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The Mechanics of Ovophagy in the Beaded Lizard (*Heloderma horridum*)

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ABSTRACT.—The beaded lizard (*Heloderma horridum*) is a large diurnal predator that feeds predominantly on juveniles in vertebrate nests and eggs. Bird eggs constitute a special problem for predators as the energetic content is shielded by a hard calcareous shell. Still, eggs of ground nesting birds such as quail constitute a large part of the diet of *Heloderma horridum*. We investigated the mechanics of the egg eating behavior in *H. horridum*. We examined the morphology of the feeding system, measured egg toughness, and calculated bite forces of *H. horridum*. Additionally, we videotaped feeding sequences and simultaneously recorded the activity patterns of the jaw muscles. Egg eating behavior consists of a fixed behavioral pattern including five distinct stages: approach, piercing, uptake, crushing, and swallowing. Two of these (piercing and crushing) can be directly related to the egg eating behavior in *H. horridum*. The piercing stage consists of several bites during which the anterior teeth are used to puncture (but not crush) the egg. Next, during the crushing stage the egg is crushed within the oral cavity (no longer any tooth contact). Based on our results, we conclude that behavioral adaptations and subtle modifications of the motor patterns during feeding are present in *H. horridum* which allow the lizard to be an efficient ovophageous predator.

Helodermatid lizards (the gila monster and beaded lizard) have fascinated man ever since the Spaniards set foot in Mexico in the sixteenth century. Soon helodermatids acquired a sinister reputation, mainly due to their venom. Ever since, researchers mainly focussed on the poison glands (Fahrenholz, 1937; Kochva, 1978), the poison itself (Mebs and Raudonat, 1966, 1967) and the effects of the poison on humans (Van Den Burgh and Wight, 1900; Bogert and Del Campo, 1956). Nevertheless, the poison apparatus of *Heloderma* does not play an important role during feeding but presumably serves as a defensive mechanism (Bogert and Del Campo, 1956; Lowe et al., 1986; Beck, 1990). It is only more recently that the ecology of helodermatids has been studied in any detail (Bogert and Del Campo, 1956; Jones, 1983; Beck, 1990). The results of these studies clearly show that, in contrast to what could have been expected (Huey and Pianka, 1981), helodermatids are secretive diurnal predators with a low activity temperature (Porzer, 1981; Jones, 1983; Lowe et al., 1986; Beck, 1986, 1990). Due to their ability to take large meals and their low resting metabolism Gila monsters can spend over 83% of the year at body temperatures well below their activity temperature (Beck, 1990).

Additionally it has been shown that helodermatids show a dietary specialization on eggs and young in vertebrate nests (Arnberger, 1948; Shaw, 1948; Stahnke, 1950; Bogert and del Campo, 1956; Beck, 1990). However, a specialization on patchy prey (both spatially and temporally) requires a high efficiency in the uptake of that

prey to maximize the energy gain while foraging. However, a high efficiency in the uptake of eggs requires specific adaptations. Within squamates, several species have specialized in the eating of eggs, most notably the ovophagus snakes of the genera *Dasypeltis* and *Elachistodon*, which have become obligate egg eaters (Gans, 1974). These snakes all show modifications of the skull, the jaws and teeth, and most remarkably even the vertebral column, which allow them to successfully ingest the highly nutritious contents of the egg. In this context, eggs can be viewed as hard food objects (due to the form as well as to the calcareous shell) and these snakes can thus be considered as real durophagous specialists (Savitzky, 1983). Adaptations to durophagy widely occur within squamates and include various solutions such as hinged teeth and increased cranial kinesis (Savitzky, 1981; Patchell and Shine, 1986a, b) and modifications of the skull, teeth, and muscular architecture (Dalrymple, 1979). Even on the level of muscular control adaptations occur, as in *Trachydosaurus rugosus* where temporal summation is used to increase the force of the jaw adductors in order to break the shell of snails (Gans et al., 1985; Gans and De Vree, 1986).

As eggs constitute a major part of the diet of *H. horridum*, and as these can be considered as a patchy prey source requiring an efficient feeding mechanism, adaptations to ovophagy are expected. The goals of this paper are (1) to investigate the mechanical basis of ovophagy in *H. horridum* and (2) to investigate whether *H. horridum* shows adaptations to ovophagy.

MATERIALS AND METHODS

Specimens.—Two adult specimens (specimen 1: SVL: 35 cm, TL: 32 cm, Mass: 1102 g; specimen 2: SVL: 37.5 cm, TL: 29 cm, Mass: 1084 g) of *Heloderma horridum* were used in the experiments. The specimens were captive bred in the Detroit Zoo. The animals were kept in a glass vivarium on a 12:12 LD cycle and were offered water and food consisting of newborn mice and quail eggs. During the experiments animals were offered quail eggs of average size (Mass: 12 ± 2 g; Length: 35 ± 3 mm; Width: 26 ± 2 mm). Quail eggs were chosen as they constitute an important part of the diet of *H. horridum* in natural circumstances (Arnberger, 1948; Bogert and Del Campo, 1956). The environmental temperature varied from 26 C at daytime to 20 C at night; an incandescent bulb provided the animals with a basking place at a higher temperature (30 C). Additionally, one *H. horridum* (SVL: 40 cm, TL: 24 cm, Mass, without viscera: 572.5 g; specimen from the Smithsonian Institution) and one *H. suspectum* (SVL: 28 cm, TL: 12.5 cm, Mass: 340 g; specimen from the Carnegie Museum of Natural History) were dissected and stained (Bock and Shear, 1972) to characterize all jaw and hyolingual muscles. Drawings were made of all stages of the dissection using a Wild M3Z dissecting microscope, provided with a camera lucida.

Cineradiographic and Video Recordings.—Cineradiography was accomplished with a Siemens Tridoros-Optimatic 880 X-ray apparatus equipped with a Sirecon-2 image intensifier. Feeding bouts were recorded laterally with an Arriflex 16 mm ST camera equipped with a 70 mm lens at a film speed of 50 frames per second.

Video recordings (50 Hz) of the feeding process were made using a Panasonic camera (WVF15E) equipped with a zoom lens (Panasonic 15X TV Zoom lens) and connected to a JVC S-VHS video recorder. Video torches (2.4 kW; TRI-LITE, Cool Light Co. Inc., Hollywood, USA) provided the necessary illumination.

Electromyographic Recordings and Analysis.—The animals used in the electromyographic (EMG) experiments were anaesthetized by an intramuscular injection of Ketalar (125 mg/kg bodyweight) before electrode implantation. Bipolar 50 cm long electrodes were prepared from teflon insulated 0.076 mm stainless steel wire (Medwire Corp.). The insulation was scraped away at the tip, exposing 1 mm of electrode wire. The electrodes were implanted percutaneously into each muscle belly using hypodermic needles with 2 mm of the electrode bent back as it emerged from the needle barrel. Elec-

trode placement was checked on dorsoventral and lateral X-rays.

During these recording sessions electrodes were placed in the major jaw closers: the musculus adductor mandibulae externus (superficial-medial and deep parts; MAME1, MAME2), the musculus pseudotemporalis (MPsT) and the musculus pterygoideus (lateral and medial parts; MPtlat and MPtmed). Electrodes were also placed in the jaw openers: the musculus depressor mandibulae (MDM) and the musculus spinalis capitis (MSCa).

Electrical signals were amplified 2000 times with Tektronix 26A2 differential preamplifiers (range 100 Hz–10 kHz) and Honeywell Accudata 117 DC amplifiers and recorded on a Honeywell 96 FM 14 channel tape recorder (medium bandpass) at a speed of 19.05 cm/s.

Bite Modelling.—For each muscle the position, the three dimensional coordinates of origin and insertion and the mass were determined. Fibre lengths were obtained experimentally by submerging the muscles in a 30% nitric acid (HNO₃, 30%) solution for 24 hours to dissolve all connective tissue. Muscle fibers were then immersed in a 50% glycerol solution and the average fiber length of each muscle or muscle bundle was determined by drawing approximately 20 fibers for every muscle (using a dissecting microscope with camera lucida). The individual fibers were then digitized and the average length calculated. The physiological cross section of the muscles was calculated as the mass divided by the fiber length (i.e. assuming a muscle density of 1 g/cm³). Forces were scaled to the physiological cross section of the muscles (250 Kpa; Herzog, 1994).

The physiological cross section of the jaw muscles and their 3D coordinates of origin and insertion were used as input for the bite model. The position of the point of application of bite forces on the lower jaw (halfway across the tooth row) was chosen based on observations of feeding sequences under semi-natural conditions.

The orientation of the food reaction forces (FRF) was set to vary between -150 and -30° (Cleuren et al., 1995) and the gape angle was set at 10° . Bite forces (BFs) must be regarded as rough estimates of the forces exerted, and are calculated for one side only (BFs have to be multiplied by two to obtain the overall bite force on the prey. A theoretical situation in which all jaw closers are maximally active was simulated (see Cleuren et al., 1995 for the validity of this procedure). A more detailed description of the bite model is presented in Cleuren et al. (1995).

Estimation of Egg Toughness.—To be able to assess the ecological relevance of the results of the bite model egg toughness was estimated exper-

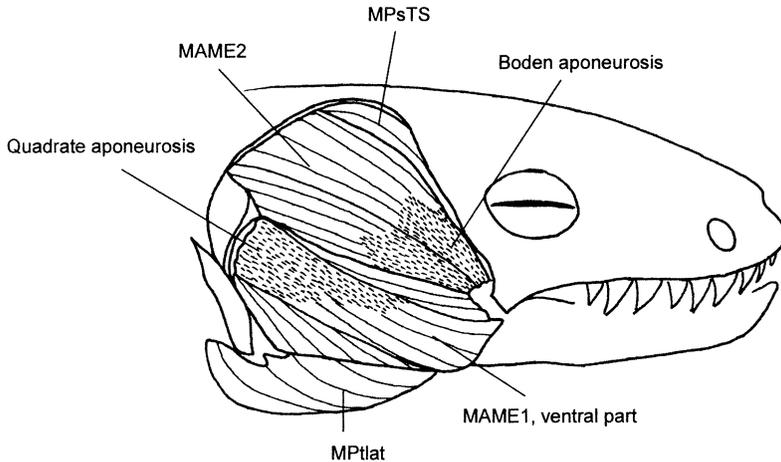


FIG. 1. Lateral view on the jaw musculature of *H. horridum* after removal of the skin and the dorsal part of the MAME1. MAME1: m. adductor mandibulae externus—superficial part, MAME2: m. adductor mandibulae externus—deep part 2, MPstS: m. pseudotemporalis pars superficialis, MPtlat: m. pterygoideus lateralis.

imentally. For this purpose the skull of the dissected specimen of *H. horridum* was used. The skull was placed on an electronic balance and provided with a fake mouthfloor in plasticine. A container was placed on top of the skull and the quail eggs were placed either between the toothrows or within the oral cavity. The container was then slowly filled until the eggshell cracked. Next the container was filled further until complete failure of the egg occurred.

RESULTS

Morphology.—The structure of the skull of anguimorph lizards in general and helodermatids more specifically has been described by several authors (Shufeldt, 1890; Boulenger, 1891; Jollie, 1960; McDowell and Bogert, 1954; Rieppel, 1980). As noted by these authors, *H. horridum* may bear teeth on both palatines and pterygooids or these may lack completely, as was observed for the specimens in this study. The jaw closers in *Heloderma* consist of several muscle groups: the m. adductor mandibulae externus (MAME), the m. pseudotemporalis (MPsT), the m. adductor mandibulae posterior (MAMP) and the m. pterygoideus (MPt). The MAME is usually subdivided into three parts: a superficial, a medial and a deep part. However, in the specimens examined by us no clear subdivision (i.e., no aponeuroses or differences in fiber orientation) between the superficial and medial parts is present. These two parts (MAME 1) will thus be treated together in this paper. Nevertheless, an aponeurosis is present within the MAME1 and separates this muscle in a dorsal and a ventral part (Fig. 1; see also Gomes, 1974). The deep part (MAME2) of the MAME is clearly recognizable and has a classic origin and insertion

(cfr. MAMEP in Gomes, 1974; Rieppel, 1980). Both the MPsT and the MPt consist of two distinct parts: a superficial (MPsTS) and deep (MPsTP) part for the MPsT and a lateral (MPtlat) and medial (MPtmed) part for the MPt as previously described (Gomes, 1974; Rieppel, 1980).

Feeding Behavior.—A typical egg feeding sequence in *H. horridum* consists of five clearly recognizable stages. First during the approach (Fig. 2A) the animal tries to localize its food by repeated tongue flicking. Both the searching and recognition of food items seems to be mediated by tongue flicking (Bogert and Del Campo, 1956; Cooper and Arnett, 1995). Once the egg has been recognized as a food item, the second stage or piercing stage (Fig. 2B) takes place. During this stage the animal rises on its front legs and orients its head towards the egg. Next, the lizard bites the egg with its front teeth thus "piercing" the egg (clearly audible cracking noise). This piercing bite (lasting approximately 2 sec.) is then repeated several times (± 10 times) during which the egg remains intact. At first glance one could get the impression (as we did initially) that the animal is unable to break the egg.

After the piercing stage the uptake (Fig. 2C) starts. This is a relatively short stage which usually comprises only three to four bites and during which the egg is maneuvered into the oral cavity. This "maneuvering" is done both by the tongue as well as by some kind of inertial mechanism. Basically, the lizard either "tosses" the egg in the air (\pm kinetic inertial) or pushes the egg against a nearby object or the ground (\pm static inertial) during which it moves its jaws

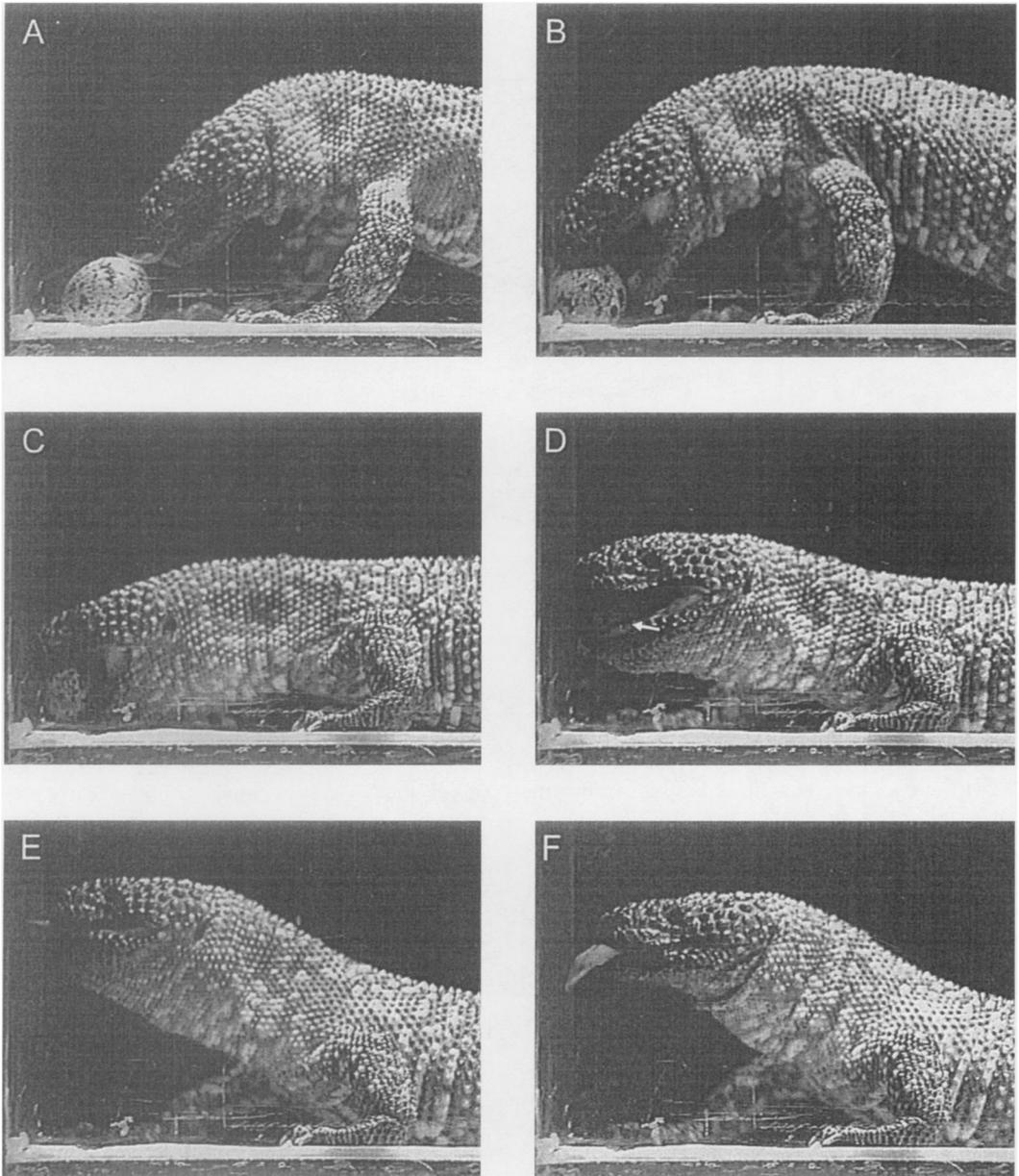


FIG. 2. Videoprints of the successive stages during an egg feeding sequence in *H. horridum*. A: tongue flick during the approach stage, B: piercing, C: uptake, D: early crushing (note that there is no longer any contact between the egg and the teeth—indicated by the arrow), E: late crushing—early swallowing, F: swallowing cycle.

around the egg (Gans, 1969 for an elaboration on inertial feeding). During the following crushing stage (Fig. 2D), the egg no longer makes contact with the teeth. Crushing consists of a varying number of bites (from 10 to 20) that are characterized by a small gape angle. During crushing bites the egg can be seen pushing the mouth floor down. During the crushing stage

the egg is slowly transported to the back of the oral cavity. Once the jaws can be closed completely, the last stage or swallowing stage (Fig. 2E) starts.

Interestingly, eggs are not always completely crushed when swallowing starts. During swallowing the tongue is positioned in front of the food and subsequently retracted, thus pushing

the food down the esophagus. Swallowing may take up to 20 bites, especially when eggs were not fully crushed before. At the end of the swallowing stage a number of aberrant swallowing cycles (Fig. 2F), characterized by a pronounced constriction of the throat region, are present.

Besides conventional video recordings, X-ray films were made. During filming the animals were immobilized and thus slightly agitated. Eggs were offered to the animal by means of a forceps. Due to the agitated condition of the animal, the eggs were not approached in the usual way but rather attacked which resulted in the immediate (less than 20 ms) crushing of the egg (see Fig. 3). Thus although in unrestrained feeding sequences eggs seem to be relatively hard (over 20 bites needed to crush the egg; sometimes not even completely crushed when swallowed) food objects, *H. horridum* is apparently perfectly capable of crushing quail eggs.

Egg Toughness.—Three series of measurements were performed on the quail eggs: (1) intact eggs were positioned between the front teeth, (2) intact eggs were positioned within the oral cavity, and (3) previously pierced eggs (10 times, using the teeth of the prepared skull) were positioned within the oral cavity. The mass of the contents of the container placed on top of the skull was recorded when the first crack was heard or seen and when total failure of the egg occurred. Measurements were repeated for at least nine randomly chosen eggs for each experiment (See Table 1). Eggs used for the different measurements did not differ in mass ($F = 0.23$, $df = 2,26$, $P > 0.05$) length ($F = 2.33$, $df = 2,26$, $P > 0.05$) or width ($F = 1.56$, $df = 2,26$, $P > 0.05$).

The average force needed to crack the egg shell with the egg placed in between the front teeth is 6.8 ± 1.4 N. In this situation total failure of the egg followed nearly immediately. However, when placed within the oral cavity the force needed to produce a crack was somewhat higher: 9.1 ± 1.6 N. Total failure in this second set-up occurred at an average force of 26.8 ± 15.4 N. In the third set-up (eggs previously pierced) the first crack occurred at a similar load (7.4 ± 2.9 N; $F = 1.48$, $df = 1,12$, $P > 0.05$). However, total failure occurred significantly sooner (12.8 ± 4.9 N; $F = 7.35$, $df = 1,18$, $P < 0.05$). A large part of the strength of the egg is thus not due to the egg shell but to the resistance of the egg membrane.

Bite Modelling.—Given an estimation of egg toughness, it would be most interesting to know how much force *H. horridum* can potentially generate when piercing or cracking an egg. To answer this question a static bite model was used and the bite forces generated by *H. horridum* while eating quail eggs were estimated. How-

ever, calculated bite forces must be regarded as only a rough estimate of the real forces exerted.

As described previously two distinct stages of explicit prey reduction take place: piercing and crushing. During piercing *H. horridum* bites the eggs with the front teeth; whereas during crushing the egg is situated within the oral cavity. The static bite model allows to calculate differences in bite forces as the result of changes in bite point. In the model the gape angle was set at 30° and all muscles were set maximally active during all simulations (i.e., the entire physiological cross section participates in biting). The following numerical values thus refer to predetermined biting points in the piercing or crushing region (Fig. 4). During piercing, bite forces of 31.0 N are generated when the bite force is perpendicular (90°) to the tooth row. A shift of the FRF away from the perpendicular axis causes an increase in bite forces. The bite forces increase to 62.4 N for FRF at -30° , and 61.6 N for FRFs at -150° . During crushing, bite forces of 43.4 N are generated when the bite force is perpendicular (90°) to the tooth row. A shift of the FRF away from the perpendicular axis again causes an increase in bite forces to 87.4 N for FRF at -30° , and 86.3 N for FRFs at -150° .

Electromyography.—The aims of the electromyographic experiments were to provide a qualitative description of the activity of the major jaw closers and openers during an egg feeding sequence in *H. horridum*. Of more specific interest were the muscle activity patterns during piercing and crushing. Only these two stages will be described here; a full description of the muscle activity patterns during feeding will be published elsewhere.

Piercing (Fig. 5).—A piercing cycle is characterized by a short bilateral activity of the jaw opener (MDM) which coincides with an activity in the dorsal cervical muscles. At maximal gape the jaw openers become silent and an activity in the jaw closers starts. Approximately 50 ms after the onset of the MDM an activity is seen in the MAME1 and the MP_{tmed}; the MP_{sT} and the MP_{tlat} becomes active approximately 100 ms later. The MAME2 remains silent during piercing. The activity patterns of the jaw closers during piercing are very characteristic and invariably of low intensity (few spikes and thus less motor units activated). Only the MAME1 shows a somewhat more intense activity which lasts about two seconds. Spikes in the MAME1 are of average to high amplitude and show a frequency of ± 6 Hz.

Crushing (Fig. 6).—Crushing cycles are characterized by short, low intensity activity in the MDM, followed by a pronounced activity in all

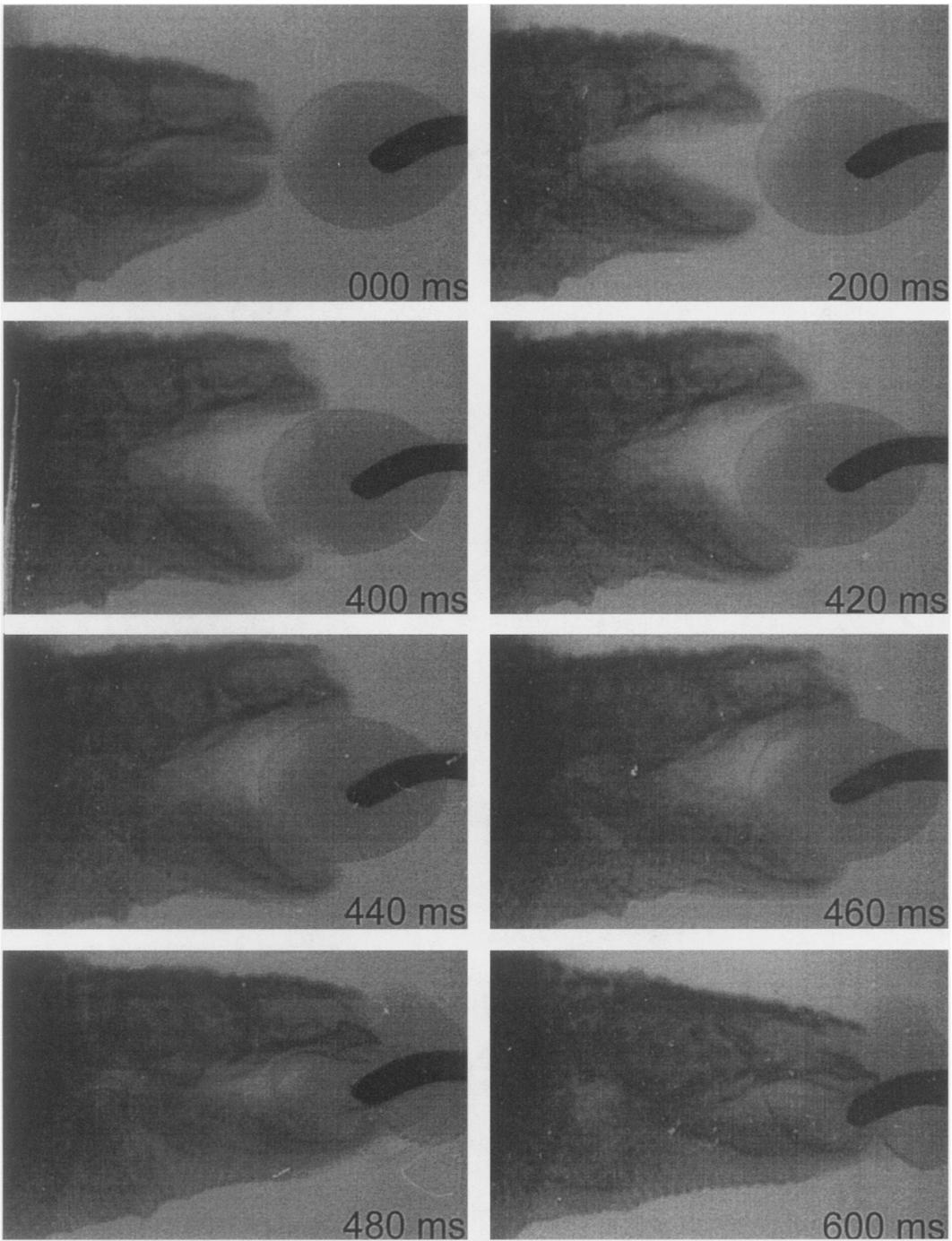


FIG. 3. Photos based on X-ray film (50 fps) of *H. horridum* while attacking an egg offered by forceps. Note that in less than 20 ms the egg is completely crushed. Time is indicated in ms at the lower right of each photo.

jaw closers with the exception of the MP_{tmed}. During the activity burst in the jaw closers the MDM shows a second activity burst of low intensity. Approximately 50 ms to 100 ms after

the onset of the MDM the jaw closers become active. Both the MAME1, the MP_{sT} and the MP_{tlat} show a strong activity (large number of spikes with a high amplitude). The MAME2

TABLE 1. Egg toughness measurements; for full explanation see text. NR = not recorded, in the first series only the first crack was recorded as total failure usually occurred shortly after. NO = not observed, in the second and third series eggs sometimes showed no cracking before total failure.

Measurement	Length (mm)	Width (mm)	Mass (g)	Force—1st crack (N)	Force—total failure (N)
1	32.80	26.20	11.91	5.85	NR
	34.50	25.50	11.69	6.61	NR
	34.50	27.05	13.13	6.54	NR
	32.45	25.15	11.02	6.24	NR
	31.25	24.50	9.92	5.64	NR
	33.80	27.75	13.90	7.50	NR
	38.15	25.65	11.74	6.84	NR
	38.10	26.70	12.93	6.88	NR
	36.75	25.85	11.54	5.04	NR
	2	33.00	25.90	11.97	8.27
33.95		25.25	11.79	11.77	53.20
32.00		26.20	12.05	NO	19.66
33.70		25.70	11.93	11.28	22.46
33.50		25.60	11.79	7.36	9.88
34.70		25.45	12.43	9.22	53.19
33.25		25.85	12.00	NO	19.68
32.75		25.20	11.22	7.85	36.14
32.55		25.30	11.37	NO	12.21
32.85		24.85	11.08	7.85	10.98
3	32.20	26.00	11.95	7.46	8.98
	34.65	25.80	12.72	7.21	9.90
	32.10	25.90	11.45	13.87	23.32
	34.25	25.00	11.71	NO	18.15
	32.85	26.20	12.39	7.46	10.32
	33.10	25.75	12.33	7.11	9.94
	35.20	25.45	12.70	NO	14.37
	32.65	26.00	12.20	NO	16.58
	31.70	25.35	10.58	4.42	9.97
	34.90	25.10	11.75	4.42	6.44

DISCUSSION

Our data suggest that egg feeding sequences in *H. horridum* occur according to a fixed behavioral pattern including five stages: approach, piercing, uptake, crushing, and swallowing. The two crucial stages within such a sequence are clearly piercing and crushing. Both stages are apparently essential and were invariably observed in our specimens while eating quail eggs. Although during both piercing and crushing it appears that the animal has great difficulties in breaking the egg shell, the X-ray sequences show that the animals have the potential to crack the eggs in one bite. Indeed, the results of the egg toughness measurements and the bite model clearly show that the potential bite force (in any situation over 30 N) is greater than the average strength needed to cause complete failure of the egg (27 N). The egg toughness measurements also indicate what the effect of piercing is on the eggs, and what its function might be. From the observation that cracking of the egg shell occurred at similar loads for previously pierced eggs and intact eggs (less than 10 N, when placed within the oral cavity) and total failure occurred at much lower loads in previously pierced eggs (not pierced: ± 27 N; previously pierced ± 13 N), it can be concluded that the piercing itself does not reduce the strength of the egg shell but does reduce the resistance of the egg membrane. Related to the piercing it can be noted that a functional subdivision of the dentition is apparently present in *H. horridum*. Whereas the four smaller and straighter premaxillary as well as the first two maxillary teeth are mainly used during piercing, the large recurved and grooved maxillary and mandibular teeth are used while subduing and holding young rodents or birds, or during defensive bites.

and the deep part of the MAME1 show an activity with spikes of intermediate amplitude. In all muscles, the stimulation frequency tends to be ± 6 Hz.

If we combine the previous conclusions with the results of the EMG experiments that demonstrate that the jaw closers show a considerably lower activity level during piercing, it becomes

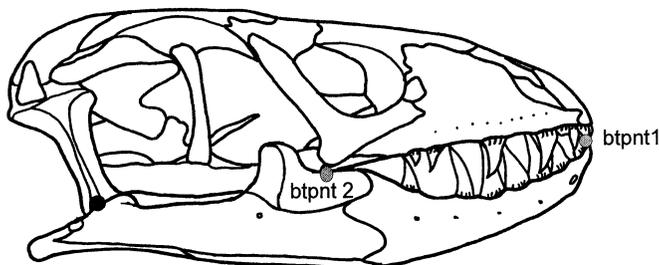


FIG. 4. Schematic representation of the bite points used in the bite model. Point 1 corresponds to the front teeth used during piercing; point 2 corresponds to the roof of the mouth where the egg is situated during crushing. btptnt1: bite point 1, btptnt2: bitepoint 2.

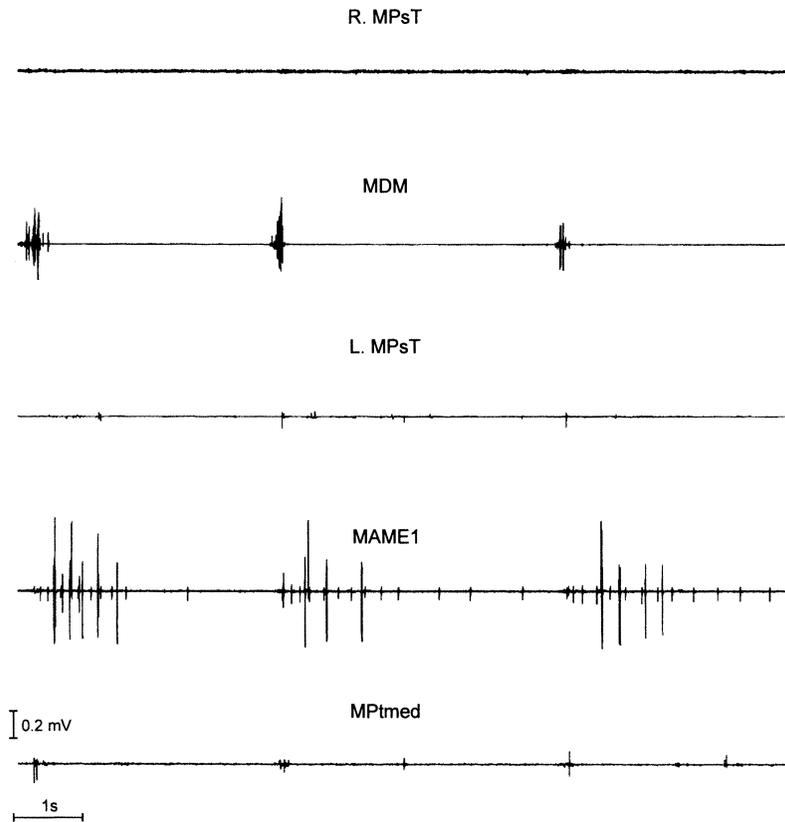


FIG. 5. Representative original electromyogram of several jaw closers and the jaw opener (MDM) during three successive pierce bites in *H. horridum*. MAME1: m. adductor mandibulae externus—superficial part, MDM: m. depressor mandibulae, MPTmed: m. pterygoideus medialis, L. MPsT: left m. pseudotemporalis, R. MPsT: right m. pseudotemporalis.

clear that the animals refrain from using their full force during this stage. The reasons why they do not use full strength can probably be related to the nature of the food: if the eggs are cracked outside of the mouth a considerable amount of the nutritious content will probably be lost in the substrate. By cracking the egg within the oral cavity, the animals avoid losing part of the content of the egg. Why then this characteristic piercing? As noted before, the act of piercing reduces the strength of the egg considerably. However, as the bite model indicates, the animals can apparently produce ample strength to crack the eggs without previously piercing it (bite forces of 43 N vs. egg strength of 27 N). This apparent paradox is presumably due to the deformable structure of the mouth floor. When the animal closes its jaws, the egg is pushed against the floor of the mouth, which, in turn, is pressed down in between the rami of the lower jaw. During such a crush bite, the gape angle reduces to almost zero, which implies a considerable shortening of the muscles involved.

Considering the fact that animals usually bite with relatively large gape angles, and that the jaw musculature is probably optimized for biting at such gape angles (as was shown for *Trachydosaurus rugosus*, Gans et al., 1985), the reduction in gape during crushing might induce the jaw muscles to be active away from the optimum in their length-tension relationship thus reducing their force output. Contraction of the intermandibularis (running between both rami of the lower jaw) musculature during crushing might counteract this deformation and thus aid considerably in crushing. However, this needs to be confirmed by EMG recordings of these muscles. Still, it can be noted that the m. intermandibularis complex is particularly well developed in helodermatids (see also McDowell, 1972). It should also be noted that during crushing the palatal and pterygoid teeth could play an important role in creating high pressure areas. However, as these teeth are absent in some specimens (as those used in this study), and generally considered to be a primitive angui-

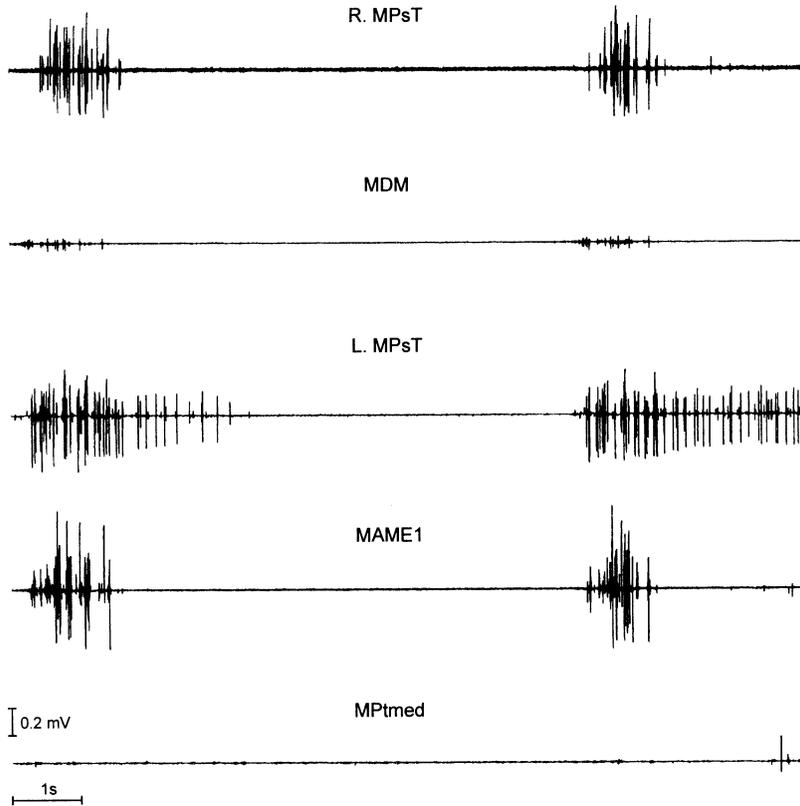


FIG. 6. Representative original electromyogram of several jaw closers and the jaw opener (MDM) during two successive crush bites in *H. horridum*. For abbreviations, see Fig. 5.

nomorph characteristic (Rieppel, 1980), they can hardly be regarded as adaptations to an ovophagous diet.

An interesting observation is that occasionally eggs seem to be not completely broken when ingested (Ditmars, 1910; Shaw, 1948; Arnberger, 1948; Stahnke, 1950). Two remarks have to be made with respect to these observations: (1) in most cases described, it was reptile eggs, and (2) in the cases we observed, the eggs, although not fully broken, were invariably previously pierced. Even if the eggs are not fully broken, piercing might still serve a function as it allows the digestive juices to make contact with and dissolve the egg membrane and the egg contents. Reptile eggs on the other hand do not possess a calcareous shell and thus the need to break or pierce it seems absent. The leathery shell of such eggs can probably be digested by the animals. If so, crushing would greatly increase the chances of losing part of the contents and thus seems superfluous in the case of reptile eggs.

However, eggs are not always processed as described in this paper. Several reports of hel-

odermatids breaking eggs outside of the mouth and lapping up the contents exist (Ortenburger and Ortenburger, 1926; Bogert and Del Campo, 1956; Beck, 1990). Two of these reports describe the breaking and lapping of hens eggs and the other deals with the eggs of desert tortoises. As the hen eggs are too large to ingest without breaking (none of our animals was able to ingest even a medium sized hen egg) they obviously have to be broken first. Breaking of eggs outside of the mouth is thus probably related to the size of the eggs. However, it must be stated that the animals used in this study were captive born and represent only a small sample. It is essential to obtain detailed descriptions of the eating of eggs in natural circumstances before the results of this study can be generalized.

If the egg eating behaviour we described can be generalized to helodermatids in general, is it then justified to say that *H. horridum* shows adaptations to ovophagy? We feel that we can state that for the specimens examined by us at least behavioral adaptations are present. These include the piercing of the eggs before ingesting and the crushing of the eggs within the oral cav-

ity. Together with these behavioral adaptations, distinct motor patterns during piercing and crushing are present. Nevertheless, the jaw apparatus of *H. horridum* seems to be constructed to serve as a high force output system. This is reflected in a hypertrophy of the external adductor (thanks to the loss of the supratemporal bar), a strengthening of the skull (including both a thickening of the dermal bones as well as an ossification of the intracranial joints), and enlargement of the maxillar and mandibular teeth (especially those teeth closest to the openings of the poison glands). Whether these characters are a plesiomorphy from an ancestral varanoid stock or adaptations in response to high predatory pressures remains unknown. Nevertheless, it seems that the bauplan of the jaw apparatus in *H. horridum* is primarily suited for defensive purposes. Despite this observation, we can state that due to mainly behavioral as well as subtle mechanistic adaptations *H. horridum* is an efficient ovophagous predator.

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Leptoseps: A New Genus of Scincid Lizards from Southeast Asia

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ABSTRACT.—Two previously described lygosomine scincid lizards known from three specimens from Southeast Asia—*Larutia osellai* Böhme, 1981 and *Siaphos poilani* Bourret, 1937—are described as a new genus, *Leptoseps*. The relationships of these two species and eight other species of limb-reduced lygosomine skinks from southeast Asia (genera *Isopachys* and *Larutia*) are analyzed cladistically.

In 1937 Bourret described the skink *Siaphos* (= *Saiphos*) *poilani* from Dong-Tam-Ve, Vietnam. He made no comparisons with other species. In 1981 Böhme described the skink *Larutia osellai* from Mea Kuong, Chiang Mai Province, Thailand. He only compared it with four species of the southeast Asian "*Sphenomorphus*" *larutensis* species group (Greer, 1977) and placed all five species in a new genus, *Larutia* (type species: *Lygosoma larutense* Boulenger, 1900, by original designation). I have recently examined and compared the three known specimens of Bourret's (MNHN 1948.61–62) and Böhme's (Mus. Civ. St. Nat. Verona C.E. No. 35) two species (Fig. 1) and believe that they are each others' closest relatives. I further believe that they are distinctive enough to be accorded separate generic status. The purpose of this paper is to diagnose the genus and discuss its relationships.

Leptoseps, sp. nov.

Type Species.—*Siaphos poilani* Bourret, 1937, designated herein.

Diagnosis.—A member of the *Sphenomorphus*

major group of lygosomine skinks (Greer, 1979), but differing from these skinks in the following combination of derived characters (based on *Eumeces* as the only currently reliably known outgroup for the *Sphenomorphus* group, but with the primitive number of premaxillary teeth nine instead of seven—see Appendix 1): supranasals absent; prefrontals absent; frontal smaller than interparietal; loreal single; first supraciliary in contact with frontal, sixth supraciliary large and projecting medially between third and fourth supraoculars; lower eyelid with opaque window; supralabials six, fourth subocular, fifth largest; infralabials five, fourth very large; external ear opening absent (Fig. 2); dorsal scales smooth, in 18 longitudinal rows at midbody.

Size small (maximum SVL = 45 mm); limbs relatively small (front limb 6 percent and rear limb 7–8 percent of SVL; Fig. 1); pes with four digits; all digits very short; supradigital scales in a single row; body elongate (SVL approximately 8.3–8.5 times head length). A more restricted diagnosis based on comparison with other limb-reduced southeast Asian lygosomines is given below.