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THE FUNCTIONAL ANATOMY OF THE TEETH OF THE WESTERN TERRESTRIAL GARTER SNAKE, *THAMNOPHIS ELEGANS*

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ABSTRACT: In the western terrestrial garter snake, *Thamnophis elegans*, three tooth types can be recognized based on their shape: recurved, curved, and linear. Recurved teeth are a shallow S-shape in appearance, curved teeth are crescent-like in shape, and in linear teeth the curve in the base does not continue distally so the tooth tip is straight. Each functional tooth bears a pair of dental ridges positioned opposite one another along the sides of the tooth. These ridges vary progressively in length and position from anterior to posterior teeth. They begin at the cusp and continue toward, but do not reach the base. The posterior maxillary teeth are distinctive. Their distal dental ridges are long and elevated into prominent edges which make the teeth appear blade-like.

Three aspects of the functional anatomy of the teeth are considered. First, in pythons and probably garter snakes, recurved teeth likely serve as prey snaring rather than manipulating adaptations. Second, dental ridges function during jaw closure as cutting edges that promote penetration and thus aid secure tooth engagement. Third, the posterior maxillary teeth are the first teeth of the maxilla to engage prey and these teeth have a distinctive anatomy (long, blade-like, prominent distal edge). Thus the posterior maxillary teeth penetrate deeper into the integument than any other teeth. This suggests that the posterior maxillary teeth function to impale the struggling prey and aid in holding and manipulating the prey.

Key words: Reptilia; Serpentes; Colubridae; *Thamnophis*; Teeth; Anatomy; SEM; Feeding

A few general studies on reptile dentition have been completed (Edmund, 1960; Peyer, 1963, 1968) and a summary by Edmund (1969) is available. However, only a few references describe snake teeth in particular and give attention to tooth surface features (Anthony, 1955; Bogert, 1943; Brattstrom, 1964; Frazzetta, 1966; Klauber, 1939). The purpose of this paper is to report the detailed tooth surface anatomy and tooth form in *Thamnophis elegans* and to discuss the functional significance of these features.

MATERIALS AND METHODS

Four skulls of *Thamnophis elegans* were cleaned for scanning electron microscopy (SEM) with dermestid beetles, washed in distilled water, immersed in acetone, and then dried at 100C for approximately 5–9 hours. The skulls were sputter coated with approximately 30 nanometers of gold and examined with a scanning electron microscope. All imaging was in the secondary mode except when viewing dental ridges. Backscattered imaging was instead used to enhance the relief of the ridges. All observations of surface features were made on functional teeth which for purposes of this investigation were classified as to type (recurved, curved, linear), and the positions of dental ridges on the sides were noted.

Two videotape cameras were used to photograph *T. elegans* engaged in prey manipulation and swallowing. Both dorsal and lateral views were filmed. A Sony videocassette recorder with pause control permitted us to stop the tape and examine actions of specific interest. All observations of feeding motions were made on snakes presented with live mice. All snakes were live captured in Whitman County, Washington, and ranged in snout–vent length from 30.4–52.8 cm.

Whenever possible we follow the terminology of Edmund (1969). Each tooth is divided into three approximately equal parts (Fig. 2). From base to tip they are the basal third, middle third, and occlusal third. No sharp anatomical landmarks delineate these divisions, but they are

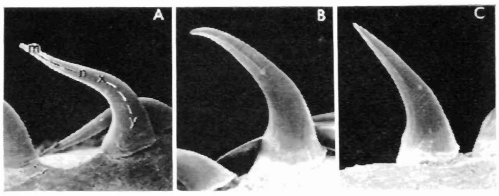

FIG. 1.—Basic tooth types of *Thamnophis elegans*: (A) recurved, (B) curved, and (C) linear. In addition to the primary curve of the tooth (x – – – y), another reverse curve (m – – – n) occurs in the tip of the recurved tooth. The end is curved backward in the curved tooth and the linear tooth is straight. Examples A–C are taken from left maxilla, right dentary, and right dentary, respectively.

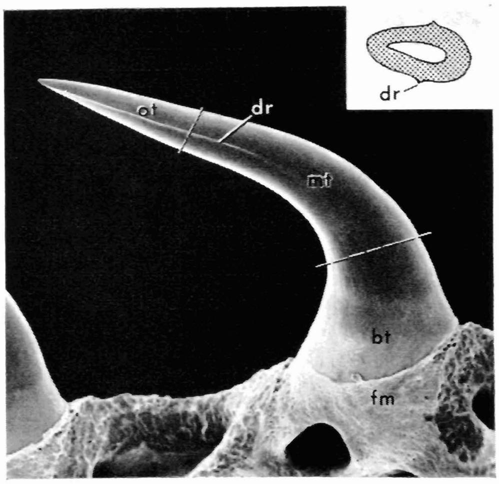

FIG. 2.—Parts of a tooth of *Thamnophis elegans*: (ot) occlusal third, (mt) middle third, and (bt) basal third. One of the two dental ridges (dr) and fibrous membrane (fm) are shown. This micrograph gives a labial view of a pterygoid tooth. The inset shows a cross-section in the middle third of the tooth.

simply established by dividing the tooth into the three equal parts.

RESULTS

Growing replacement teeth lie procumbent at the lingual (maxilla, dentary), or the labial (palatine, pterygoid) bases of functional teeth. Each functional tooth is pleurodont and ankylosed at its base to the crest of the socket.

There are three types of teeth (recurved, curved, linear), distinguished primarily by the shape of the occlusal third of the tooth. In the recurved condition the occlusal third curves forward, in a curved tooth it curves posteriorly, and in a linear tooth it is straight (Fig. 1).

Each tooth bears two dental ridges (Fig. 2) formed opposite one another in the surface enamel. These ridges run parallel to the curvature of the tooth. These ridges begin at or very near the tip and extend part way along the length of the tooth towards the base. Although they are present on all teeth, their position and length varies.

SPECIFIC TOOTH CHARACTERISTICS

Palatine teeth.—The palatine articulates at its posterior end with the pterygoid. The tooth bearing ventral edge of the former is slightly curved outward (Fig. 3) and contains 13–14 dental sockets. The teeth project posteriorly. Compared to the pterygoid teeth, the palatine teeth have only a slight inward orientation and all teeth are of about equal height.

All three tooth types are present although recurved teeth tend to predominate anteriorly. The paired dental ridges of approximately equal length were found on all teeth. One ridge was labial in position and the other was lingual. The length of the paired ridges varies. They are short on anterior teeth (through the occlusal third) and longer (extending into the middle third of tooth) on more posterior teeth (Fig. 4).

Pterygoid teeth.—At its anterior end the pterygoid articulates with the palatine. From this articulation, the pterygoid extends posteriorly along a straight axis until near its posterior end. There the end projects outward in a latero-posterior direction (Fig. 3). Teeth are borne along the ventral surface from the anterior end to the beginning of the lateral projection. Dental sockets number 24–26.

Functional teeth at the cranial end project postero-medially, but toward the

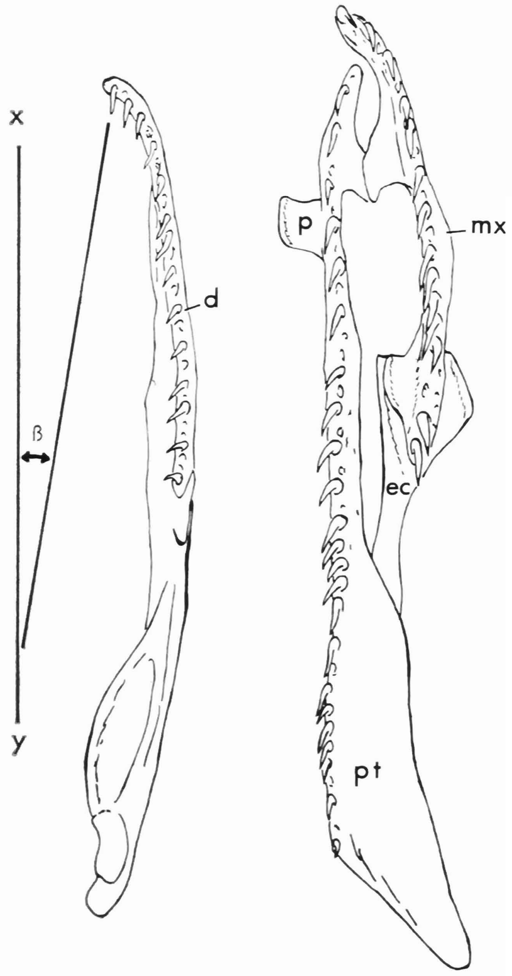

FIG. 3.—Occlusal view of the mandible and palato-maxillary arch of *Thamnophis elegans* showing tooth bearing bones: (d) dentary, (mx) maxilla, (p), palatine, (pt) pterygoid, and (ec) edentulous ectopterygoid. The line of cusp projection is carried to the midline of the cranium (xy). The angle β indicates orientation which is negative if the tooth slants inward and positive if the tooth slants outward. Anterior dentary teeth make the smallest and posterior teeth the largest angle with the cranial axis. Note that anterior maxillary teeth project outward but this changes progressively in posterior teeth.

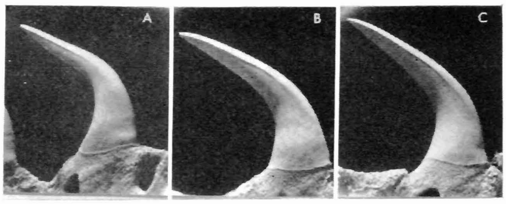

FIG. 4.—Palatine and pterygoid teeth of *Thamnophis elegans*. The three teeth are in labial view and were taken from anterior palatine (A), middle pterygoid (B), and posterior pterygoid (C) regions. The dental ridge occurs primarily in the occlusal third in (A), more extensively in the middle third in (B), and into the basal third in (C).

caudal end they change gradually to a posterior or a slight postero-lateral slant. These teeth are of the linear and curved types. Anterior teeth are about equal in height but decrease in size in the posterior dental arcade. Each tooth carries two dental ridges of approximately equal length on the labial and lingual sides of the teeth. The ridges on anterior teeth extend only through the occlusal third but in posterior teeth they extend farther along the tooth into the basal third (Fig. 4).

Dentary teeth.—From its posterior articulation with compound and splenial bones, the dentary extends forward curving medially toward the mandibular symphysis (Fig. 3). The dentaries do not form a synovial articulation with each other, but are joined loosely by connective tissue, muscles, and integument. Each dentary bears 24–25 sockets. When the mouth is closed, the tips of the teeth are directed posteriorly and slightly medially. The anterior teeth project posteriorly. However, toward the posterior end of the bone, they progressively become more sharply directed inward (Fig. 3). The tooth types present are linear and curved, and they become progressively shorter posteriorly. Two dental ridges of approximately equal length are present. These are labial and lingual in position and are opposite one another on the sides of each tooth.

Maxillary teeth.—The maxilla is suspended at its middle from the prefrontal and articulates posteriorly with the expanded end of the ectopterygoid which in turn articulates at its opposite end with the pterygoid. The maxilla is a curved bone that anteriorly bends in a medial direction.

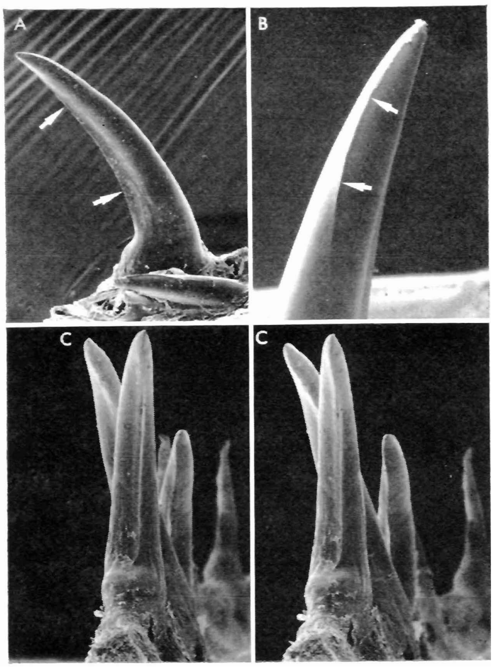

FIG. 5.—Posterior maxillary tooth of *Thamnophis elegans*. (A) Medial view of the left posterior maxillary tooth. Note the ridge (arrows) along the inside bend of its curvature. This prominent ridge can be seen best in the stereopair (C) taken of the distal face of the posterior maxillary tooth. (B) Close view of the short mesial ridge (arrows) that extends only a short distance away from the cusp.

It carries 21–24 dental sockets along the long axis of the bone. The teeth on the maxilla show greater variation than is found in sets of teeth on any other bones. This difference is primarily evident between posterior and anterior teeth. The caudal 2–3 teeth are relatively longer than the more anterior teeth. The former are curved and bear a long distal dental ridge and short mesial dental ridge. The distal dental ridge also forms a long, unique blade-like edge (Fig. 5). In contrast, the middle and anterior teeth are relatively short and bear lingual and labial dental ridges of approximately equal length.

There is some difference in tooth structure between the middle and anterior teeth. The anterior teeth (6–8 sockets) are recurved with the tips directed postero-laterally whereas the middle teeth can be any of the three tooth types and the tips are directed postero-medially (Fig. 3).

FUNCTION

Prey capture/swallowing.—The feeding sequence of *T. elegans* includes striking, holding, and deglutition phases. Considerable manipulation of the struggling prey may occur before swallowing begins. If the strike has resulted in a grasp on the prey at midbody, the jaws move by alternating left and right side-stepping motions to either end of the struggling prey. Swallowing begins when one end is reached. Alternating left and right cranial motions then advance the jaws over the prey and pass it into the esophagus. The teeth secure the prey during manipulation and swallowing.

The actions of the maxillae are of special note because of their unique posterior teeth. During swallowing the jaws of one side open and lift the maxillary teeth away from engagement with the prey. The maxilla is carried forward by horizontal swivel of the head and horizontal rotation about the point of suspension of the maxilla from the prefrontal. This movement causes the posterior end of the maxilla to swing laterally and the anterior end to swing medially. When the jaw is closed the posterior end of the maxilla is rotated downward and the rear teeth are the first to make contact with the prey. These rear teeth are longer than the more anterior maxillary teeth, and they securely hook into the integument so that upon retraction they carry along any tissue in which they are embedded.

Recurved teeth.—Frazzetta (1966) proposed that the S-shaped curve of recurved teeth serves two functions in *Python sebae* and *Python molurus*. The primary bend (located in the basal third) directs the axis of the tooth posteriorly so that if a prey tries to pull back out of the snake's mouth, the tooth sinks in deeper to more securely impale the prey. The reversed curve in the occlusal third serves to change the angle of attack of the tooth cusp during the strike so it is brought into line with the impact force (Frazzetta, 1966). In *T. elegans* the recurved teeth are borne by maxillae and palatines and are positioned at the anterior ends of those bones. The anterior teeth are the most likely teeth to make contact during the strike, and thus may be recurved in *T. elegans* for the same reasons as in pythons. The fact that posterior teeth tend not to be recurved suggests that they may be more important in other functions such as manipulating the captured prey.

Dental ridges.—Frazzetta (1966) proposed that the dental ridges ("cutting" edges) function in pythons to cut the teeth free from the prey during jaw opening. In *T. elegans* this seems to be unlikely for several reasons. First, the best developed ridges are on the wrong side of the tooth. During jaw opening the bones move forward relieving pressure on the back of the tooth and placing pressure on the leading anterior tooth face as it meets tissue during forward opening motion. If the teeth become stuck when the jaws are opened, then it is the leading anterior face that is the most likely side to become bound and the best developed ridges should be on these anterior surfaces to cut them free. However, just the opposite is true in *T. elegans*. The longest ridges are on the posterior sides of the teeth. It thus seems more likely that the better developed posterior ridges function when force is greatest during retraction. This means that the posterior ridges serve while the mouth is closing and hence they more likely function to cut the teeth into, not out of, the prey. Second, the teeth sink into the integument only part way during swallowing. This partial penetration creates less of a problem as the teeth are cut free from the tissue. Perhaps the ridges help the teeth slip out of the prey, but it seems more likely that their major function is to aid in tooth engagement, not disengagement.

Posterior maxillary teeth.—The rear maxillary teeth are distinctive. They are longer than anterior teeth, the distal dental ridge runs almost the entire length of the tooth, and this distal ridge forms a prominent, sharp edge. As the jaws close, the posterior end of the maxilla swings downward toward the prey so that rear teeth are the first to engage. Having engaged the prey, the maxilla is then retracted thus making the posterior face of the teeth the leading edge of the posteriorly directed motion (Fig. 6). The presence of a prominent edge on the posterior face of the teeth can serve to cut through tissue and promote penetration. Deep penetration permits more effective holding and manipulation of slippery, struggling prey. The prominent ridge may also promote entrance of oral secretions into prey tissue. It has not been established that garter snakes possess oral gland secretions injurious to their prey. However, there is some evidence that on occasion they can inflict a bite painful to humans (Goellner, 1975), and Taub (1965) found an enlarged oral gland (Duvernoy's) associated with the rear teeth. This evidence may suggest the presence of an oral gland secretion that serves to tranquilize or envenomate struggling prey.

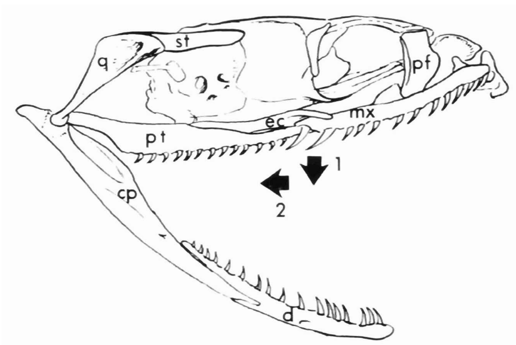

FIG. 6.—Skull of *Thamnophis elegans*. Arrows show sequence and direction of the closing (1) and retraction (2) motions. The posterior teeth on the maxilla (mx) are the first teeth on this bone to engage the prey. The dentary bone is indicated by (d), the compound by (cp), the ectopterygoid by (ec), the prefrontal by (pf), the pterygoid by (pt), the quadrate by (q), and the supratemporal by (st).

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