Kinematics of Egg-eating by the Specialized Taiwan Snake
Oligodon formosanus (Colubridae)

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ABSTRACT.—The Taiwan colubrid snake *Oligodon formosanus* feeds almost exclusively upon the eggs of other reptiles. Snakes that specialize on the eggs of birds usually swallow eggs whole then crush them. *Oligodon* instead uses enlarged, blade-like rear maxillary teeth to make repeated slashes in the leathery egg shell, inserts its head, and swallows the yolk. The mechanics of cutting involve cycles of extreme displacement of the maxillary bone, whose blade-like teeth are swung in arcs to make ever deeper slashes in the shell until a slit is formed. The cycles during cutting involve protraction, engagement, and retraction of the palatomaxillary arch of one side while the contralateral jaws maintain a continuous hold on the egg surface. The slit is enlarged by repeated cutting motions until the snake can push its head through this opening and into the interior of the egg, where it swallows the yolk and young embryo. The basic feeding behavior of colubrids has been modified in *O. formosanus* in two ways. First, the reciprocating, unilateral pattern has become repeating and unilateral. Second, palatomaxillary arch displacements characteristically arising during deglutition in other colubrids arise earlier in feeding by *O. formosanus* during egg opening. The egg-eating specializations of *O. formosanus* give it access to an energy rich food (yolk) and to a wider range of foods (small to large eggs) than are available to generalized snakes of similar size.

Snakes that specialize on bird eggs for food are a familiar subject of study (Gans and Oshima, 1952; Fukada, 1959; Broadley, 1979). Characteristically, the egg is swallowed whole, the calciferous shell is crushed by forceful contraction of axial musculature that may press the egg against vertebral processes to separate the embryo and its yolk from the shell; the shell is often regurgitated afterward (Gans, 1952). However, snakes that specialize on the eggs of reptiles must necessarily employ different feeding mechanisms to address the different mechanical problems of opening a reptile egg. Unlike stiff, brittle-shelled avian eggs, the compliant, leathery-shelled eggs of most oviparous reptiles yield to mechanical stress. Furthermore, the relatively large size of reptilian eggs compared to egg predators may prevent swallowing of the egg whole and thus does not allow an opportunity for deployment of axial musculature.

Species of the genus *Oligodon* feed primarily on reptile eggs. This is done not by cracking the egg shell but by first slitting the shell, then inserting the head through the cut to drink the contents (Minton and Anderson, 1963; Toriba, 1987). This behavior has been suggested for the genus *Cemophora* with both box turtle eggs and corn snake eggs (Dickson, 1948; Minton and Bechtel, 1958), and for species of *Stegonotus* (McDowell, 1972). Egg shells were also recovered in the feces of *Oligodon* (Toriba, 1987), suggesting that on occasion these snakes might simply ingest the entire egg. Other genera such as *Prosymna* (Broadley, 1979) also exhibit a tendency to eat entire reptile eggs and pass parts of the undigested shell. Both *Oligodon* and *Prosymna* have also been recorded feeding on other prey such as small lizards and mammals (Minton and Anderson, 1963; Broadley, 1979).

The purpose of our study was to gather details of the basic feeding behavior specialized for egg eating and to propose a kinematic model for egg entry by *Oligodon*.

MATERIALS AND METHODS

Basic cranial osteology was determined from skulls of *Oligodon formosanus* cleaned by dermestid beetles. They were examined under a dissecting microscope and sketched with camera lucida drawing tube.

The feeding behavior of four *O. formosanus* (47–53 cm snout–vent length, SVL) were filmed using both artificial and actual reptile eggs, as well as newborn mice. Artificial eggs were made using two sizes of gelatin capsules (2.2 cm long × 0.5 cm diameter, and 4 × 1.5 cm) filled with chicken egg yolk. The reptile eggs (average 5.9 cm in length and 2.4 cm in width) were from *Lampropeltis* spp., and had been laid about one month before. Newborn mice were *Mus musculus* (5–6 g). Three snakes (SVL 47.0–53.1 cm) were examined in feeding trials. The animals inside their cages (50 × 30 × 30 cm) were placed in the filming room on a table in a quiet environment with overhead lights dimmed. A

hide-box was available and the cage floor covered with newspaper. The snakes were left in the room from 30 min to 24 h. They were filmed before two tungsten lights with a Hycam high speed 16 mm camera (Kardong, 1975). During feeding trials, the top to the cage was lifted and capsule, egg, or mouse was placed on a low plastic platform inside. Lights were turned on and filming began when the snake opened its mouth and began to cut the egg. Each of the three snakes was tested five to ten times with eggs or capsules. In addition to egg or capsule, one snake was presented with newborn mice. Snakes placed in feeding trials had access to water but had not eaten for at least 45 days; a total of 18 feeding trials (eggs/capsules) was filmed or carefully observed thereafter. No significant differences were observed in feeding behavior on eggs and on capsules. Therefore, descriptive events are based equally on both.

Following the initial analysis of the basic feeding behavior, two snakes were lightly anesthesized (isoflurane) to the point at which tail reflex (retraction to pinch by forceps) was extinguished. Then the mouth was opened and the palatomaxillary arch grasped with tweezers and slid forward-and-back in a horizontal plane relative to the braincase to simulate as closely as possible the displacements observed earlier during basic feeding. Restrictions noted during these arch manipulations are the basis for characterizing the joint mobilities within the palatomaxillary arch. Also while snakes were anesthesized, the teeth borne on maxilla, palatine, pterygoid, and dentary bones were firmly pressed with tweezers in anteroposterior directions, and in mediolateral directions to determine if they could be folded (e.g., Savitzky, 1981), or if any significant movement relative to their bases of attachment to the bones was possible.

RESULTS

Morphology.—The basic skull morphology of *Oligodon* is similar to that of other colubrids (e.g., Cundall, 1981). Of special note is the palatomaxillary arch, which is a central mechanical unit of egg-opening behavior. Within the arch, the ectopterygoid is firmly joined at its posterior end with the mid-dorsal pterygoid. Together, ectopterygoid and pterygoid constitute the biforked "body" of the arch. Each forms a joint with anterior elements (palatine and maxilla), respectively the palatopterygoid and ectopterygo-maxillary joints. These are hingelike and establish axes of rotation inclined at oblique angles to the midsagittal plane of the braincase (Fig. 1). The prefrontal is firmly joined at its dorsomedial side to the braincase. Its ventral end offers a fixed site that suspends both the
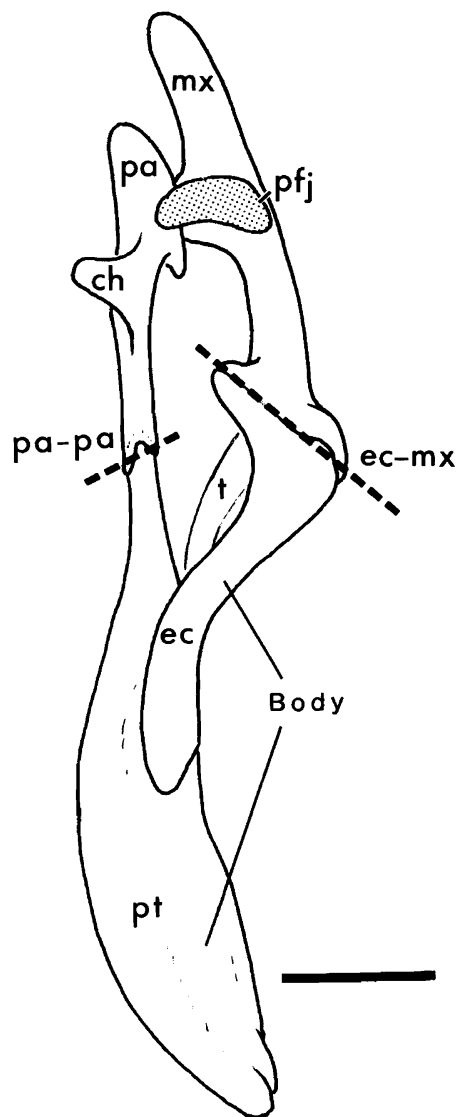

FIG. 1. Right, palatomaxillary arch of *Oligodon formosanus*, dorsal view, resting position. The arrow lies along the midsagittal axis of the braincase. Firm attachment between ectopterygoid (ec) and pterygoid (pt) produce a structural unit, the "body" of the arch. The shaded area (pfj) represents the articular faces on palatine (pa) and maxilla (mx) where suspension from the prefrontal is established. The dashed lines indicate the hingelike axes of rotation about the palatopterygoid joint (pa-pt) and the ectopterygo-maxillary joint (ec-mx). Abbreviations: ch, choanal process of the palatine; t, an enlarged posterior maxillary tooth. Bar equals 2 mm.

palatine and maxilla. This point of suspension is established dorsally in the middle of the maxilla and defines a point of pivot about which the maxilla rotates. In the palatine, this fixed

point of suspension is also established dorsally, but within its anterior region; the palatine establishes a second point of sliding contact with the skull through its choanal process.

Palatine, pterygoid, maxilla, and dentary all bear teeth. Some teeth carry dental ridges (sensu Wright et al., 1979), none is grooved, and all are homodont except for those carried on the posterior end of the maxilla. The posterior one or two maxillary teeth are distinctly longer than those in mid- or anterior shaft. Further, these teeth are laterally compressed and blade-shaped, with the posterior margin forming the sharpest edge on the tooth (Mori et al., 1992).

Basic Feeding Behavior.—Rodents: Swallowing of young mice was characterized by reciprocating, unilateral feeding (sensu Gans, 1961). Following movement about the cage, the snake made contact with the mouse. It pushed its nose into the mouse, jaws parted, and reciprocating motions of left and right sides to the jaws began. Successive alternating advances of palatomaxillary arches "walked" the jaws over the prey in a feeding pattern qualitatively the same as that described for other colubrids (Albright and Nelson, 1959; Cundall, 1983; Kardong, 1986).

Eggs/Capsules: A feeding episode of *Oligodon formosanus* consisted of four phases when large eggs or yolk-filled capsules were presented.

Phase I (Movement). Following introduction of egg or capsule, the snake often exhibited only slight increases in tongue flicks ($\bar{x} = 15.4$/min). Onset of active movement about the cage and eventual investigation of the egg/capsule began within about 10 min, although on two occasions the snake did not begin activity for over 1 h. During movement about the cage, the head was carried about 1 cm above the surface of the cage floor. This movement was interrupted at irregular intervals by pauses or by pushing the nose into cage corners. Such movements eventually brought the snout of the snake into contact with the egg/capsule.

Phase II (Contact). During contact the head was moved close to and across the surface of the egg/capsule, as the rate of tongue flicking increased ($\bar{x} = 64.3$/min). The head was held close enough so that the ventral surface of the tongue upon protrusion made contact with the egg/capsule surface. The snake also pushed its snout between egg/capsule and cage floor in a rooting-like action that could be vigorous enough to cause the egg to roll. Often the snake discontinued the contact phase and returned to the movement phase. Occasionally this ended the trial as the snake apparently lost interest in feeding and entered its hide-box. On 11 occasions, the snake returned to the contact phase and exhibited for the first time jaw motions that marked the onset of the cutting phase.

Phase III (Cutting). The cutting phase began when the jaws opened wide and grasped the egg/capsule. The jaws of one side maintained their hold on the egg/capsule surface without release during the cutting phase, while the opposite jaws actually moved through repeated slashing cycles, each cycle composed of three stages—protraction, engagement, retraction.

Stage 1 (Protraction). The jaws of one side closed so that their teeth engaged the surface of the egg/capsule. With these teeth engaged, the jaws of the opposite side opened and simultaneously the palatomaxillary arch of this opening side was now protracted. Protraction produced more acute angles through the joints within the arch. Protraction also swung these joints forward and slightly ventrally.

Arch protraction imparted a rotation to the maxilla about its suspension with the prefrontal, but no significant forward sliding on this articulation occurred. This rotation about the prefrontal was characterized by the ventral swing of the posterior, and dorsal rotation of the anterior, end of the maxilla. No individual teeth moved on their sockets (see below). Instead, the posterior blade-like teeth rode forward on the rotating maxilla describing an anteroventrally directed arc relative to the braincase. Because the axis of rotation within the ectopterygo-maxillary joint was inclined from a transverse to a more lateral-facing position, protraction of the arch added a lateral component of motion to this arc that the posterior maxillary teeth followed. The palatine underwent displacements similar to the maxilla, namely, its posterior end swung forward and ventrally. This rotated the palatine from a horizontal orientation of its long axis at the start of protraction to an almost vertical position relative to the braincase by the end of protraction.

In addition to arch protraction, jaw opening and rotation of the braincase about its longitudinal axis contributed further to displacements of the rear maxillary teeth. Thus, palatomaxillary arch protraction swung rear maxillary teeth in an anteroventrally (and slightly outward) directed arc. Acting alone, this would bring tooth tips immediately into contact with the egg/capsule surface. However, because the palatomaxillary arch is suspended from the braincase, jaw opening and rotation of the braincase about its longitudinal axis lifts the arch away from the egg/capsule surface so that the tips of rear maxillary teeth clear the surface during arch protraction. Consequently, by the end of the protraction stage, rear maxillary teeth have been moved forward above and advanced over the surface of the egg/capsule.

Stage 2 (Engagement). By the end of the protraction phase, forward advance of the posterior
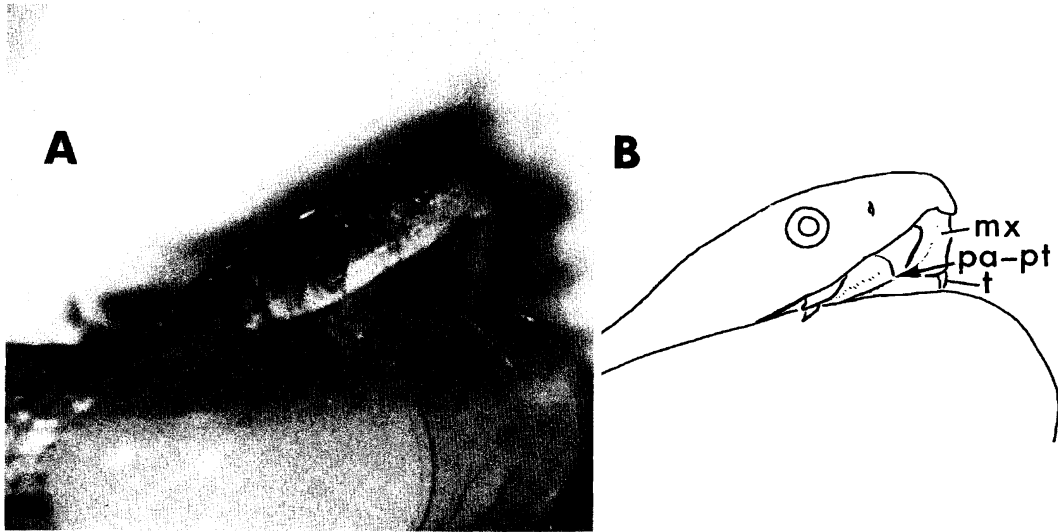
FIG. 2. Cutting phase in *Oligodon formosanus*, gelatin capsule: (A) photograph taken from a frame of high speed film; (B) outline of this photograph. Jaws of the right side hold the capsule and the contralateral (left) jaws are producing the slashing cycles. This frame is taken at a point of a cutting cycle at the end of protraction. Notice that palatopterygoid joint (pa–pt) of the left side forms an acute angle and that the enlarged posterior maxillary tooth (t) has just engaged the surface of the capsule.

end of the maxilla relative to the egg/capsule surface usually brought its elongated, bladelike teeth into close proximity with the surface of the egg/capsule. If the teeth did not make contact by the end of rotation, then the jaws closed slightly to push the points of these posterior teeth into contact with the surface of the egg/capsule. This is recognized as the short engagement phase (Fig. 2).

Stage 3 (Retraction). Once the teeth were engaged, retraction of the palatomaxillary arch pulled the teeth across the egg/capsule to produce a shallow cut in its surface. The acute angles between the body of the arch and anterior elements became less acute as maxilla and palatine returned to a more horizontal position relative to the braincase.

The same side repeated this cycle (protraction, engagement, retraction) while the contralateral side maintained its continuous engagement with the capsule. Thus, unlike unilateral feeding (sensu Gans, 1961) wherein jaws of opposite sides walk through reciprocating advances over the prey, *Oligodon* exhibited repeated jaw displacements of only one side that were not alternately repeated by the contralateral set of jaw elements.

Phase IV (Swallowing). Once an opening through the shell was produced, the snake probed the opening with its snout and usually pushed its entire head inside. This forceful penetration of the head tended further to enlarge the opening as well as now give the snake access

to the contents. The yolky contents were swallowed by drinking motion, in which the lower jaws were raised and lowered simultaneously in a slow pumping motion that involved the floor of the buccal cavity and adjacent throat. Withdrawal of the head was occasionally hindered by the edges of the slit that caught on neck scales. "Backing up" of the snake eventually resulted in temporary binding of the egg/capsule between objects in the cage, giving the snake a chance to pull itself free.

Mechanics of Cutting.—During the cutting phase, entry into the capsule was gained by the elongated teeth located at the posterior end of the maxilla (Fig. 3). Repeated cycles of protraction, engagement of the posterior maxillary teeth, and then retraction resulted in these tooth tips making several repeated slashes in the surface of the egg/capsule. Unlike swallowing by most snakes wherein the head progresses along a swallowing axis (sensu Kardong, 1986), in *Oligodon* the closed jaws of one side establish a fixed point on the egg/capsule surface. Opposite jaws are held consequently at a set radius from this fixed point. Because the contralateral jaws remained fixed in position, the repeated slashes of ipsilateral maxillary teeth were confined to a single location on the surface of the egg/capsule. Consequently, these teeth usually cut in a previous slash and deepened it. The overall result after approximately 20 such cycles was for the cuts to break through the surface of the egg/capsule. Thereafter, the snake con-
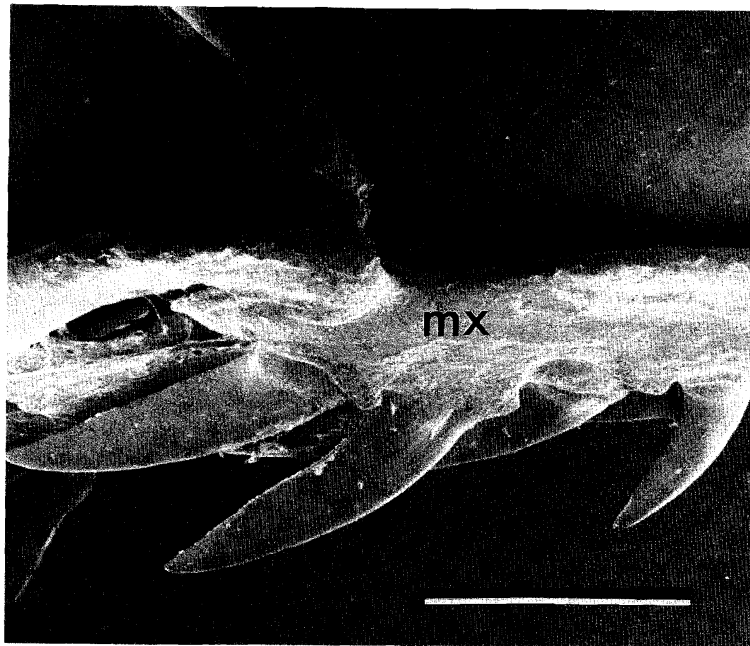
FIG. 3. Posterior teeth on the right maxilla (mx). Note the bladelike shape and relatively greater length of posterior teeth compared to more anterior teeth on the maxilla. A slight foreshortening of the maxilla has occurred in this low power, scanning electron micrograph. Bar equals 1.5 mm.

tinued to make slashing motions of its maxillary teeth, with the teeth actually passing into the opening. This allowed the sharp posterior edge of the tooth to directly cut the open edge of the egg/capsule's skin rather than to slash its surface. Like a knife blade drawn along an open cut, action of the sharp tooth edge now extended the size of the opening. After about 30 cycles following first initiation of the cutting phase, the snake released the hold its contralateral jaws had until then maintained and pushed its head into the egg/capsule through the hole, to begin swallowing the contents.

Kinematics.—In anesthetized snakes, forces applied to the palatomaxillary arch failed to produce significant anteroposterior sliding of the maxilla upon its articulation with the fixed prefrontal. However, considerable maxillary rotation was possible so that the posterior end of the maxilla described a ventrally directed arc of almost 80° from its resting, horizontal position. The supratemporal exhibited a range of rotation about its proximal articulation with the skull through almost 45°. Manipulation of the palatine confirmed that it was freely rotatable about its suspension from the prefrontal and that the choanal process established a sliding articulation with the base of the braincase. Forced forward displacement of the palatomaxillary arch resulted in rotation of the palatine characterized by the upward swing of its an-

terior end and ventral rotation of its posterior end.

Manipulation of maxillary, dentary, pterygoid, and palatine teeth of the anesthetized snakes failed to produce any movement of functional teeth within their sockets (cf. Savitzky, 1981). Thus, all functional teeth are firmly ankylosed at their bases, and exhibit no ability to fold or change position during feeding.

KINEMATIC MODEL

Based upon these observations of feeding and jaw kinematics, the following model for egg opening by *Oligodon formosanus* is proposed (Fig. 4).

1. The supratemporal–quadrate articulation rotates dorsally to its maximum excursion at the onset of cutting phase but thereafter remains fixed in position during a feeding episode.

2. During the protraction stage, the distal end of the quadrate rotates forward about its articulation with the supratemporal, and reverses this motion during the retraction stage.

3. During protraction, the two joints within the palatomaxillary arch (palatopterygoid and ectopterygo-maxillary joints) travel in an anteroventral direction relative to the braincase. This action produces acute angles in these joints and results in rotation of anterior arch elements (maxilla and palatine) about their points of suspension from the prefrontal.

4. The ectopterygo-maxillary joint permits rotation that pushes the posterior maxilla forward, ventrally, and laterally relative to the braincase. In order for this movement to occur, the maxilla rotates, but does not slide, about its articulation with the prefrontal.

5. Enlarged posterior teeth are carried by the rotating maxilla along an arc that displaces them from a resting position next to the upper lip and into an erect position where they can engage the surface of the egg.

6. On the same side undergoing palatomaxillary arch protraction, opening of the jaws and rotation about the long axis of the braincase lift the arch slightly away from the egg to ensure that protracting rear maxillary teeth clear, and thus successfully advance over, the surface of the egg.

7. Initially the tips of the enlarged posterior maxillary teeth score and deepen the surface cut; once a slit is opened, later in the cutting phase, the bladelike edge on the tooth extends the opening during protraction engagement/retraction cycles.

DISCUSSION

The teeth of snakes must puncture the tissues of prey to gain a firm hold on resisting animals (Frazzetta, 1966) or penetrate the skin so that venom might be delivered (Kardong, 1980). Slender, pointed teeth readily puncture prey tissues; however, such puncture wounds are not extended. As Frazzetta (1988) has argued, cutting presents a different mechanical problem from puncturing because skin is compliant and so undergoes large deformations before yielding to mechanical stress. This makes pointed teeth much less effective in slicing, compared to puncturing. Thus, those snake teeth that must cut compliant skin are not pointed but instead are bladelike (Wright et al., 1979; Kardong, 1980).

Egg-eating snakes specialized for bird eggs do not encounter soft, pliable surfaces. The avian egg shell is hard and brittle, and swallowing specializations center around axial musculature and projecting bony processes that crack the shell (Gans, 1952; Fukada, 1959; Broadley, 1979). However, egg-eating snakes such as *O. formosanus* that specialize upon reptile eggs meet a different mechanical problem than that encountered by avian egg specialists. The egg shell of most reptiles is leathery and compliant, and swallowing specializations center around teeth that cut the shell. The blade-like, rear maxillary teeth of *O. formosanus*, along with the kinematics involved in egg-eating, address the problem of opening an egg with such a compliant shell.

Displacements of the palatomaxillary arch used during the cutting phase to slash the egg shell are quite similar to, and presumably de-
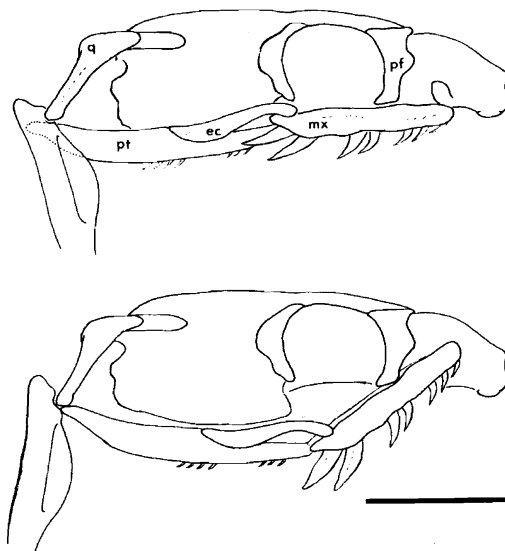

FIG. 4. Kinematic model. Once the open jaws of one side have established a hold on the egg surface, the contralateral jaws shown here protract. This motion swings the enlarged, posterior maxillary teeth in a ventral, anterolateral arc bringing them into contact with the surface of the egg. Bar equals 5 mm.

rived from, displacements used during swallowing by other species of colubrids. In the generalized colubrid *Elaphe obsoleta quadrivittata* swallowing advances of the palatomaxillary arch produce rotations of the maxilla about its fixed suspension from the prefrontal, swing its posterior end ventrally, and upon closure move the maxillary teeth toward and into contact with the surface of the prey (Albright and Nelson, 1959; Kardong, 1986). The mechanics of jaw advance in *Elaphe* are such that as the maxilla rotates about its suspension from the prefrontal, subsequent jaw closure results first in the engagement of the posterior maxillary teeth with the prey. Although posterior maxillary teeth of *Elaphe* are unspecialized, Kardong (1986) argued that such a kinematic action makes this site, the posterior maxilla, especially well-suited to carry specialized teeth that might address specialized mechanical problems. For example, where slipper prey are caught and swallowed, teeth residing on the posterior maxilla are often long to increase purchase (Kardong, 1979, 1980). Since a similar rotation of the palatomaxillary arch occurs in *O. formosanus*, it is not surprising to discover specialized posterior maxillary teeth addressing the specialized mechanical demands.

Thus, not only are posterior maxillary teeth morphologically specialized for cutting, but the kinematic displacements that bring them into

contact with the surface of the egg are motions amplified from the closing phase exhibited during swallowing by other colubrids. In other colubrids, although the closing phase of swallowing brings the maxilla toward the prey, its teeth may not always make actual contact (Cundall, 1983). However, in *O. formosanus* the rear maxillary teeth almost always make contact with the surface of the egg/capsule during the cutting phase. Consequently, this downward travel of the maxilla during closing, characteristic of other colubrids, is both incorporated into egg-opening behavior and accentuated in *O. formosanus* during the engagement phase to ensure frequent contact of rear maxillary teeth with the egg surface.

Two basic features of the swallowing mechanics characteristic of other colubrids are modified in *O. formosanus*. Firstly, the characteristic reciprocating, unilateral pattern of swallowing has been modified to a repeating, unilateral pattern. Whereas most colubrids swallow by alternating advance of left and right sets of jaws, *O. formosanus* cuts into the egg by repeated jaw cycles of only one side without alternating displacements of the opposite side. Occasionally colubrids exhibit several repeated advances of jaws on one side (Gans, 1970, pers. comm.), an apparent adjustment to prey shape or to initial improper engagement of teeth. This occasional repeating, unilateral pattern of other colubrids has, in *O. formosanus*, been expanded into the characteristic motor pattern deployed during opening of the egg shell. Secondly, the characteristic colubrid pattern of jaw advance during swallowing (protract, close, retract) occurs in *O. formosanus* not during the swallowing phase but earlier, during opening of the egg. Thus, this motor pattern occurs earlier in the feeding behavior, and participates not in advancing the jaws over the prey (deglutition), but instead during the preceding egg-opening behavior.

Once inside, the yolk contents can be drunk. Mature eggs may be encountered occasionally by *O. formosanus* so that more alternating advances of jaws, like feeding in most colubrids, may be used to swallow the near-term embryo. Such reciprocating advances of jaws were observed when *O. formosanus* showed interest in and swallowed newborn mice. Thus, such an alternating motor pattern is retained in the swallowing repertoire of *O. formosanus*. However, when the egg contents were yolk, deglutition was more characteristically a drinking pattern (e.g., Kardong and Haverly, 1993) with synchronous and simultaneous elevation and depressions of both left and right sets of jaws.

The specialized morphology, jaw mechanics, and feeding behavior of *O. formosanus* give it

access to food resources less available to snakes of a similar size. By producing an opening in the tough, leathery shell, *O. formosanus* is able to feed on eggs too large to swallow whole. These feeding specializations of jaws and teeth thus give *Oligodon* access to both a high energy resource (egg yolk) and also expand the relative size range of available foods (large eggs).

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