Tanner, L.H., Spielmann, J.A. and Lucas, S.G., eds., 2013, The Triassic System. New Mexico Museum of Natural History and Science, Bulletin 61.

TOOTH FORM AND FUNCTION IN TEMNOSPONDYL AMPHIBIANS: RELATIONSHIP OF SHAPE TO APPLIED STRESS

LARRY F. RINEHART AND SPENCER G. LUCAS

New Mexico Museum of Natural History and Science, 1801 Mountain Road NW, Albuquerque, NM 87104

Abstract—Temnospondyl amphibians were important members of the tetrapod fauna and the terrestrial vertebrate food chain during the Paleozoic and early Mesozoic. The “labyrinthodont” teeth of these amphibians are not simple cones; they exhibit an overall tooth form that is relatively complex and generally conserved over large temporal and phylogenetic ranges. We assess the functional morphology of these teeth and show the relationship of tooth shape to applied stress in three species of temnospondyl amphibians: the Pennsylvanian-Permian eryopid *Eryops*; the Middle Triassic capitosaurid *Eocyclotosaurus*; and the Late Triassic metoposaurid *Koskinonodon*. Beam theory was employed to develop strength profiles of the study teeth, which were then compared to their bending moment and shear stress profiles. These profiles are a graphic representation of the stress and strength along the longitudinal tooth axis at any position along the length of the tooth crown. This analysis showed that the teeth were best adapted to loading in the labiolingual direction, and that their strength varied as a cubic parabola, increasing from tip to base. In labial aspect the teeth have an approximately triangular shape. When such a tooth has penetrated a prey item and is loaded in the labiolingual direction, its triangular shape produces a uniformly varying load along the tooth length that results in a cubic parabola bending moment profile. Whereas no correlation was seen between tooth strength profiles and shear stress profiles, the bending moment stress profiles and tooth strength profiles were identical. Thus, shape has evolved to resist the applied bending moment while maintaining good penetration and crack propagation in hard parts of the prey items and for optimal performance during normal usage rather than to survive a relatively rare catastrophic impact.

INTRODUCTION

Jaws and teeth are of primary importance in the evolution of vertebrate life and are the most commonly fossilized skeletal parts and the most-studied biological apparatus. Some have considered the relative size of the feeding structures of vertebrates to be evidence of speciation and niche partitioning (Hutchinson, 1959) and as indicators of feeding strategies and behavioral patterns (e.g., Henderson, 1998). Numerous studies of the relationships of tooth form, function, and wear are present in the biological and paleontological literature. Some investigations of strength, both of complete tooth structures and their component materials, are also available. As an example, Gianninia et al. (2004) experimentally determined the tensile strength of human tooth enamel and dentin, as well as their juncture. They found that all strengths were in the tens of megapascals (units of pressure = force/area: 1 Pascal = 1 Newton/m^2 and 1 MPa = 1 Newton/mm^2) range, but varied based on location within the tooth and orientation of the prismatic structure of the enamel.

Evans and Sanson (2003) explored the relationship of form and function in mammalian teeth to answer the question of how close these teeth are to their ideal functional form, that is, as mechanical devices for shearing, crushing, puncturing and so forth. Their mechanical analyses suggested that many forms (e.g., canine, carnassial, tribosphenic, etc) are close to ideal, and they supported this conclusion by pointing to the geologically long (~140 million year) evolutionary conservation of these types. Yet, these same workers (Evans and Sanson, 2005) also noted that in some bat teeth, ideal functionality was sacrificed for strength. This seems an adaptive strategy in a mammal that cannot repeatedly replace its teeth as do reptiles and amphibians. Clearly, adaptive trade-offs and compromises are important factors in natural selection.

In studies of the mechanics of tooth shape, the teeth are often treated as cantilevered beams. Christansen and Adolfssen (2005) used a cantilevered beam model to determine canine tooth strength in various felid, canid, and ursid species, noting that felids have the strongest canines.

In experiments using deer and pig hides, Freeman and Lemen (2007) investigated the trade-offs between the shapes of felid canine teeth that are best designed for penetration and those designed for maximum strength. To calculate strength they assumed the tooth to be a simple cantilevered beam with a point load applied to the tip, and thus that the bending moment profile along the length of the tooth was linear (we discuss this point below). They calculated strengths at 5% and 20% of length from the tooth tip. They found that a single parameter, the taper of the essentially conical tooth, was the critical determining factor. If the tooth taper was long and slender it penetrated well but was more vulnerable to breakage, whereas a less acutely tapered tooth was stronger but penetrated poorly. They found a strong correlation between their predicted optimum taper and the taper seen in extant felids.

Here, we examine what was a very long-lived and evidently successful tooth type of temnospondyl amphibians. This tooth type first evolved in the Carboniferous and persisted little changed until the Early Cretaceous, a geological time span of more than 300 million years. We employ several lines of inquiry to assess the functional morphology of these teeth and attempt to determine the biomechanical pressure that directed the evolution of this successful morphology.

INSTITUTIONAL ABBREVIATIONS/TERMINOLOGY

Institutions: MCZ, Museum of Comparative Zoology, Harvard University; MNHN, Muséum National D'Historie Naturelle, Paris; NMMNH, New Mexico Museum of Natural History; NMNH, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; SMNS, Staatliches Museum für Naturkunde, Stuttgart; UCMP, University of California Museum of Paleontology, Berkeley; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

Terminology: We chose to use the standard dental terminology of Peyer (1968, fig. 10) where labial and lingual indicate directions toward the outside and the inside of the mouth, respectively, and mesial and distal indicate direction along the curvature of the tooth rows. Mesial is toward the midline of the dental series (anterior center of the jaws) and distal is toward the jaw joint, although intuitively one might suppose that distal would refer to the direction away from the jaw joint. This choice was made to eliminate possible confusion over the orientation of the major and minor axes of teeth with elliptical cross-sections that may be found in the transversely-oriented anterior of the mouth or along the longitudinally-oriented lateral margin of the mouth. Teeth are counted from the anterior center of the jaws proceeding toward the jaw joint.

TEMNOSPONDYLI

The temnospondyl amphibians were a diverse and successful group that were among the dominant tetrapods of the Paleozoic–early Mesozoic (Schoch and Milner, 2000) (Fig. 1). By the end of the Triassic, most of the temnospondyls had become extinct, but they persisted at low diversity until the Early Cretaceous, which was their final extinction. Most workers have indicated that their dentition is adapted for a diet of fish (e.g., Damiani et al, 2000; Dias and Schultz, 2003). Their teeth are often described as conical, and indeed, they appear simple and conical, but close examination reveals a highly adapted shape that varies from base to tip (Fig. 2).

The teeth of temnospondyl amphibians are structurally "labyrinthodont," a form presumably inherited from crossopterygian ancestors (Peyer, 1968) and so-named for the complex infolding of their enamel and dentine (Romer, 1947, 1956) (Fig. 2). The infolding is indeed labyrinthine, often showing secondary and tertiary folds on the primary folds. All of the teeth of this study show longitudinal grooving, particularly on the lower portion of the crown, which is an external indication of the internal folding (Romer, 1933, 1956).

Possession of labyrinthodont teeth has in the past been given phylogenetic significance and considered by some workers as diagnostic of a family (Abel, 1919) or order-level systematic assignment (Kuhn, 1939a, b; Romer, 1947), or even a subclass-level taxon (Romer and Parsons, 1977). More recently the "Labrynthodontia" have been recognized as a paraphyletic group (e.g., Milner et al., 1986; Benton, 1990; Carroll, 1990), and the term is currently used only as indicative of tooth structure.

Temnospondyl teeth are emplaced in shallow pits along the jaws or on the palate where they are welded to the substrate bone by cementum. There are no tooth sockets as such and no "roots" to the teeth. Tooth replacement is accomplished by resorbing the cementum until the tooth is freed from its emplacement. The replacement tooth is then grown and cemented to the underlying bone.

CANTILEVERED BEAM TOOTH MODEL

As mentioned above, many researchers have rightly assumed individual teeth to act as transversely-loaded cantilevered beams, rigidly supported at one end and free-standing. In this study, we used a cantilevered beam model to calculate the strength of the tooth along its entire length, thus creating a strength profile. Mechanical beam theory (e.g., Laurson and Cox, 1950; Marks, 1951) defines the bending moment profiles and shear stress profiles associated with such beams under various loading regimes (Fig. 3). Below, we consider the three most applicable loading scenarios as they may be applied to teeth.

1. A cantilevered beam model is analyzed with a transverse point load (W) applied at the tip (Fig. 3A), as would be the case if a tooth suffered the impact of a hard object on its distal end (occlusal tip). In this senario the bending moment (M) increases linearly with distance (x) along the total tooth length (l) proceeding from the tip toward the base, and the shear stress is equal to -W.

2. A cantilevered beam with a load distributed uniformly along its length (Fig. 3B) would approximate a tooth of rectangular shape in labial view (analogous to a human incisor) having penetrated a prey or food item and then having transverse force applied in the labiolingual direction. In this scenario the bending moment increases as a parabola (square

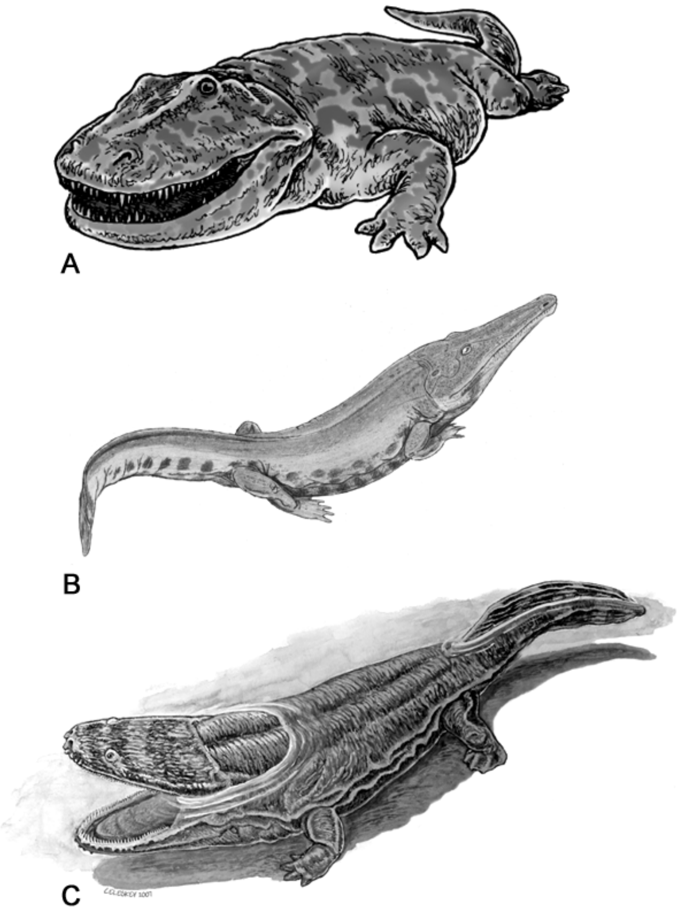

FIGURE 1. Reconstructions of typical temnospondyl amphibians, all two to three meters in length: **A**, The Pennsylvanian-Permian eryopid *Eryops* (artwork by Matt Celeskey); **B**, the Middle Triassic cyclotosaurid *Eocyclotosaurus* (by permission of the artist, Dmitry Bogdanov); and **C**, the Late Triassic metoposaurid *Koskinonodon* (artwork by Matt Celeskey).

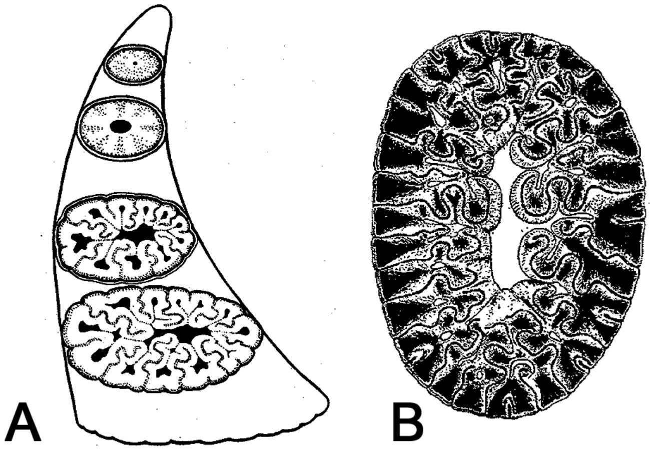

FIGURE 2. Labyrinthodont tooth structure (after **A**, Peyer, 1968, fig. 73, and **B**, Carroll, 2009, fig. 4.2A). **A**, Labyrinthodont structure varies with height in a mature temnospondyl tooth. **B**, Detailed cross section showing the labyrinthine enfolding of enamel and dentin in a temnospondyl tooth.

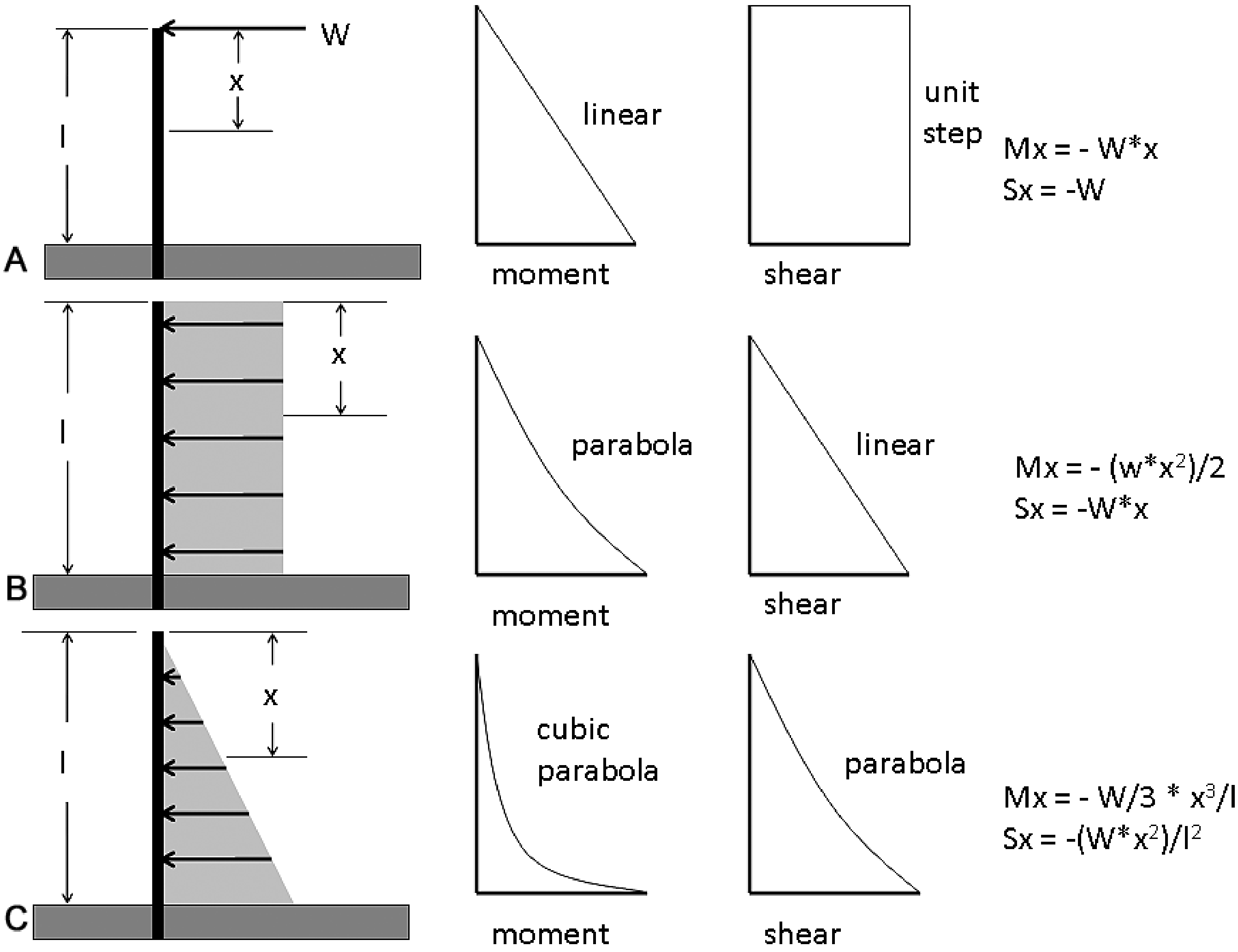

FIGURE 3. Three cantilevered beam loading scenarios that are applicable to teeth. **A**, A cantilevered beam with a single-point transverse load applied at the tip producing a linearly increasing, bending-moment profile and a unit-step shear profile along the beam length. **B**, A cantilevered beam with a uniformly distributed transverse load producing a parabolic bending-moment profile that increases from tip to base as the square of the distance and a linear shear profile. **C**, A cantilevered beam with a transverse load that increases uniformly from tip to base producing a cubic parabola bending-moment profile that increases from tip to base and a parabolic shear profile. This is the best model for the study teeth in normal usage. **Mx** = bending moment along distance, x; **Sx** = shear along distance, x; **W** = total distributed load; **w** = distributed load per distance unit; **x** = distance proceeding from beam tip toward the base.

of the distance, x) from the tip to the base of the tooth, and the shear stress increases linearly along that distance.

3. A cantilevered beam with a uniformly increasing load applied from tip to base (Fig. 3C) is considered. A tooth of triangular shape in labial view (as in the temnospondyl teeth studied here) having penetrated a prey or food item and then subjected to a transverse force applied in the labiolingual direction would experience this type of loading. This scenario is a close approximation of the loading experienced by the study teeth if a bitten prey animal struggles to escape by pulling away from the predator. The resultant bending moment along the length of the tooth from tip to base increases as a cubic parabola (x^3), whereas the shear stress increases as a parabola (x^2).

Thus, the simple cantilevered beam model often used in strength studies (number 1 above) only applies when the tooth impacts a hard object at a single point. We find models that fit the tooth in normal use (example numbers 2 and 3 above), where it is sunk into a food object and pulled upon, to be the most instructive.

MATERIALS AND METHODS

The study teeth (Table 1) were carefully selected to be of typical size and shape for their representative species and were further prepared where necessary. Marginal teeth, being by far the most abundant, were selected for study rather than the larger palatal fangs or tusks. Maxillary, premaxillary, and dentary teeth are all included in the study. With the exception of a few clearly specialized teeth such as palatal fangs, no difference in structure could be discerned.

Our observations on the shapes of typical temnospondyl marginal teeth revealed that basally they have an elliptical cross section in which the major axis of the ellipse is oriented in the labiolingual direction (Table 2, Fig. 4). From the base of the crown to its tip, cross sections first become circular and then elliptical again, but with the major axis of the ellipse oriented mesiodistally. All the teeth show longitudinal grooving, especially near the base, and possess a sharp, mesiodistally-oriented carina on the upper portion of the crown. The carina is weakly developed and present only very near the tooth tip in *Eocyclotosaurus*, mod-

TABLE 1. Measurements of study teeth. *Eryops* – NMMNH P-46379, tooth position 19 on left side of skull. *Eocyclotosaurus* – NMMNH P-64410, tooth position ~ 55 on dentary. *Koskinonodon* – NMMNH P-64352, isolated tooth from NMMNH locality 1176.

Eryops	Height above base (mm)	Labiolingual (mm)	Mesiodistal (mm)
	0	11.7	6.3
	1	8.1	6.2
	2	6.4	5.6
	4	5.5	5
	6	4.6	4.5
	8	3.8	3.7
	10	3.2	3.3
	12	2.2	2.6
	14	1.3	1.6
	15	0 (tip)	0 (tip)
Eocyclotosaurus			
	0	4.55	2.67
	1	3.23	2.42
	2	2.58	2
	3	1.95	1.8
	4	1.41	1.64
	5	1.19	1.45
	6	0.92	1.12
	8 original height	0 (tip)	0 (tip)
Koskinonodon			
	~0	6.34	4.57
	2	4.68	3.87
	4	3.5	3.15
	6	2.41	2.48
	8	1.85	2.79
	10	1.43	2.27
	12	1.81	1.12
	13	0 (tip)	0 (tip)

erately developed in *Eryops*, and strongly developed and extending far down the tooth crown from the tip in *Koskinonodon*. Photographs of the study teeth show their shapes in mesiodistal and labiolateral aspects (Fig. 5).

Relative Strength

Tooth strength calculations here are relative rather than absolute because the absolute strength of the tooth materials is unknown. Even if the strengths of the enamel and dentine were known, their labyrinthine infolding makes the problem intractable. We have assumed that because the infolding of the dentine and enamel is similar among the closely related study taxa the infolded materials should be treated as a single material with similar properties across taxa. Given this, relative tooth strength reduces to the cross-sectional shape of the teeth with respect to the direction of the applied force. We have shown that tooth shape, if not size, is similar for the study taxa.

In generating the tooth strength profiles we used the simple, rectangular, cantilevered beam strength formula,

$$s = d^2 * w$$

where s is strength, depth (d) is the beam thickness in the direction of the applied force, and width (w) is the beam thickness in the direction perpendicular to the applied force.

We have modified the original beam equation (Marks, 1951) by removing the material strength constant. Thus, the equation no longer yields the absolute beam strength, but rather the strength in relative terms. Finally, because the strength calculations are relative rather than absolute, the difference between the assumed rectangular cross section and the actual elliptical cross section is negated.

Using a scale under magnification, height increments were marked on the study teeth with a very fine-tipped pen, and careful measurements of the major and minor diameters were then made using digital calipers under magnification at each height increment. Strength profiles (strength as a function of height above the base) were calculated using the beam strength equation (above).

TABLE 2. A brief assessment of tooth shape in 15 genera belonging to eight temnospondyl families shows that the generalized tooth morphology assumed in this study (Fig. 4) is the "default" morphology across temnospondyl taxa. Taxonomy according to Schoch and Milner (2000). Except where literature is cited, these data are based on observations by the authors. In the last column, “model” refers to the basally labiolingually-elongate tooth transitioning through a circular cross section to become mesiodistally-elongate in its upper portion.

Taxon	Institution	Specimen #	Tooth base labiolingually elongate?	Preserved teeth fit model?
Eryopidae				
Eryops	NMMNH	46379	yes	yes
Mastidonsauridae				
Mastodonsaurus	SMNS	80704	yes	yes
Thoosuchhidae				
Hyperokynodon	SMNS	16670	yes	yes
Plagiosauridae				
Gerrothorax	SMNS		yes	yes
Actinodontidae				
Sclerocephalus	SMNS		yes	yes
Cyclotosauridae				
Cyclotosaurus	SMNS	13014	yes	yes
Wellesaurus	UCMP	36729	yes	yes
Quasicyclotosaurus	UCMP	37754	yes	none
Eocyclotosaurus	NMMNH	P-64410	yes	yes
Metoposauridae				
Metoposaurus	ZPAL	AbIII/3	yes	none
Apachesaurus	UCMP	63845	yes	yes
Dutuitosaurus	MNHN	XIp/4/66	yes	yes
Arganasaurus	MNHN	XIX/1/66	yes	none
Koskinonodon	UCMP	113554	yes	Yes
Chigutisauridae				
Siderops	*	*	yes	yes

*Warren and Hutchinson, 1983, figure 1.

Shape and calculated strength profiles were then plotted (Fig. 6). The left column in Figure 6 quantifies morphology by showing how the cross-sectional shape of the teeth varies as a function of height above the base. Cross-section ellipticity > 1 signifies labiolingual elongation, 1 = circular cross-section, and ellipticity < 1 indicates mesiodistal elongation. The plots in the right column of Figure 6 show tooth-strength profiles; that is, strength in the labiolingual direction as a function of height above the base. The strength units are identical in each plot, so relative strength of the study teeth can be compared directly. The calculated bending moment profile for each tooth is scaled and overlain on the strength data points to show the degree of similarity between the strength profile and the bending moment profile.

RESULTS

Eryops

NMMNH specimen P-46379, a 410-mm-long partial skull of *Eryops*, was collected from NMMNH locality 6121 in the Upper Pennsylvanian El Cobre Canyon Formation of the Cutler Group of Cañon del Cobre, New Mexico (Lucas et al., 2005). This specimen, described in detail by Werneburg et al. (2010), contains a well-preserved dentition. All the marginal teeth in this specimen are curved lingually (Fig. 5A), and the palatal fangs are directed posteriorly so as to snag and entrap prey. This curvature is not considered significant in the transverse strength calculations below. Forty-five tooth positions are present in each upper

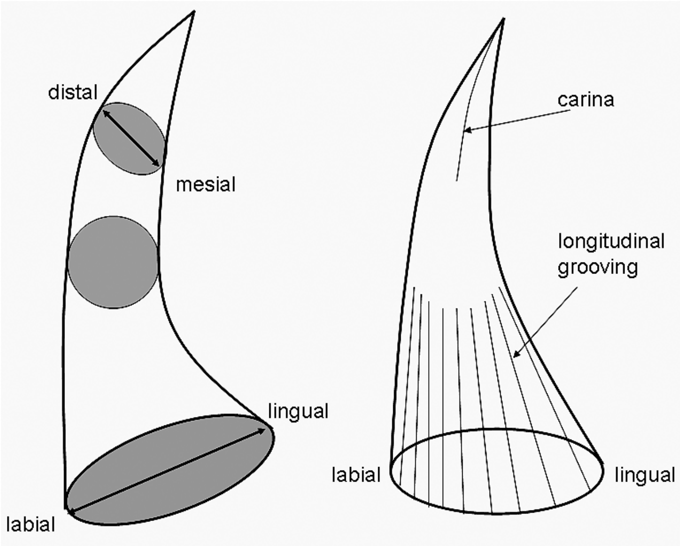

FIGURE 4. Shape and external structure of typical temnospondyl teeth. **A**, Oblique view showing the basal labiolingually-elongate ellipse cross section (shaded) transitioning through a round central segment to a mesiodistally-elongate ellipse as height along the tooth increases. **B**, Mesial view showing the typical external form including longitudinal grooving, especially near the base, and in some cases, a sharp carina near the tip.

marginal toothrow: 12 in the premaxilla and the remainder in the maxilla. In addition to the marginal toothrows, the specimen has three pairs of palatal fangs, one pair each on the vomers, palatines, and ectopterygoids. Additionally, nearly the entire palate is covered with a shagreen of sharp denticles that are canted posteriorly. The dentition of *Eryops* appears well-suited to seize and maintain control of slippery prey.

Description/analysis

Tooth number 19 of the left maxilla of NMMNH P-46379 was selected for study because it is particularly well-preserved and of characteristic size and shape (Fig. 5A-B). Measurements of the 15 mm-tall tooth were made incrementally from base to tip in the labiolingual and mesiodistal directions (Table 1).

At its base the tooth is elliptical in cross section, with the major axis in the labiolingual direction. The labiolingual axis length is 1.85 times the mesiodistal axis length (Fig. 6A). Proceeding from the base to the tip of the crown, the diameter diminishes and the tooth approaches a circular cross section at about 6 mm height. The cross section remains approximately circular with further reduction in diameter between 6 and 10 mm height. Between 10 and 15 mm the tooth becomes elliptical in the mesiodistal direction and continues to diminish in diameter until it comes to a moderately sharp point at its tip. The mesiodistally-elongate upper portion supports a carina of the same orientation (Fig. 5A).

The *Eryops* tooth is the largest and strongest of the study teeth. Its strength profile is a near-perfect cubic parabola, increasing from tip to base (Fig. 6B).

Eocyclotosaurus

NMMNH P-64410 is a partial mandible of a small individual of the cyclotosaurid amphibian *Eocyclotosaurus* collected from NMMNH locality 5193. This locality lies in the uppermost meter of the Middle Triassic (Perovkan, early Anisian) Anton Chico Member of the Moenkopi Formation (Lucas and Schoch, 2002; Lucas, 2010; Rinehart et al., 2010). Several skulls and jaws from the Anton Chico locality, varying in midline length from 180 to 380 mm, have been prepared. Approximately 98 teeth are present in each of the upper toothrows of *Eocyclotosaurus*, and pairs of palatal fangs are present on the vomers and on the palatines. The palate bones are essentially smooth, lacking the denticulation seen in *Eryops*.

Description/analysis

We selected tooth number 55, just posterior to mid-position on the dentary in P-64410 (Fig. 4C-D), for detailed preparation and measurement (Table 1). About 2 mm of the tooth tip are missing from this approximately 8 mm-tall tooth, but otherwise it is in good condition and characteristic of the entire series.

The cross-sectional ellipticity of this tooth is plotted (Fig. 6C). Basally, the cross section is elliptical with a labiolingual axis that is 1.7 times greater than the mesiodistal axis. The tooth cross section is circular at a height of 3.5 mm. Above 3.5 mm the cross section is elliptical, with the major axis oriented mesiodistally. Although the tip of this tooth is missing, preparation of other teeth revealed a small, weakly-developed carina near the tip.

Because of its smaller diameter, the *Eocyclotosaurus* tooth is only about 1/16 as strong as the *Eryops* tooth. As in the *Eryops* tooth, strength increases from tip to base as a cubic parabola (Fig. 6D).

Koskinonodon

NMMNH P-64352 (Fig. 5E-F) is an isolated tooth of *Koskinonodon* (previously *Buettneria*: Mueller, 2007) from NMMNH locality 1176, the well-known Lamy Amphibian Quarry (e.g., Romer, 1939) of north-central New Mexico. Of the very numerous skulls and jaws of *Koskinonodon* periodically collected at this quarry over the past seven decades by MCZ, NMNH, and NMMNH, no specimens contain a single complete tooth in place. The teeth were undoubtedly lost during transport of the bones (Lucas et al., 2010). The quarry has yielded numerous broken, isolated "labyrinthodont" amphibian teeth that were apparently transported together with the skulls and jaws. Because of the monodominant and near monotaxial character of the quarry assemblage, we assess these to be teeth of *Koskinonodon*.

Description/analysis

The 13 mm-long tooth analyzed here is elliptical near its base where the labiolingual axis is 1.39 times greater than the mesiodistal axis (Fig. 6E). We assume that a small basal segment is missing as evidenced by its broken margin. Ellipticity decreases above the base, and the tooth shows a circular cross section at a height of 4.5 mm. As in the other study teeth, above the point where the cross section is circular, the tooth is elliptical, with the major axis oriented mesiodistally. In *Koskinonodon* the carina is quite pronounced and accentuates the ellipticity of the upper portion of the tooth.

As in the *Eryops* and *Eocyclotosaurus* teeth, the *Koskinonodon* tooth has a cubic parabola strength profile (Fig. 6F). The bending moment calculation could not be extended to the base of the tooth, because the exact position of the base is not known. Due to its smaller size, its strength is approximately one fifth that of the *Eryops* tooth.

DISCUSSION AND FURTHER ANALYSIS

Our examination of numerous temnospondyl taxa shows that, with rare exceptions, their marginal teeth have a uniform morphology. Table 2 demonstrates that the tooth morphology outlined here (Fig. 4) is common to most temnospondyls. This is also true generally of ectopterygoid teeth and dentary teeth as well as maxillary and most premaxillary teeth. This suggests that this tooth morphology is a primitive character of the clade. Exceptions exist in that some taxa possess a few specialized teeth such as essentially conical, caniform teeth in the marginal dentition and on the palate. Additionally, the premaxillary teeth of *Eocyclotosaurus* are exceptional in that they are transversely elongated, even in the anteriormost part of the premaxilla. We hypothesize that this is an adaptation for side-strike feeding behavior. This morphological variation is currently under analysis by the authors and will be published as a separate study.

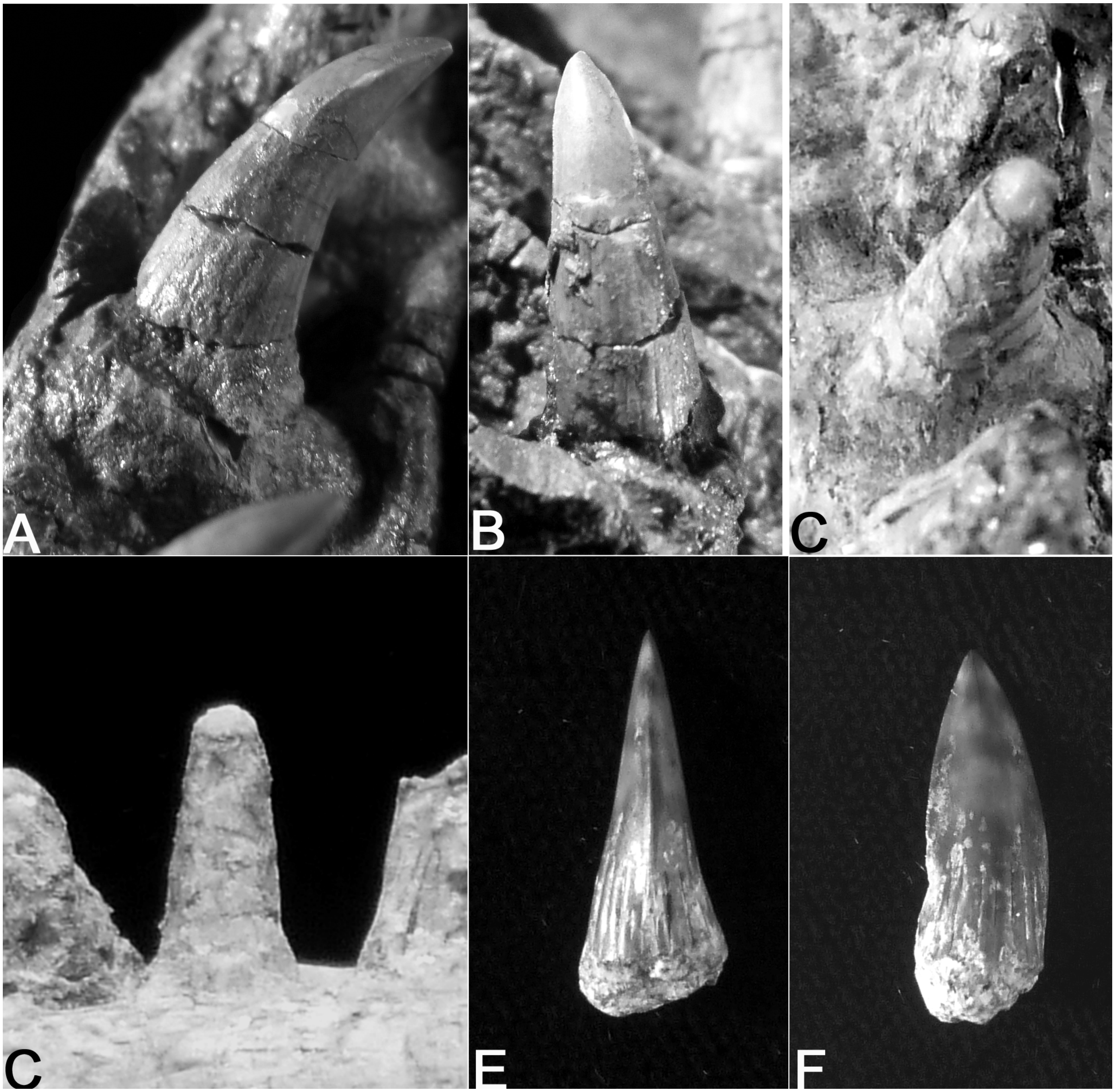

FIGURE 5. Photos of the study teeth. **A-B**, *Eryops*, NMMNH P-46379, tooth number 19 on the left maxilla, 15 mm-tall in **A**, mesial, and **B**, labial views. **C-D**, *Eocyclotosaurus*, NMMNH P-64410, tooth number ~ 55 on a partial right dentary, 6 mm-tall as preserved in **C**, mesial or distal, and **D**, labial views. **E-F**, *Koskinonodon*, NMMNH P-64352, a 13 mm-tall isolated tooth in **E**, mesial, and **F**, labial views.

Tooth Size and Shape, and Mouth Shape

Whereas tooth shape varies little across taxa, size varies greatly, even in animals of similar overall size. The largest and smallest teeth among the taxa studied vary in length by approximately a factor of two (*Eryops* = 15 mm, *Eocyclotosaurus* ~ 8 mm) and basal cross sectional area by a factor of nearly six (*Eryops* = 57 mm^2, *Eocyclotosaurus* = 9.5 mm^2), whereas the estimated length of the animals ranges only from 2 to 2.5 m (*Eryops*: Case, 1911, *Eocyclotosaurus*: Schoch, 2008). We conclude that tooth size in these temnospondyls does not necessarily scale with body size, and instead reflects a specific diet and/or predation technique.

Similarly, whereas basic tooth shape is conserved across many temnospondyl taxa, snout (mouth) shape varies greatly (Fig. 1). For example, *Eryops* has a very broad snout, the snout of *Koskinonodon* is somewhat narrower, and that of *Eocyclotosaurus* is quite long and narrow. Several taxa (e.g., *Mastodonsaurus*, *Quasicyclotosaurus*) have snout widths intermediate between those of *Koskinonodon* and *Eocyclotosaurus*.

Using geometric morphometrics and comparative methodology, Linde et al. (2004) examined the relationship of patterns of diet and phylogeny to tooth and premaxilla (mouth) shape. They found that in sparid fishes (spiny-finned, warm-water marine fish with well-developed teeth, e.g., porgie or bream) tooth shape was conservative and more

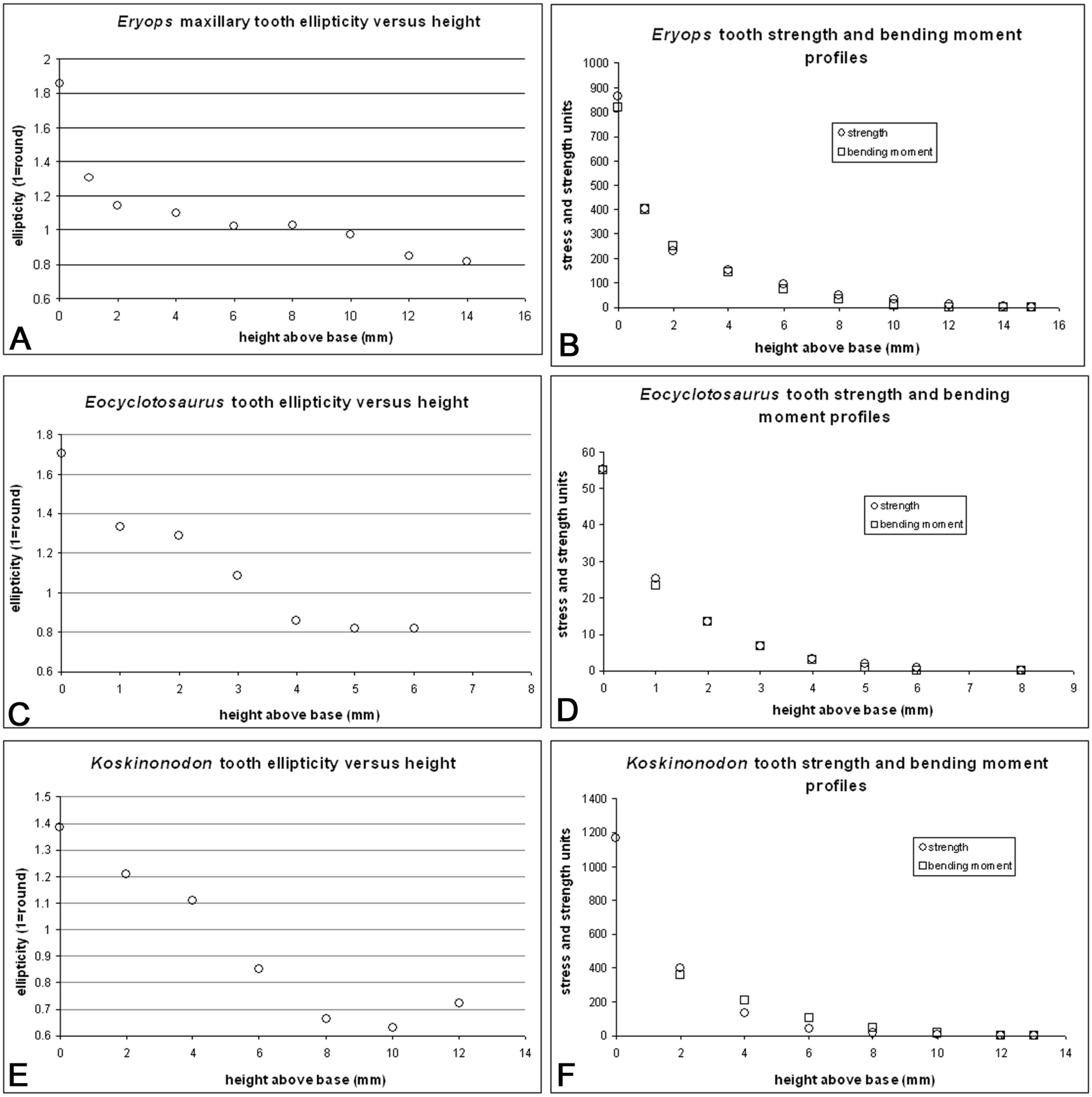

FIGURE 6. Plots of tooth ellipticity (labiolingual diameter/mesiodistal diameter) define tooth shape by showing cross sectional shape as a function of height (**A**, **C**, **E**). In ellipticity plots, ellipticity >1 indicates ellipticity in the labiolingual direction, = 1 indicates circular cross section, <1 indicates ellipticity in the mesiodistal direction. Plots **B**, **D**, and **E** show the labiolingual strength profile and scaled bending moment profile as a function of height above the tooth base. Bending moment is scaled and overlain on strength data for comparison of the mathematical function form. Strength units are equal in each plot and may be compared across species. **A-B**, *Eryops*; **C-D**, *Eocyclotosaurus*; **E-F**, *Koskinonodon*.

allied with phylogeny than with diet, whereas premaxilla (mouth) shape varied based on diet. We hypothesize that this is the case in the genera of this study, in which the teeth are similar in shape, but the muzzle shapes are quite different. Apparently, whereas tooth shape is conservative across these taxa, tooth size and snout shape vary according to diet (ecological niche) and hunting technique.

Carinae

Development of a carina in the three study teeth varies across taxa. *Eocyclotosaurus* teeth exhibit minimal development of the carina, *Eryops* a moderate development, and *Koskinonodon* a strong development of an almost blade-like carina, at least in portions of the mouth (Fig. 5E-F). It seems obvious that the purpose of such a structure would be to aid penetration of the tooth by cutting through tissue. However, evidence has been presented to support an additional function of the carina. Freeman (1992) determined that sharp edges on the canines of some bats concentrate stress and are for the purpose of crack propagation in hard food items. These edges are positioned so as to direct a crack initiated by the canines toward the incisors and premolars, where it may be further propagated. The carinae of temnospondyl teeth are aligned mesiodistally.

Thus, as the tooth penetrates a hard object and stress concentrates at the sharp edges of the carinae, any resultant cracks will be propagated toward the cracks initiated by the preceding and following teeth in the dental series, so that a complete separation of the hard object is more efficiently accomplished.

Inferred Feeding Behavior

The feeding behaviors of temnospondyls must be inferred from anatomical evidence. Based on flat skull morphology and on the fact that their legs are short and therefore enforce a low standing profile, some workers have reasoned that in temnospondyl feeding the lower jaw would lie flat on the substrate and the skull would be adducted against it (Watson, 1951). The teeth of temnospondyls show no capacity for shearing or crushing, only for penetrating and holding on to prey. Several studies supply evidence that may be incorporated to formulate a generalized scenario.

1. Wilson (1941) identified the probable origin of the *m. retractor bulbi*, on the pterygoid at the posteriormost margin of the palatal vacuity of *Koskinonodon*. Presumably, swallowing in this animal, and probably all temnospondyls (Clack, 2002), was assisted by retraction of the eyeballs posteroventrally into the buccal cavity by the *m. retractor bulbi*, as it is in most extant amphibians (Duellman and Trueb, 1986; Levine et al, 2004). The presence of large palatal vacuities in the Temnospondyli, which probably evolved to assist in buccal pumping (Clack, 1992), made this adaptation possible.
2. The presence of a hyoid apparatus in temnospondyls indicates the presence of a tongue (e.g., Warren and Hutchinson, 1983).
3. Lingually-directed curvature of the marginal teeth appears to be the norm for temnospondyls, although the extent of curvature is highly variable. In *Eryops*, the teeth are strongly curved, whereas curvature is less pronounced in *Eocyclotosaurus* and very slight in *Koskinonodon*. Other temnospondyls (e.g., *Siderops*: Warren and Hutchinson, 1983) show an intermediate degree of curvature. Apparently, the purpose of such lingual tooth curvature is to resist the escape of struggling prey from the mouth.

Thus, the anatomical evidence indicates some probability that prey were seized in the teeth, manipulated into swallowing position with the help of a tongue, and swallowed with assistance from the tongue and the *retractor bulbi* musculature. This is the method of feeding employed by most extant amphibians (Duellman and Trueb, 1986). Exceptions have been noted in that some modern species are tongueless, and some (e.g., Gymnophonia) show little evidence of using the *m. retractor bulbi* in swallowing, apparently due to their greatly degenerated eyes.

Inertial feeding, where the head is thrust forward during swallowing so that the inertia of the food object helps propel it down the throat, may also have been employed by the temnospondyls. However, the length of the neck of buccal breathing animals is severely restricted due to the problem of pumping air down such a structure (Clack, 1992). The lack of a significant neck would have limited the ability to aggressively thrust the head forward, a significant disadvantage in inertial feeding.

Implications of the Shape and Strength Data

The similarity of tooth shapes and strength profiles across taxa indicates that the teeth of all the study animals were "designed" for similar use. The cubic parabola strength profiles indicate that the tooth shape of temnospondyls was a response to the applied bending moment generated by struggling prey attempting to pull away from these predators.

Catastrophic breakage could result from the impact of a hard object, either during predation or by accident, but the strength profiles do not show that the teeth were designed primarily to resist such an event. Rather, the principal evolutionary pressure has been toward maximizing strength for "normal" usage, which is capturing and maintaining control of prey.

The question of why the teeth are principally strengthened in the labiolingual direction must be addressed considering that struggling prey could apply force in almost any direction. The answer may lie in the fact that neighboring teeth in the toothrow reinforce each other mesiodistally, leaving the teeth most vulnerable to labiolingual loading.

We conclude that in temnospondyls the upper, mesiodistally elongated portion of the tooth crown with its carina is best suited to initiate penetration of the prey item and to propagate cracks in hard tissues, whereas the overall crown shape maximizes resistance to bending. Given that the tooth materials are brittle and essentially cannot bend, deformation can only result in fracturing.

Is the Bending Moment-Strength-Shape Relationship Universal?

It seems probable that the relationship between bending moment and strength profiles described here in temnospondyls may be applied to other taxa, and may be a universal rule for penetrating teeth subjected to lateral loading. To test for a more general biological application of this principle we have examined a marginal tooth from a crossopterygean fish, the extant coelacanth, *Latimeria chalumnae*, a distant relative to temnospondyl ancestors, and an incisor of an amniote sister group, humans.

Latimeria chalumnae

Latimeria is the sole surviving representative of the crossopterygean fishes. The teeth of the ancestral crossopterygeans were of labyrinthodont form (e.g., the Late Triassic coelacanth, *Quayia zideki*, as exemplified by NMMNH specimen P-16918), which was presumably inherited by their temnospondyl descendants, but the teeth of *Latimeria* have lost this complex structure. However, whereas most extant fish have lost the enamel from their teeth, *Latimeria* retains a true enamel component (Meinke and Thomson, 1983). The teeth of *Latimeria* are more simple and conical than those of the temnospondyls, though the teeth of *Quayia* are intermediate in complexity.

The dentition of *Latimeria* is impressive (Fig. 7A), comprising hundreds to thousands of teeth and denticles covering a wide size range and distributed both marginally and over most of the palate. A large (cm-sized) marginal tooth (Fig. 7B-C) was selected for analysis from photographic plates published by Millot and Anthony (1958). Unlike the temnospondyls, this tooth had its strong axis oriented mesiodistally. Similar to the temnospondyl teeth, the *Latimeria* tooth exhibits a cubic parabola strength profile and bending moment profile (Fig. 7D).

Homo sapiens

A human incisor, diagrammatically illustrated in cross-section (Fig. 8A), was chosen for analysis. An incisor functions similarly to the teeth analyzed above because in normal use, it penetrates directly into a food item and then is pulled upon in a direction normal to its long axis (think of biting into an apple and pulling it away to separate a piece). The incisors of some other amniotes (e.g., Biknevicius et al., 1996) show similar overall morphology and therefore can be expected to behave in a similar fashion.

The human incisor should be particularly exemplary in demonstrating whether the bending moment to strength relationship generally holds true. This is because the human incisor is rectangular in labial aspect rather than triangular, as in all the previously analyzed teeth. The rectangular shape should produce a parabolic (x^2) bending moment profile (Fig. 3B) as opposed to the cubic parabola (x^3) profile (Fig. 3C) of the triangular teeth if it has evolved in response to applied bending moment. Indeed, comparison of the strength profile to the bending moment profile (Fig. 8B) demonstrates that both profiles are of identical form and are parabolic rather than cubic. This is significantly different from those of the *Latimeria* and amphibian teeth. This result greatly strengthens the argument that the shape of all penetrating teeth develops in response to the applied bending moment.

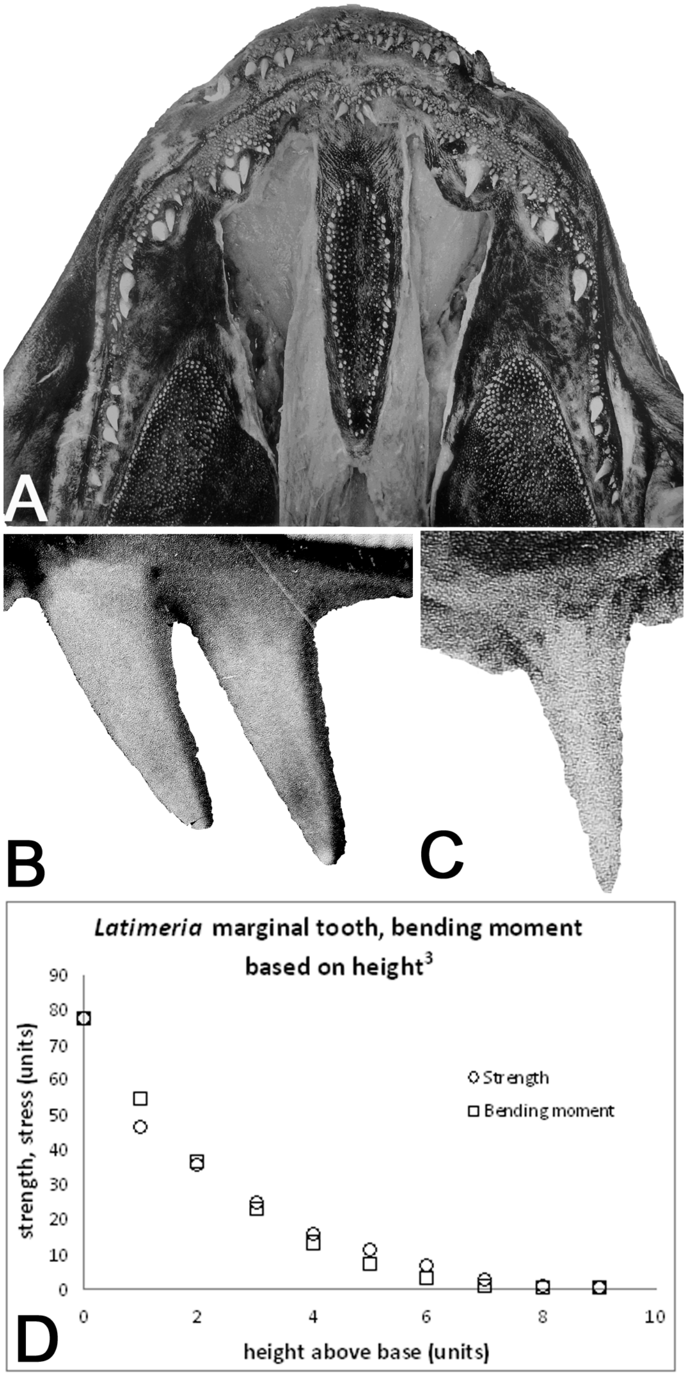

FIGURE 7. **A**, The dentition of *Latimeria*. **B-C**, A large marginal tooth in **B**, lingual view and **C**, mesial view (modified from Millot and Anthony, 1958, plates 36, 8, and 62, respectively). The right tooth in B was used in the analysis. No scale; the tooth is approximately 9.5 mm long. **D**, Cubic parabola strength and bending moment profiles.

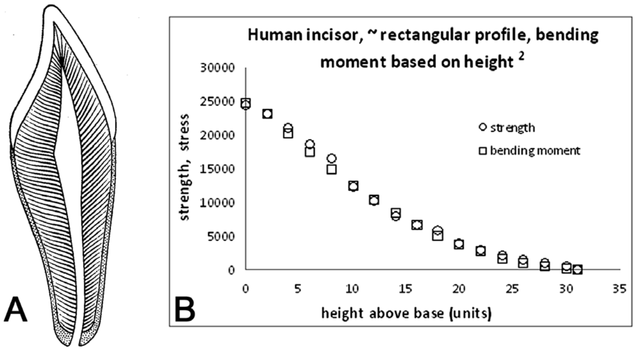

FIGURE 8. **A**, Human incisor in cross section, mesial view (after Peyer, 1968, fig. 8); stippling = cementum, hachure = dentin, clear = enamel. **B**, Parabolic strength and bending moment profiles measured from base of crown (widest point of enamel portion).

CONCLUSIONS

1. Applied bending moment during normal use is the biomechanical force that drives the evolution of penetrating tooth shape in temnospondyls and many other, possibly all, vertebrate taxa.

2. The shape of the temnospondyl amphibian teeth studied here, as well as numerous other taxa, is not a simple cone. Rather, it is highly derived, being labio-lingually elongate at the base, circular in cross-section at some distance above the base, and mesiodistally elongate at the tip of the crown with a variably developed carina. This shape is optimized to facilitate penetration, resistance to the bending moment applied by struggling prey, and the propagation of cracks in the hard parts of the food item.

3. Tooth shape, regardless of the size or shape of the mouth, is conserved over a long temporal span and across the taxonomic range of temnospondyls. Similar to the results of Linde et al. (2004), we find that mouth shape and tooth size is more indicative of diet or hunting strategy than is tooth shape.

4. The simple bending moment calculation that assumes a force applied at a single point along the tooth length does not reflect the behavior of penetrating teeth during normal use. Their shape is explained by a model (Fig. 3B-C) that considers their three dimensional shape with a distributed, transverse load along their entire length.

5. The results of the strength and bending moment calculations in *Latimeria* and *Homo* argue strongly that the strength and bending stress-to-tooth shape relationship is universal for penetrating teeth. However, more work is required to corroborate this hypothesis conclusively.

ACKNOWLEDGMENTS

The authors thank the many volunteers of NMMNH who assisted in the excavation, collection, and preparation of the material used in this study. We appreciate the reviewers, David S Berman and Ralf Werneburg, who improved the manuscript with their comments and suggestions. Matt Celeskey allowed the use of his artwork of *Eryops* and *Koskinonodon*. Dmitry Bogdanov granted permission to use his artwork of *Eocyclotosaurus*.

REFERENCES

Abel, O., 1919, Die Stämme der Wirbeltiere: Berlin and Leipzig, 353 p.

Benton, M. J., 1990, Phylogeny of the major tetrapod groups: Morphological data and divergence dates: Journal of Molecular Evolution, v. 30, p. 409-424.

Biknevicius, A.R., Valkenburgh, B. Van, and Walker, J., 1996, Incisor size and shape: Implications for feeding behaviors in saber-toothed "cats": Journal of Vertebrate Paleontology, v. 16, p. 510-521.

Carroll, R.L., 1990, A tiny microsaur from the Lower Permian of Texas: Size constraints in Paleozoic tetrapods: Palaeontology, v. 33, p. 893-909.

Carroll, R.L., 2009, The rise of amphibians: 365 million years of evolution: Baltimore, Johns Hopkins University Press, 360 p.

Case, E.C., 1911, Revision of the Amphibia and Pisces of the Permian of North America: Carnegie Institution of Washington, Publication 146, 179 p.

Christiansen, P., and Adolfssen, J.S., 2005, Bite forces, canine strength and skull allometry in carnivores (Mammalia, Carnivora): Journal of the Zoological Society of London, v. 266, p. 133-151.

Clack, J.A., 1992, The stapes of *Acanthostega gunnari* and the role of the stapes in early tetrapods; *in* Webster, D., Fay, R.R., and Popper, A.N., eds., Evolutionary biology of hearing: New York, Springer-Verlag, p. 405-420.

Clack, J.A., 2002, Gaining ground: The origin and evolution of tetrapods: Bloomington, Indiana University Press, 369 p.

Damiani, R., Neveling, J., Hancox, J., and Rubidge, B., 2000, First trematosaurid temnospondyl from the *Lystrosaurus* assemblage zone of South Africa and its biostratigraphic implications: Geological Magazine, v. 137, p. 659-665.

Dias, E.V., and Schultz, C.L., 2003, The first Paleozoic temnospondyl postcranial skeleton from South America: Revista Brasileira de Paleontologia, v. 6, p. 29-42.

Duelman, W.E., and Trueb, L., 1986, Biology of the amphibians: Baltimore, The Johns Hopkins University Press, 670 p.

Evans, A.R., and Sanson, G.D., 2003, The tooth of perfection: Functional and spatial constraints on mammalian tooth shape: Biological Journal of the Linnean Society, v. 78, p. 173-191.

Evans, A.R., and Sanson, G.D., 2005, Correspondence between tooth shape and dietary biomechanical properties in insectivorous microchiropterans: Evolutionary Ecology Research, v. 7, p. 453–478.

Freeman, P.W., 1992, Canine teeth of bats (Microchiroptera): Size, shape and role in crack propagation: Biological Journal of the Linnean Society, v. 45, p. 97–115.

Freeman, P.W., and Lemen, C.A., 2007, The trade-off between tooth strength and tooth penetration: Predicting optimal shape of canine teeth: Journal of Zoology, v. 273, p. 273-280.

Gianninia, M., Soaresb, C.J., and Carvalho, R.M., 2004, Ultimate tensile strength of tooth structures: Dental Materials, v. 20, p. 322-329.

Henderson, D.M., 1998, Skull and tooth morphology as indicators of niche partitioning in sympatric Morrison theropods: Gaia, no. 15, p. 219-226.

Hutchinson, G.E., 1959, Homage to Santa Rosalia or why are there so many kinds of animals?: The American Naturalist, v. 93, p. 145-159.

Kühn, O., 1939a, Ein neuer rachitomer Stegocephale aus dem unteren Rotliegenden: Palaeontologische Zeitschrift geologische Gesellschatt, v. 42, p. 377-385.

Kühn, O., 1939b, Die Fossilen Amphibien: Berlin, 98 p.

Laurson, P.G., and Cox, W.J., 1950, Mechanics of materials, 2nd edition, New York, John Wiley and Sons, Inc., 422 p.

Levine, R.P., Monroy, J.A., and Brainerd, E.L., 2004, Contribution of eye retraction to swallowing performance in the northern leopard frog, *Rana pipiens*: The Journal of Experimental Biology, v. 207, p. 1361-1368.

Linde, M., Palmer, M., and Gomez-Zurita, J., 2004, Differential correlates of diet and phylogeny on the shape of the premaxilla and anterior tooth in sparid fishes (Perciformes: Sparidae): Journal of Evolutionary Biology, v. 17, p. 941-952.

Lucas, S.G., 2010, The Triassic timescale based on nonmarine tetrapod biostratigraphy and biochronology, *in* Lucas, S.G., ed., The Triassic timescale: Special Publication 334, Geological Society, London, p. 447-500.

Lucas, S.G., and Schoch, R.R., 2002, Triassic temnospondyl biostratigraphy, biochronology and correlation of the German Buntsandstein and North American Moenkopi Formation: Lethaia, v. 35, p. 97-106.

Lucas, S.G., Rinehart, L.F., and Hunt, A.P., 2005, *Eryops* (Amphibia, Temnospondyli) from the Upper Pennsylvanian of El Cobre Canyon, New Mexico: New Mexico Museum of Natural History and Science Bulletin, v. 31, p. 118-120.

Lucas, S.G., Rinehart, L.F., Krainer, K., Spielmann, J.A., and Heckert, A.B., 2010, Taphonomy of the Lamy amphibian quarry: A Late Triassic bonebed in New Mexico, USA: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 298, p. 388-398.

Marks, L.S., 1951, Mechanical engineer's handbook: New York, McGraw-Hill Book Company, Inc., 2236 p.

Meinke, D.K., and Thomson, K.S., 1983, The distribution and significance of enamel and enameloid in the dermal skeleton of osteolepiform and rhipidistian fishes: Paleobiology, v. 9, p. 138-149.

Millot, J., and Anthony, J., 1958-1965, Anatomy de *Latimeria chalumnae* (2 volumes): Paris, Editions du Centre National de la Recherche Scientifique, v. 1, 122 p., v. 2, 131 p.

Milner, A.R., Smithson, T.R., Milner, A.C., Coates, M.L., and Rolfe, W.D.I., 1986, The search for early tetrapods: Modern Geology, v. 10, p. 1-28.

Mueller, B.D., 2007, *Koskinonodon* Branson and Mehl, 1929, a replacement name for the preoccupied temnospondyl *Buettneria* Case, 1922: Journal of Vertebrate Paleontology, v. 27, p. 225-225.

Peyer, B., 1968, Comparative odontology: Chicago, The University of Chicago Press, 347 p.

Rinehart, L.F., Voigt, S., Lucas, S.G., Cantrell, A., and Suazo, T., 2010, Preliminary taphonomy of a Middle Triassic (Perovkan) amphibian bonebed in northeastern New Mexico, USA: Geological Society of America, Abstracts with Programs, v. 42, p. 633.

Romer, A.S., 1933, Vertebrate paleontology: Chicago, University of Chicago Press, 468 p.

Romer, A.S., 1939, An amphibian graveyard: The Scientific Monthly, v. 49, p. 337-339.

Romer, A.S., 1947, Review of the Labyrinthodontia: Bulletin of the Museum of Comparative Zoology at Harvard College, v. 99, 368 p.

Romer, A.S., 1956, Osteology of the reptiles. Chicago, University of Chicago Press, 772 p.

Romer, A.S., and Parsons, T.S., 1977, The vertebrate body, 5th edition: Philadelphia, W. B. Sanders Company, 624 p.

Schoch, R.R., 2008, The Capitosauria (Amphibia): characters, phylogeny, and stratigraphy: Palaeodiversity, v. 1, p. 189–226.

Schoch, R.R., and Milner, A.R., 2000, Stereospondyli: Handbuch der Paläoherpetologie, part 3B, 203 p.

Warren, A.A., and Hutchinson, M.N., 1983, The last labrynthodont? A new branchyopoid (Amphibia, Temnospondyli) from the Early Jurassic Evergreen Formation of Queensland, Australia: Philosophical Transactions of the Royal Society London B, v. 303, p. 1-62.

Werneburg, R., Lucas, S.G., Schneider, J.W., and Rinehart, L.F., 2010, First Pennsylvanian *Eryops* (Temnospondyli) and its Permian record from New Mexico: New Mexico Museum of Natural History and Science, Bulletin 49, p. 129-135.

Wilson, J.A., 1941, An interpretation of the skull of *Buettneria*, with special reference to the cartilages and soft parts: Contributions to the Museum of Paleontology, University of Michigan, v. 6, p. 71-111.