1974) and Whittle and Rose (1988).

codilians commonly dive and remain submerged without them indicates a triturating role as in birds. In addition, crocodilians with gizzard stones have significantly higher gut assimilation efficiencies than those without them (Davenport et al., 1992). Understanding the function of the gizzard in birds and crocodilians gives us valuable inferential information in tracing the evolution of prey processing in archosaurs. Even though there has been a lot of extinction in the Archosauria, the presence of the gizzard as the chewing mechanism in crocodilians and birds suggests that the gizzard is common to all archosaurs (Fig. 5). Further evidence for widespread occurrence of the gizzard among archosaurs comes from the presence of gastroliths in fossil taxa along both archosaur branches and extensive evidence of them in both the ornithischian and saurischian lineages. New techniques are being used to show that gastroliths were ground in the gizzards in these paleospecies (Whittle and Rose, 1988; Manley, 1991; Johnston et al., 1994) and it seems clear that the gizzard was used as a chewing mechanism across the archosaurs. In addition, given how well the size of the gizzard and the use of gastroliths correlates with the foods hardness in extant forms, it is perhaps not surprising that gastroliths are common in herbivorous fossil ar-

chosaurs and usually not found in carnivorous forms.

The gizzard is often considered to be the *compensatory* organ for the loss of teeth (e.g. Stevens and Hume, 1995) which seem obvious in birds. But birds are among the few archosaurs that have lost all of their teeth. The rest of the Archosaurs have plenty of teeth in an otherwise fairly simple arcilneal jaw system. Why is it that propaliny is not found in the rather extensive radiations of the archosaurs? Perhaps the advent of chewing with the gizzard (that we know is an extremely effective chewing system) precluded further chewing modifications of the jaw. Minor chewing by the jaws would facilitate the reduction and swallowing of rough plant matter (such as cycads, conifers) that would be stored in the crop and processed in the gizzard. This would explain why many very large herbivorous forms had heads considered to be too small to have *processed* enough food — they were gathering food and preparing it enough for the gizzard as in modern forms. In archosaurs, arcilneal jaws worked in concert with gizzard chewing to provide food processing on a par with that of mammals. Furthermore, advent of the gizzard may have shifted the functional role of the jaws away from a prey processing function toward the essentially prey-gathering (prey capture) function it has in modern archosaurs. In terms of the predatory archosaurs, the gizzard freed the head to function as a prey gathering device for which arciliny was not only sufficient but perhaps a better design for forceful killing bites. The presence of the gizzard may also explain why there were so many large predatory forms. In terms of the birds, the gizzard did not compensate for the loss of teeth, its appearance in archosaurs was probably one of several key innovations in the evolution of flight-facilitating the loss of teeth, the reduction of head mass, and shifting the chewing organ towards the center of mass. Clearly archosaurs possess the functions of chewing defined from mammalian jaws whether processing prey with the jaws and gizzard or with the gizzard alone.

##### 5. Filling in the gap: arcilneal prey processing behavior in lizards

Among extant amniotes, the mammals (tribosphenic chewing system), archosaurs (arciliny

with a gizzard) and turtles (propaliny) are derived in their feeding mechanisms and lepidosaurians (except for *Sphenodon* and *Uromastix*) are the only group using a simple arcilneal system to feed. In addition, the skulls of lizards are often taken as a primitive model for amniotes (Smith, 1993). Therefore, analyses of feeding behavior in lizards can provide information on the basic functioning of arcilneal jaws in prey processing.

Several species of lizards have independently developed morphological changes associated with durophagy of molluscs and crabs. Species with spheroid peg-like teeth bordering on molariform in shape appear in several lizard families (Iguanidae, Teiidae, Xantusiidae, Lacertidae, Scincidae, Anguidae, and Varanidae; Estes and Williams, 1984). These 'molariform' teeth, however, are produced by wearing down of essentially normal teeth and only two genera (*Dracaena*: Teiidae; *Tiliqua*: Scincidae) develop molariform teeth early in development (Estes and Williams, 1984). Durophagous lizards generally do exhibit changes in adductor muscle and jaw size, enlarged muscle attachment sites, and modified motor patterns that facilitate increased crushing forces (Lonnberg, 1903; Dalrymple, 1979; Krebs, 1979; Rieppel and Labhardt, 1979; Wineski and Gans, 1984; McBrayer and White, unpublished data). Durophagous lizards clearly have increased their ability to crush hard food in ways similar to arcilneal herbivores in other amniote taxa. However, these species are not obligate molluscivores and there are other species known to consume molluscs with no evidence of changes in the basic arcilneal jaw and simple dentition (Smith, 1993). This reflects a common observation in lizards — that phenotypically generalized lizards often consume the same food items as morphologically specialized lizards (Greene, 1982). Thus, in general lizards are opportunistic feeders.

However, in terms of feeding behavior, lizards fall into two phylogenetic groups employing different foraging strategies that result in different diets (Fig. 6). The major basal lizard radiation (the Iguania) are *sit-and-wait predators* that sally forth from perches to catch passing prey and they generally eat larger active prey that are homogeneously distributed. The top two major branches of the lizards (the Autarchoglossa) are *active foragers* which cruise through their relatively larger home ranges, poking and digging through litter, and rely more on chemosensory specializa-

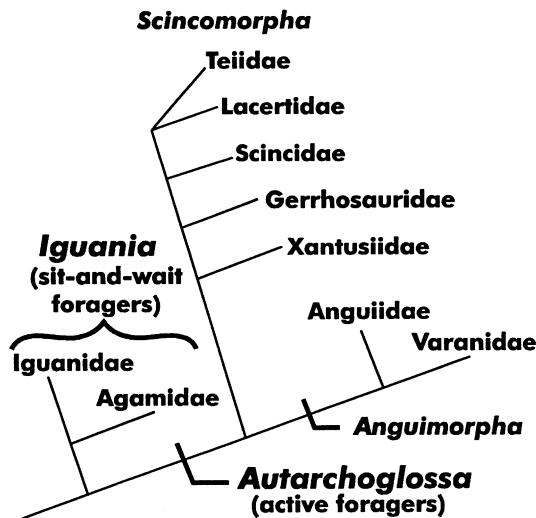


Fig. 6. Patterns of foraging behavior in the Lepidosauria (Cooper, 1994).

tions to locate prey (Cooper, 1994; Huey and Pianka, 1981). They often focus on concealed prey and locate pockets of heterogeneously distributed prey resources (like termites or nests). Much has been written about the ecological, behavioral, social, and dietary differences of the two foraging strategies and how these taxa interact on the community level (Regal, 1978; Vitt and Price, 1982; Huey and Pianka, 1981; Day et al., 1999; Perry, 1999). How they differ in terms of feeding behavior and jaw mechanics has been the focus of our recent work and preliminary results reveal several interesting patterns that relate to evolution of prey processing in lizards.

#### 5.1. Behavioral and biomechanical contrasts of sit-and-wait vs. active foraging lizards.

Lizards have been predicted to have extensive intraoral prey processing behaviors (Bramble and Wake, 1985; Reilly and Lauder, 1990). Because the nature of and extent of prey processing and manipulative behaviors in lizards has not been quantified (Elias et al., 2000) we have undertaken a broad scale behavioral and morphological analysis of feeding in lizards not only to compare the two feeding strategies known in lizards but understand lizard feeding in the context of other amniotes. Based on our preliminary data (McBrayer and Reilly, unpublished data) the prey processing repertoire of 16 lizard species we have examined (those behaviors after the capture and before

transport to swallowing begins) involves: (1) *puncture crushes* essentially identical to those of mammals; (2) *side-to-side transports* of the prey item; (3) *general transports* repositioning the prey within the jaws for another processing stroke; and (4) an as yet undescribed behavior where the prey item is pressed between the tongue and palate as the jaws close tightly with little penetration of the teeth within the prey. In addition, species with highly derived chemosensory tongues (*Tupinambis* and *Varanus*) utilize inertial transport behaviors with or without the use of the tongue (Smith, 1982, 1984; Condon, 1987; Elias et al., 2000). It is clear that lizards are performing prey crushing cycles (puncture crushes and the novel compression behavior) often separated by various types of transport movements (side-to-side, general, and inertial) to reposition the prey that are essentially identical to puncture crushing and manipulation behaviors of mammals. Thus, lizards appear to 'chew' their prey more than had been expected given that they eat prey more or less whole. Even more interestingly, the active foragers appear to be using more complex prey processing behaviors. Preliminary comparisons show several quantitative differences in the feeding repertoires of sit-and-wait vs. active foraging lizards (Fig. 7). First, in the sit-and-wait species the prey compression movements (Fig. 7, stippled bars) are dominated by the novel jaw compression behavior which is usually done in a series of compression cycles without repositioning, and thus, they have significantly fewer transport cycles (Fig. 7, white bars). They appear to employ the novel behavior to crush and presumably moisten the prey within the oral cavity. Second, the active foraging species exhibit significantly more cycles (approximately twice the amount) of prey processing jaw movements between the strike and the onset of prey transport cycles (Fig. 7, mean numbers of behaviors). Third, the increase in the number of processing cycles is produced by an increase in the number of puncture crushes (Fig. 7, black bars) and an increase in the intervening unilateral, side-to-side, and inertial repositioning transport movements (Fig. 7, gray and white bars). Thus, the active foragers have more cycles of prey processing and a repertoire dominated by organized positioning and puncturing of prey items prior to swallowing. Finally the autarchoglossans consistently scrape the sides of the head on the substrate while feeding to shear off part of the prey

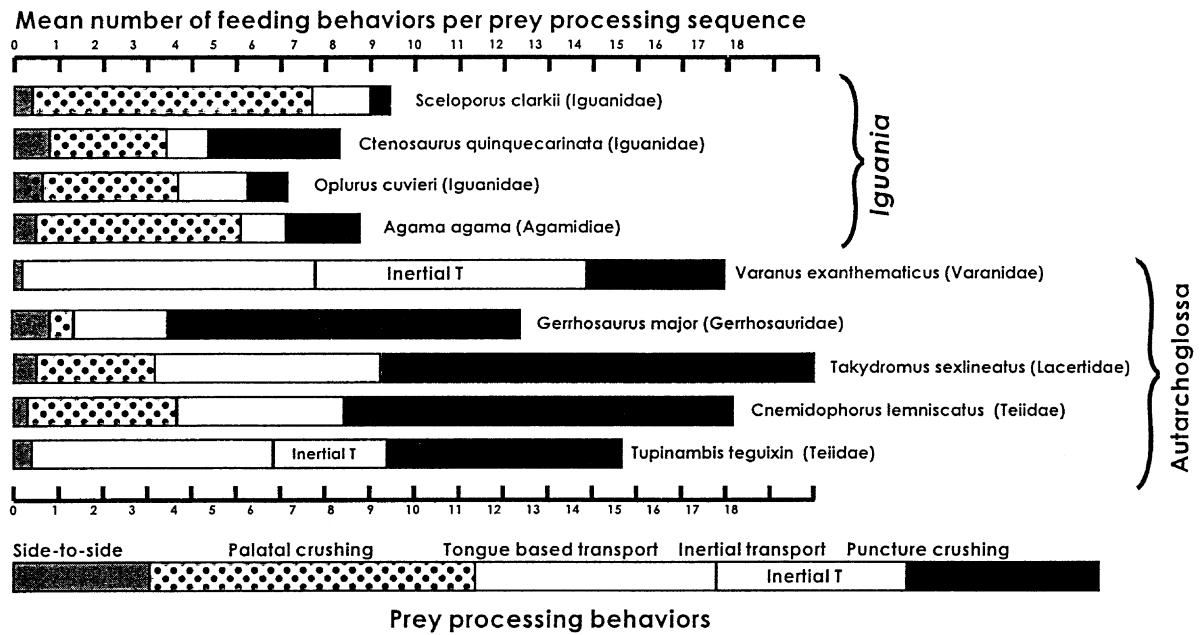


Fig. 7. Preliminary analysis of prey processing behavior in sit-and-wait (Iguanian) vs. active foraging (Autarchoglossan) lizards. Note the increase in side-to-side, tongue-based transports and puncture crushing behaviors in the active foraging species. Behavioral data are from high-speed video recordings of individual feeding bouts of lizards feeding on prey sizes adjusted to the same relative to head length. Sample sizes from individual lizards studied are indicated in parentheses.

outside the jaws — often biting the heads or limbs off to be consumed subsequently (personal observation). Clearly, lizards meet the functions of chewing (facilitation of swallowing, facilitation of digestive penetration) and there is an obvious increase in the extent and nature of chewing behavior in the autarchoglossans that appears to be correlated with their active foraging strategy. In fact, the intermixing of puncture crushes and various transport behaviors provides compelling evidence that lizards (and particularly the autarchoglossans) are chewing. And species with highly specialized chemosensory tongues have even developed inertial transport behaviors (not known in most other lizards) to make up for the inability of the tongue to carry out manipulative transports (Elias et al., 2000). How do biomechanical patterns in the feeding mechanism relate to these differences in feeding behavior?

The primitive condition for lizard jaw mechanism based on fossil outgroups is a jaw built for rapid bites and weak chewing (Robinson, 1976; Dalrymple, 1979). However, several comparative studies of the jaw adductors in lizards have shown that across extant lizards the jaw adductors are positioned to work at their greatest mechanical

advantage when the jaws are near closure with maximal forces produced in the region of the maxillary teeth (McDowell and Bogert, 1954; Olson, 1961; Carroll, 1969; Haas, 1974; Rieppel, 1978; Wineski and Gans, 1984; Gans et al., 1985). Thus, although they have arcilneal jaws and pointed simple teeth, biomechanically modern lizards are built for static bites used for chewing rather than for the kinetic bite used in prey capture (McDowell and Bogert, 1954).

In comparing the sit-and-wait and active foraging taxa, the only major morphological differences in the two feeding strategies noted to date are in the tongue and hyoid apparatus (Schwenk, 1988). The iguanians have a relatively large fleshy tongue supported by a robust hyobranchial apparatus and generally have short wide jaws. The tongue is projected, at least partially, out of the mouth to capture prey and used extensively in prey processing. The autarchoglossans have narrow pointed jaws and more streamlined, forked tongues supported by lighter more gracile hyobranchial elements. Their tongues are functionally adapted to a chemosensory function (Schwenk, 1993; Cooper, 1994, 1995) and, although tongue protrusion is greater than in igua-

nians, it is only protruded during olfactory behavior; very rarely is it involved in prey capture (Schwenk and Throckmorton, 1989). In terms of tongue morphology, the predominance of the novel compression behavior in iguanians may be related to the generalized form of their tongue. The switch to increased use of the teeth with puncture crushing in the autarchoglossans parallels the skull streamlining and decreased prey manipulative function of their tongue.

We have also found several additional biomechanical differences among the active foragers that appears to relate to their more complex prey processing repertoire (McBrayer, unpublished data). First, although the internal adductors are essentially similar in size and shape, the active foragers exhibit various modifications of the lower jaw (e.g. larger coronoid processes) to facilitate muscular and tendinous insertions. Second, the active foragers tend to have strikingly larger internal tendons and increased angles of pinnation in the external adductors that attach to the skull and lower jaw over a relatively longer portion of the jaw. In addition, the dorsal attachments of the external adductors to the cranium are expanded relative to iguanians (Costelli, 1973). Third, the external adductors in some autarchoglossans (Teiidae; McBrayer, unpublished data) have what one could call an atlanto-occipital ligament running through the muscle to the lower jaw. This ligament increases in size considerably up the scincomorph branch of the group. Fourth, in autarchoglossans, the pterygoideus muscles exhibit larger internal tendons and increased pinnation angles, and a variety of modifications to the retroarticular processes (e.g. longer, flatter, or expanded processes) to facilitate muscle attachments and extend the lever arm. All of these changes, paralleling the kinds of changes to increase mechanical advantage in chewing used by other amniotes, suggest that the autarchoglossans have modified the jaw mechanism in ways to increase bite forces during prey processing compared to iguanians. If one combines these biomechanical shifts with the increased chewing complexity of their prey processing repertoire, it seems clear that the active foraging crown lizard taxa have increased the degree to which they manipulate and chew prey over the basal sit-and-wait iguanians.

## 6. Conclusions and future directions

So what can we say about patterns of prey processing in amniotes? It is clear from the simple review we have made that chewing is not limited to mammals. Based on the defined functions of chewing (Hiimae and Crompton, 1985) it appears that most amniote taxa and indeed several major radiations of amniotes process their food in ways that prepare it for swallowing and increase surface area for digestive enzymes. The new information on prey processing in extant lizards shows that even the default jaw system of arcilneal jaws with simple pointed teeth can be used to reduce prey for swallowing, and to puncture and crush even large prey items to facilitate digestion. Furthermore, given the widespread retention of this system historically, and its widespread use in herbivores, our basic impression of primitive amniote feeding should realize that arcilneal jaws with simple or leaf-shaped teeth and adductors aligned for static bites is the most widespread feeding mechanism in both herbivores and omnivores and that chewing should be considered as one of the functions of this system.

Biomechanically how have amniotes improved chewing? Although taxonomically most amniotes have the arcilneal jaw system, six basic modifications have occurred to 'improve' chewing mechanics. First, it is universal among herbivores using the arcilneal jaw system to see a shift from simple pointed teeth (of omnivores) to various forms of leaf-shaped teeth that appear better suited for shearing, cropping and chopping plants. Second, a few herbivores and durophagous omnivores have added molariform teeth to the arcilneal jaw. This includes the development of gomphodont-like teeth in the Therocephalians (synapsids) and Trilophosaurians (diapsids) and the appearance of peg-like teeth (by development or by wear) in durophagous lizards and the Rhynchosaurians (diapsids). Third, a few herbivores adopted propalinal jaw movements with molariform teeth (several synapsids and one lepidosaurian) or cornified beaks and jaws (one synapsid and the Testudines). Fourth, the mammals developed several novel modifications of their complex chewing system (anisognath, tribosphenic molars, unilateral occlusion with transverse movement and dentary-squamosal jaw joint)

although many mammalian herbivores have reverted to propaliny with molars. Finally, the advent of the gizzard in archosaurs made possible the fifth and sixth additional chewing systems. In the predominant one, the default arcilneal jaw is involved in some prey processing before passing the food to the gizzard (most extinct archosaurs and some birds) and thus, the jaws and gizzard both process food. In the other archosaur system, chewing is done by the gizzard only and the jaws, freed from the function of prey processing, have radiated into a myriad of forms for prey gathering (crocodilians and most birds).

#### 6.1. Historical patterns in amniote feeding systems

Though each of the major amniote clades seems to have started with the default arcilneal system, each moved in a different direction. The synapsids moved early and often to propaliny with molars and were very successful with changes in the jaw joint, adductors and teeth (and secondary palate, cheeks) setting the stage for the series of novel changes enabling the mammalian system to emerge (note, however, that the immediate outgroups to the Theria had arciliny with shearing teeth). The anapsids tried propaliny with leaf-shaped teeth and settled on propaliny with a beak. Among the diapsids, lepidosaurians retained arciliny with pointed or leaf-shaped teeth while arcilneal chewing aided by the gizzard dominated the large radiation of the archosaurs. Contrasting the dominant historical patterns in each major clade with patterns remaining in extant amniotes reveals some interesting patterns. Today, the lepidosaurians remain generalized with the arcilneal jaw used for chewing in both omnivory and herbivory. Similarly, extant archosaurs retain the generalized gizzard dominated system common to their ancestry but the novel advent of the gizzard was a key innovation for the archosaur radiation. The basal mammals (tribosphenic chewing system) and turtles (propaliny with beaks) also have novel feeding systems compared to their ancestors. In addition, a secondarily derived version of propaliny has emerged in the most rodents and a few other modern mammals from the tribosphenic chewing system in the mammals. Thus, except in the lizards, novelty seems to have played a role in the success of modern forms.

More interestingly, however, is the observation

that each of the major amniote clades feeds with a different mechanism, and thus, they are somewhat functionally segregated. Historically, the simple arcilneal system (including its retention as part of chewing in most archosaurs) is the most common, and thus, the most successful jaw mechanism across the amniotes. In terms of the number extant species, the basic arcilneal system extant in lizards (~ 4503 species) is more successful than the derived tribosphenic chewing system of mammals (~ 2629 species [4629 mammalian species minus most of the rodents (~ 2000) which are propalineal]). Thus, the basic arcilneal system has worked well for both omnivory and herbivory throughout the history of amniotes. Propaliny would appear to easily evolve from arciliny but in fact it has not appeared that often in the amniotes. Among extant forms propaliny remains only in the turtles (~ 294 species) and in only two lepidosaurian species among the diapsids. However, a secondarily derived version of propaliny emerged in multituberculates and from the tribosphenic chewing system in most of the rodents (~ 2000 species). Thus, propaliny (with teeth) has only really remained in its secondarily derived form in mammals and is as much a part of food acquisition as it is a part of prey processing. Far and away the most common feeding system in amniotes throughout history and today is the combination of arcilneal jaws and a gastric mill. Archosaurs have dominated amniote biodiversity throughout amniote history and continue to do so today. In terms of modern diversity, amniotes using arcilneal jaws and a gizzard (~ 9835 bird species + ~ 23 crocodilian species) are twice as common as arcilneal (~ 4503 lizards) and propalineal forms (~ 294 turtles and ~ 2000 rodents) and four times more common than tribosphenic chewing mammals (~ 2629 species). A major point of this review is how under appreciated the addition of a gastric mill to arcilneal jaws has been in amniote evolution. While amniotes appear to have jack-of-all-trade digestive systems malleable for any diet and functional over a range of temperatures (Stevens and Hume, 1995), the jaw-based food processing system appears to have been more constrained in its range of forms. In fact, modern archosaurs chew primarily with their gizzards and thus, their jaws have perhaps the least chewing function of any amniote. Thus, it was the adaptability of the amniote digestive system (in evolving the crop and gizzard) that usurped the role of

chewing from the jaws in archosaurs and enabled them to become the most successful amniote group.

We further emphasize the significance of the adaptability of the amniote digestive system with patterns of extinctions among the mammalian herbivores. The Tertiary was witness to numerous adaptive radiations of clades of large bodied subungulate (e.g. proboscideans) and ungulate-grade herbivores (e.g. perissodactyls, South American ungulates, and artiodactyls). Except for the ruminant artiodactyls, these taxa are now extinct or relictual. The extant perissodactyls and proboscideans are represented by only 20 species. Non-ruminant artiodactyls (e.g. pigs and allies, camels and allies) presently include 28 species. In the last 10 million years, bovids (137 species) and to a lesser extent cervids (44 species) have come to dominate mammalian herbivore faunas. These taxa share a relatively new innovation of the foregut (stomach fermentation). The complexly chambered stomach of the ruminants has been interpreted as a key innovation enabling the exploitation of high volumes of low quality plant material. The rumen acts in an similar manner to the crop of archosaurs, providing storage space for fermentation of materials processed by the jaws but as yet indigestible. Muscular churning in the rumen is performed but further processing is provided by the jaws (e.g. regurgitation of the cud) in lieu of a gizzard. Similar modifications of the foregut are observed in the macropodids, leaf-eating primates, and some rodents. In a way these most successful of modern mammalian herbivores share with the archosaurs the use of the foregut to both ferment and 'chew' food.

## 6.2. *Is more efficient chewing related to increased metabolic rate?*

We appreciate the myriad other factors potentially confounding interpretations of evolutionary differences in the jaw systems of amniote groups. For example, changes associated with the evolution of flight had multiple effects on the changes in the feeding system in birds, and the common association of hindgut fermentation with herbivory leads to more specialized grinding adaptations in the feeding mechanism. However, the general correlate most often invoked to explain the increased chewing efficiencies of birds and mammals is homeothermy and the associated de-

mands of maintaining a high metabolic rate. Clearly the second function of chewing (to increase the surface area for chemical digestion) must improve in order to increase digestive efficiency to meet the needs of increased metabolic rate. Mammals have done this with fancy teeth and lots of cycles of complex chewing movements. Birds have done it with a gastric mill. Thus, increased chewing efficiency is related to the development of higher metabolic rates in birds and mammals. Do we see trends toward increased chewing efficiency and increased metabolic rate in other amniotes? The answer is yes. In many extinct herbivorous forms among the synapsids and archosaurs, large size, improved chewing systems (propaliny with molars, a gizzard with arciliny with or without molars) and gut fermentation are combined to suggest that these animals could have been homeothermic or at least gigantothermic (homeothermic just on the basis of being a large fermentation chamber). Perhaps more interestingly (and certainly more testable!) there appears to another example among extant amniotes — in the lizards. Above we showed that the autarchoglossan lizards exhibit greater complexity of chewing behavior involving the increased use of puncture crushing and prey manipulation compared to the sit-and-wait iguanians. Increased puncture crushing of prey, though nowhere near the level of chewing seen in birds and mammals, appears to function to increase the surface area of food for digestion. Thus, we are seeing a trend toward increased chewing in the active foraging lizards that by definition have higher field metabolic demands owing to their foraging strategy. In fact, a recent review of vertebrate metabolic rates in 48 species of sit-and-wait and active foraging lizards (Brown, 1999; Nagy et al., 1999) has shown that the active foraging lizards have higher field and resting metabolic rates than sit-and-wait foragers. Therefore, the shift from sit-and-wait to active foraging strategies in lizards, that is so well based in ecological terms, also appears to be associated with a parallel increase in metabolic rate and the complexity of chewing behavior. Lizards may be giving us a fine scale look at the evolution of feeding function as it relates to the demands of increasing metabolic rate.

To conclude, we reiterate that this rather simple review is based on our comparative understanding of the many aspects of feeding biology to

date which are lucid and well supported in a few areas but foggy and undigested for most areas and taxa. Thus, the message we can convey is that much more work is needed in most areas and for most taxa in order to test the kinds of ideas and issues we have discussed. Of foremost importance is the need for functional and behavioral studies of feeding and its variation across amniotes. Most, if not all, of the general conceptual ideas about the evolution of feeding in amniotes are based on mammalian patterns. Our understanding of turtle, lizard, and bird feeding is in an embryonic stage and outgroup comparisons in studies of amniote feeding are difficult at this point due to the lack of comparative data. Of special interest would be an examination of feeding in omnivorous turtles compared to herbivorous forms. Within lizards descriptive and biomechanical studies across the group are underway (Urbani and Bels, 1995; Herrel et al., 1996, 1997, 1998, 1999; Delheusy and Bels, 1999; Herrel and De Vree 1999; Elias et al. 2000; McBrayer, unpublished data). Yet, we have only begun to probe the behavioral, functional, and performance differences across foraging strategies and many additional studies of the details of the ecomorphological patterns of morphology, behavior, function and biomechanics are needed at many levels of analysis. A large scale comparison of the jaw adductors of amniotes, their homologies, variation, functions, and relationships to feeding behavior and diet, though a daunting task, is one that we need to be working toward. And finally, a serious examination of the evolution of the gizzard and jaw function is needed not only within the birds but within the archosaurs as a whole, because the evolution of the most important of the amniote feeding systems is the one we know the least about. To chew or not to chew is not the question — it is knowing *how* amniotes chew that will lead us into new directions.

## References

- Beecher, W.J., 1962. The biomechanics of the bird skull. *Bull. Chicago Acad. Sci.* 11, 10–33.
- Bock, W.J., 1964. Kinetics of the avian skull. *J. Morphol.* 114, 1–14.
- Bock, W.J., 1966. An approach to the functional analysis of bill shape. *Auk* 83, 10–51.
- Bock, W.J., Kummer, B., 1968. The avian mandible as a structural girder. *J. Biomech.* 1, 89–96.
- Bown, T.M., Kraus, M.J., 1979. Origin of the tribosphenic molar and metatherian and eutherian dental formulae. In: Lillegraven, J.A., Kielan-Jaworowska, Z., Clemens, W.A. (Eds.), *Mesozoic Mammals: The First Two-Thirds of Mammalian History*. University of California Press, Berkeley, CA, pp. 172–181.
- Bramble, D.M., 1974. Occurrence and significance of the Os transiliens in gopher tortoises. *Copeia* 102–109.
- Bramble, D.M., Wake, D.B., 1985. The feeding mechanisms of lower tetrapods. In: Hildebrand, M., Bramble, D.M., Liem, K.F., Wake, D.B. (Eds.), *Functional Vertebrate Morphology*. Harvard Univ. Press, Cambridge, MA, pp. 230–261.
- Brown, B., 1907. Gastroliths. *Science* 25, 392.
- Brown, T.K., 1999. The physiological ecology of desert lizards (*Phrynosoma platyrhinos*) in the Mojave desert (California). Ph.D. Dissertation, University of California, Los Angeles.
- Browne, T.G., 1922. Some observations on the digestive system of the fowl. *J. Comp. Pathol. Ther.* 35, 12.
- Buhler, P., 1981. Functional anatomy of the avian jaw apparatus. In: King, A.S., McLelland, J. (Eds.), *Form and Function in Birds*, vol. 2. Academic Press, New York, pp. 439–468.
- Carroll, R.L., 1969. Problems of the origin of reptiles. *Biol. Rev.* 44, 393–432.
- Carroll, R.L., 1991. The origin of reptiles. In: Schultze, H.P., Trueb, L. (Eds.), *Origins of Higher Groups of Tetrapods*. Cornell University Press, Ithaca, NY, pp. 331–353.
- Clemens, W.A., Kielan-Jaworowska, Z., 1979. Multituberculata. In: Lillegraven, J.A., Kielan-Jaworowska, Z., Clemens, W.A. (Eds.), *Mesozoic Mammals: The First Two-Thirds of Mammalian History*. University of California Press, Berkeley, CA, pp. 99–149.
- Cloudley-Thompson, J.L., 1972. The classification and study of animals by feeding habits. In: T-W-Fiennes, R.N. (Ed.), *Biology of Nutrition*, vol. 18. Pergamon Press, New York, pp. 439–470.
- Condon, K.A., 1987. Kinematic analysis of mesokinesis in the Nile monitor *Varanus niloticus*. *Exp. Biol. (Berlin)* 47, 73–87.
- Cooper, W.E., 1995. Evolution and function of lingual shape in lizards, with emphasis on elongation, extensibility, and chemical sampling. *J. Chem. Ecol.* 21, 477–505.
- Cooper, W.E., 1994. Chemical discrimination by tongue-flicking in lizards: a review with hypotheses on its origin and its ecological and phylogenetic relationships. *J. Chem. Ecol.* 20, 439–487.
- Corbet, P.S., 1960. The food of a sample of crocodiles *Crocodilus niloticus* L. from Lake Victoria. *Proc. Zool. Soc. Lond.* 133, 561–572.



- Costelli, J., 1973. Iguanid trigeminal musculature and its role in the phylogeny of the Iguanidae. Ph.D. Dissertation, City University of New York, New York.
- Crompton, A.W., 1971. The origin of the tribosphenic molar. In: Kermack, D.M., Kermack, K.A. (Eds.), Early Mammals (special issue). J. Zool. J. Linn. Soc. (suppl. 1) 65–87.
- Crompton, A.W., Hiiemae, K., 1970. Molar occlusion and mandibular movements during occlusion in the American opossum, *Didelphis marsupialis*. Zool. J. Linn. Soc. 49, 21–27.
- Crompton, A.W., Hylander, W.L., 1986. Changes in mandibular function following the acquisition of a dentary-squamosal jaw articulation. In: Hotton, H.N., MacLean, P., Roth, J., Roth, E. (Eds.), The Ecology and Biology of Mammal-Like Reptiles. Smithsonian Institution Press, Washington, DC, pp. 263–287.
- Currie, P.J., Padian, K. (Eds.), 1997. Encyclopedia of Dinosaurs. Academic Press, New York.
- Dalrymple, G.H., 1979. On the jaw mechanism of the snail-crushing lizards, *Dracaena* DuRoi 1802 (Reptilia, Lacertilia, Teiidae). J. Herpetol. 13, 303–311.
- Davenport, J., Andrews, T.J., Hudson, G., 1992. Assimilation of energy, protein and fatty-acids by the spectacled caiman *Caiman crocodilus* L. Herpetol. J. 2, 72–76.
- Day, L.B., Crews, D., Wilczynski, W., 1999. Spatial and reversal learning in congeneric lizards with different foraging strategies. Ann. Behav. 57, 393–407.
- Delheusy, V., Bels, V.L., 1999. Feeding kinematics of *Phelsuma madagascariensis* (Reptilia: Gekkonidae): testing differences between Iguania and Scleroglossa. J. Exp. Biol. 202, 3715–3730.
- Dodson, P., 1997. Neoceratopsia. In: Currie, P.J., Padian, K. (Eds.), Encyclopedia of Dinosaurs. Academic Press, New York, pp. 473–478.
- Duke, G.E., Dzuik, H.E., Evanson, O.A., 1972. Gastric pressure and smooth muscle electrical potential changes in turkeys. Am. J. Physiol. 222, 167–176.
- Edmond, A.G., 1960. Tooth replacement phenomena in the lower vertebrates. Life Sciences Division, Royal Ontario Museum, Contr. 52.
- Elias, J.A., McBrayer, L.D., Reilly, S.M., 2000. Prey processing kinematics in *Tupinambis teguixin* and *Varanus exanthematicus*: conservation of feeding behavior in 'chemosensory tongued' lizards. J. Exp. Biol. 203, 791–801.
- Estes, R., Pregill, G. (Eds.), 1988. Phylogenetic relationships of the lizard families: essays commemorating Charles L. Camp. Stanford University Press, Stanford, CA.
- Estes, R., Williams, E.W., 1984. Ontogenetic variation in the molariform teeth of lizards. J. Vert. Paleontol. 4, 96–107.
- Gans, C., DeVree, F., Carrier, D., 1985. Usage pattern of the complex masticatory muscles in the shingle-back lizard, *Trachydosaurus rugosus*: a model for muscle placement. Am. J. Ant. 173, 219–240.
- Gauthier, J.A., Kluge, A.G., Rowe, T., 1988. The early evolution of the Amniota. In: Benton, M.J. (Ed.), The Phylogeny and Classification of the Tetrapods, vol. 1: Amphibians, Reptiles, Birds. Clarendon Press, Oxford, UK, pp. 103–155.
- Gillette, D.D., 1994. Seismosaurus, the Earth Shaker. Columbia University Press, New York.
- Glut, D.F., 1997. Dinosaurs the Encyclopedia. McFarland and Company, London.
- Gorniak, G.C., Rosenberg, H.I., Gans, C., 1982. Mastication in the tuatara, *Sphenodon punctatus* (Reptilia: Rhynchocephalia): structure and activity of the motor system. J. Morph. 171, 321–353.
- Grant, R.B., Grant, P.R., 1989. Evolutionary Dynamics of a Natural Population: The Large Cactus Finch of the Galapagos. University of Chicago Press, Chicago, IL.
- Greene, H.W., 1982. Dietary and phenotypic diversity in lizards: why are some organisms specialized? In: Mosakowski, D., Roth, G. (Eds.), Environmental Adaptation and Evolution. Gustav Fischer, Stuttgart.
- Haas, G., 1974. Muscles of the jaws and associated structures in the Rhynchocephalia and Squamata. In: Gans, C., Parson, T. (Eds.), Biology of the Reptilia, vol. 4. Academic Press, New York, pp. 285–490.
- Herrel, A., De Vree, F., 1999. Kinematics of intraoral transport and swallowing in the herbivorous lizard *Uromastix acanthanurus*. J. Exp. Biol. 202, 1127–1137.
- Herrel, A., Cleuren, J., De Vree, F., 1996. Kinematics of feeding in the lizard *Agama stellio*. J. Exp. Biol. 199, 1727–1742.
- Herrel, A., Cleuren, J., De Vree, F., 1997. Quantitative analysis of jaw and hyolingual muscle activity during feeding in the lizard *Agama stellio*. J. Exp. Biol. 200, 101–115.
- Herrel, A., Aerts, P., De Vree, F., 1998. Static biting in lizards: functional morphology of the temporal ligaments. J. Zool. Lond. 244, 135–143.
- Herrel, A., Verstappen, M., De Vree, F., 1999. Modulatory complexity of the feeding repertoire in scincid lizards. J. Comp. Physiol. A 184, 501–518.
- Herring, S.W., 1993. Functional morphology of mammalian mastication. Am. Zool. 33, 289–299.
- Hiiemae, K.M., 1976. Masticatory movements in primitive mammals. In: Butler, P.M., Joysey, K.A. (Eds.), Mastication. Wright, Bristol, pp. 105–118.
- Hiiemae, K.M., Crompton, A.W., 1985. Mastication, food transport, and swallowing. In: Hildebrand, M., Bramble, D.M., Liem, K.F., Wake, D.B. (Eds.), Functional Vertebrate Morphology. Harvard Univ. Press, Cambridge, MA, pp. 262–290.

- Hotton, N., Olson, E.C., Beerbower, D., 1997. Amniote origins and the discovery of herbivory. In: Sumida, S.S., Martin, K.L.M. (Eds.), *Amniote Origins: Completing the Transition to Land*. Academic Press, San Diego, CA, pp. 207–264.
- Huey, R.B., Pianka, E.R., 1981. Ecological consequences of foraging mode. *Ecology* 62, 991–999.
- Johnston, R.G., Lee, W.G., Grace, W.K., 1994. Identifying *Moa* gastroliths using a video light-scattering instrument. *J. Paleontol.* 68, 159–163.
- Kear, J., 1972. Feeding habits of birds. In: T-W-Fiennes, R.N. (Ed.), *Biology of Nutrition*, vol. 18. Pergamon Press, New York, pp. 471–503.
- King, G., 1996. *Reptiles and Herbivory*. Chapman and Hall Publ, London, UK.
- Krebs, U., 1979. Der Dumeril-waran (*Varanus dumerilli*): ein spezialisierter Kriechfresser? *Salamandra* 15, 146–157.
- Lederer, R.J., 1975. Bill, size, food size, and jaw forces of insectivorous birds. *Auk* 92, 385–387.
- Lonnberg, E., 1903. On the adaptations to molluscivorous diet in *Varanus niloticus*. *Arkiv. Für Zoologie* 1, 67–83.
- Manley, K., 1991. Two techniques for measuring surface polish as applied to gastroliths. *Iconos* 1, 313–316.
- McDowell, S.B., Bogert, C.M., 1954. The systematic position of *Lanthonotus* and the affinities of the Anguimorph lizards. *Bull. Am. Mus. Nat. Hist.* 105, 1–142.
- Moore, S.J., 1998a. The comparative functional gizzard morphology of several species of birds. *Aust. J. Zool.* 46, 359–368.
- Moore, S.J., 1998b. The gizzard morphology of an avian herbivore: the domestic goose, *Anser anser*. *Aust. J. Zool.* 46, 345–357.
- Nagy, K.A., Girard, I.A., Brown, T.K., 1999. Energetics of free-ranging mammals, reptiles and birds. *Annu. Rev. Nutr.* 19, 247–277.
- Nakahiro, Y., 1966. Studies on the method of measuring the digestibility of poultry feed. *Mem. Fac. Agri. Kagawa Univ.* No. 22.
- Norman, D.B., Weishampel, D.B., 1985. Ornithopod feeding mechanisms: their bearing on the evolution of herbivory. *Am. Nat.* 126, 151–164.
- Olson, E.C., 1961. Jaw mechanism: rhipidistians, amphibians, reptiles. *Am. Zool.* 1, 205–215.
- Perry, G., 1999. The evolution of search modes: ecological versus phylogenetic perspectives. *Am. Nat.* 153, 98–109.
- Raath, M., 1974. Further evidence of gastroliths in prosauropod dinosaurs. *Arnoldia* 7, 1–5.
- Regal, P.J., 1978. Behavioral differences between reptiles and mammals: an analysis of activity and mental capabilities. In: Greenberg, N., MacLean, P.D. (Eds.), *Behavior and Neurology of Lizards*. National Institute of Mental Health, Rockville, MD, pp. 177–188.
- Reilly, S.M., Lauder, G.V., 1990. The evolution of tetrapod feeding behavior: kinematic homologies in prey transport. *Evolution* 44, 1542–1557.
- Richardson, K.C., Wooller, R., 1990. Adaptations of the alimentary tracts of some Australian lizards to a diet of pollen and nectar. *Aust. J. Zool.* 38, 581–586.
- Rieppel, O., 1978. Streptostyly and muscle function in lizards. *Experientia* 34, 776–777.
- Rieppel, O., Labhardt, L., 1979. Mandibular mechanics in *Varanus niloticus* (Reptilia: Lacertilia). *Herpetologica* 35, 158–163.
- Robinson, P.L., 1976. How *Sphenodon* and *Uromastix* grow their teeth and use them. In: Bellairs, A.d'A., Cox, C.B. (Eds.), *Morphology and Biology of Reptiles*. Linnean Society Symposium Series 3. Academic Press, London, pp. 43–46.
- Schumacher, G.H., 1973. The head muscles and hyolaryngeal skeleton of turtles and crocodylians. In: Gans, C., Parsons, T.S. (Eds.), *Biology of the Reptilia*, vol. 4. Academic Press, London, pp. 101–199.
- Schwenk, K., 1988. Comparative morphology of the lepidosaur tongue and its relevance to squamate phylogeny. In: Estes, R., Pregill, G. (Eds.), *The Phylogenetic Relationships of the Lizard Families: Essays Commemorating Charles L. Camp*. Stanford University Press, Palo Alto, CA, pp. 569–598.
- Schwenk, K., 1993. The evolution of chemoreception in squamate reptiles: a phylogenetic approach. *Brain. Behav. Evol.* 41, 124–137.
- Schwenk, K., Throckmorton, G.S., 1989. Functional and evolutionary morphology of lingual feeding in squamate reptiles: phylogenetics and kinematics. *J. Zool. Lond.* 219, 153–175.
- Simonetta, A.M., 1960. On the mechanical implications of the avian skull and their bearing on the evolution and classification of birds. *Q. Rev. Biol.* 35, 206–220.
- Smith, H.M., 1960. *Evolution of Chordate Structure*. Holt, Rinehart and Winston, New York.
- Smith, K.K., 1982. An electromyographic study of the function of jaw adducting muscle in *Varanus exanthematicus* (Varanidae). *J. Morph.* 173, 137–158.
- Smith, K.K., 1984. The use of the tongue and hyoid apparatus during feeding in lizards (*Ctenosaura similis* and *Tupinambis nigropunctatus*). *J. Zool. Lond.* 202, 115–143.
- Smith, K.K., 1993. The form of the feeding apparatus in terrestrial vertebrates: studies of adaptation and constraint. In: Hanken, J., Hall, B.K. (Eds.), *The Skull*, vol. 3. University of Chicago Press, Chicago, IL, pp. 150–196.
- Sokol, O., 1967. Herbivory in lizards. *Evolution* 21, 192–194.
- Stevens, C.E., Hume, I.D., 1995. *Comparative Physiology of the Vertebrate Digestive System*, 2nd ed. Cambridge University Press, Cambridge, UK.