Dental morphology of the cannibal morph in the tiger salamander, *Ambystoma tigrinum*

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Abstract. Cannibalistic behavior is accompanied by a robust dental and skeletal polymorphism in cannibal tiger salamanders, *Ambystoma tigrinum*. This study describes the dental polymorphism in terms of hypertrophy, recurvature, and surface detail as revealed by scanning electron microscopy. Vomerine and dentary teeth in cannibals are longer than those of non-cannibals of the same head size. While cannibals exhibit recurved teeth on each dentigerous bone, straight peg-like teeth appear occasionally. Conversely, isolated recurved teeth may be present in non-cannibals. No consistent differences between cannibal and non-cannibal teeth with respect to the surface geography of the pedicel, shaft, or pedicel shaft junction were observed. Hypertrophy of the horizontally ankylosed vomerine teeth is associated with a distortion of the underlying vomer. This suggests that alterations in odontogenesis may effect changes in the morphogenesis of underlying dentigerous bones. Differential rates of development (heterochrony) between the skull (dentigerous bones) and the dentition may be a characteristic feature in the evolution of cranial morphology in cannibal tiger salamanders.

Introduction

Morphological and behavioral polymorphisms—the coexistence or sequential appearance of two or more discrete phenotypes—appear frequently in natural populations. When constituent morphs of a polymorphic population inhabit different trophic levels as adults or at different stages in development, the population is said to exhibit a trophic polymorphism (e.g., *Asplanchna*: Gilbert, 1980; *Cichlasoma*: Sage and Selander, 1975; Liem and Kaufman, 1984; *Ambystoma*: Collins and Holomuzki, 1984). Cannibalism is a trophic polymorphism that commonly appears as an opportunistic behavior (reviewed by Crump, 1983; Fox, 1975; Polis, 1981; Polis and Myers, 1985). Structural cannibals, predatory individuals with mouth parts adapted for

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macrophagy, have been described in several taxa including invertebrates (*Asplanchna*, *Glaucoma*, *Blepharisma*, and *Amoeba*) and vertebrates (*Scaphiopus* and *Ambystoma*) (Polis, 1981). For example, cannibalistic tadpoles of the anuran *Scaphiopus* are well equipped with hypertrophied jaws and jaw musculature for eating conspecifics (Bragg, 1964).

Cannibal morphs have been described in larval forms of three subspecies of the common tiger salamander, *Ambystoma tigrinum* (Ambystomatidae) (*mavortium*, *nebulosum*: Collins, 1980; *tigrinum*: Lannoo and Bachmann, 1984). The enlarged heads, increased gape and enlarged teeth of cannibal *Ambystoma* may circumvent gape restrictions on prey size selection (Zaret, 1980), and ensure a firm purchase on prey items. The effect of this cannibalistic polymorphism on population dynamics can be dramatic. Gehlbach (1969) reported that 128 *Ambystoma* cannibals consumed 1,700 conspecifics in a two-week period, representing a 25% reduction in that particular population (0.21-1.30 conspecifics per day per cannibal). Cannibalistic *Ambystoma* have much larger heads (width and length) than non-cannibals of the same age class and possess elongate, recurved teeth (Gehlbach, 1969; Holomuzki and Collins, 1987; Lannoo and Bachmann, 1984; Pierce et al., 1983, Powers, 1907; Rose and Armentrout, 1976). Though the external morphology of the cannibal head has been described in detail, cannibal teeth which differ from the more common short, straight teeth of non-cannibal *Ambystoma* have received only marginal attention.

In this study, I describe and compare tooth structure in larval cannibal and non-cannibal tiger salamanders. Particular attention has been paid to tooth length, distribution of recurved teeth on each dentigerous bone, and the superficial geography of the shaft, pedicel, and shaft-pedicel junction as documented by scanning electron microscopy.

I asked the following questions: 1) Are elongate, recurved teeth found only in cannibals? 2) Is the polymorphism characteristic of all dentigerous bones? 3) Apart from tooth size and shape, are there other distinguishing characteristics of the cannibal dentition, e.g., are cannibal teeth constructed differently from non-cannibal teeth? Finally, I describe the characteristic vomerine mounding in cannibals, patterns of tooth replacement, adult tooth morphology, and briefly speculate as to the functional implications of this dental polymorphism.

Material and methods

Specimens examined

All specimens were *Ambystoma tigrinum nebulosum* larvae of intermediate body size (eleven cannibals, 40-95 mm, and nine non-cannibals, 55-96 mm trunk length; see Appendix 1). At capture, specimens were classified as either cannibal or non-cannibal based on the exaggerated head width typical of the cannibal morph. Trunk vertebrae length (TVL) (anterior dorsal tip of atlas to posterior face of last post-sacral vertebrae) was measured from radiographs (Hewlett-Packard Faxitron portable X-ray unit) and
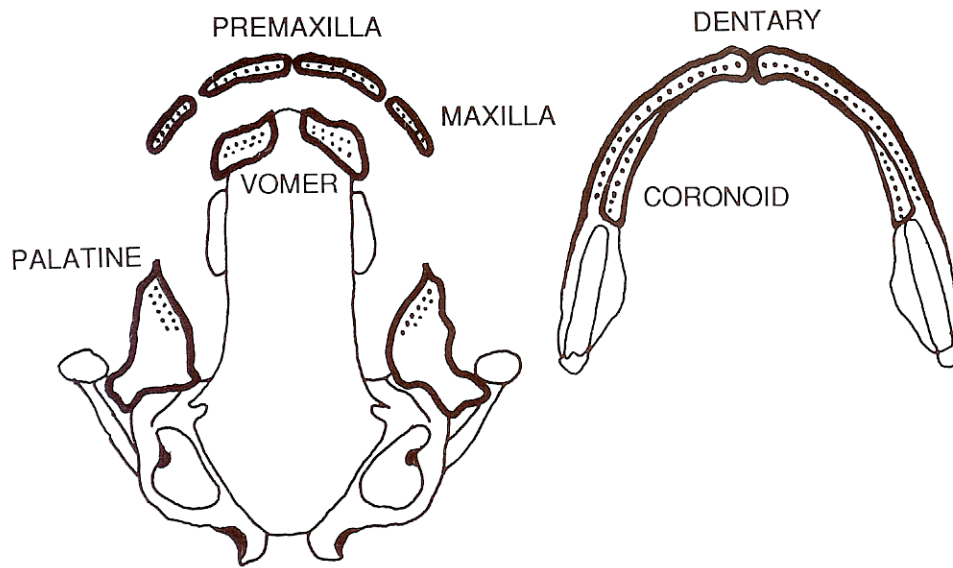
Figure 1. The six dentigerous bones in the skull (ventral view) and mandible of *Ambystoma tigrinum*.

used as a measure of body size; braincase width (BCW) (width of skull across parietals anterior to otic capsules) characterized head size. The standard measure of body size, snout-vent length, was avoided because it incorporates head size, which differs between morphs. All six dentigerous bones (fig. 1: dentary, coronoid, premaxilla, maxilla, vomer, and pterygoid) were removed from the right side of each specimen.

The junction between the tooth shaft and pedicel is characterized by a hinge-like region. The teeth of several preserved specimens (10% neutral buffered formalin) were manipulated with forceps and a blunt probe to examine the flexibility of this hinge region.

Scanning Electron Microscopy

After staining with alizarin red S (Hanken and Wassersug, 1981), each dentigerous bone was clearly visible through the adherent tissue which facilitated tissue removal without damaging the underlying teeth and bone. Connective tissue that could not be removed with forceps was removed chemically by maceration in a 10% trypsin solution in 30% aqueous sodium borate. Remaining tissue was easily removed by cleaning each bone with 5% aqueous KOH in a sonicator. Air dried material was glued to SEM mounting stubs with silver paint, sputter coated with 500 angstroms of gold (Technics hummer sputterer II), and stored in a desicator. High resolution micrographs were made with either an AMR-1000A or a SCI stereoscan S4-10 scanning electron microscope.

The shape and superficial geography of the pedicel, tooth shaft, and shaft/pedicel junction in cannibal and non-cannibal teeth on each of the six bones was documented with micrographs. Tooth length (cusp tip to the deepest lingual point of tooth/bone ankylosis) was measured directly from the SEM micrographs (five teeth per photograph). Lingual measurements were used so as to limit variability in tooth length due to the intrinsic differences in the type of ankylosis characteristic of each bone (e.g., horizontal ankylosis: coronoid, vomer, palatopterygoid; pleural ankylosis: dentary, maxilla, premaxilla).

Tooth distribution

Dentary, premaxillary, and vomerine teeth from 128 (55 cannibal, 73 non-cannibal, see Appendix 2) specimens cleared and differentially stained for bone and cartilage (Hanken and Wassersug, 1981) were classified as straight teeth if the tooth shaft and tooth pedicel were aligned coaxially, or as recurved teeth if there was any deviation from this coaxial arrangement. Each specimen was scored conservatively. In cannibals, for instance, any number of straight teeth found on a particular bone would cause that particular tooth patch to be classified as straight. The converse was true in non-cannibals; any recurved teeth appearing in an otherwise homogenous patch of straight teeth would cause the entire patch to be classified as cannibal.

Results

General observations

Larval dentition. — Typically, the larval teeth of non-cannibal *Ambystoma tigrinum* are sharply pointed, undivided monocuspids while the teeth of cannibal larvae are recurved, undivided monocuspids. The marginal teeth of both morphs (maxilla, premaxilla, dentary, coronoid) are monostichous (single row of teeth) and pleurally ankylosed, except the teeth of the coronoid which are horizontally ankylosed. Teeth located on the roof of the mouth (vomer, palatine) are polystichous (serial rows of teeth) and horizontally ankylosed with adjacent pedicel bases fused into a common pulp cavity.

Tooth replacement. — As larvae, replacement teeth in each morph remain monocuspid but exhibit an increasingly distinct pedicel/shaft division with successive tooth generations. The pattern by which bicuspid teeth replace monocuspid teeth prior to metamorphosis is shared by cannibals and non-cannibals; bicuspid teeth first appear in the vomer and premaxilla followed by the maxilla and dentary. In cannibals however, the junction between pedicel and shaft of these incoming bicuspid teeth is often angled rather than curved.

Adult dentition. — At metamorphosis, the coronoid bones (and teeth) are resorbed while each palatopterygoid divides to form separate pterygoid and palatine bones as well as

the post-choanal process of each vomer in both morphs. After metamorphosis, marginal tooth batteries remain monostichous while the polystichous vomer (vomeropalatinum; Clemen, 1979) becomes monostichous.

Scanning Electron Microscopy

Tooth shaft. — In both morphs, the crown of the tooth shaft is covered with a thin sheath of enamel which appears to be approximately 0.2μm thick (fig. 2a,b). The
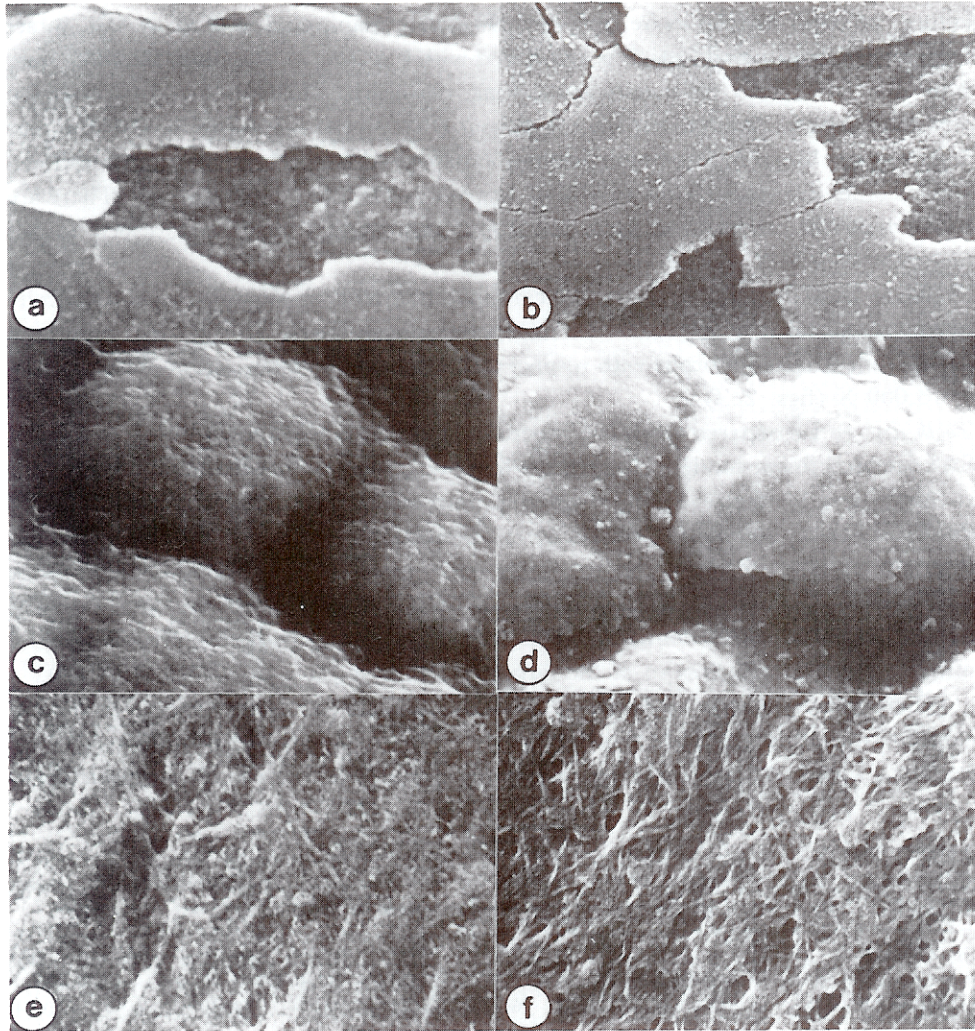

Figure 2. Scanning electron micrographs of dentary tooth shafts (a,b), hinge regions (c,d), and pedicels (e,f) at 13000 X of non-cannibals (a,c,e) and cannibals (b,d,f). There are no differences between cannibal and non-cannibal tooth surfaces in any of the three regions at this magnification. Tooth base is to the left of each photograph.

longitudinal fracture lines, which penetrate the enamel thereby exposing the underlying dentine core of the tooth, may be artifactual. Whether or not this chipping and flaking is indicative of tooth wear or is a preparation artifact, the pattern does not appear to differ between morphs when viewed at 13,000 X (fig. 2a,b).

Shaft-pedicel junction. — The division between the shaft and the pedicel corresponds with the gum-line and appears to be little more than a weak zone at which buckling occurs (fig. 2c,d). Lingual buckling occurs in both cannibals and non-cannibals but whether this flexion is "hinge-like" or is evidence of a "controlled" mechanical failure, or both, has yet to be resolved. However, manipulation of preserved, intact teeth shows that lingual flexion is associated with buckling on the inner (lingual) face, while the same teeth resist outward (labial) extension. This would suggest that the observed flexion of teeth in the micrographs is not a preparation artifact. The granular nature of the hinge region becomes more apparent with successive tooth generations, and becomes distinctive when bifid teeth appear just before metamorphosis. There are no obvious differences between cannibal and non-cannibal teeth with respect to this region at 13,000 X (fig. 2c,d).

Pedicel. — Superficially, the pedicel of cannibals and non-cannibals is characteristically fibrous in appearance, presumably a matrix of collagen fibers. No particular difference is apparent between morphs with respect to the density or organization of these fibers at 13,000 X (figs. 2e,f).

Tooth size. — I compared tooth lengths from cannibals and non-cannibals with GLM-SAS (general linear models procedure – Statistical Analysis System) and adjusted for covariation in head size. Palatine and coronoid teeth were omitted from the analysis due to an inadequate sample size (table 1). Cannibal teeth ranged from 25-39% longer than non-cannibal teeth on dentary, premaxilla, maxilla, and vomer bones, but only differences involving the dentary and vomerine teeth were significant ($p < .05$). The hypertrophied cannibal dentition is most obvious at intermediate body sizes (50-70 mm TVL) and much less so at the largest body sizes (90+ mm TVL) (fig. 3a).

When plotted against body size (TVL), cannibal teeth appear longer than non-cannibal vomerine teeth, but this was expected due to the hypertrophy of the cannibal skull as a whole. When tooth length is plotted against head size (vomerine tooth length

Table 1. Cannibal and non-cannibal mean tooth lengths. Individual means presented in Appendix 2. Abbreviations: DENT = dentary, PMAX = premaxilla, MAX = maxilla, VOM = vomer, TVL = trunk length, BCW = braincase width. Asterisk indicates significance level ($p < .05$).

SPECIMEN	n	TVL	BCW	DENT	PMAX	MAX	VOM
CANNIBAL	11	66.84	7.51	0.69	0.59	0.48	0.64
NON-CANNIBAL	9	69.93	6.68	0.52	0.47	0.38	0.46
F VALUE				6.82*	2.78	3.79	9.74*
Cannibal tooth length as a percent of non-cannibal tooth length				32%	25%	26%	39%

against BCW; fig. 3b), the difference between morphs is still obvious but not to the same extent as before (fig. 3a). This illustrates that cannibal teeth are not only absolutely longer than non-cannibal teeth, but relatively longer as well.

Tooth recurvature. — In general, cannibals exhibit recurved teeth, and non-cannibals possess more typical, peg-like teeth in the dentary, premaxilla and vomerine tooth batteries. However, recurved teeth are interspersed among peg-like teeth in 22% of the non-cannibals, while normal peg-like teeth occasionally appear (16%) among rows of
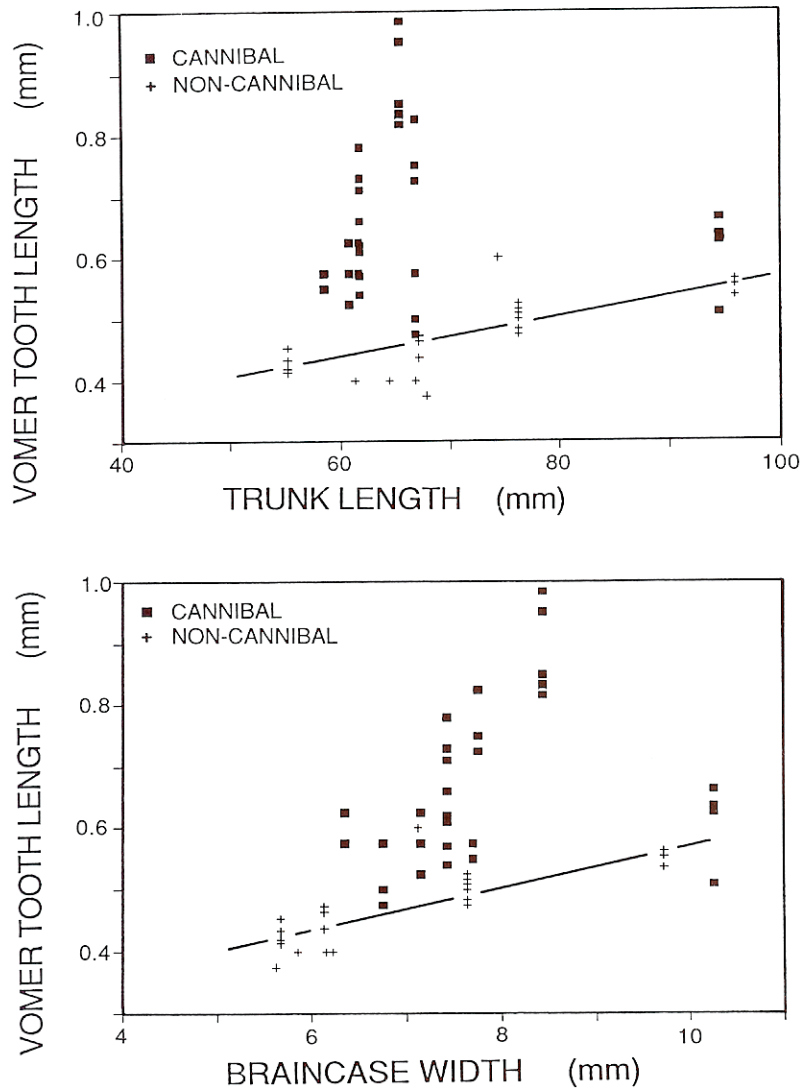

Figure 3. Scatterplot of vomerine tooth length against (a) trunk-vertebral length, and (b) braincase width-head size (mm).

Table 2. Incidence of recurved teeth on dentary, vomer, and premaxillary bones (number of specimens = 128). Recurvature is indicated by (+), its absence by (–), and both (mosaic) by (M). Nine of 55 cannibals and 16 of 73 non-cannibals express both straight and recurved teeth (mosaics).

	CANNIBAL (n = 55)				NON-CANNIBAL (n = 73)		
n	Dentary	Vomer	premaxilla	n	Dentary	Vomer	Premaxilla
46	+	+	+	57	–	–	–
6	M	+	+	12	–	–	M
3	+	M	+	3	–	M	–
				1	M	–	–

recurved teeth in cannibals (table 2). These aberrant teeth occur randomly along the length of each dentigerous bone or as tooth buds still embedded in the adjacent dental lamina, either singly or in a series of 2-3 teeth. These dental mosaics appear most frequently in the premaxillary lamina of both morphs.

The degree to which cannibal teeth are recurved varies from the absence of curvature in straight teeth to lingually curved shafts that form a 30 degree angle from the vertical axis of the tooth (figs. 4-5). The straight shafts of premaxillary and maxillary teeth are often placed obliquely on the pedicel giving the false impression of recurvature. These angular or bent teeth do not appear to be damaged (buckled) and may be characteristic of the premaxillary and maxillary tooth rows of metamorphosed cannibals and non-cannibals (fig. 5c-f).

Vomerine mounding. — Cannibal vomer and palatine bones are mounded ventrally from the roof of the mouth into the buccal cavity. The greatest distortion appears to be around the long axis of each bone (fig. 6, Lannoo and Bachmann, 1984). Non-cannibals do not possess either vomerine or palatine mounding, subsequently, the resident teeth appear in linear clusters of 2-3 teeth. When the underlying bone buckles into the mouth cavity, this linear arrangement is disrupted causing the teeth to point in different directions (fig. 4b).

Discussion

Dental polymorphism

It is not unusual for amphibians of different age classes and/or trophic levels to possess different tooth morphologies (Tihen, 1958; Wake and Wurst, 1979). Larval salamanders and caecelians generally undergo a dentitional metamorphosis at or just before metamorphosis. The typical, cone shaped larval teeth are usually replaced by the adult dentition (Tihen, 1958) which may exhibit a taxon specific cusp shape (Greven, 1984; Greven and Laumeier, 1987; Moury et al., 1985; Tihen, 1958; Wake and Wurst, 1979). Even paedomorphic species which do not undergo somatic metamorphosis, may nevertheless undergo a dentitional metamorphosis (Parker and Dunn, 1964; for a review of amphibian dentition, see: Greven, 1989). Though two
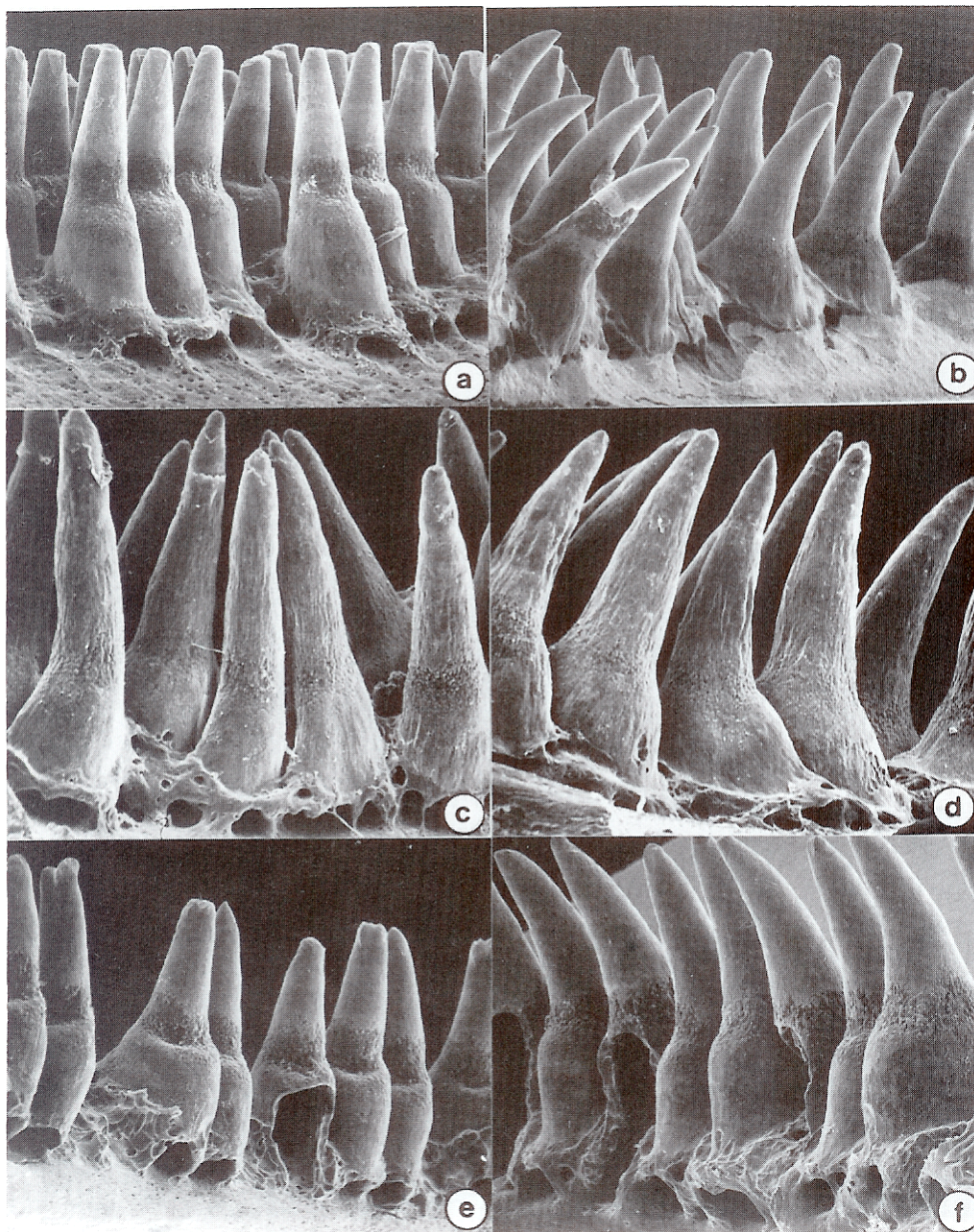
Figure 4. Postero-lingual views of vomerine teeth (a,b), palatine teeth (c,d), and dentary teeth (e,f) in non-cannibals (a,c,e) and cannibals (b,d,f). Note the recurvature and wide pedicel bases in cannibal vomerine and palatine teeth (b,d). Also note the difference in the orientation of teeth on the underlying vomer: rows in non-cannibals (a) and an irregular arrangement in cannibals (b).
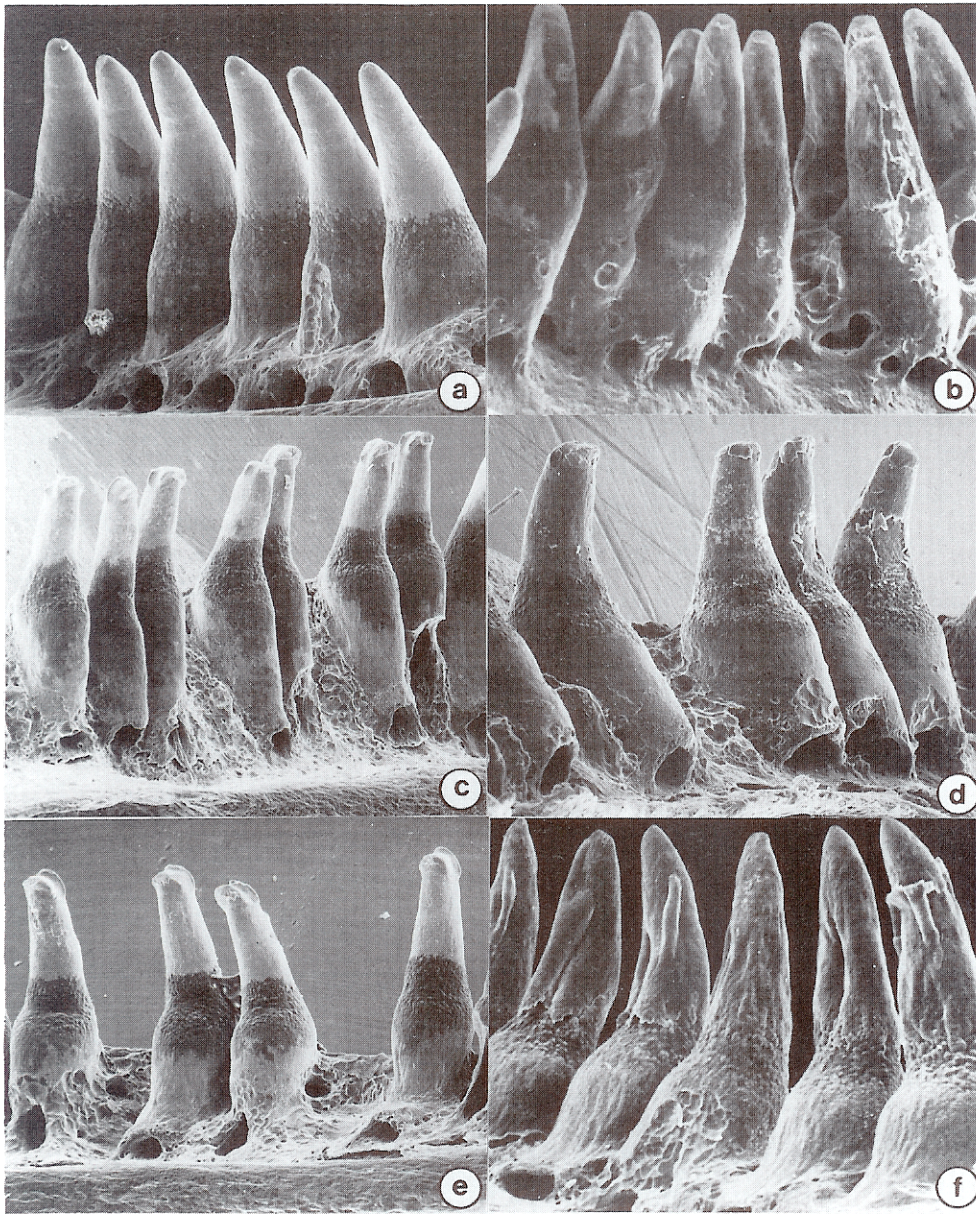
Figure 5. Postero-lingual views of coronoid teeth (a,b), premaxillary teeth (c,d) and cannibals (b,d,f). Note the limited recurvature and relatively wide pedicel bases in cannibals (b,d,f), and the non-cannibal adult bifid teeth (c,e).
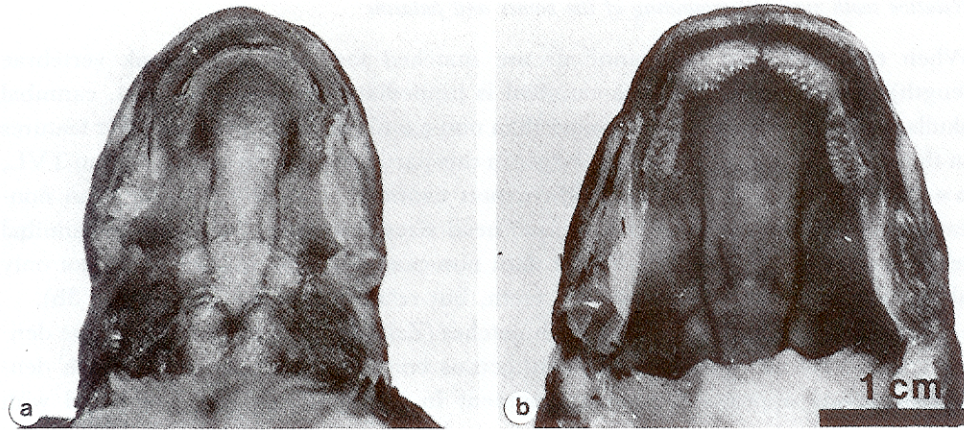
Figure 6. Photograph of the roof of the mouth of (a) non-cannibal and (b) cannibal *Ambystoma tigrinum* (duplicated with permission, Lannoo & Bachmann, 1984). Note the flat vomer and palatine tooth patches in the non-cannibal and the grossly distorted palatine and vomerine tooth patches and bones in the cannibal.

morphologically distinct tooth series are common, Wake (1976) describes three sequential tooth morphs in live-bearing caecilians that includes a highly specialized fetal tooth morphology used for scraping nutritive secretions from the uterine wall. Aside from normal variation in tooth size and shape within a particular age class or taxa, I have not found any record of a dental polymorphism of the type observed in cannibal tiger salamander larvae.

The tooth recurvature found in cannibal *A. tigrinum* is characteristic of other paedomorphic urodeles (*Gegeneophis*, *Andrias*: Greven and Clemen, 1980; Greven, 1984) but occurs infrequently in non-cannibal *A. tigrinum* larvae. Therefore, recurved teeth are not a derived character unique to cannibals, but may represent a shift from a dental morphology that already exists at low frequency in non-cannibals.

Very little empirical data concerning dental form and function appears in the literature. Nevertheless, recurved teeth in other carnivores are commonly believed to insure a firm purchase on the prey item as well as the unidirectional travel of food items into the mouth (fish: Fink, 1981; snakes: Savitzky, 1981). Similarly, several urodelan genera (e.g. *Triturus*: Clemen and Greven, 1979; *Salamandra*: Clemen et al., 1980; *Andrias*: Greven and Clemen, 1980; *Hynobius*: Greven and Clemen, 1985; *Plethodon*: Moury et al., 1985) and the caecelian *Gegeneophis* (Greven, 1984) exhibit a pedicel-shaft function that is variably calcified, forming a hinge that may act in a ratchet-like fashion to keep food items in the mouth. This weakened region may also permit a clean break with the pedicel in order to prevent damage to the underlying bone, surrounding teeth, and dental lamina in the event of excessive stresses incurred during prey capture (Moury et al., 1985). In unison, tooth recurvature and a defined "crush-zone" may insure unidirectional travel of prey items into the mouth in cannibal *Ambystoma*.

Relative tooth size and mounding of the vomer and palatine

When cannibals and non-cannibals are matched for body size (trunk vertebrae length), the larger head of the cannibal is immediately apparent. In fact, cannibal skulls are 19% wider and 13% longer than non-cannibal skulls, whereas other features in the cranium range from 6-21% larger in this particular size range (40-96 mm TVL, n = 72; Pedersen, 1988). One might expect cannibal teeth to be longer than non-cannibal teeth on the basis of increased head sizes alone (fig. 3a). Indeed, cannibal teeth average 30% (25-39%) longer than non-cannibal teeth making them not only absolutely longer than non-cannibal teeth, but relatively longer as well (fig. 3b).

Clemen (1988) has shown that tooth patches (Zahnfelder) and their generative dental lamina rely on an underlying dentigerous bone to remain active. As each dentigerous bone appears during development in the cannibal, it is populated with recurved teeth, including the coronoid which is eventually lost at metamorphosis. Competition for the limited ankylosis space between adjacent, hypertrophic vomerine and palatal teeth may distort the underlying, typically planar, vomer and palatine bones resulting in a "mounded" appearance (fig. 7; Powers, 1907; Lannoo and Bachmann, 1984)). To what extent this dental hypertrophy has affected morphological changes in other dentigerous bones in the cannibal is unknown.

Possibly, dental hypertrophy has triggered morphogenetic changes that, through functional or developmental integration, are grossly observable in surrounding features (e.g. rostrum length, head width, jaw size, jaw musculature; Zelditch, 1988). The characteristically wide head, elongate recurved teeth and hypertrophied musculature of a cannibal becomes obvious in the as yet incompletely ossified skull (Pedersen, 1988, Masters unpub. thesis) while it is still too small to eat conspecifics and must filter-feed on small invertebrates (e.g., *Daphnia*). Because this suite of characters appears when the skull is yet too small to take full advantage of its "carnivourus dentition", it is necessary to investigate events that occur very early in development, such as the hormonal integration of skull growth, in order to identify the mechanism(s) by which this dental polymorphism is effected.

Established polymorphisms are an integral part of the conversion of intraspecific variation into interspecific variation. It could be argued that cannibalism, as a trophic polymorphism, has allowed tiger salamanders to "functionally speciate" (Collins and Holomuzki, 1984) at the ecological level. Dental polymorphism is a predominant feature of the cannibal morph. If a shift in dental morphology has affected the structure and/or functional integration of trophic structures in salamander larvae, to what extent have similar mechanisms effected changes in the evolution of the skull and jaws in other vertebrates?

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Appendix 1. Individual cannibal and non-cannibal tooth lengths. Each volume is the mean length of five teeth on the same bone; cannibals: mean trunk length = 66.85 mm, n = 11; non-cannibals: mean trunk length = 69.93 mm, n = 9. Abbreviations: DENT = dentary, PMAX = premaxilla, MAX = maxilla, VOM = vomer, TVL = trunk length, BCW = braincase width. Specimen numbers are collector field numbers: M = Mitton and C = Collins.

	CANNIBALS							NON-CANNIBALS					
SPECIMEN	TVL	BCW	DENT	PMAX	MAX	VOM	SPECIMEN	TVL	BCW	DENT	PMAX	MAX	VOM
C11776	40.6	4.74	0.58				C15381	67.8	5.62	0.50	0.33	0.28	0.38
M1241	61.7	6.35	0.87	0.68	0.48	0.59	C22984	55.2	5.67	0.52			0.43
M1229	66.8	6.75	0.72	0.63	0.56	0.52	C15373	61.3	5.85	0.50	0.30	0.30	0.40
M1240	60.8	7.15	0.73	0.51	0.45	0.58	C22981	67.2	6.13	0.42	0.72	0.43	0.46
C24809	61.8	7.43	0.58			0.65	C15382	64.5	6.15	0.55	0.38	0.38	0.40
M1800	75.0	7.50			0.38		C15377	66.8	6.22	0.58	0.35	0.35	0.40
M1234	58.5	7.70	0.43	0.57	0.47	0.57	C15212	74.5	7.12	0.74	0.53	0.50	0.60
M1245	66.8	7.75	0.78	0.63	0.53	0.77	C24836	76.3	7.64	0.41	0.57		0.50
M24808	65.4	8.44	0.80			0.87	C24835	95.8	9.72	0.50	0.56	0.46	0.55
C15153	83.5	8.61	0.58	0.52									
C15151	94.5	10.26	0.80			0.61							
MEAN TOOTH LENGTH			0.69	0.59	0.48	0.64				0.52	0.47	0.38	0.46

Appendix 2. Specimens utilized in the study: 20 specimens were used in the SEM analysis (*) while another 128 specimens were utilized in the morphometric analyses. All numbers are collectors field numbers.

Bernardine Lake, Taos Co., New Mexico, collected Aug. 8, 1978 by J. Mitton and B. Pierce (n = 27). 1, 2, 1227, 1229*, 1230, 1234*, 1235, 1237-1939, 1940-1241*, 1245*, 5001*, 5002*, 5004-16*

Dexter National Fish Hatchery, 2.6 km S-SE of Dexter, elev. 1042 m, Chaves Co., New Mexico, collected Aug. and Sept. 1984 by J. Collins (n = 80). 15195-211, 15212*, 15213, 15373*, 15374-75, 15377*, 15378, 15381-82*, 16112-21, 16123, 16125-31, 16135-38, 16140-41, 16143, 22975-22980, 22981*, 22982-83, 22984*, 22985-90, 24808-09*, 24257-58, 24310-18, 24320

Dude Sink, 21.1 km E-NE of Pine, elev. 2304 m, Coconino Co., Arizona collected June 11, 1983 by J. Collins (n = 16). 11776*, 14212, 14214-16, 14221, 14224-25, 14230-34, 14236, 14241-42

Five Springs Tank, 24.3 km E-NE of Reserve, elev. 2523 m, Catron Co., New Mexico, collected July 24, 1984 by J. Collins (n = 2). 15151*, 15153*

Myrtle Lake, 27 km E of Pine, elev. 2372 m, Coconino Co., Arizona, collected May 11, 1984 by J. Collins (n = 8). 16081-86, 16088-89

Unnamed stock tank, 16.3 km E of Elida, Roosevelt Co., New Mexico, collected Jan. 2, 1986 by J. Collins (n = 2). 24835*, 24836*

Vallecitos #2, Taos Co., New Mexico, collected June 8, 1978 by J. Mitton and B. Pierce (n = 16). 1025, 1026, 1035, 1038, 1042-44, 1049, 1051, 1055, 1060, 1074, 1077, 1082, 1097, 1119