

Mastication in the Tuatara, *Sphenodon punctatus* (Reptilia: Rhynchocephalia): Structure and Activity of the Motor System

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ABSTRACT The masticatory pattern of *Sphenodon punctatus*, the sole remaining rhynchocephalian, now restricted to islands off the coast of New Zealand, has been analyzed by detailed anatomy, cinematography, cinefluoroscopy, and electromyography. Food reduction consists of a closing, crushing bite followed by a propalinal sliding of the dentary row between the maxillary and palatine ones. The large, fleshy tongue can be protruded to pick up small prey, and also plays a major role in prey manipulation. The rotational closing movement of the jaw, supporting the basic crushing movement, is induced by the main adductor musculature. It is followed by a propalinal anterior displacement relying heavily on the action of the *M. pterygoideus*. The fiber lengths of the several muscles reflect the extent of shortening. The most obvious modification appears in the *M. pterygoideus*, which contains a central slip of pinnately arranged short fibers that act at a period different from that of the rest of the muscle; their action increases the power during the terminal portion of the propalinal phase. This also allows the animal to use its short teeth in an effective shearing bite that cuts fragments off large prey.

The action of single cusped dentary teeth acting between the maxillary and palatine tooth rows provides a translational crushing-cutting action that may be an analog of the mammalian molar pattern. However, this strictly fore-aft slide does not incorporate capacity for later development of lateral movement.

As the sole Recent representative of the order Rhynchocephalia, the tuatara *Sphenodon punctatus* has been the subject of a disproportionately large number of anatomic studies (see Dawbin, '62; Robb, '73). The skull of *Sphenodon* differs from that of other lepidosaurians in being fully diapsid. A quadratojugal bone, a squamosal-jugal brace, and a fixed quadrate are retained, although there is some question about the degree of cranial kinesis (Versluys, '12; Kuhn-Schnyder, '54; Ostrom, '62; Iordansky, '66; Rieppel, '78). Both the dentitional pattern (Robinson, '76) and the cephalic musculature (Haas, '73; Poglayen-Neuwall, '53) show further differences. Earlier investigations, both descriptive and functional, relied on preserved material. More recently, field investigations (Crook, '75; Gans, '82) and laboratory studies of living specimens (e.g., Hill and Dawbin, '69; McDonald and Heath, '71; Gans and Wever, '76; Ireland and Gans, '77) have begun to increase our understanding of the physiology and behavior of the tuatara (Robb, '77). The present report of the relation of cranial architecture, musculature, and dentitional patterns to feeding behavior and muscle action in the tuatara provides

a base line for comparisons among lepidosaurians.

Lepidosaurians feed in various ways and their varied feeding behaviors are reflected in the structures they use. Snakes swallow their prey whole by means of alternating, unilateral movements of their highly kinetic skulls (Cundall and Gans, '79; Gans, '61). Amphisbaenians bite into their prey, ripping pieces loose by rotation of the body (Gans, '74). Herbivorous lizards crop vegetation, then swallow it with minimal reduction (Throckmorton, '76). Carnivorous lizards chew small food items (Frazzetta, '62) or utilize inertial feeding to bolt down large prey (Gans, '61). Neither the occurrence nor the absence of cranial kinesis correlates clearly with particular feeding strategies.

The skull of *Sphenodon* differs from those of Recent lizards because it has two fixed and parallel rows of teeth on each side of the upper

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This paper is dedicated to the memory of George Haas in appreciation of his profound contributions to the cephalic anatomy of Recent and fossil reptiles

jaw. The lateral teeth of each set lie on the medial edge of the maxilla and the medial ones on the lateral edge of the palatine; between them they form a narrow tooth-fringed channel into which the mandibular tooth row closes. The teeth are subtriangular in profile, with the bases fused in series along each row. Reconstructions have suggested that sphenodontids reduce their food by powerful, relatively slow shearing bites (Gunther, 1867; Robinson, '73).

The origin of the difference between food processing by *Sphenodon* and lizards apparently dates back to the pre-Triassic separation between sphenodontid rhynchocephalians and carnivorous prolacertilians (Robinson, '73). The latter probably used weak, relatively fast, piercing bites. The dichotomy of masticatory patterns seems to have been sharpened further as the lizards lost the quadrate-jugal arcade and mobilized their quadrate bones (streptostyly); this permitted the swallowing of relatively larger prey. *Sphenodon* has a fully diapsid skull with a fixed quadrate and is apparently unable to increase the lateral distance between the jaw joints. It apparently compensates for the limited size of the bolus that may be swallowed by subdividing larger prey into manageable pieces.

Through the courtesy of the government of New Zealand, four living specimens of *Sphenodon* were available for study. We here describe how *Sphenodon* capture and masticate different prey and how the major muscles then drive their jaws. Analysis of some of the smaller muscular components is relegated to a second study.

MATERIALS AND METHODS

Specimens available

The following animals were used in this study: For osteology, AMNH 75705, AMNH 89835, CU 8568; for myology, two preserved but partially dissected (brains removed for neuroanatomic study) heads (CG 5369, 5370) and one intact specimen (CG 5321); for observation of feeding movements three living specimens (two females, one male; weight range 582-822 gm; CG 5320, 5322, 5323); the last two were used for the electromyography.

Dissection

Photographs of all stages of dissection served as a basis for illustrations and descriptions. Contrast between muscle and the surrounding connective tissue was increased by use of an iodine solution (Bock and Shear, '72). Muscle terminology follows Haas ('73).

The animal (female; weight 242 gm; snout-vent length 22.1 cm) used for myologic analysis had died of a protozoan infection that left its muscles relaxed. Fixation was in 10% formalin about 2 hr. after death (time required for postmortem veterinary examination). An estimate of muscle weight, fiber and sarcomere lengths, and muscle architecture (Table 1) of the major masticatory muscles was obtained by 1) dissecting out the preserved muscles (on one side), 2) weighing each three times (being blotted dry between each weighing), 3) immersing each in 30% nitric acid for three to five days to dissolve the connective tissue, and 4) then placing them in 50% glycerol. The fiber arrangement of the muscles was then traced from camera lucida projection on a Wild dissecting microscope. The length of five entire fibers from adjacent positions within the muscle was measured on a millimeter scale and ocular micrometer on a dissecting microscope. Several fibers were then placed in glycerol on a microscope slide and examined under oil immersion. The overall length of 20 sets of 10 sarcomeres was measured for part of each muscle by means of a calibrated micrometer located in the ocular. The muscles were then washed with water and 70% alcohol, air-dried, and weighed to obtain dry weights of the fiber masses.

Behavioral observations and movement records

Specimens were observed while they were housed individually in large (1m × 1m × 1m), screened, glass-fronted cages located in an air-conditioned room maintained at 15°-17°C and illuminated for 12-hr. periods by both GroLux and white fluorescent lamps. A heat lamp focused on one corner of the cage provided a basking site. Tuataras were fed crickets, cockroaches, and newly born mice that had been dusted with Pervinal vitamin powder. Fresh drinking water and pans large enough to let the animals immerse themselves were always available.

For detailed observations of feeding, tuataras were temporarily transferred to smaller cages or a table top and then conditioned to accept food manipulated by hand. Chilled crickets (length: 2.0-2.4 cm; weight: 0.3-0.6 gm) and cockroaches (length: 2.8-3.0 cm; weight: 0.5-0.7 gm), as well as newly born (length: 3.5-4.0 cm; weight: 2.1-2.4 gm) and juvenile mice (length: 5.5-6.0 cm; weight: 6.1-7.0 gm), were offered individually to facilitate observation and cinematography. Feeding sequences were filmed on 16-mm film with a strobe-synchronized camera (Gans, '66)

using either direct lateral or biangular lateral-frontal (mirror) views. Cineradiographs of one specimen were taken at the Museum of Comparative Zoology of Harvard University (courtesy of Professor F. Jenkins) with a Siemens cinefluoroscopy unit operated at 50 kV and 120 mA. The Siemens image intensifier was filmed with an Auclair 16-mm camera at about 50 frames per second. All films were analyzed with a Lafayette 16-mm analytical projector and a Vanguard motion analyzer.

Mercury strain gauge records

During many of the feeding sequences, a vertically directed mercury strain gauge was placed on one side of the head. Patches of Velcro were attached by contact adhesive to the skin over the postorbital-squamosal bar and to the midventral surface of the lower jaw. Complementary patches of Velcro were bonded to each end of the gauge. The gauge was then placed so that it was under slight tension when the mouth was closed.

Electromyography

EMGs were recorded from those masticatory muscles into which electrodes could be placed using bony landmarks and pal-

pation. Because of the high risk to the animal involved, we recorded from the small and deeply positioned muscles of the head in only one specimen. The activity of the infrahyoid and suprahyoid muscles and of the muscles of the tongue is excluded.

Electrodes formed of 0.076-mm Teflon-insulated stainless steel wire (Medwire Corp.) were inserted through the skin and into each muscle via 25-gauge hypodermic needles (see Gans and Gorniak, '80, for details of electrode construction). The outside ends of the electrodes were soldered to Teflon-insulated silver wires placed into PE tubing or to earphone wires (later experiments) that were connected to cables leading to the preamplifiers by Amphenol Mighty-Mite circular connectors. The coating of the connecting wires was fixed to the animal by short patches of Velcro. This kept the leads from shifting and relieved strain on the electrodes.

EMG signals were amplified by means of Tektronix 122 and 26A2 preamplifiers and Honeywell 117 amplifiers. EMG signals, strobe photocell outputs, and those from the mercury strain gauge amplifier were stored on a Honeywell 5600 intermediate-band tape recorder and simultaneously displayed on a

TABLE 1. Wet and dry whole muscle weights (in grams) and ranges of the fiber lengths (in mm) of the major masticatory muscles of *Sphenodon*

Muscles	Weights		Fiber length	N ¹
	Wet	Dry		
M. depressor mandibulae	0.49	0.11		
anterior portion			8.0-21.0	45
posterior portion			23.0-29.0	35
M. adductor mandibulae externus superficialis	0.90	0.35		
anterior portion			7.0-18.0	50
posterior portion			10.0-15.0	50
M. adductor mandibulae externus medialis				
MAMEM-a	0.50	0.10	9.0-13.0	70
MAMEM-b	0.34	0.06	12.0-17.0	75
MAMEM-c	0.20	0.05	13.0-15.0	100
M. adductor mandibulae externus profundus	0.10	0.04	5.0-11.0	180
M. pseudotemporalis superficialis	0.54	0.12	8.0-18.0	105
M. pseudotemporalis profundus	0.18	0.06	14.0-17.0	100
M. pterygoideus typicus				
dorsalmost (deep) portion	0.08	0.02	5.0-10.0	80
middle portion	1.65	0.57		
medial part			17.0-18.0	70
lateral part			7.0-15.0	70
ventrolateral portion	0.30	0.08	18.0-20.0	40
M. pterygoideus atypicus	0.11	0.05	16.0-17.0	60

¹N equals number of fibers measured

Tektronix 565 oscilloscope and a Gould (Brush 481) multichannel chart recorder.

Animals were anesthetized by an intramuscular injection of Brevital Sodium (Eli Lilly; dosage: 1.2 mg/kg of body weight). After they had recovered from anesthesia, the conditioned animals were placed on a grounded stainless steel tray (moistened with saline solution) that was fixed in front of the chart recorder. A movie camera recorded a lateral view of the animal and the chart record showing EMG signals, a transducer signal, and a 1-Hz time signal.

Frame-by-frame projection of films allowed measurement of the displacement of the lower jaw. Velocity and acceleration were determined, first graphically and later by means of a computer. The displacement record was also correlated with muscular activity and transducer signals. Up to seven simultaneous EMGs were digitized and processed by a Hewlett Packard 21MX minicomputer to obtain the number of spikes and their average amplitude for intervals correlated with the cine frames. Digitized records were stored on cassette tape and then displayed on a Tektronix 4051 Graphic Display System with 4662 digital plotter. Previous studies suggest that the product of the number of spikes times their amplitude correlates best with tension (Gorniak and Gans, '80); hence, this value was plotted for each muscle as a bar graph. The plot showed individual records as a percentage of the maximum value for each feeding sequence. Percentage graphs allow intersequence comparisons even though the level of amplification of EMGs has not been controlled in some experiments. Recent studies show that EMGs thus recorded and analyzed are highly repeatable (Gans and Gorniak, '80).

We here report on 80 feeding sequences combining EMG and strain gauge records, as well as on additional observations of EMGs without synchronized displacement recordings. Fifty-five of the feeding sequences were filmed, and 31 of these contain strobe-triggered photocell outputs. EMGs with simultaneous movement records were obtained from the following muscles (N = the number of reduction sequences): anterior (N = 17) and posterior (N = 38) portions of the M. depressor mandibulae; anterior (N = 8) and posterior (N = 8) portions of the M. adductor mandibulae externus superficialis *sensu stricto*; anteromedial (N = 59), posterior (N = 14) and ventrolateral (N = 6) portions of the M. adductor mandibulae externus medialis; M. adductor

mandibulae externus profundus (N = 4); M. pseudotemporalis superficialis (N = 15); M. pseudotemporalis profundus (N = 5); M. pterygoideus atypicus (N = 4) and the superficial (N = 26) and deep (N = 19) parts of the medial half of the middle portion of the M. pterygoideus typicus, as well as the superficial (N = 5) and deep (N = 5) parts of the lateral half of the middle portion and the ventrolateral portion of the M. pterygoideus typicus.

RESULTS

General

Detailed descriptions of the skull (Romer, '56), dentition (Robinson, '76), and cephalic musculature (Byerly '25; Haas, '73) of *Sphenodon* are already available. However, we here provide a brief description of the dentition and descriptions of the muscles from which recordings were made including their fiber lengths (Table 1) in order to provide a foundation for the interpretation of the movements they generate. Sarcomere lengths from different muscles are equivalent at 2.6 μm . Measurements of fiber and sarcomere lengths are for one specimen and one side only.

Descriptions of the dentition and myology are followed by a description of the feeding movements observed when *Sphenodon* chews crickets, cockroaches, and mice of various sizes. Descriptions of the muscular activities recorded during reduction sequences are then presented.

Dentition

Sphenodon has a mandibular and maxillary pair of canine-like teeth and a maxillary pair of incisor-like teeth. The large canine-like mandibular teeth lie just posterolaterally to the mandibular symphysis; the smaller maxillary teeth lie posterior to the mandibular ones and are each preceded by three small conical teeth. All of these canine-like teeth are larger than the remaining marginal teeth. In frontal view, the mandibular canines slant slightly laterally and in lateral view slightly posteriorly; the maxillary canines extend directly ventrally. Both anterior and posterior surfaces of the canine-like teeth are rounded, whereas their medial and lateral surfaces are relatively flat.

The upper pair of incisor-like teeth protrudes straight downward from the premaxilla; these are the largest teeth. Each of the more posterior teeth generally has two pointed cusps, a small medial (which may be absent) and large lateral one. The anterior and lateral surfaces of these teeth are rounded, the

posterior surface is flat, and the medial surface shows a sharp edge. In frontal projection, each tooth lies well medial to the quadratoarticular joint; the lateral margins of the teeth line up with the lateral margins of the palatine tooth rows and their medial margin ends just medial to the inner surface of the pterygoid flange. When the jaws are closed, the maxillary incisor-like teeth lie anterior to the mandibular symphysis and anteromedial to the canine-like mandibular teeth; neither pair contacts the other.

Sphenodon also has maxillary, palatine, and mandibular (dentary) marginal teeth. These teeth are triangular in lateral view and increase in size as one proceeds posteriorly along the tooth row. The medial side of the maxillary and mandibular teeth and the lateral side of the palatine teeth are flat; the opposite side is rounded. The rounded surface of the maxillary and palatine teeth flattens posteriorly, meets the flat surface of the tooth and forms a sharp posterior edge; their anterior surface is rounded. In contrast, both the anterior and posterior surfaces of the mandibular teeth are rounded. The maxillary and palatine teeth slant slightly posteriorly, whereas the mandibular teeth slant anteriorly.

The maxillary, palatine, and mandibular tooth rows diverge posterolaterally from the symphysis. The palatine teeth lie parallel to the posterior half of the maxillary tooth rows, forming a narrow trough between them. This trough is slightly wider posteriorly than anteriorly. The posterior mandibular teeth fit snugly within this trough and this fit restricts lateral movements of the mandible when the teeth are occluded.

Myology

Weights

The air-dried weights of the masticating muscles of one side totaled 1.61 gm (wet weights, blotted, totaled 5.39 gm). The *M. depressor mandibulae* makes up 6.8% of the total dry weight, the *M. pterygoideus atypicus* 3.1%, and the entire *M. pterygoideus typicus* 41.6%. The remaining 48.5% comprises the superficial, medial, and deep adductors. The *M. adductor mandibulae externus medialis* makes up 13.0% of the total, the *M. adductor mandibulae externus superficialis* 21.7%, the *M. pseudotemporalis superficialis* 7.5%, the *M. pseudotemporalis profundus* 3.7%, and the *M. adductor mandibulae externus profundus* 2.5%. Thus, even though the *M. pterygoideus typicus* is the largest single muscle, its mass is

less than that of all the adductors (compressors) combined. Apparently, the compressors are capable of generating the greatest forces.

M. depressor mandibulae (MDM; Figs. 1,2)

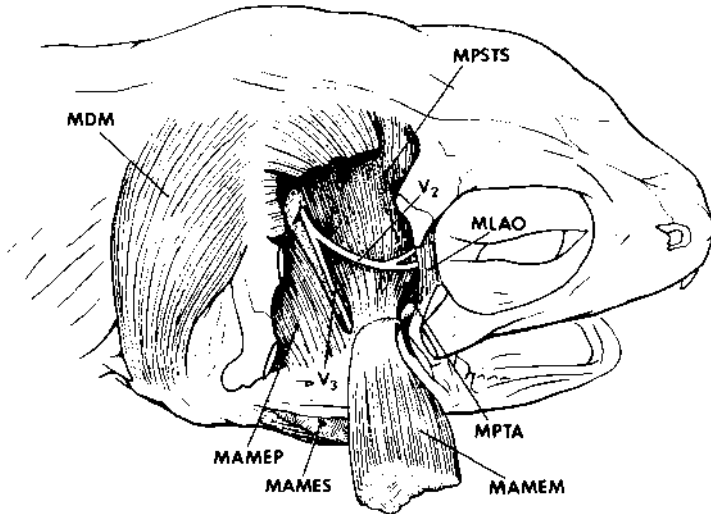
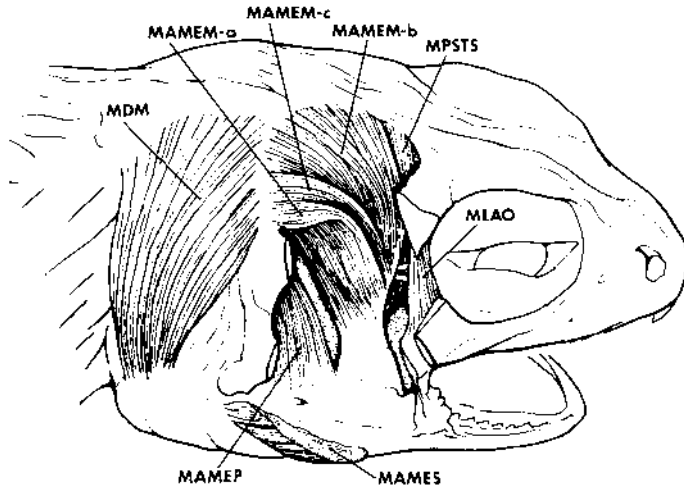
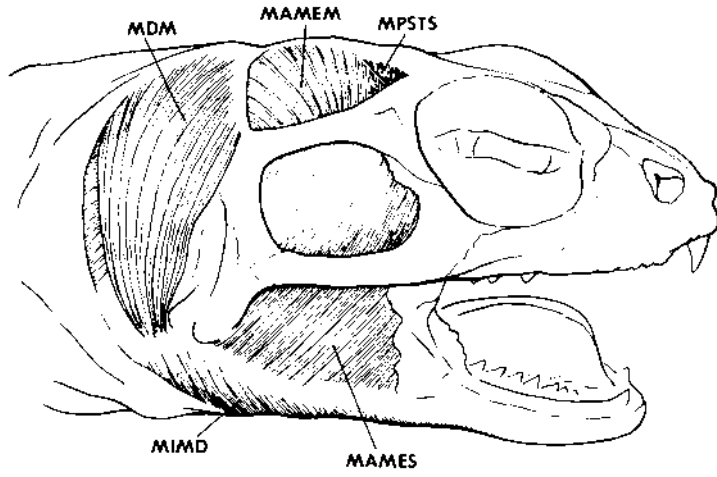
The posterior fibers of the *M. depressor mandibulae* originate from the dorsoposterior portion of the parietal and dorsal posteriormost part of the squamosal, and the anterior fibers originate from the posterior aspect of the dorsal process of the squamosal; some deep anterior fibers also originate from a middorsal section of connective tissue. The sharp difference in the origin and the difference in fiber lengths (Table 1) between the posterior half of the muscle and the anterior half suggests that the MDM may have an anterior and posterior subdivision, even though there is no obvious connective tissue plane separating them.

The posterior fibers first run laterad and slightly ventroposteriorly and then curve sharply posteriorly near the lower margin of the dorsal temporal fossa. These fibers curve around the posterior end of the jaw and insert on its ventral surface. The anterior fibers run ventroposteriorly and slightly laterad and then insert on the posterolateral end of the jaw. The superficial posterior and anterior fibers insert more ventrally on the mandible than the deeper fibers. The dorsal third of the depressor is thin, the middle third relatively thick, and the ventral third tapers towards the insertion. Loose connective tissue attaches the medial surface of the dorsal two-thirds of the muscle to underlying structures, whereas the ventral third is relatively free.

The lengths of the superficial fibers of the anterior portion of the MDM (range 19–21 mm) are greater than those of its deep fibers (range 8–15 mm). In the posterior portion, the lengths of the superficial and deep fibers are similar (superficial: range 25–29 mm; deep: range 23–25 mm), and their lengths are greater than those of the anterior portion. In both parts, the lengths of the superficial and deep fibers increase as one proceeds posteriorly; the increase is greatest in the deep fibers of the anterior portion.

M. adductor mandibulae externus superficialis sensu stricto (MAMES; Figs. 1,2)

The *M. adductor externus superficialis sensu stricto* fills the lateral part of the ventral temporal fossa and forms a bulge on the lateral surface of the posterior part of the lower jaw. It is covered by the lower temporal fascia and is



not immediately visible after removing of the skin. The MAMES originates from the medial surfaces of the postorbital and squamosal; the anterior one-fourth of the origin is fleshy, the deep portion of the middle half is fleshy, and the superficial part aponeurotic (the aponeurosis is wide anteriorly and tapers posteriorly), and the posterior one-fourth of the origin is aponeurotic. The fibers pass in a posteroventrad and slightly laterad direction dorsal and medial to the jugal. Ventral to the jugal the fibers curve medially to insert along the lateral surface of the dentary, posterior to the mandibular tooth row. The most superficial fibers insert most ventral and the deepest fibers most dorsal on the dentary.

The superficial anteriormost fibers of the anterior one-fourth of the MAMES show the longest fiber lengths (range 17-18 mm) and decrease thereafter (13-14 mm), whereas the underlying deep fibers of this part are short (range 7-10mm). As one proceeds posteriorly through the middle half of the MAMES, the length of the superficial fibers originating from the wide aponeurosis first decreases to 11-12 mm but then increases to 14-15 mm as the aponeurosis tapers. In contrast, the length of the deep fibers of this portion first increases to 12-14 mm and then decreases to 10-12 mm posteriorly. In the posterior one-fourth of the MAMES, there is no significant difference between the lengths of the superficial and deep fibers. The lengths of these fibers range between 10-12 mm anteriorly and 8-9 mm posteriorly.

M. adductor mandibulae externus medialis (MAMEM; Figs. 1, 2)

The compound *M. adductor mandibulae externus medialis* lies posterior to the *M. pseudotemporalis superficialis*. The muscle has fleshy origins, but all of its subdivisions in-

sert on the basal aponeurosis that lies deep to the MAMES. This aponeurosis is the insertion for several other adductors of the lower jaw, and transmits the forces to the dorsal margins of the coronoid and postcoronoid portion of the lower jaw. The bulk of the MAMEM fills the dorsal temporal fossa. It is difficult to see its individual heads, as the ventral half of the muscle is covered by loose connective tissue, by the MAMES, and by the upper temporal bar. In vivo, the components of the MAMEM may be located relative to the bony landmarks. Haas ('73) lists five heads of the MAMEM (but only diagrams four); there appears to be a discrepancy between the labels used in his text description of the MAMEM and those in his diagrams. Only three (a-c) heads were found in the present study and their labels follow the convention used in the diagrams.

The anteromedial head of the MAMEM (MAMEM-b) originates as a set of laterally and slightly anteriorly directed fibers from the dorsolateral surface of the parietal. A short distance from their origin, the superficial fibers of the anterior head curve sharply to run nearly straight ventrad and slightly anteriorly; the deeper fibers curve less sharply than the superficial ones and the deepest run nearly straight ventrolaterad. The superficial and deep fibers taper ventrally to insert on an anterodorsal extension of the basal aponeurosis with the anterior fibers inserting dorsal to the posterior ones. The lengths of the superficial and deep fibers of the anterior portion of the MAMEM-b are similar (12-14 mm). In the posterior portion, the deep fibers (15-17 mm) are slightly longer than the superficial ones (14-16 mm) but both are longer than those anteriorly.

The posterior head (MAMEM-c) originates as a set of fibers that runs in a markedly anterolaterad direction from the dorsal, posterolateral surface of the parietal and the anterodorsal surface of the squamosal. The superficial fibers then curve sharply ventrad, continue anteriorly, and pass deep to the postorbital bar and the MAMES. The deep fibers of the MAMEM-c run anteriorly and nearly straight ventrolaterad. The superficial and deep fibers converge ventrally to form a thin muscular sheet; the anterior fibers form the anterior part of this sheet and the posterior fibers the posterior part. The anterior part inserts dorsal to the posterior part on the lateral surface of the anterior and central portion of the basal aponeurosis. In the anterior part of the MAMEM-c, the deep fibers (14-15 mm) are slightly longer than the superficial ones (13-14

Fig. 1. *Sphenodon punctatus*. Top: Lateral view of dissection after removal of skin and connective tissues. Note that adductor muscles are bound by the dorsal and ventral arches of the diapsid skull. Middle: Lateral view of dissection after removal of both bony arches and most of the MAMES. Note the subdivisions of the MAMEM and how this bulky muscle tapers to insert onto the thin basal aponeurosis. Bottom: Lateral view of the dissection after removal of both bony arches, most of the MAMES, and displacement of the MAMEM. Note the large MPSTS and the relations of the maxillary (V_2) and mandibular (V_3) branches of the trigeminal nerve. MAMEM, *M. adductor mandibulae externus medialis*; MAMEP, *M. adductor mandibulae externus profundus*; MAMES, *M. adductor mandibulae externus superficialis*; MDM, *M. depressor mandibulae*; MIMD, *M. intermandibularis*; MLAG, *M. levator anguli oris*; MPSTS, *M. pseudotemporalis superficialis*; MPTA, *M. pterygoideus atypicus*.

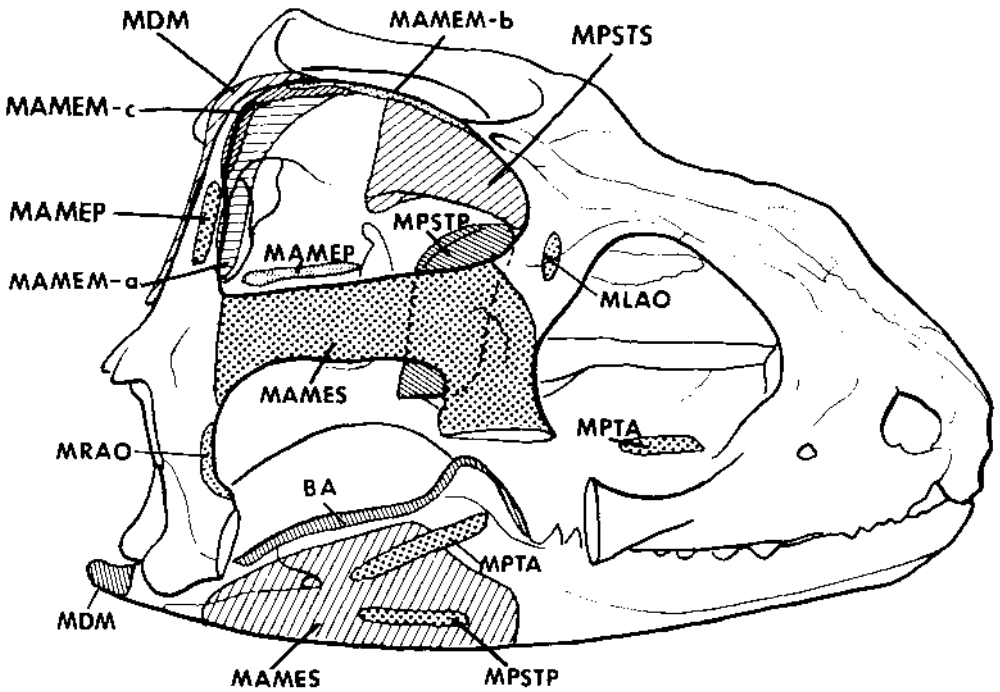
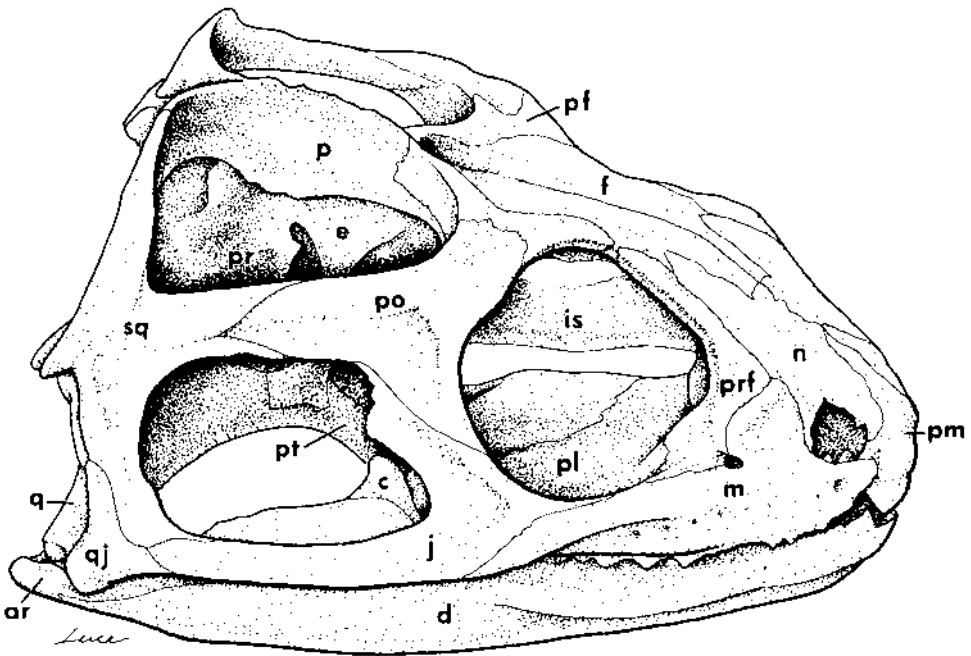


Fig. 2. *Sphenodon punctatus*. Top: Lateral view of skull. Note fully diapsid skull having two temporal fenestrae completely encircled by bone. Bottom: Lateral view of the skull (with lower arch removed) and lower jaw. The sites of attachment of cephalic muscles are indicated. ar, articular; BA, basal aponeurosis; c, coronoid process; d, dentary; e, epipterygoid; f, frontal; is, interorbital septum; j, jugal; m,

maxilla; MPSTP, *M. pseudotemporalis profundus*; n, nasal; p, parietal; pf, postfrontal; pl, palatine; pm, premaxilla; po, postorbital; pr, prootic; prf, prefrontal; pt, pterygoid; q, quadrate; qj, quadratojugal; sq, squamosal. For completeness, we show attachment sites of the *M. levator anguli oris* (MLAO) and the *M. retractor anguli oris* (MRAO). Other abbreviations as in Figure 1.

mm). However, the lengths of the superficial and deep posterior fibers are similar to each other (14–15 mm) and similar in length to the deep fibers of the anterior portion.

The largest part of the MAMEM is the ventrolateral head (MAMEM-a) that originates from the posterolateral and posteroventral surface of the parietal and from the anterior surface of the dorsal process of the squamosal. The superficial fibers initially run in a markedly anterolateral direction, then curve sharply ventrad, continuing anteriorly to pass deep to the postorbital bar and MAMES. The deep fibers curve less than the superficial, running nearly straight ventrolateral and slightly anteriorly. The superficial fibers insert on the lateral surface and deep fibers on the medial surface of the anterior and central portion of the basal aponeurosis just ventral to the insertion of the anterior and middle heads. The anterior fibers of the MAMEM-a also insert dorsal to the posterior ones. The fibers of the anterior part of the MAMEM-a are shorter than those of the posterior part (anterior: 9–11 mm; posterior: 11–13 mm). However, the lengths of the superficial and deep fibers of the anterior part are similar to each other as are those of the posterior part.

M. adductor mandibulae externus profundus (MAMEP; Figs. 1,2)

The *M. adductor mandibulae externus profundus* lies deep to the MAMEM and posterior to the *M. pseudotemporalis superficialis*. It has a lateral head originating from the posterolateral surface of the prootic and a medial head originating from its anterolateral surface. The fibers of the lateral head pass ventrad and anteriorly to converge onto a flat tendon, inserting on the medial surface of the posterior part of the basal aponeurosis. The anterior fibers of the medial head run almost directly ventrad to join the tendon of the lateral head. The posterior fibers of the medial head pass ventrad and slightly anteriorly to insert directly on the basal aponeurosis posterior to the insertion of its anterior fibers and those of the lateral head.

The anterior superficial fibers of the lateral head of the MAMEP are slightly shorter than the anterior deep fibers (superficial: 7–8 mm; deep: 8–9 mm). As one proceeds posteriorly, the length of the superficial fibers decreases (5–6 mm), whereas the lengths of the deep fibers remain relatively constant. The anterior superficial fibers of the medial head are also slightly shorter than those of its deep counterparts (superficial: 6–7 mm; deep: 7–8 mm).

However, as one moves posteriorly the lengths of both the superficial and deep fibers increase and become similar to each other (superficial: 10–11 mm; deep: 9–11 mm).

M. pseudotemporalis superficialis (MPSTS; Figs. 1, 2)

The anterodorsal portion of the *M. pseudotemporalis superficialis* is visible in the anterior corner of the dorsal temporal fossa, but most of the muscle lies deep to the MAMEM. The maxillary division of the trigeminal nerve (V_2) crosses the lateral face of the MPSTS and the mandibular branch of the trigeminal nerve (V_3) lies against its posterior margin.

The MPSTS originates from the posterior part of the postfrontal, the anterolateral part of the parietal, and the dorsoposterior part of the epipterygoid. Its anterior fibers initially pass ventrad and slightly anterolaterad dorsal to the postorbital, but then curve medially deep to the postorbital to run nearly straight ventrad. The anterior fibers converge to insert on the medial surface of a tendinous extension of the anterior part of the basal aponeurosis. The central and posterior fibers also run ventrad and slightly laterad dorsal to the postorbital and then curve slightly medially ventral to it. However, the orientation of these fibers becomes progressively more anterior as one moves caudally. The central fibers insert onto the anterior tendinous extension, ventral and posterior to the anterior fibers. The posterior fibers insert directly onto the medial surface of the anterior and central portion of the basal aponeurosis. The most superficial of the anterior, central, and posterior fibers insert most dorsally and the deepest fibers most ventrally.

The superficial anteriormost fibers of the MPSTS are longer than the deep ones (superficial: 17–18 mm; deep: 14–15 mm). As one moves posteriorly, the lengths of the superficial fibers remain relatively constant until the posterior margin of the MPSTS, where the fiber lengths decrease to 15 mm. In contrast, the length of the deep fibers first increases (15–17 mm) but then decreases (11–8 mm) as the posterior border of the muscle is reached.

M. pseudotemporalis profundus (MPSTP; Fig. 2)

The *M. pseudotemporalis profundus* is composed of a long lateral and a short medial part and lies between the MPSTS and the epipterygoid bone. The mandibular branch of the trigeminal nerve separates the posterior margin of the MPSTP from the anterior margin of the

M. adductor mandibulae externus profundus. The lateral part originates deep to the anterior portion of the MPST'S from the ventroanterior region of the parietal and the dorsoanterior part of the epipterygoid. The medial part of the MPSTP lies deep to the lateral part and originates from the anterior part of the epipterygoid and the posterior part of the membranous braincase. The fibers of the lateral part pass ventroposteriorly and slightly laterad, whereas those of the medial part pass posterolaterad and slightly ventrad. The lateral and medial parts join near the upper margin of the mandible and the fibers then run ventroposteriorly and slightly laterad to insert on the ventromedial surface of the dentary, ventral to the coronoid process.

The lengths of the anteriormost and posteriormost fibers of the lateral part are similar (14-15 mm), as are the lengths of the anterior and posterior fibers of the medial part (14-15 mm). However, the fibers in the middle of the lateral part are longer (16-17 mm) than those at its anterior and posterior margins.

M. pterygoideus typicus (MPTT; Fig. 3)

The bulky *M. pterygoideus typicus* has a complicated internal architecture. It may be subdivided into 1) a dorsalmost (deep) portion, 2) a middle portion, and 3) a ventrolateral one. Haas's brief description (1973) of this muscle only mentions its several bony points of attachment.

The dorsalmost (deep) portion of the MPTT fills the ventral half of the space lying medial to the pterygoid and pterygoid wing of the quadrate. The muscle originates from the anterodorsal region of the medial surface of the pterygoid. From here its fibers run sharply ventrad and curve slightly posterolaterally to insert on the dorsal surface of the postero-medial end of the lower jaw by means of fine tendons and fleshy attachment.

The fibers of the dorsalmost portion of the MPTT are short dorsally and ventrally and long in the center of the muscle. As one moves dorsally, the length of the fibers increases from 5-6 mm (ventral) to 8-10 mm but then decreases to 6-7 mm.

The middle portion is the bulkiest part of the MPTT. It bulges ventrally from the two sides to form a deep, narrow ridge in the roof of the posterior part of the oral cavity. The middle portion of the MPTT originates from the ventral and medial surface of the ectopterygoid-ptyerygoid process (ptyerygoid flange), the medial margin and ventroposterior half of the

ptyerygoid and the ventromedial process of the quadrate. Its superficial (i.e., ventral) fibers originate from the pterygoid by an aponeurosis, whereas the deeper fibers attach directly. The middle portion of the MPTT may be subdivided into medial, intermediate, and lateral parts and each of these into superficial and deep fiber layers.

The superficial fibers of the medial part show a parallel arrangement. These fibers first run posteromedially and slightly ventrad; thereafter they curve posterolaterad toward the ventroposterior margin of the mandible. The superficial fibers of the intermediate part also show bundles of parallel fibers that initially pass caudad, then turn sharply ventrad and slightly laterad to the ventral margin of the mandible; thereafter they curve sharply caudad and slightly ventrolaterad. The deep fibers of both these parts are parallel and pass straight posterolaterad and slightly caudad. Both superficial and deep fibers of the medial and intermediate parts converge posteriorly to insert on the medial surface of the posterior end of the lower jaw, just anterior to the insertion of the dorsal portion of the MPTT.

As one moves farther laterad, the fiber arrangement of the MPTT changes from a parallel to a bipinnate one. This change in fiber arrangement is not obvious from a superficial ventral view, as the middle portion of the MPTT is covered partially by the ventrolateral portion. Haas ('73) does not describe this change in the MPTT of *Sphenodon* and no such condition has been mentioned for the MPTT of *Uromastyx aegyptius* (Throckmorton, '80), *Varanus exanthematicus*, *Ctenosaura similis*, and *Tupinambis nigropunctata* (Smith, '80).

This bipinnate arrangement marks the boundaries of the distinct lateral one-third of the MPTT. This lateral part is further subdivided into a lingual and buccal half by the insertion sites of the fibers. The medialmost fibers of the lingual half are long, curve posterolaterally, and insert near its posterior end. As one continues toward the plane of insertion, the fibers curve less and their lengths gradually decrease as they insert farther anteriorly along this plane. The fibers of the buccal half run ventromedial to meet those of the lingual half; the more posterior insert more posteriorly than the anterior fibers. The lengths of the fibers of the buccal half are equivalent to each other.

The ventrolateral portion of the MPTT has a tendinous origin from the lateral and ventral aspect of the ectopterygoid-ptyerygoid process.

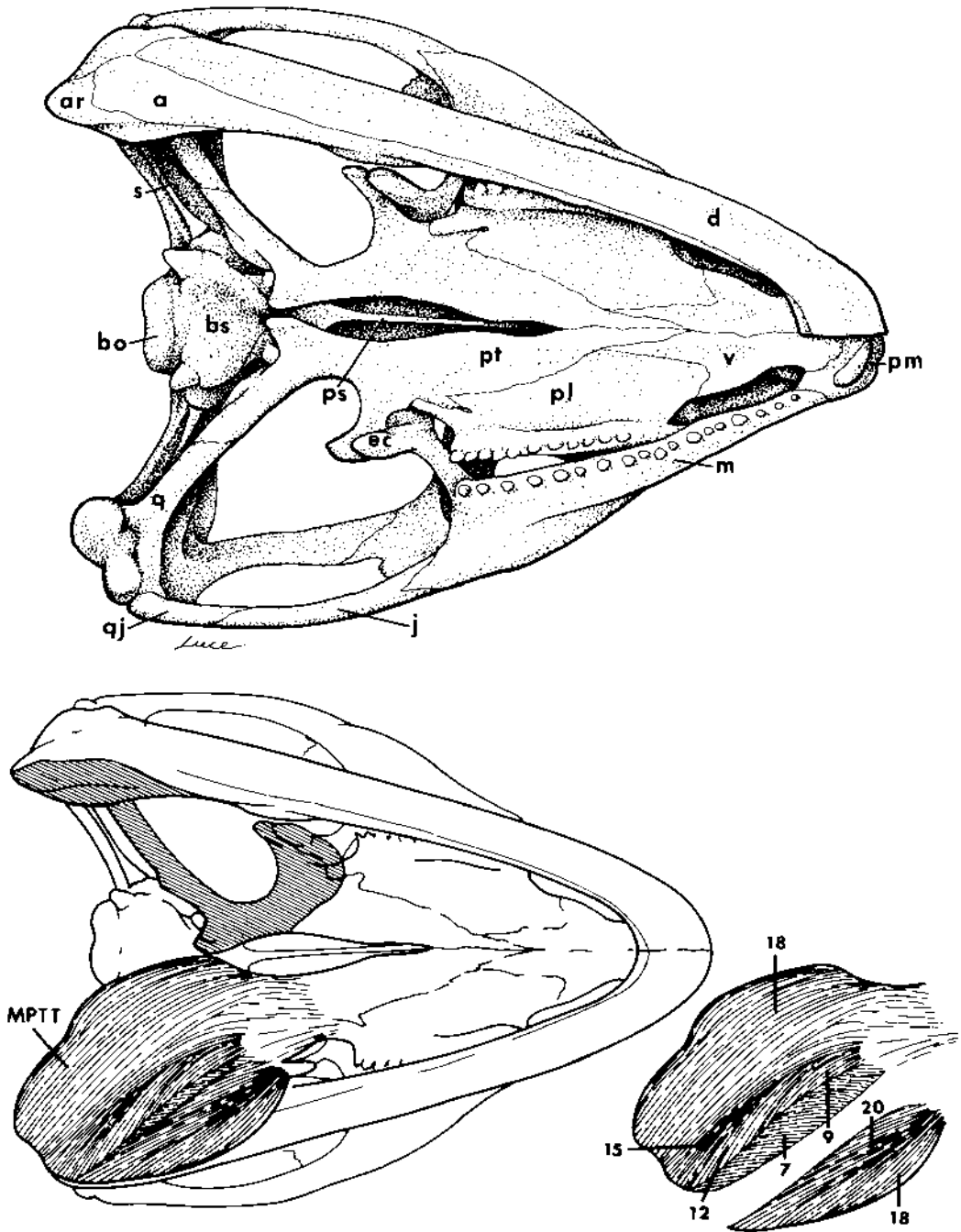


Fig. 3. *Sphenodon punctatus*. Top: Ventral view of skull and right half of lower jaw. Note the close proximity of the coronoid process of the lower jaw and the pterygoid flange and the arrangement of maxillary and palatine tooth rows. Bottom: Ventral view of the dissection after removal of the intermandibular and throat musculature. The cross-hatched areas represent sites of attachment of the MPTT. Ventral

view of the middle portion of the MPTT with the ventrolateral portion displaced. Note the shape and fiber arrangement of the MPTT. The numbers give the lengths of the fibers (in mm) in the regions indicated. a, angular; bo, basioccipital; bs, basisphenoid; ec, ectopterygoid; MPTT, M. pterygoideus typicus; ps, parasphenoid; s, stapes; v, vomer. Other abbreviations as in Figure 2.

Its fibers first pass ventrolaterally and slightly caudad to the ventral margin of the mandible; they then curve posterolaterally to run along the ventral margin up to the posterior third of the jaw, where they insert on its medial, ventral, and ventrolateral surfaces. The ventralmost fibers insert most posteriorly on the mandible and the medial and lateral fibers anteriorly. The fiber lengths for the different regions of the middle and ventrolateral portions are shown in Figure 3.

M. pterygoideus atypicus (MPTA; Figs. 1,2)

The M. pterygoideus atypicus is the largest of the deep jaw muscles. It originates ventral to the eye on the dorsal surface of the palatine and can be exposed by elevating the eye and its loose connective tissues. The lateralmost fibers originate most anteriorly and the medialmost most posteriorly. Its fibers pass caudad and slightly dorsolaterad, bridging the gap between the posterior end of the palatine and the pterygoid. From here they continue caudad, passing medially through a slightly rounded depression in the ectopterygoid-ptyerygoid process. After bending through about 80°, they continue posteroventrad to insert on the medial surface of the lower jaw, just ventral and posterior to the coronoid bone. The lateralmost fibers insert anteriorly and the medialmost posteriorly. The fiber lengths of the MPTA (16-17 mm) are relatively constant from its medial to lateral margins.

Feeding movements

Introduction

General terminology. A feeding sequence consists of prey capture, mastication, and swallowing. Mastication is subdivided into reducing, repositioning, and terminal phases. Each single swing of the mandible, starting with opening of the mouth and continuing through closing, is referred to as a cycle. Each cycle is divided into phases defined by obvious changes in the movement pattern.

Preliminary information about muscular activity is provided by the externally visible movements of the jaws and tongue and by the bulging muscles, specifically of the Mm. adductor mandibulae externus medialis (dorsal temporal fossa) and superficialis (ventral temporal fossa) and the M. depressor mandibulae. The bulky tongue is highly mobile, plays an important role in capture and manipulation of food, and is visible whenever the mouth is open. Individual cycles of masticatory phases differ when the animals are reducing the food,

when they are repositioning it between the jaws, and during the terminal phase, just prior to swallowing.

Reducing movements. Reducing movements usually comprise groups of two to four cycles during which the prey is positioned between the teeth on one side of the head. In each cycle, the mouth first opens slowly and then continues to open more rapidly until maximum gape for the cycle is reached. It next closes rapidly and then slows down as the food is contacted. During slow closing, the mandible first continues to move upward and then moves anteriorly. The mouth then opens slightly and the mandible remains immobile until the start of the next cycle. During these reduction cycles, strain gauges placed at right angles to the tooth row generate a double-peaked output (see below).

Changes in the size of the prey do not produce fundamental changes in mandibular movement. However, the horizontal and vertical excursions of the head are greatest when large prey is being reduced. Also the duration of certain phases of the masticatory cycle then increases.

Repositioning movements. Food is shifted posterolaterad during the individual chewing cycles of a group. Subsequently, it is repositioned between the tooth rows of the same or the opposite side. At the start of a repositioning movement, the mouth opens farther than during reducing movements. The tongue shifts the food as the mouth opens and displaces it anteriorly and laterally. Repositioning movements produce single peaks of greater amplitude and duration than chewing cycles on the strain gauge records. Occasionally, the food may be repositioned without a significant change in the pattern of chewing movements.

Terminal movement. At the very end of a reduction sequence, the tongue moves the food towards the back of the oral cavity. In such terminal movements, the mouth opens slightly wider and longer than it does during chewing cycles. Strain gauge records show a single peak of relatively long duration.

Feeding on crickets and cockroaches

Capture. Tuataras respond to moving prey by cocking their head towards it. While they ordinarily ignore motionless prey, they may ingest it after it has been moved around with tweezers.

When a (hungry) tuatara notices insects moving on the ground, it points its head towards the prey, opens the mouth, and then

everts the tongue. The tongue first lifts slightly out of the buccal floor and then begins to protrude; during this movement its dorsal surface remains straight and the tongue appears thin in profile (Fig. 4B). As the tongue protrudes beyond the symphysis, its upper surface curves. The middle of the tongue then seems to be pushed upward and forward, but the anterior portion appears to be fixed to the symphyseal region so that the tongue starts to double back under itself (Fig. 4C). The head continues to move towards the prey and cineradiographs show that the hyoid (supporting the trachea and posterior lingual portion) is protracted. This protraction of the hyoid moves the posterior aspect of the tongue towards the symphysis.

During capture, the sticky dorsal surface of the anterior portion of the tongue rotates around the symphysis to lie ventrally. The ventrally directed surface is pushed against the food (Fig. 4D) by a combination of tongue eversion and the forward and downward movement of the head (Fig. 4E). Hyoid, tongue, and adherent prey are then withdrawn into the oral cavity (Fig. 4F) and the mouth closes.

Reducing movements. Retraction of the tongue pulls the adherent prey into the mouth, where it generally comes to rest partially across one set of tooth rows; two to three preliminary masticatory or immobilizing cycles follow. The tongue then repositions the cricket posteriorly near the corner of the mouth and between either set of teeth, after which mastication proper begins. The cricket generally remains in a fixed position relative to the upper jaw for two to four masticatory cycles. Occasionally, propalinal shearing movements of the lower jaws shift the cricket slightly anteriorly. The cricket is then repositioned by the tongue either to the same or the opposite side as the mouth opens; two to three more masticatory cycles follow. Such groups of cycles occur repeatedly during a reduction sequence. Increasing amounts of secretion become visible around the cricket and it becomes reduced to a saliva-covered, mushy mass after approximately 15 chewing cycles.

A masticatory cycle (Figs. 5, 6) may be subdivided into six phases: 1) slow-opening, 2) fast opening, 3) fast-closing, 4) crushing, 5) shearing, and 6) resting; all are best described from lateral views (Fig. 5).

During the slow opening phase (1), the lower jaw first rotates open slowly. Cineradiographs show that the retroarticular process of the mandible simply rotates about a transverse

axis through the quadrate. During the fast-opening phase (2), the lower jaw rotates open more rapidly; but the entire jaw also moves posteriorly. Cineradiographs show that the retroarticular process of the mandible continues to rotate, but simultaneously translates posteriorly along the articular surface of the quadrate. The fast opening phase ends with the mouth wide open and with the retroarticular process shifted posteriorly in the mandibular fossa.

During the fast-closing phase (3), the mandible first rotates closed rapidly and only decelerates when the teeth contact the food. The anterior shift of the mandibular tip at the end of fast closing is so minor that the articular process shows no obvious translation in cineradiographs. Next follows the distinct crushing phase (4). The dorsal and lateral adductor masses on the working side of the head bulge obviously and one may hear chitin being fractured. During the crushing phase, the mandible slowly rotates toward closure; it also moves slightly forward as the retroarticular process both rotates about the quadrate and translates anteriorly. During the shearing phase (5), the mandible obviously moves anteriorly; food held fixed against the maxillary and palatine tooth rows is sheared by the mandibular row acting like a saw. Large food items tend to be rotated slightly and the skin of the mouth adjacent to the food is pulled taut during this propalinal (anterior) shift. The shearing phase lasts until the mandible drops slightly and moves slightly posteriorly, separating the upper and lower teeth. During the resting phase (6), the lower jaw remains slightly depressed until the start of the slow opening phase of the next cycle.

During the crushing phase, the muscles bulge noticeably out of the dorsal temporal fossa. Normally the food is asymmetrically positioned; the muscles of the working side then bulge slightly earlier and more obviously than do those on the balancing side. During the fast-closing and crushing phases, muscles on the working side also bulge slightly out of the ventral temporal fossa. Muscles of the anterior portion of the ventral fossa begin to bulge during fast closing; those of the posterior portion bulge next, during the crushing phase.

Records from the strain gauge (Fig. 6) crossing the gape reflect the jaw movements during a chewing cycle as a double-peaked curve; the first peak is larger than the second. The rise of the first peak correlates with the start of fast opening, the peak indicates the transition from

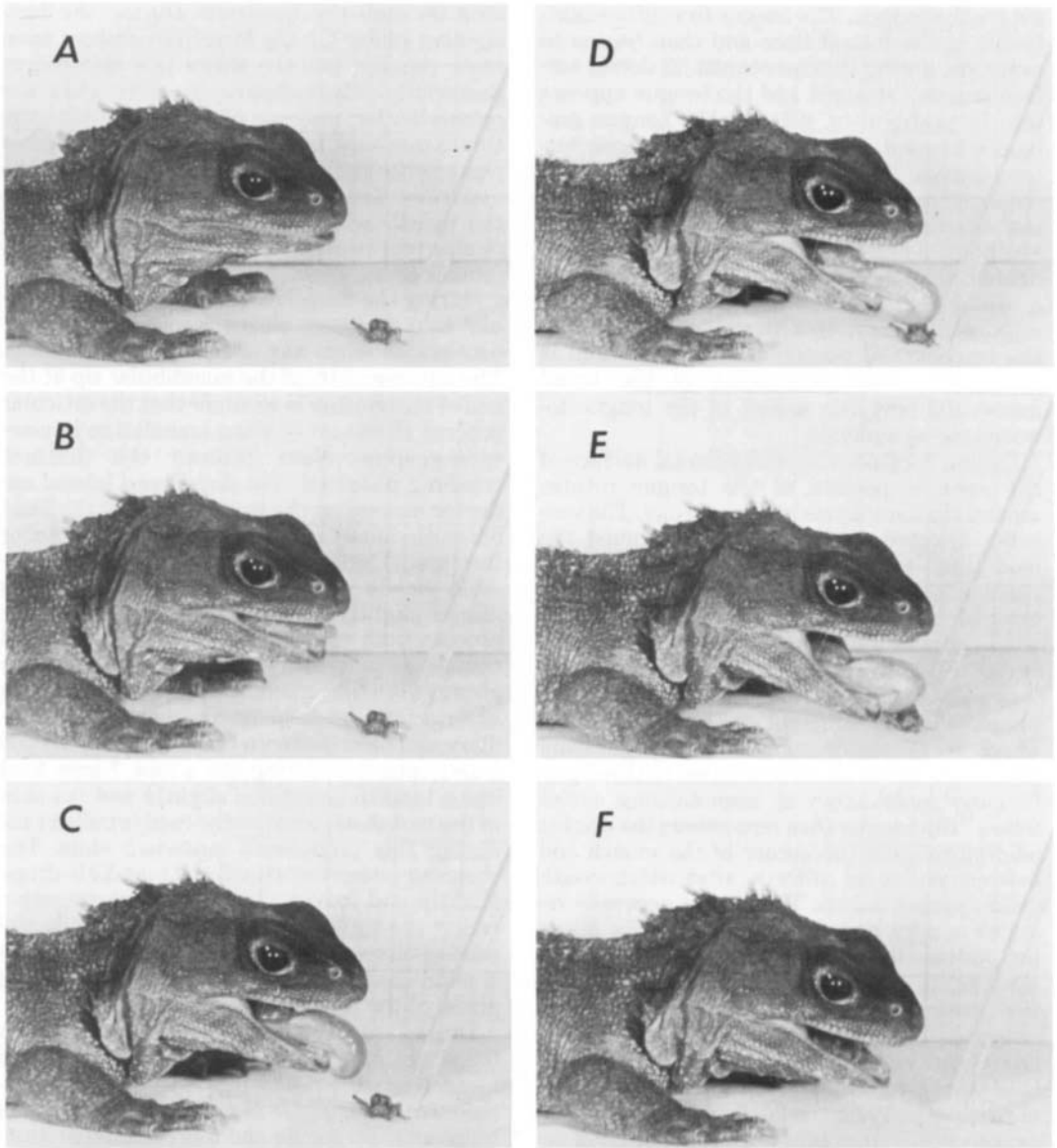


Fig. 4. *Sphenodon punctatus* capturing a cricket. Successive frames (24 frames/sec.) from a 16-mm, strobe-exposed film. An immobilized (chilled) cricket was

manipulated by a plastic rod to attract the tuatara and elicit feeding within a circumscribed area. This procedure was used in most recording sessions.

fast opening to fast closing, and the signal returns to base line at the end of the fast closing phase. The small secondary peak is produced by the bulging of the dorsal adductor mass and consequently correlates with the crushing phase. The relative height of this secondary peak is higher on the working than on the balancing side. No strain gauge dis-

placements occur during the slow opening and shearing phases, nor do the strain gauges indicate anteroposterior movements and the relative opening of the mouth during the resting phase.

In general, the length of all phases, except for the resting one, decreases as does the excursion of the jaws throughout a reduction se-

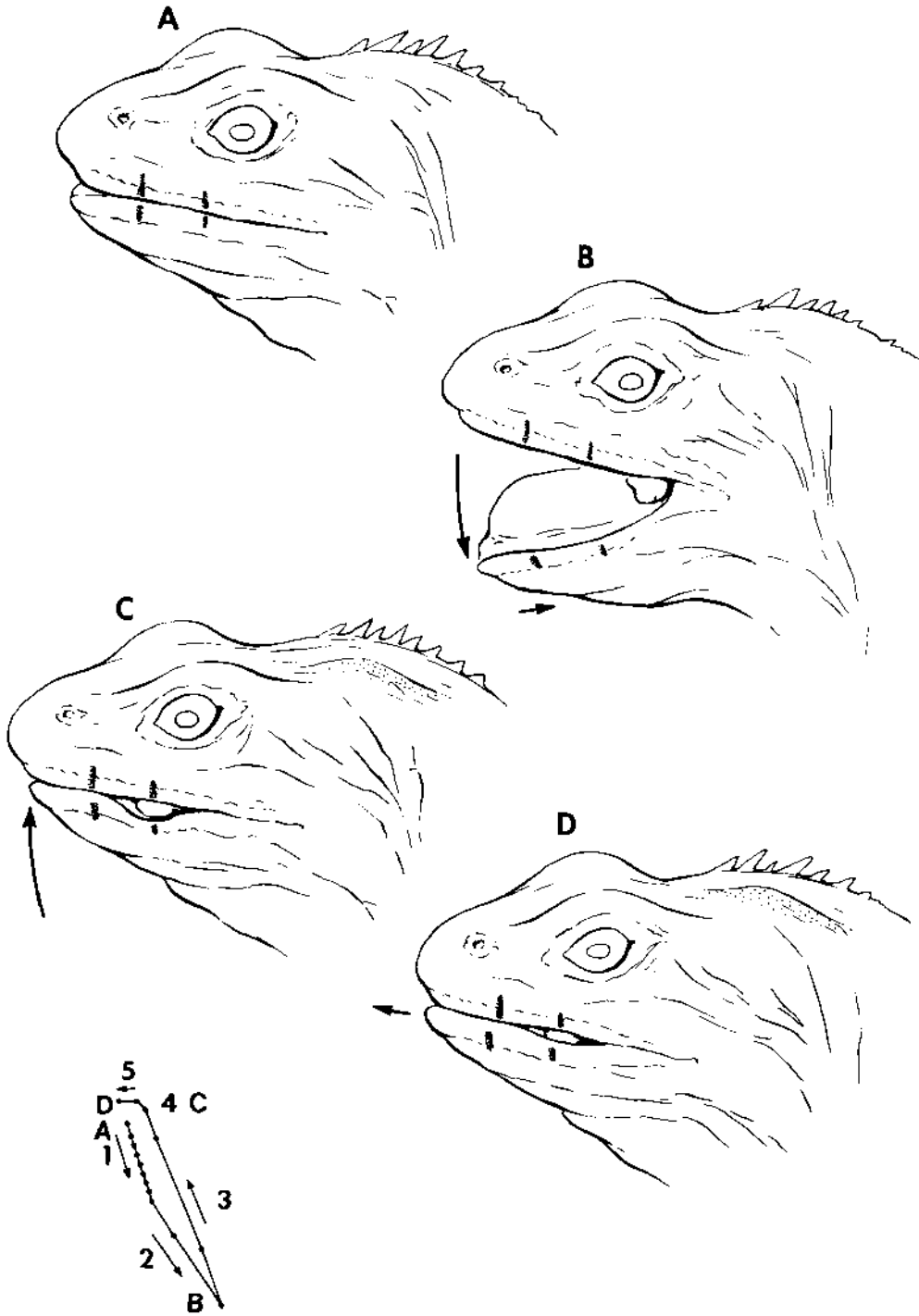


Fig. 5. *Sphenodon punctatus*. Displacement of lower jaw during a chewing cycle traced from 16-mm movie. Arrows indicate the movement of the jaw between frames as food is reduced between the left tooth rows. The vertical bars crossing the labial zone are painted reference markers indicating the extent of the propalinal shift. The stippled area

represents the bulging of the working side adductors during crushing and shearing phases. The insert shows the path of the tip of the mandible relative to the head during a reducing cycle. 1, slow-opening phase; 2, fast-opening phase; 3, fast-closing phase; 4, crushing phase; 5, shearing phase.

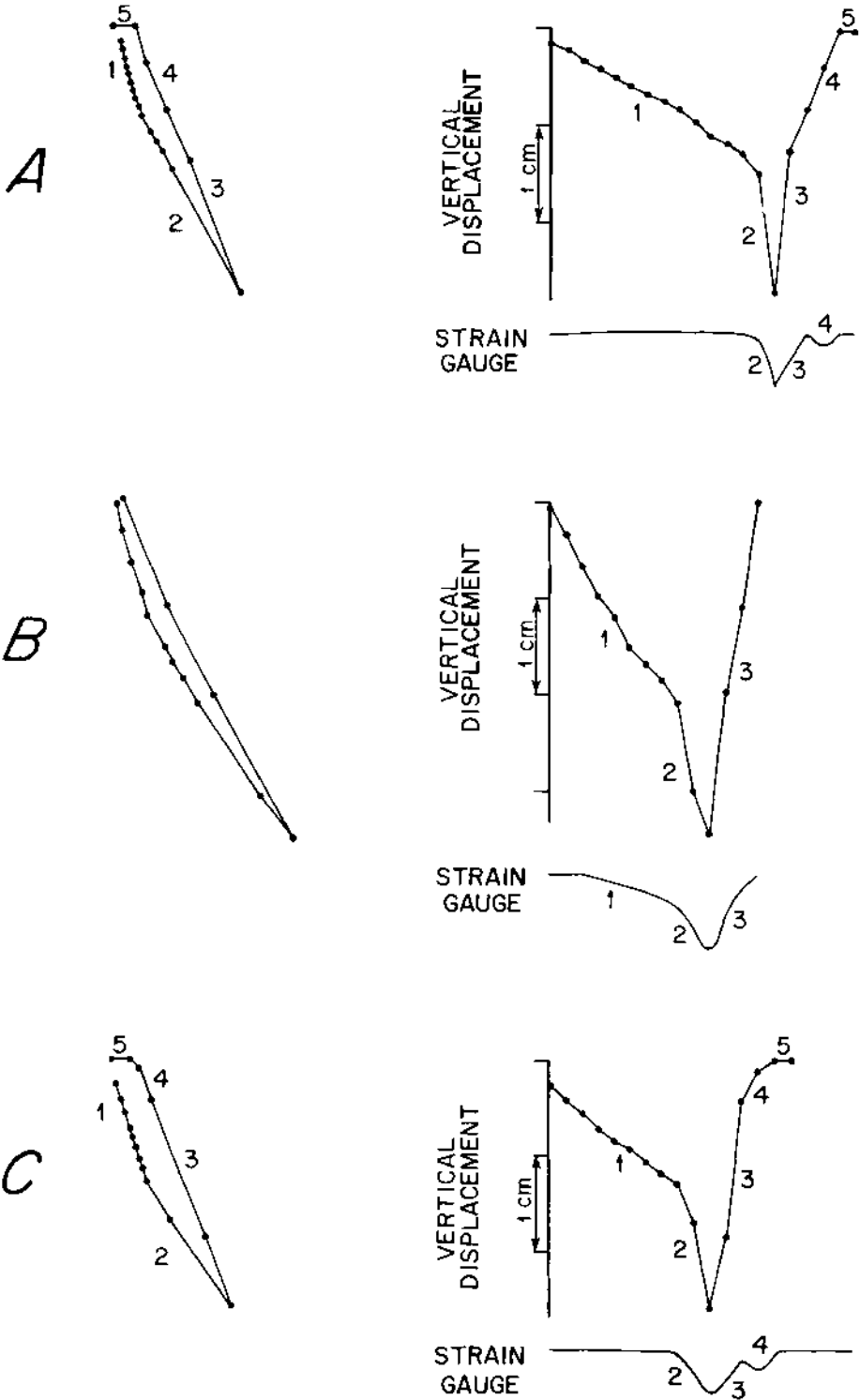


Fig. 6. *Sphenodon punctatus*. Three successive cycles of the left tip of the jaw (left) and their corresponding vertical displacement graph and strain gauge record (right) when a tuatara reduces a cricket. A: The working side is on the left.

B: Food is repositioned to the right. C: The balancing side is on the left. The numbers accompanying the cycles, displacement graphs, and strain gauge records indicate five of the six phases of a reduction cycle.

quence. Neither direct observations nor analysis of films suggests that the mandible moves laterally, or that the lower jaws rotate about their long axes.

The lower jaws reach maximum opening velocity during the initial one-third of the fast opening phase (Fig. 7). The velocity then smoothly reverses to a maximum closing value that occurs during the first one-third of the fast-closing phase. Maximum closing velocities tend to be greater than or equal to (rarely less than) maximum opening velocities. Maximum opening acceleration of the lower jaws occurs at the start of fast opening and the two- to three-times greater maximum closing acceleration is reached at the start of the fast closing phase.

Repositioning movements. Insects are repositioned every three to five cycles. Repositioning cycles occur about 100 msec. after the end of the shearing phase of the previous reduction cycle; the resting phase before a repositioning cycle is only 40% as long as that between two reduction cycles.

As the mouth begins to open, the tongue twists towards the working side to contact and slide the cricket off the double tooth rows. The mouth opens wider than during a chewing cycle and the tongue arches dorsally, first centering the cricket in the oral cavity and, as the mouth closes, repositioning it laterally for the first cycle of the next chewing sequence.

As the mandible reaches a wide open position during repositioning, the skin covering the dorsal temporal fossa sinks inward slightly but then rises and straightens during the fast-closing phase. Strain gauge records do not show a secondary peak.

Terminal movements. As the cricket becomes crushed, it is gradually worked posteriorly to the central region of the oral cavity; reduction cycles then pass smoothly into terminal ones.

Terminal movements are characterized by dorsal and anterior arching of the tongue which usually rubs against the roof of the mouth (and collects food from it). During this movement the lingual tip extends beyond the anterior margin of the maxillary tooth row. The tongue (and hyoid) then retract, carrying the food into the buccal cavity. The mouth opens slightly wider and for a longer interval during terminal cycles than during masticatory cycles.

The dorsal adductor musculature does not bulge obviously (so the strain gauge records do not show a secondary peak). Furthermore,

there is less propalinal displacement of the mandible during terminal cycles than during masticatory ones; the path of the mandibular tip shows only a slight anteroposterior displacement when the mouth opens and closes. During the fast opening phase, the mandible and its articular process show only a slight posterior translation and during the crushing and shearing phases only slight anterior translation. There are usually five terminal cycles at the end of a reduction sequence.

Mandibular displacement during terminal cycles is similar to that during reducing ones. Maximum opening velocity occurs during the last one-third of jaw opening, and maximum closing velocity takes place during the first one-third of closing. Maximum opening acceleration coincides with the start of fast opening and the two-times-greater maximum closing acceleration coincides with the start of fast closing.

Feeding on mice

General. *Sphenodon* ingests newly born mice in the same way that it does crickets and roaches. Portions of the feeding pattern change during ingestion of juvenile mice. Tables 2 and 3 show changes in reducing movements among reduction sequences for crickets, roaches, and juvenile mice.

Capture and immobilization. *Sphenodon* captures mice by biting them and obtaining a secure grip with the anterior teeth. The tongue plays no role during capture nor is it protruded. After capture, mice are shifted gradually deeper into the mouth by inertial movements of the head. These involve a rapid drop of the mandible with a simultaneous upward and forward movement of the head relative to the prey. The mouth then snaps closed and the head again moves downward. Captured mice are generally positioned transversely in the mouth across the tooth rows of both sides.

Coincident with or following the capture and posterior shift, *Sphenodon* makes a series of crushing bites that kill the mouse. The tooth rows on both sides are used simultaneously and the prey is not repositioned as long as it remains centrally located in the mouth. Repositioning occurs by rapid lateral movements of the head (with a simultaneous opening cycle) and effectively shifts the prey to the side opposite to that towards which the head moves. Both during capture and during inertial movements *Sphenodon* rotates its skull slightly dorsal around the head joint; this occurs coincident with mandibular depression.

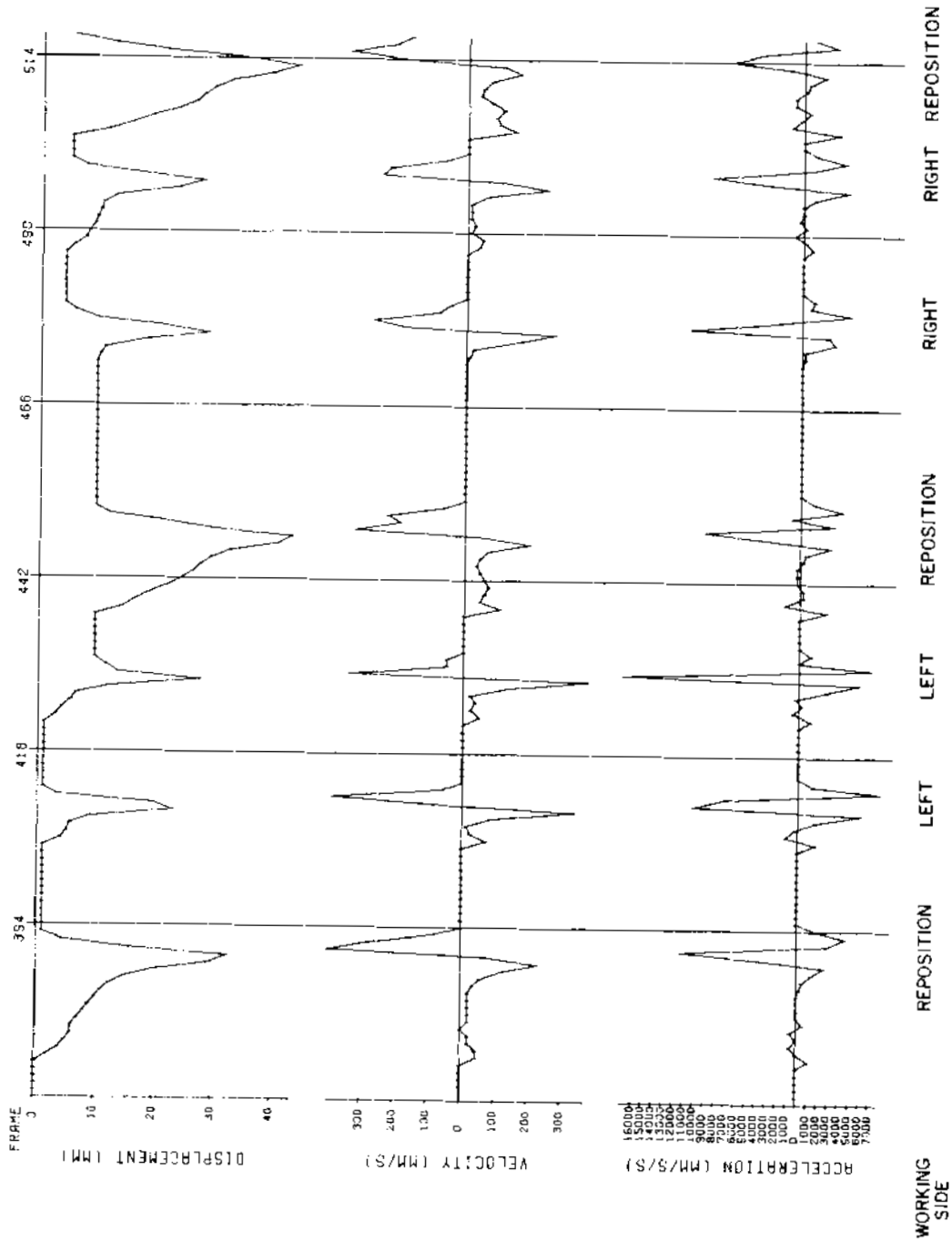


Fig. 7. *Sphenodon punctatus*. Vertical displacement, velocity, and acceleration graphs of the tip of the mandible relative to the head: when tuatara reduces a cricket.

TABLE 2. Comparison of masticatory cycles when *Sphenodon* chew crickets, cockroaches, and juvenile mice¹

Food	Bites per second	Total number of bites per sequence	Duration of bite ²	Duration of repositioning movements ²	Duration of terminal movements ²
Crickets	0.84 ± 0.13 (N=190)	21.2 ± 3.39 (N=12)	502.6 ± 80.4 (N=50)	709.3 ± 98.4 (N=23)	891.7 ± 305.5 (N=16)
Cockroaches	0.83 ± 0.87 (N=130)	32.0 ± 5.63 (N= 9)	620.7 ± 140.6 (N=50)	831.9 ± 151.3 (N=31)	1072.2 ± 180.4 (N=20)
Juvenile mice	0.55 ± 0.06 (N=192)	38.4 ± 4.82 (N= 5)	877.4 ± 187.4 (N=42)	1391.1 ± 237.4 (N=15)	1300.5 ± 398.9 (N=11)

¹Bites are defined as the start of slow opening to the start of the resting phase. Data are mean ± SD.

²Milliseconds.

TABLE 3. Duration (msec.) of the six phases of masticatory cycles when *Sphenodon* chew crickets, cockroaches, and juvenile mice¹

Food	N	Slow-opening	Fast-opening	Fast-closing	Crushing	Shearing	Resting
Crickets	10	141.04 ± 29.5 (21%)	95.53 ± 20.5 (14%)	82.00 ± 20.5 (12%)	68.06 ± 20.5 (10%)	63.55 ± 21.6 (9%)	232.06 ± 114.0 (34%)
Cockroaches	10	145.55 ± 41.4 (21%)	86.51 ± 13.5 (12%)	77.08 ± 13.5 (11%)	63.96 ± 21.3 (9%)	63.55 ± 21.6 (9%)	264.04 ± 134.5 (38%)
Juvenile mice	10	414.51 ± 116.4 (25%)	132.02 ± 18.0 (8%)	113.57 ± 18.0 (7%)	86.51 ± 13.5 (5%)	91.02 ± 27.1 (5%)	843.37 ± 203.4 (50%)

¹Number in parenthesis directly below each mean equals the duration in percentage of the entire cycle. N equals number of cycles.

Reducing movements. At the start of reduction, the mice are shifted inertially to one side of the mouth by rapid mouth opening with coincident lateral shifts of the head. Simultaneously, mice tend to be shifted posteriorly as the head moves forward relative to the prey. The mice are repositioned inertially after each set of four to seven cycles. The tongue is not noticeably involved in the manipulation of large prey during these early stages of mastication.

As reduction of mice proceeds, movements of the mandible resemble those during the reduction of crickets. However, reduction of mice differs by upward movements of the entire head as the mouth opens, and downward movements as it closes; the head also tilts towards the balancing side during the first half of a reduction sequence. Thereafter, head movements cease, only the lower jaw cycles, and the tongue becomes involved in the manipulation of the food. During terminal cycles, the tongue protrudes but does not arc upward as it does during the reduction of crickets; nor does it appear to rub against the roof of the mouth.

Portions of mice may remain outside of the mouth during most of the reduction sequence.

Protruding limbs and even the heads of mice will then be cut off, but the severed portions are not picked up and only the part in the mouth is ingested. This observation may explain the comments that decapitated petrels were found in areas inhabited by tuataras (Crook, '75).

Electromyography - Capture

As the mouth starts to open, the anterior and posterior portions of the M. depressor mandibulae (MDM) begin to fire bilaterally. The anterior portion first reaches its maximum level and continues at this level until the mouth is almost completely open. However, the posterior portion first reaches a 25-30% level, becomes more active to a 50-60% level, and then reaches its maximum level near the end of opening. As the mouth reaches a wide-open position, the anterior portion of the M. adductor mandibulae externus superficialis (MAMES) starts to fire at a 20-25% level. Both portions of the MDM first become less active and then silent as the mouth starts to close.

Closing of the mouth is accompanied by increased activity in the anterior portion of the

MAMES and by the start of activity in the posterior portion of the MAMES, the anteromedial and posterior portions of the *M. adductor mandibulae externus medialis*, the *M. pseudotemporalis superficialis*, as well as the superficial and deep parts of the middle portion of the *M. pterygoideus typicus*. All of these adductors become more active during closing and attain maximum activity when the teeth contact and then crush (or penetrate) the prey. Thereafter, the adductors become less active as the mouth is closed and then silent as it opens slightly and stops moving. All of these adductors, as well as the MDM, remain silent as the mouth stays motionless, even though crickets and cockroaches lie partially across one set of lower teeth and juvenile mice across both sets.

Electromyography—Reduction

M. depressor mandibulae (MDM). The *M. depressor mandibulae* of the working and balancing sides are active bilaterally and symmetrically during the opening phase of a reduction cycle. However, the pattern of activity differs between the anterior and posterior portions of this muscle. Maximum voltages are 1.84 mV for the anterior and 2.32 mV for the posterior portion.

The anterior portion of the MDM starts to fire at a 10-15% level at the beginning of the slow-opening phase and continues to fire at this level throughout this phase; the posterior portion remains silent. At the start of the fast-opening phase, activity of the anterior portion reaches 40-60%, increases to 80-100% about midway through the fast-opening phase, and then drops to 20-30% as the lower jaw reaches its furthest ventral excursion (Fig. 8). The posterior portion of the MDM becomes active at a 40-60% level and maintains this level throughout fast opening. Both portions of the MDM become silent once the mouth reaches the wide-open position and remain inactive during the fast-closing, crushing, shearing, and resting phases.

Activity of both the anterior and posterior portions of the MDM is greater at the start than at the end of a reduction sequence and least during terminal cycles. When food is repositioned, the start and cutoff of activity in both the anterior and posterior portions are similar to those seen during a reduction cycle. However, the level of activity of the posterior portion reaches 100% during the repositioning movements, which is more than 40% greater than its maximum activity level during reduction cycles.

M. adductor mandibulae externus superficialis sensu stricto (MAMES). The anterior and posterior portions of the MAMES are active asymmetrically during reduction cycles and the level of activity is greater for the muscle on the working than on the balancing side. Maximum voltage is 0.86 mV for the anterior portion and 2.28 mV for the posterior one.

As the mouth starts to close, the anterior portion of the MAMES of the working side begins to fire at a 20-30% level (Fig. 8). Activity increases during closing to reach levels of 90-100% on the working side and 40-60% on the balancing side during the crushing phase. Activity of the MAMES of the working side then drops to 0-30% as the lower jaw starts to move anteriorly during the shearing phase. However, the posterior portion of the MAMES is silent until the start of the crushing phase. The level of activity then builds rapidly to 70-100% on the working side and then decreases sharply to below 40% as the crushing phase ends. The posterior portion of the muscle is generally silent during the shearing phase. Both portions of the MAMES are silent during the resting and opening phases of a reduction cycle.

During repositioning cycles, the anterior portion of the MAMES starts to become active at a 10-20% level at the end of the fast-opening phase and throughout the fast-closing phase. Unless the repositioning cycle has placed food between the tooth rows, the activity remains at 20-50% during the next crushing phase. When food has been positioned between the teeth, the MAMES becomes more active, reaching 70-100% during the crushing phase.

M. adductor mandibulae externus medialis (MAMEM). The anteromedial (-b-), posterior (-c-), and ventrolateral (-a-) heads of the *M. adductor mandibulae externus medialis* are bilaterally and asymmetrically active during a reduction cycle, and the level of activity is greater for the head on the working side than for that on the balancing one. Activity decreases as the food is reduced, as it is repositioned, and during terminal cycles. Maximum voltage is 1.74 mV for the anteromedial, 2.48 mV for the posterior, and 1.94 mV for the ventrolateral head.

All heads of the MAMEM of the working and balancing sides are silent at the start of closing; those of the balancing side remain silent throughout the fast-closing phase. However, as the teeth approach the food late in the fast-closing phase, all three portions of the working side start to fire at a 20-30% level (Fig. 8). Their activity increases rapidly at the

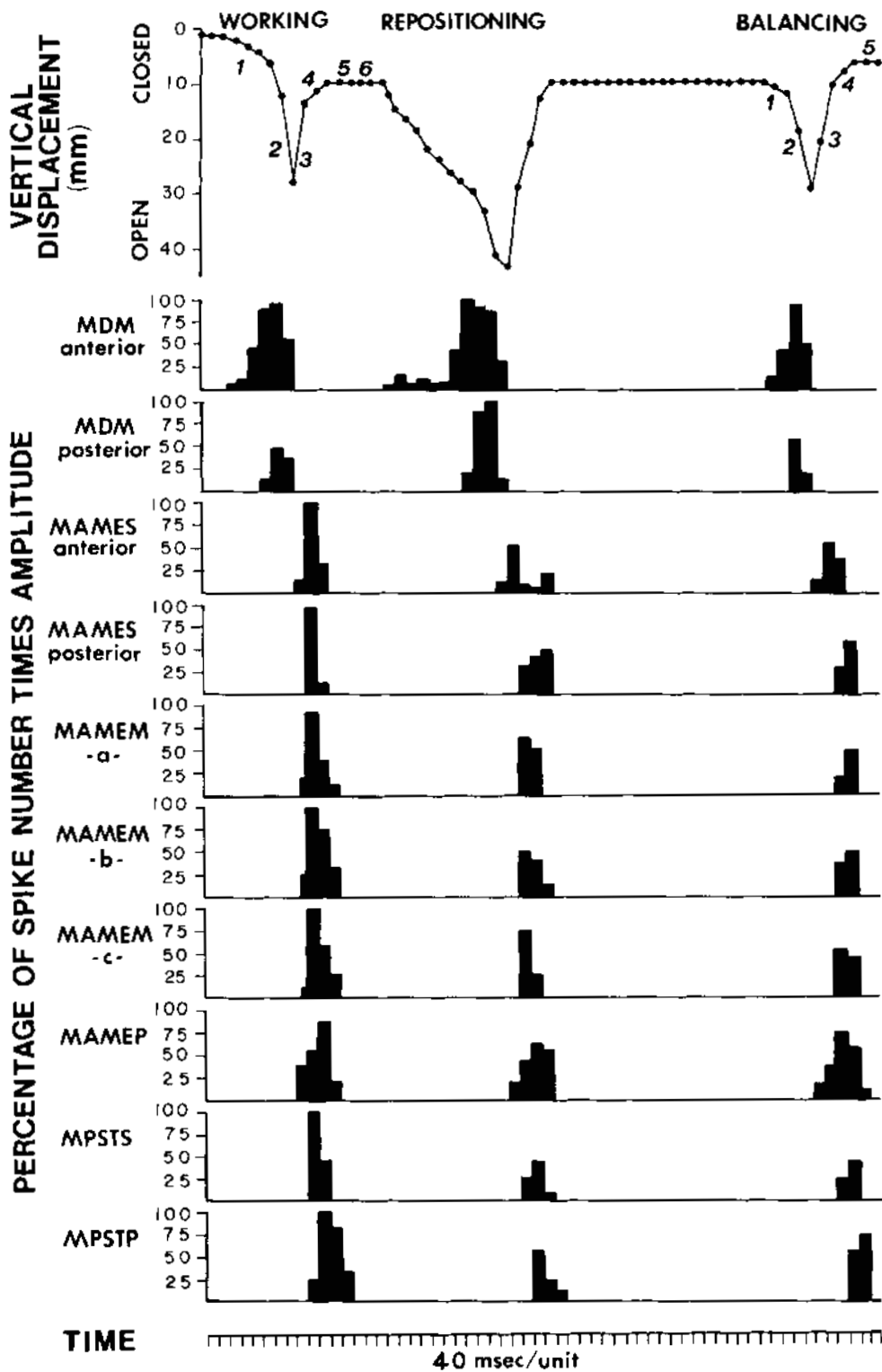


Fig. 8. *Sphenodon punctatus*. Synthetic summary of a sequence of vertical displacements of the lower jaw and bar graphs of the percentage of the number of EMG spikes times the mean spike amplitude when a tuatara reduces a

cricket. Muscle abbreviations as in Figure 1. The numbers (1-6) along the displacement graph indicate the six phases of a reduction cycle.

start of the crushing phase, reaching 70–100%. Activity of the posterior and ventrolateral heads then drops to a 40–60% level and the anteromedial one to a 50–70% level as this phase ends. The posterior and ventrolateral portions of the MAMEM of the working side show a 10–20% level of activity at the start of the shearing phase, whereas the anteromedial portion shows a 20–40% level. The three heads then become silent and remain so through the resting phase. Activity of the anteromedial and ventrolateral portions of the balancing side builds to a 30–40% level at the start of the crushing phase, increases to 50–60%, and then drops to 0–10% as the crushing phase ends; activity of the posterior head first increases rapidly to 50–60% and then drops to a 30–40% level. They become silent at the start of the shearing phase and remain so throughout the resting and opening phases.

M. adductor mandibulae externus profundus (MAMEP). The *M. adductor mandibulae externus profundus* is bilaterally active during a reduction sequence. Activity is greater on the working side than on the balancing one and decreases on both sides as the food becomes reduced. Maximum voltage is 1.28 mV.

The muscles on both sides start to fire at a 20–40% level at the start of fast closing (Fig. 8). Activity increases to 50–60% and reaches 90–100% on the working and 60–80% on the balancing side during the last half of the crushing phase. Thereafter, activity decreases bilaterally to a 0–30% level during the first half of the shearing phase. Both muscles are silent during the resting phase.

M. pseudotemporalis superficialis (MPSTS). The *M. pseudotemporalis superficialis* of the working side is more active than the MPSTS of the balancing side, which shows variable activity during reduction cycles. Both sides also show variable and low levels of activity during terminal cycles. Maximum voltage is 1.72 mV.

The MPSTS of both the working and balancing sides are silent at the start of closing and during the fast-closing phase of reduction cycles. The MPSTS of the working side becomes active at the start of the crushing phase. Activity increases rapidly to 80–100% and then drops quickly to below 50%, to end at the start of the shearing phase (Fig. 8). Simultaneously, the MPSTS of the balancing side is active at a 20–40% level. Both sides are silent throughout the shearing, resting, and opening phases.

M. pseudotemporalis profundus

(MPSTP). The *M. pseudotemporalis profundus* of the working side is more active than that on the balancing side. Maximum voltage is 0.71 mV.

The MPSTP of the working side begins to fire at the start of the crushing phase. Activity increases rapidly to reach 75–100% at the start of the shearing phase but then decreases rapidly to 20–30% at the end of shearing. The MPSTP of the balancing side fires later and is active for a shorter period than the muscle of the working side. Activity of the balancing side MPSTP begins at the end of the crushing phase and increases rapidly to a 60–80% level early during the shearing phase; it rapidly drops to zero near the end of shearing. The MPSTP of both the working and balancing sides are inactive during the resting and opening phases.

M. pterygoideus typicus (MPTT). Both the superficial and deep medial parts of the middle portion of the *M. pterygoideus typicus* of the working and balancing sides are active asymmetrically. The level of activity of both parts is greater for the working than for the balancing side and activity decreases as the food is reduced. Maximum voltage is 1.86 mV for the superficial medial part, 1.90 mV for the superficial deep part, 1.46 mV for the superficial lateral part, 1.54 mV for the deep lateral part, and 1.30 mV for the ventrolateral part.

The superficial medial part of the middle portion of the MPTT of the working side begins to fire at a 10–30% level during the fast-closing phase (Fig. 9). Activity increases during the crushing phase to reach 70–100% at the start of the shearing phase, then decreases rapidly to 10–25% at the end of this phase, and ceases at the start of the resting phase. The deep medial part of the MPTT of the working side begins to fire later than the superficial one, only starting to show a 20–40% level of activity during the crushing phase. Activity increases throughout the crushing phase and reaches 70–100% at the start of the shearing phase. The deep part rapidly becomes less active to 10–30% and is silent throughout the resting phase.

The superficial medial part of the middle portion of the MPTT of the balancing side shows an activity pattern similar to but of lower amplitude than that of the working side. However, the deep part of the MPTT of the balancing side is active later than that of the working side. For the deep part of the balancing side, activity starts during the last half of the crushing phase and then increases rapidly to

reach 40-60% at the start of the shearing phase. Activity then decreases rapidly and ceases at the start of the resting phase.

The superficial and deep lateral parts of the middle portion of the MPTT of the working side fire asymmetrically (Fig. 9). The superficial lateral part begins to fire at a 10-40% level at the start of the crushing phase. Activity then increases during the first part of the shearing phase, reaches 80-100% near the end of shearing, and decreases rapidly thereafter. The deep lateral part of the working side is active at a 10-30% level during the fast-closing phase, remains so during crushing, increases to 70-100% during the shearing phase, but then decreases rapidly to a 0-20% level.

The superficial lateral part of the balancing side begins to fire at the start of shearing. Activity first increases rapidly to 20-30% and then decreases rapidly at the end of shearing. The deep lateral part of the balancing side shows an activity pattern similar to the working side but at a lower level. Both the superficial and deep lateral parts of the working and balancing side are silent during the resting and opening phases.

The ventrolateral portion of the MPTT is active throughout most of a masticatory cycle but at varying activity levels. The ventrolateral portions of the working and balancing sides show similar activity patterns; however, the activity levels of the working side muscle are greater than those of the balancing side.

The ventrolateral portion of the working side shows two bursts of activity as the mouth closes and variable low level activity during the resting phase. The first burst of activity begins at the start of fast closing. Activity increases rapidly to 40-60%, but then decreases rapidly to 0-20% during crushing. This decreased level is followed by a second burst during which the activity level reaches maximum at the start of the shearing phase. Activity then decreases to 10-20% as the shearing phase ends. The ventrolateral portions remain active at a level varying between zero and 25% during the resting phase.

During terminal cycles, the activity pattern of the medial and lateral parts of the middle portion of the MPTT, as well as the ventrolateral portion differ from that during chewing (Fig. 9). The deep medial part starts to fire at a 5-20% level at the start of the shearing phase and continues throughout the resting phase at a 20-50% level and into the start of slow opening at a 5-20% level. In contrast, the

superficial medial and lateral parts and the deep lateral part and the ventrolateral portion of the MPTT now are silent during closing of the mouth and active when it opens. The superficial medial and lateral parts become active at a 10-25% level at the end of the resting phase, continue through slow and fast opening at a 20-60% level, and end as the mouth starts to close. The deep lateral part and the ventrolateral portion become active at the start of the resting phase and remain so through slow opening.

M. pterygoideus atypicus (MPTA). The *M. pterygoideus atypicus* of the working and balancing sides are active during the fast-closing, crushing, and shearing phases of a reduction cycle. However, the activity level of the working side MPTA is greater than that of the balancing side MPTA. Maximum voltage is 1.06 mV.

The MPTA of the working side begins to fire at a 20-30% level during the fast closing (Fig. 9). Activity then increases to 50-75% during the first part of the crushing phase and then reaches maximum near the end of crushing and the start of the shearing phase. During shearing, the activity level remains high (60-75%) but then decreases rapidly as the shearing phase ends. Activity of the MPTA of the balancing side initially reaches a 15-20% level during fast closing. Activity then increases slightly to 30-40% during crushing and remains so during the first part of the shearing phase; it then drops to zero as shearing ends. Both the MPTA of the working and balancing side are inactive during the resting and opening phases and during terminal cycles.

DISCUSSION

Masticatory pattern

General

The dentition of *Sphenodon* is functionally heterodont. As already noted (Robinson, '76), the large anterior (successional) marginal teeth are analogous to canines. As none of the acrodont teeth are replaced and new teeth develop at the rear of the series, the tooth series retains a sequence of teeth that show size increases from front to rear.

However, the size increase is uneven; thus Robinson's reference ('76) to "successional," "remnant hatchling," and "additional" dental regions. As earlier stated by Günther (1867), old individuals still retain the small remnant hatchling teeth anteriorly; as these teeth become smaller, wear marks gradually develop on the dentary itself (Robinson, '76). The wear

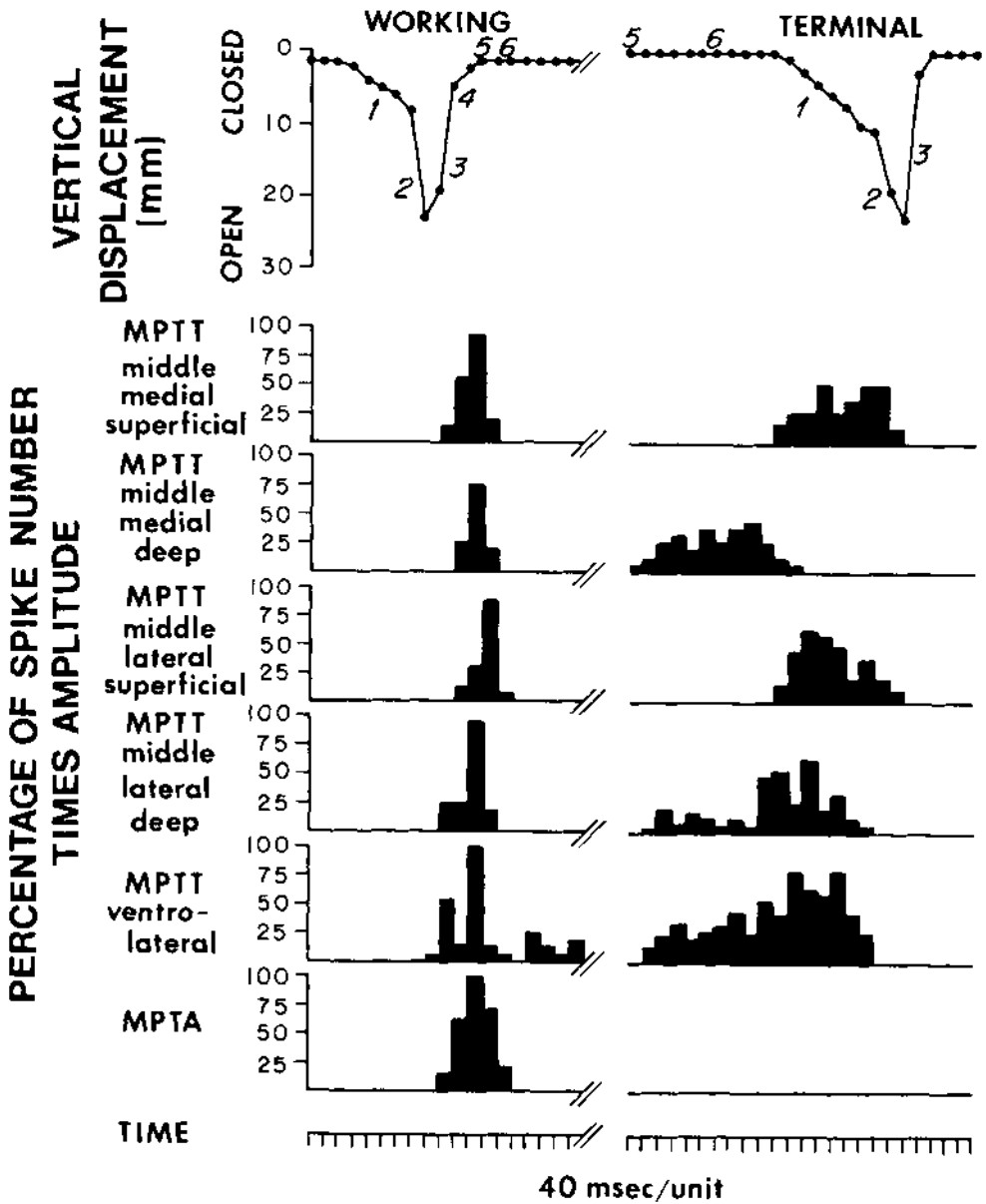


Fig. 9. *Sphenodon punctatus*. Synthetic summary of the percentage of the number of EMG spikes times the mean spike amplitude of the different portions of the *M. pterygoideus typicus* (MPTT) and *M. pterygoideus atypicus* (MPTA) on the working side and during a terminal cycle

when a tuatara reduces a cricket. Note the difference in the activity pattern of the MPTT and the absence of activity of the MPTA during a terminal cycle. The numbers along the displacement graph indicate the six phases of a reduction cycle.

of these anterior teeth increases the vertical distance between the upper and lower tooth rows in this region; more important, it increases the effective height of the enlarged successional teeth (which show less wear) and pre-

mits adult animals to impale larger prey. The few small remnant hatchling teeth provide a rough contact surface that will hold large prey; however, such prey must be repositioned before reduction. In adult *Sphenodon*, the small

surface area of the remnant hatchling teeth limits their shearing capacity and thus this section is not used during reduction of large prey.

Our X-ray movies of feeding sequences suggest that *Sphenodon* lacks cranial kinesis and this observation agrees with some reports (Versluys, '12; Kuhn-Schnyder, '54; Jollie, '60). However, Romer ('56) described a movable articulation between the basiptyergoid process of the basisphenoid and the pterygoid. Jordan-sky ('66) considered a special metakinesis as a possible feature of the tuatara skull. One should realize that even cineradiographs of lizards with kinetic skulls have not provided measurable displacement of bones because of the limited resolution of available methods (Throckmorton, '76). Whatever the condition in juvenile animals (Ostrom, '62), manipulation of skulls and of living adults shows no trace of cranial kinesis. [Since the preparation of this report, one of us (C.G.) was able to examine two living specimens, each younger than 5 years. Neither showed any capacity for palatal motility.]

The pattern of food reduction seen in *Sphenodon* would seem to represent an interesting and important variant in the development of reptilian masticatory patterns. It is a rather specialized behavior, as most living reptiles use their feeding apparatus as an "organ of prehension" (Davis, '61). The most significant aspect is probably indicated by Robinson's comments ('76) about the "poor occlusal relationships." One could even modify this comment to state that *Sphenodon* lacks occlusion of the kind seen in mammals. The tooth rows do not meet but interdigitate. A staggered interdigitation of tooth positions may occur among the individual teeth of other reptiles (crocodilians are a good example), but *Sphenodon* shows an interdigitation of tooth rows, rather than of individual teeth. On each side of the mouth, the food is contacted by two sets of teeth on its dorsal and one set on its ventral surface. The close approximation of the pterygoid flanges and coronoid processes assures that the mandible can only move parallel to the upper tooth rows. The food object is thus exposed to short-distance bending or shear, the effect of which differs with the consistency of the prey. Consequently, we have here a food-handling system unique in vertebrates.

The static forces applied to the dorsal and ventral tooth rows differ only slightly (the latter is greater by the mass of the bolus). However, the tooth/prey contact area is likely

to be greater on the dorsal (two rows of teeth) than on the ventral (a single row) surface. Consequently, the stress level will be much larger on the ventral side. This arrangement assures that the mandibular rather than the maxillo-palatine teeth will first perforate uniform prey. The effects of mandibular deceleration and the closing forces will differ depending upon the position of the food. If the bolus moves with the mandible, deceleration forces will decrease the differential. If the tongue holds the bolus against the palate, the forces will enhance it.

As shear during sliding movements is again greater on the mandibular than on either the maxillary or palatine rows, the cutting action will also begin on the mandible. The asymmetry of anteroposterior edges becomes critical during the propalinal translation at the end of crushing; the anteroiad shift of the mandible then exposes the food to the sharply sloping vertical aspects of the three tooth rows. This angulation increases the probability that the cusps will hook into surface irregularities of the prey; the forward slide of the mandible thus induces localized shear and cutting.

In interpreting any of the several patterns seen, it remains critical to remember that the stress induced and the strain effected in the prey surface will be less when more teeth or a greater cutting surface contact the prey; other things being equal, prey deformation or rupture is thus greatest for the cutting element that has fewest contact points. This, of course, assumes that the translational movement occurs while the teeth are pressed together, as they are in *Sphenodon*. Should the prey be impaled on the dentary or held against it by the tongue, it might then be slid past the palatine tooth array and its inertia would enhance rasping or cutting of its surface.

The crushing and shearing phases shown by *Sphenodon* have a markedly different significance for the two food types tested. In dealing with the exoskeleton of relatively large hard prey, the closing movement must effect a major force so that the teeth will induce initial penetration at high angles of incidence among teeth and prey. This initial perforation by the crushing action weakens the exoskeleton, as it provides stress-concentrating points; the shearing phase then rips apart the armor. Although we did not test prey items with truly heavy exoskeletons, the large orthopterans and beetles ingested by tuataras in the wild probably represent the kinds of prey for which this process is critical.

For soft prey, the relative significance of

these two phases of each masticatory cycle differs. The initial bite then serves not only to crush and incapacitate prey but also to fold up the soft tissues, compressing them against the internal skeleton. To make the propalinal shearing movement effective, the direct crushing force must continue to be applied; thus compressors may be seen to fire at full level during the beginning of the sliding movement. (Continuation of compression during shearing may be visualized by considering the use of a sharp knife to cut a folded piece of fabric resting on a wooden block. If the blade presses the fabric against the block, and then slides along the surface, all pleats and folds will be separated simultaneously. If the knife only presses the cloth against the block in some regions, only these will be separated, the loose cloth will stretch and a much longer horizontal movement is required for its separation.) Thus, the effectiveness of cutting is markedly increased by holding the dorsal and ventral tooth rows together during the slide. The crushing also permits more rapid approach of teeth to the internal skeleton of the prey. When *Sphenodon* reduces adult birds or mice, the relatively short mandibular cusps are unlikely to reach bone until several shearing strokes have occurred.

The combination of the crush-induced holding action and of the differential stress levels noted at the upper and lower tooth rows have major effects on the length of the stroke needed for penetration. As the jaws close, the distance between them decreases. This changes the force application to the bolus from long bending to shear and increases the risk of local failure of the integument and of the soft tissues in the prey. The greater local stresses imposed by the mandibular teeth are more likely to exceed the elastic limit of the prey than are the lower stresses induced where the bolus contacts the upper jaw. Thus, the bolus is likely to hang on the palatal surface and cutting will be concentrated between bolus and mandibular teeth. This means that the full anteroiad stroke of the mandible induces a cut at a single site of a fixed prey item. It assures maximal utilization of the rather limited capacity of the mandible for propalinal movement.

Both the crushing and the shearing mechanism make the continuous posterior shift of the prey advantageous. First of all, posterior shift of the prey improves the effective moment arm of the jaw. Secondly, the acrodont dentition only adds additional cusps at the rear; this assures that the posterior teeth are

larger, less worn, and better able to perform the slicing action. There may be a trade-off as very large prey would, when placed between the posteriormost teeth, require a very wide gape and thus place the crushing muscles into a less advantageous portion of the length-tension curve. This may be the reason why some of the dorsalmost crushing muscles (*M. adductor mandibulae externus medialis*, *M. pseudotemporalis superficialis*) have relatively long fibers that curve ventrolaterally and only start to fire effectively after the mouth has partially closed. The placement of the pterygoid muscles suggests that their activity should not shift on the length-tension curve, as displacement is relatively independent of gape (see below).

Capture

Sphenodon uses different approaches to capture small and large prey. Small prey are retrieved by rapid movement of the tongue, pulled into the back of the mouth and bitten initially between the cheek teeth. Large prey are captured by moving the head toward them, biting them while the tongue remains at rest and impaling them on the incisor-like successional teeth. The difference may involve several factors.

Small prey are relatively flat and their bodies tend to be close to the ground; this would force the tuatara to bend its neck sharply in order to bring the jaws into position for the bite. Most small prey, such as crickets and cockroaches, are also very mobile and acceleration of the tongue is less costly (and hence likely to be more rapid) than that of the entire head. The adhesive mechanism for prey capture is inherent in the dorsal surface of the tongue and is reflected in its long, densely packed papillae and mucous cells (Gabe and Saint Girons, '64); these give the tongue the appearance of a deep-pile carpet. *Sphenodon* rarely uses its tongue during the capture of large and slowly crawling prey, such as juvenile mice. *Sphenodon* then moves its snout close to the prey, opens its mouth, and shifts it into position for a bite. The projecting successional teeth will hold the soft prey, even when the initial bite does not otherwise incapacitate it. Thus, *Sphenodon* captures prey with a pattern reflecting prey size, configuration, and mobility.

Transport of prey also reflects its size, weight, and texture. Small prey is transported by the tongue; large prey is shifted by inertial movements of the head. Large prey occupies much of the oral cavity and thus limits move-

ments of the tongue. Also, feathered and furred prey provide poor surfaces for lingual adhesion.

Reduction

Sphenodon reduces both small and large prey with similar mandibular movements. Two factors that may explain this stereotyped pattern of movement are: 1) the limited degrees of freedom of the cranial joints force the movements to follow a set path, and 2) the activity pattern of the muscles generating the movements remains relatively constant throughout reduction sequences.

In *Sphenodon*, the degrees of freedom of the mandible are indeed limited by the position of the tooth rows and the close approximation of the pterygoid flanges and coronoid processes; this would by itself tend to produce the repeatable movement pattern observed. However, even though the pattern of movement remains relatively constant, other aspects of the masticatory cycle, such as motor activity, change with food type (Tables 2,3); so does the degree of head and tongue movement. Thus, whereas mandibular excursion is stereotyped because of the constraints of the hard tissues and absence of intracranial movement (kinesis), the size and consistency of the food have significant effect on movements of the head and tongue.

Throckmorton ('76) suggested that the slow opening may be assisted by gravity. However, duration of the slow-opening phase during reduction of juvenile mice (weight 6-7 gm) is twice that during reduction of crickets (0.3-0.6 gm). If slow opening were gravity-assisted, it would be more rapid during the reduction of heavier than of lighter prey items.

The duration of the slow-opening phase does reflect the size of the food. Obviously, large prey occupies more space within the oral cavity than does small prey. Perhaps, as there is less space to manipulate it, the risk of loss is greater. However, prolongation of the slow-opening phase increases the length of time the prey is secured and decreases the risk of losing it. By opening the mouth slowly and for a short distance (beyond the diameter of prey), *Sphenodon* can quickly snap it closed to keep prey from slipping out of the mouth.

Terminal

During terminal movements, *Sphenodon* uses its tongue to clean the oral cavity in two different ways. After reduction of crickets and cockroaches, *Sphenodon* seems first to clean

the anterior part of the tongue by passing it between the tips of the upper and lower jaws, and then clean the floor and roof of the mouth by arcing the tongue and moving it posteriorly. After mice are reduced, *Sphenodon* again uses the jaws to clean the tongue first but then uses the tongue to clean only the floor of the mouth. Perhaps the fluid content of mice does not adhere to the roof of the mouth, eliminating the need to clean it; also most cutting action takes place along the ventral surface of the prey.

Myology and electromyography

General

The review of Haas ('73) indicates that the head muscles of *Sphenodon* are similar to those of a generalized lizard, but retain some indications of arrangements primitive among reptiles. The tuatara differs from squamates in having an anterior *M. pterygoideus atypicus*. Also the separation among adjacent muscles is less pronounced in *Sphenodon* than in lizards or snakes (Haas, '73). The latter condition may reflect an absence of mobility among cranial elements, but it also raises the question whether the muscular separation is retained from an earlier form with a less rigid skull. Alternatively one may ask whether the described subdivisions are real or based upon expectations derived from the study of squamates. For instance, the two posteriormost portions of the *M. adductor mandibulae externus medialis* may be defined morphologically and have slight differences in fiber direction (and fiber length); however, their activity shows no significant differences. In contrast, the *M. depressor mandibulae* and *M. adductor mandibulae externus superficialis sensu stricto* are not morphologically separated into distinct portions, but their sections do differ in fiber length and in activity pattern.

In *Sphenodon*, the anterior movement of the lower jaw during the shearing phase is an important component of mastication. The *M. pterygoideus typicus* is the largest single muscle and its anteroposterior line of action directs the forces primarily anteriorly and to a small degree vertically and horizontally, even when the mouth is wide open. Thus, although the MPTT is active during crushing, its maximum activity levels during reduction occur during the shearing phase, when movement of the lower jaw follows the main line of action of the muscle. Furthermore, the fixed quadrates of *Sphenodon* would keep the main line of action of the MPTT in a constant anteroposterior

line. Smith ('80) notes the forward movement of the quadrate and activity of the *M. pterygoideus* of *Varanus* during closing. She argues that a movable quadrate lets the *M. pterygoideus* function as an adductor during ingestion, and moves the lower jaw anteriorly during biting. However, *Sphenodon* also has a large *M. pterygoideus*, which clearly facilitates the generation of large forces during the shearing phase. Even though the *M. pterygoideus* of *Varanus* may assist in closing the mouth, its size and primarily anteroposterior line of action suggest additional functions. Size and position indicate that the muscle would tend to generate large propalinal forces during the bite. These would be less important in shifting the lower jaw than in maintaining its position relative to the midline when prey is struggling or being shaken.

Capture

The activity pattern of most of the muscles studied differs between the times during which *Sphenodon* makes a capture bite and those in which it engages in reduction cycles. These differences seem to reflect the need to 1) open the mouth rapidly during the capture bite (so that the tongue can be quickly protruded), and 2) then to snap the mouth closed to secure and kill the prey. Opening for a bite proceeds uniformly and fast; the slow-opening phase characterizing reduction, terminal, and repositioning cycles is then absent. Consequently, both portions of the *M. depressor mandibulae* become active bilaterally; in contrast, only the anterior portion of the muscle is active during slow opening. The simultaneous firing at the start of opening not only rotates the mandibles, but also induces posterior translation of the fossa on the condyle, so that the mandible drops most rapidly.

The closing movement is similarly distinct. Not only do the various adductors fire more symmetrically during capture than during a reduction bite, but the *M. pterygoideus* immediately becomes active symmetrically. It contributes to the closing component and thus accelerates the jaw and adds to its impact, but it also induces maximum propalinal action at the very beginning of closure. This brings the successional teeth into opposed position so that they approach each other before closure, rather than at the end of the shearing phase.

Reduction

In *Sphenodon*, slow opening is generated by the anterior portion of the *M. depressor mandibulae* (MDM). The nearly vertical path of these

fibers to their insertion just posterior to the quadratoarticular joint would simply rotate the mandible about the quadratoarticular joint, opening the mouth straight downward. In the herbivorous lizard *Uromastyx* the MDM inserts at the caudal end of the lower jaw, well posterior to the jaw joint; it is silent during slow opening (Throckmorton, '78). This position and activity pattern are similar to those of the posterior portion of the MDM in *Sphenodon*. These results suggest that those fibers of the MDM lying close to the joint may induce slow opening of the mouth, whereas those lying farthest away from the joint induce fast opening. Consequently, studies on reptilian feeding should examine not only various subdivisions of the complex adductors, but also different areas of comparatively simple muscles, such as the MDM.

During a reduction cycle, the activities of the superficial and deep adductors and the pterygoids allow them to be classified into three functional groups (Fig. 10). The first is the closing-compressor group. It consists of the *M. adductor mandibulae externus superficialis*, the *M. adductor mandibulae externus profundus*, and the *M. pseudotemporalis superficialis*. The second group is the compressor-shear group. It consists of the *M. pseudotemporalis profundus* and the *M. pterygoideus atypicus*. The third group is the shear group and it consists of the *M. pterygoideus typicus*. Group 1 generates closing forces that initially close the mouth and then compress or crush the prey. Group 2 generates compressive forces during crushing but continues to apply these forces during shearing. Simultaneously, group 3 induces anteriorly directed forces on the lower jaw and the food is compressed and sheared by action of groups 2 and 3. The activity levels of the adductors apparently reflect instantaneous local changes in tension due to changes in the consistency and position of the bolus during reduction cycles.

Olson ('61) contrasted the concepts of "static pressure" and "kinetic inertial" systems of jaw mechanics. In the former the adductor muscles exert maximum force when the mouth is nearly closed and thoroughly reduce the food. In the latter, the adductors supposedly exert maximum forces when the mouth is wide open, food is not reduced and the muscles apparently function for prey capture. In *Sphenodon*, the activity level of the adductors generally supports the concept of a "static pressure" system. However, the activity levels generated by the

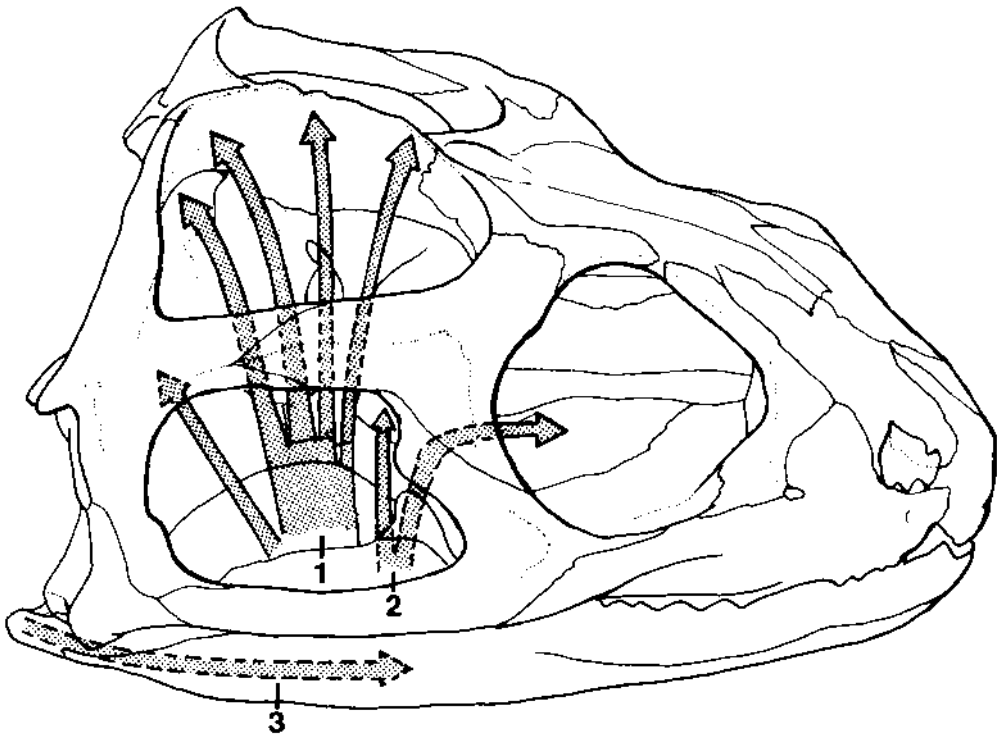


Fig. 10. *Sphenodon punctatus*. Lateral view of the skull showing a summary of the three mechanical adductor

groups. 1, Closing-compressor group; 2, compressor-shear group; 3, shear group.

adductors of both the working and balancing sides change from bite to bite during a reduction sequence: presumably these muscles respond to changes in the position and texture of the bolus. (This pattern is equivalent to that shown by some masticating mammals.) Thus, the present results support the hypothesis of a "static pressure" system only in that forces exerted by the adductors during an individual bite are greatest when the mouth is nearly closed. However, they conflict with the hypothesis in that the forces generated by the adductors during a bite are not the maximum forces that these muscles are capable of exerting, nor are the forces generated then equivalent among bites of a reduction sequence. The concept of "maximum" force involves too many variables to be meaningful in this context.

In the reduction cycles of *Uromastyx aegyptius*, the *M. depressor mandibulae* (MDM) is active when the mouth closes and the deep portion of the *M. pterygoideus* (MPTT) is active when the mouth opens (Throckmorton, '76);

these thus differ from activities recorded in *Sphenodon* during reduction. These differing activity patterns seem to relate to the degree to which the quadrate can move. In *Uromastyx*, the quadrate is held only by supratemporal and pterygoid. Thus, action of the MDM and MPTT not only moves the mandible about the quadrate but also increases mandibular excursion by movement of the quadrate itself; these muscles may also function to stabilize the quadrate. In *Sphenodon*, the quadrate is fixed and mandibular movements are restricted to the quadratoarticular joint. Consequently, the activity patterns of at least the MDM and MPTT are apparently affected by the degree of cranial kinesis. Unfortunately, we still lack detailed descriptions of feeding movements and the activity patterns of the other masticatory muscles in *Uromastyx aegyptius* or other lizards that show varying degrees of cranial kinesis. Thus, comparisons relating the degree of intracranial movements and the activity patterns of the masticatory muscles are premature.

Terminal

The fibers of the middle portion of the *M. pterygoideus typicus* (MPTT) lie anteroposteriorly when the mouth is closed; activation of these fibers would then tend to pull the mandible directly anteriorly. During terminal cycles, activity of the ventrolateral and medial and lateral deep parts would bring the tips of the upper and lower jaws into close approximation, but would not generate significant closing forces on the mandible. Such activity, while the anterior part of the tongue pushes against the aligned tips of the jaws during terminal cycles, allows the mouth gradually to open while conforming to the shape of the protruding tongue; the incisor-like teeth are then rubbed against the surface, cleaning the tongue.

The fiber direction of the medial and lateral superficial parts of the MPTT suggests that it would also tend to move the mandible anteriorly when the mouth is closed and that it would maintain the closed position. However, during terminal cycles the superficial part of the MPTT is active coincident with the *M. depressor mandibulae* (MDM) as the mouth opens. Simultaneously, activity of the ventrolateral and lateral deep parts increases. Their actions form a bilateral force couple. These parts of the MPTT and the MDM insert as a sling on the posterior end of the articular. Upward pull by the MDM rotates the mandible about the quadrate while the anterior pull of the MPTT limits posterior translation of the mandible. Consequently, the mandible opens by simple rotation, accounting for the decrease in propalinal movement during terminal cycles.

Fiber length relationships

While the fiber lengths of the muscles considered in this study differ by a ratio of almost 6 to 1, the extreme lengths are represented by only three muscles. The dorsalmost (deep) portions of the *M. pterygoideus typicus* and the *M. adductor mandibulae externus profundus* have the shortest fibers and the posterior portion of the *M. depressor mandibulae* has the longest ones (Table 1). However, most muscles show a wide range of fiber lengths, with the exception of such muscles as the *M. pterygoideus atypicus*. Fiber lengths generally differ within subdivisions. This variability emphasizes the importance of sampling many sites before assuming that the fiber length is constant.

When the fiber lengths are viewed in relation to their position and activity times, a very in-

teresting pattern emerges. The first example is given by the anterior and posterior portions of the *M. depressor mandibulae*. The fibers of the anterior portion are shorter than the posterior ones. The anterior portion also inserts close to the quadratomandibular joint and thus has a short moment arm. This anterior portion fires during slow opening, inducing initial separation of teeth from the bolus. The muscle then appears to be close to its resting length; however, the length-tension relation may not be particularly critical, as the muscle is then active only at a low level. Initially the teeth are still embedded in the food and the muscle induces pure rotation. After the start of the fast-opening phase, muscular activity increases and contributes to further opening; however, at this time the muscle incurs a slight relative lengthening as the mandible is translated posteriorly at the jaw joint; this might improve the length-tension relationship.

The more posterior portion of the *M. depressor mandibulae* not only has a longer lever arm and much greater bulk, but has markedly longer fibers than the anterior portion. The former is active only when the mandible is being rapidly depressed, inducing both rotation and translation. Quite clearly the much greater length of its fibers reduces relative shortening and retains the muscle in the advantageous portion of the length-tension curve.

Similar patterns are seen in the fast-closing and crushing movements. The anteriormost portions of the MAMES have long fibers and the MAMEP has relatively short ones, although both muscles start the fast-closing movement. The MAMEP has a relatively short lever arm, but the fibers of the MAMES lie superficially along the side of the face and have a relatively long lever arm. Toward the end of fast closing (before the cusps reach firm contact with the prey), one notes the start of activity 1) of the posterior portion of the MAMES, 2) of the three portions of the MAMEM, and 3) of the MPTS. Four of these five muscles show similar and relatively narrow ranges in fiber lengths, and the other (MPTS) shows a wide range. The MAMEM-a has the shortest fibers and lever arm of the MAMEM complex; the posterior portion of the MAMES also has shorter fibers and lever arm than the anterior one. The short fibers of the MPTS reach from the parietal straight ventrally to the basal aponeurosis, whereas its long fibers curve laterad and then run ventrad. The long fibers of the MAMEM also curve ventrolaterally and will in the resting position form

an angle of close to 40° in their course. Apparently these curving fibers are much straighter when the mandible is fully depressed. Thus, those adductors in which the direction of action is straight dorsoventral have short fibers and those in which the path of the muscle incurs a curve to a more posteriorly displaced origin have long ones. Furthermore, in spite of their different origins, the lengths of most fibers of the MAMEM and MPTS are similar, though the latter has a group of deeply placed, short fibers. These similarities appear to be achieved by the attachment of these muscles on various continuations of the basal aponeurosis rather than directly on the mandible.

In the *M. pterygoideus typicus* (MPTT) the origin of the fibers varies, whereas all of them insert in close juxtaposition. Thus, there is a regional change in fiber arrangement from long-fibered parallel to short-fibered bipinnate. The long-fibered portion is apparently capable of greater absolute shortening than the short-fibered one. It is activated before the short one and induces the initial propalinal forces during shearing. In contrast, the short fibers induce the forces at the end of the shearing phase. The long, medial fibers would also induce a medial component to the force, which may be disadvantageous for generating propalinal movement. The medial component would shift the jaw very slightly toward the working side at the start of shearing when the teeth are slightly separated. However, the line of action of the short, lateral, bipinnate fibers is nearly straight anteriorly and parallel to the toothrows. Thus, at the end of the shearing phase these fibers tend to keep the lower teeth aligned between the upper rows while generating a final thrust to shear the food. The fiber arrangement and parallel arrangement of long and short fibers do raise some questions about preliminary firing patterns that may bring the fibers to a length at which stimulation will induce effective action.

Neural control

Little is known about the neural mechanism controlling the feeding movements of lizards and of the activity patterns of the muscles generating them. Almost all work on the neural control of mastication has been carried out on mammals (Dubner and Kawamura, '71; Gans et al., '78). Three observations relate generally to control systems and may deserve brief mention.

The duration of the different phases of a

reduction cycle is affected by the size of the food object. Similarly, the activity levels of the adductors reflect the size and position of the bolus. The increased adductor activity, when food is in contact with the teeth, suggests that the timing and level of adductor activity are controlled by an oral afferent feedback system. Whether this feedback system is similar to that of mammals remains subject to test. The present observations suggest the likelihood that the afferent information on the size and position of the bolus is derived from the sense organs of the tongue.

The masticatory muscles of *Sphenodon* do not have to restrain the jaw movements to the propalinal plane, as the mechanical constraints preclude lateral movements. In lizards with cranial kinesis, the muscles presumably have a greater role in guiding the movements of the jaw and in stabilizing cranial elements during the bite. One would expect more complex control systems in such cases.

In spite of this mechanical simplicity, the neural control mechanism in *Sphenodon* appears to be relatively complex. Olfactory cues mediate the prey attack response and visual cues are used to steer the capture of prey. The size and position of the bolus are monitored during reduction and will affect the activity of the masticatory, lingual, and nuchal musculature. These oral sensory signals steer not only the overall food handling, but are obviously responsible for differences between the EMG patterns of successive cycles.

Phylogeny

The capacity for inducing not only perforating and crushing forces but for applying shear in an anterior-posterior direction may be critical in the further development of sphenodontid dentition, as well as in that of the rhynchosaur (which may or may not be related to *Sphenodon*; Carroll, '77; Sill, '71). These animals tend to widen the maxillary-palatine tooth area in which each row is composed of an array of variously shaped teeth. The mandibular tooth row is much narrower and its teeth perhaps larger, a pattern that has been variously ascribed to adaptation to a herbivorous diet. Cutting action by the upper teeth would presumably require that the food object move past them. This cutting action could occur only if the prey were impaled on dentary teeth and cutting-slippage occurred against the palatal surface. The effect here would be equivalent to those achieved when the tooth cusps are widened and serve as slic-

ing or shaving devices while they move at right angles to the prey.

Although this study does not deal with fossils to any significant extent, the pattern in *Sphenodon* permits some very interesting speculations. Most textbooks argue that heterodonty and complex tooth shapes are characteristic of mammals and absent in Recent reptiles. While this is an overstatement (Edmund, '69), the pattern of mandibular movement is obviously more complex in modern mammals. The nature of the complexity generally reflects translatory movements between the tooth rows.

Such translation has apparently arisen a number of times independently. Thus, it occurs in turtles (Gaffney, '75), in *Sphenodon*, and presumably within the therapsid-mammalian transition. In each case, this horizontal movement apparently involves sliding along the craniomandibular joint and is independent of the phenomenon of cranial kinesis. The latter primarily reflects movement between and about the occipital, the medial, and the nasal portions of the braincase, as well as between the variously fixed dental arcades and the quadratic suspension of the mandible.

While translatory movements do occur in some turtles, the broad crushing surfaces and continuous cutting edges of the Testudines would involve few problems with occlusion. The occlusion of dental arrays is assumed to be much more difficult to develop and investigators have predicated a complex series of stages with gradual development of additional cusps and basins (Peyer, '68).

The solution found by the Rhynchocephalia (and rhynchosauroids) appears to reflect a rather simple avoidance of the occlusion problem. The teeth need never contact, and the wear marks between them are as likely to reflect interaction of tooth and prey as grinding of tooth on tooth. The system is effective even when the inter-row distance changes. Local variants in tooth shape have much less effect than do those in mammals. In this sense, one can assume that these small reptiles developed a food niche that was later to be expanded by mammals.

While we see an initially equivalent solution, the pattern also incorporates a profound future limitation. As long as the mandible has to slide between maxilla and palatine, it is restricted to strict propalinal movements. Reptiles with such a pattern are therefore precluded from shift to any of the transverse masticatory types that proved so successful in mammals.

More important, the avoidance of the need for a precise matching bite eliminated any tendency for later development of different kinds of "molar occlusions." The dentition in the sphenodontid upper jaw may be conceived as a mammalian molar row with a medial separation. It presumably represented a significant advance over a general crushing bite, but the solution adopted may have blocked the path to continuing development.

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