

SKULL GROWTH IN CANNIBALISTIC TIGER  
SALAMANDERS, *AMBYSTOMA TIGRINUM*

SCOTT C. PEDERSEN

*Department of Environmental, Population and Organismic Biology, University of Colorado,  
Boulder, CO 80309-0334*

*Present address of author: University of Nebraska State Museum, University of Nebraska,  
Lincoln, NE 68588-0118*

**ABSTRACT**—This study compared skull growth in cannibal and non-cannibal tiger salamanders, *Ambystoma tigrinum*. Skull measurements from cleared and stained larvae suggested that the development of small cannibals less than 70 mm SVL was characterized by the differential, accelerated growth of the skull. Though the skulls of cannibals remained larger than those of non-cannibals, the trophic apparatus of non-cannibals exhibited accelerated growth so that it was difficult to accurately identify cannibals or non-cannibals on the basis of skull size at snout-vent lengths greater than 70 mm. This study suggests that the soft-tissue, functional matrix of the head dictates head size, and that the increased head size in cannibals is compensatory growth responsive to the increased functional demands of macrophagy.

The ephemeral environments and high larval densities which typically characterize amphibian populations often lead to intense intraspecific competition, stress, and/or starvation. Under these conditions, cannibalism, an extreme form of trophic polymorphism, is sometimes observed (Collins and Cheek, 1983; Polis and Myers, 1985). Opportunistic cannibalism is the most common form and may benefit both the cannibalistic individual(s) and the host population (Semlitsch and Caldwell, 1982). However, predatory individuals with mouth parts specialized for macrophagy, i.e., structural cannibals, appear in several amphibian taxa: *Scaphiopus* and *Ambystoma* (Bragg, 1964; Polis, 1981).

Structural cannibals have been reported in three of the seven subspecies of tiger salamanders, *Ambystoma tigrinum* (Gehlbach, 1967): *A. t. mavortium*, *A. t. nebulosum*, and *A. t. tigrinum* (Collins, 1980; Lannoo and Bachmann, 1984). The "characteristic" recurved teeth and broad heads of the cannibal morph have been described in numerous studies (Powers, 1907; Rose and Armentrout, 1976; Pierce et al., 1983; Lannoo and Bachmann, 1984; Lannoo, 1985; Pedersen, 1991). These authors have hypothesized that the cannibals' cranial hypertrophy must confer some biomechanical advantage to the cannibal larvae during prey capture. However, Reilly et al. (1992) have shown that increased head size and jaw gape did not

improve cannibal feeding performance but that dental polymorphism did.

In this report I examine the degree to which inter-morph differences in external head size and shape are mirrored by differences in skull size and shape in developmental series of cleared and stained larvae. I also address the question of whether the apparent cranial hypertrophy (head size) of cannibals is limited to growth in trophic structures, or does it represent allometric growth of the entire skull?

**MATERIALS AND METHODS**—One hundred twenty-nine larval *Ambystoma tigrinum mavortium* were collected in New Mexico and Arizona by James Collins (Arizona State University, ASU) and Jeffrey Mitton (University of Colorado, CU) and were returned to the ASU zoological collections at the termination of the project. Collins identified specimens in the field as either "typical" or "cannibal" based on relative size and shape of the head. Collins' and Mitton's identifications were modified such that only individuals exhibiting both recurved teeth and a wide head were classified as morphological cannibals. Identification of the reproductive status or the dietary preference of each animal was not possible because many specimens were either previously gutted or poorly preserved.

The museum voucher specimens utilized in this study do not reflect a random, cross-section of a single natural population. Instead, specimen availability dictated that developmental series for both cannibals and non-can-

nibals were constructed by combining animals collected from several populations from a limited geographic area in western New Mexico. Still, these series are incomplete (non-continuous), and the statistical analyses concerning small larvae were biased by the large number of very small cannibal larvae and the near absence of intermediate-sized cannibal larvae.

All specimens were cleared and differentially stained for bone and cartilage (Hanken and Wassersug, 1981). The total length of the trunk vertebrae (TVL: anterior face of atlas to posterior surface of last pre-caudal vertebrae) was measured ( $\pm 0.01$  mm) with Helios dial calipers. I chose TVL as a measure of body size because the more commonly used measure, snout-vent length (SVL), includes the length of the head (dependent variable). Eleven cranial osteological characters were measured with an ocular micrometer mounted inside a Wild M8 dissecting microscope (SL, greatest skull length; QW, skull width across quadrates; PMW, premaxilla width; PML, premaxilla length; ML, maxilla length; FL, frontal length; VL, vomer length; VW, vomer width; OCW, skull width across otic capsules; BCW, braincase width across anterior tip of parietals; PL, parietal length; Fig. 1).

Based on my subsamples, individuals began to metamorphose at 50 mm TVL or 67 mm SVL in these populations as evidenced by the initiation of gill resorption. I used this body length to separate smaller individuals (non-cannibal larvae, small cannibalistic larvae) from the larger specimens (non-cannibal branchiatae—i.e., typical individuals with delayed metamorphosis—and large cannibal branchiatae).

An analysis of variance (ANOVA—SYSTAT; Wilkinson, 1990) was performed on each log-transformed variable within each size range; e.g., small non-cannibal larvae compared with small cannibalistic larvae, and non-cannibal branchiatae compared with cannibalistic branchiatae. The significance level of  $P = 0.05$  was adjusted using the Bonferroni correction ( $P = 0.05/n = 0.05/12 = 0.004$ ) to control for group-wide, Type I error during the multiple comparisons presented in Table 1.

Each log-transformed character was then regressed against log TVL for each group (small non-cannibal larvae, small cannibal larvae, branchiatae, cannibal branchiatae; SYSTAT: Wilkinson, 1990). Cannibal and non-cannibal regression coefficients for each variable were compared with a test for homogeneity of slopes (ANCOVA). The significance level of  $P = 0.05$  was adjusted using the Bonferroni correction ( $P = 0.05/n = 0.05/11 = 0.0045$ ) to control for group-wide, Type I error during these multiple comparisons.

To evaluate the variance-covariance relationships among cranial characters and between cannibal larvae and non-cannibal larvae, a principal component analysis was performed utilizing log-transformed data for the eleven osteometric characters. Three principal components were subsequently extracted from the corre-

lation matrix by the root curve method (STATVIEW: Feldman et al., 1988). Structures associated with the trophic apparatus (i.e., jaws, dentigerous bones, suspensorium) appear to grow more rapidly in small cannibals (Lannoo and Bachmann, 1984). To test this observation, I calculated a crude, cranial index to evaluate the relationship between the neurocranium and the rest of the skull by dividing the projected area of the braincase (width of braincase at the otic capsules  $\times$  length of braincase) by the projected area of the trophic apparatus ((width of skull at the quadrates  $\times$  length of skull) – braincase area).

**RESULTS**—Non-cannibal larvae <50 mm TVL exhibited skulls that were significantly larger than the skulls of the small cannibal larvae in eight of eleven characters including TVL (Table 1). These results were not predicted and they clearly reflected the collecting bias in the study (see above). This sampling bias and the resulting statistical artifacts were somewhat ameliorated by the data presented in Fig. 2. This scatterplot of log QW against log TVL (skull width against trunk length) clearly showed that cannibal heads were statistically wider than non-cannibal heads at all TVL. Indeed, above 50 mm TVL, the large cannibals exhibited the predicted dimorphism in head size; all characters except vomer length were 12–27% larger than in non-cannibals (Table 2). The appearance of intermediate head sizes in both morphs at all TVL (Fig. 2) suggests that there is a continuum of head sizes rather than a clear dimorphism in size between cannibals and non-cannibals.

The continuum of head sizes at all TVL complicated the interpretation of the subsequent regression analyses. This was most apparent in the comparison of regression coefficients between morphs or between body size classes when these comparisons were restricted to the conservative Bonferroni  $P$  values ( $P = 0.0045$ ) necessitated by the simultaneous group-wide comparisons of several variables or coefficients. For example, the regression coefficients for the length of the maxilla, premaxilla, frontal and vomer bones were clearly larger in small cannibals than in small non-cannibals (Table 3), albeit insignificantly so. Consequently, cannibal and non-cannibal allometric trajectories for each character generally paralleled each other across the entire range of body sizes, 19–102 mm TVL.

For all characters, the slope of the regression line of small cannibals (<50 mm TVL) was not significantly different from the slope of the line

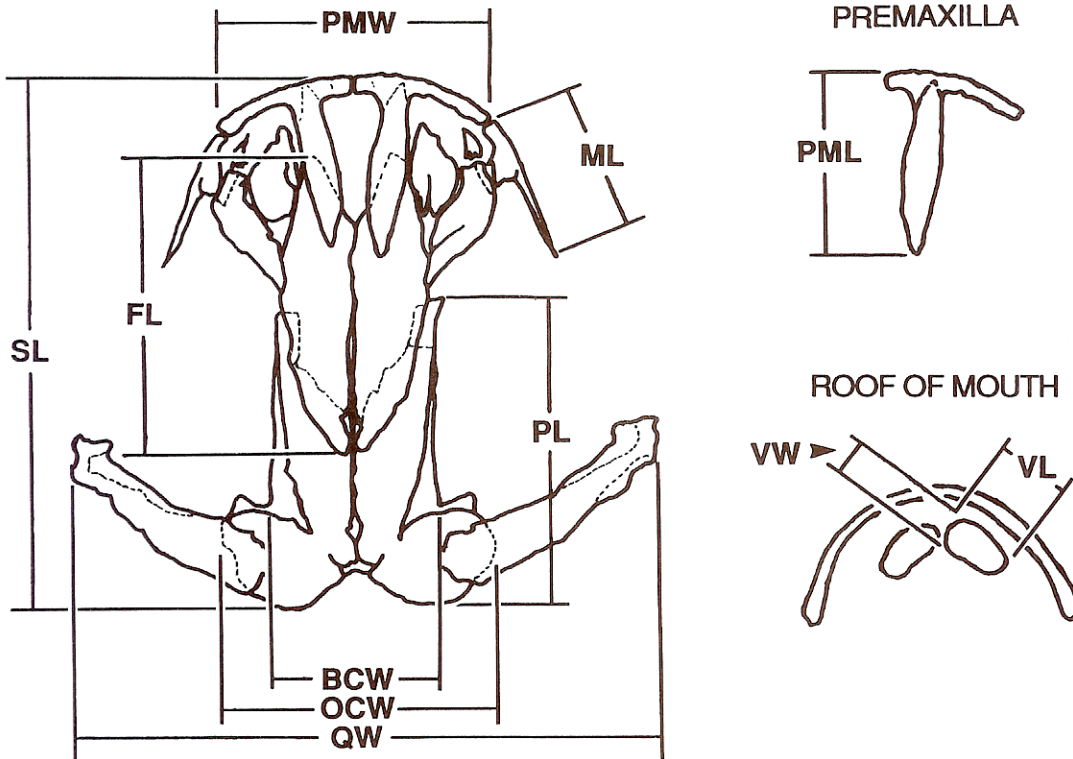


FIG. 1—The eleven osteometric characters utilized in the study are shown superimposed on a line drawing of a typical larval skull of *Ambystoma tigrinum*.

TABLE 1—Character means and standard deviations (non-transformed data) for small cannibals and non-cannibals <50 mm TVL. ANOVA results from log-transformed data (Bonferroni  $P = 0.05/12 = 0.004$ ).

Variable	Non-cannibal ( $n = 39$ ) Mean $\pm$ $SD$	Cannibal ( $n = 29$ ) Mean $\pm$ $SD$	$F$ -ratio	$P$
Trunk vertebrae length	35.58 $\pm$ 6.97	26.34 $\pm$ 9.20	28.72	0.0000
Greatest skull length	12.75 $\pm$ 2.03	12.60 $\pm$ 1.93	0.03	0.8655
Greatest skull width	12.00 $\pm$ 2.27	12.12 $\pm$ 2.29	0.09	0.7675
Premaxilla width	5.76 $\pm$ 0.79	5.38 $\pm$ 1.14	3.67	0.0598
Premaxilla length	3.12 $\pm$ 0.48	2.71 $\pm$ 0.84	10.18	0.0022
Maxilla length	3.10 $\pm$ 0.51	2.36 $\pm$ 1.03	23.67	0.0000
Frontal length	6.92 $\pm$ 1.16	5.55 $\pm$ 1.54	23.12	0.0000
Vomer length	2.81 $\pm$ 0.55	1.95 $\pm$ 0.91	36.08	0.0000
Vomer width	0.87 $\pm$ 0.20	0.56 $\pm$ 0.25	41.18	0.0000
Skull width (capsules)	8.12 $\pm$ 1.27	6.89 $\pm$ 1.63	15.16	0.0002
Braincase width	4.12 $\pm$ 0.83	3.46 $\pm$ 1.00	11.46	0.0001
Parietal length	8.47 $\pm$ 1.63	6.52 $\pm$ 2.15	22.83	0.0000

exhibited by large cannibals (>50 mm TVL). The slope remained constant for all characters across the entire range of body sizes (19–95 mm TVL; Bonferroni  $P = 0.05/11 = 0.0045$ ; Tables 3–5).

Many characters (OCW, BCW, VL, VW, SL) also exhibited the same allometry across the entire range of non-cannibal body sizes (21–102 mm TVL). However, several characters exhibited an allometric shift at 50 mm TVL. Whereas growth decreased significantly in PL, the following characters exhibited increased rates of growth in individuals larger than 50 mm TVL: FL, PMW, ML, PML, and QW ( $P = 0.0045$ ). The differential allometry of these five characters is of particular interest because each either supports, or is an integral part of, a subcomponent belonging to the trophic apparatus.

Cannibal and non-cannibal character allometries in animals less than 50 mm TVL rarely exhibited any significant differences in regression coefficients; i.e., they possessed the same allometric growth rate. However, the overall length and width of the skull in small non-cannibals grew significantly faster than in small cannibal skulls. Conversely, premaxillary length increased significantly faster in cannibals.

For most characters, the growth rates of large cannibals and large non-cannibals were not significantly different. The increases in premaxillary and maxillary length growth rates in non-

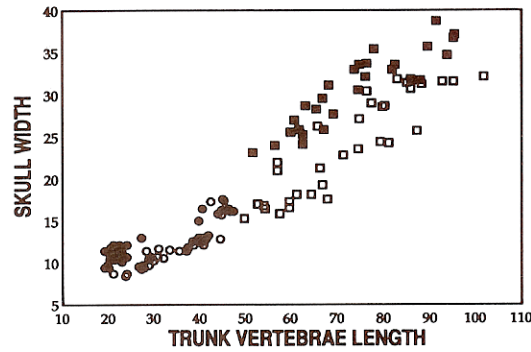


FIG. 2.—Scatterplot of skull width (QW: skull width at quadrates) and trunk vertebrae length (TVL). Open circles = typical larvae < 50 mm TVL; closed circles = cannibal larvae < 50 mm TVL; open squares = typical branchiates > 50 mm TVL; closed squares = cannibal branchiates > 50 mm TVL. Note the difference in skull width between cannibals and non-cannibals at all TVL.

cannibals were the only significant allometric differences noted in animals above 50 mm TVL.

As expected for a morphological series with a wide size range, the loadings on the first principal component (PC 1) were large and positive (Table 6). As the first component described 94.5% of the total variation in the sample, this component was predominantly one of size allometry. The second component (PC 2) described 2.3% of the total variation and contrasted vomerine length, width, and parietal length with the greatest length and

TABLE 2.—Character means and standard deviations (non-transformed data) for large cannibals and non-cannibals >50 mm TVL. ANOVA results from log-transformed data. The larger mean size of the cannibals is also reported as a percent increase in size over the non-cannibal means (Bonferroni  $P = 0.05/12 = 0.004$ ).

Variable	Non-cannibal ( $n = 32$ ) Mean $\pm$ SD	Cannibal ( $n = 29$ ) Mean $\pm$ SD	F-ratio	P	Increase
Trunk vertebrae length	72.10 $\pm$ 13.79	73.99 $\pm$ 12.63	0.34	0.5646	
Greatest skull length	21.00 $\pm$ 3.91	25.21 $\pm$ 3.19	21.13	0.0000	20%
Greatest skull width	23.89 $\pm$ 5.91	30.50 $\pm$ 4.39	23.68	0.0000	27%
Premaxilla width	10.59 $\pm$ 2.19	12.86 $\pm$ 1.95	18.10	0.0001	21%
Premaxilla length	6.32 $\pm$ 1.98	7.84 $\pm$ 1.03	15.74	0.0002	24%
Maxilla length	6.44 $\pm$ 1.94	8.10 $\pm$ 1.20	17.60	0.0001	26%
Frontal length	11.79 $\pm$ 2.37	14.63 $\pm$ 2.49	20.73	0.0000	24%
Vomer length	5.13 $\pm$ 0.98	6.08 $\pm$ 1.62	6.01	0.0172	18%
Vomer width	1.61 $\pm$ 0.40	1.95 $\pm$ 0.45	9.26	0.0035	21%
Skull width (capsules)	12.32 $\pm$ 1.93	13.78 $\pm$ 1.66	10.43	0.0020	12%
Braincase width	7.00 $\pm$ 1.12	8.10 $\pm$ 1.14	13.88	0.0004	16%
Parietal length	12.74 $\pm$ 1.37	14.97 $\pm$ 2.14	23.18	0.0000	17%

TABLE 3—Regression coefficients (slopes and intercepts) for log-transformed linear regression of head measures on TVL for small non-cannibal and cannibal larvae.

Variable	Non-cannibal		Cannibal	
	Slope $\pm$ SE	Intercept	Slope $\pm$ SE	Intercept
Greatest skull length	0.73 $\pm$ 0.04	-0.02	0.46 $\pm$ 0.03	0.45
Greatest skull width	0.81 $\pm$ 0.06	-0.17	0.55 $\pm$ 0.04	0.31
Premaxilla width	0.59 $\pm$ 0.04	-0.16	0.57 $\pm$ 0.06	-0.07
Premaxilla length	0.25 $\pm$ 0.12	0.10	0.81 $\pm$ 0.10	-0.72
Maxilla length	0.74 $\pm$ 0.05	-0.66	1.13 $\pm$ 0.12	-1.24
Frontal length	0.58 $\pm$ 0.08	-0.07	0.78 $\pm$ 0.06	-0.37
Vomer length	0.85 $\pm$ 0.07	-0.87	1.17 $\pm$ 0.09	-1.38
Vomer width	0.94 $\pm$ 0.12	-1.52	0.86 $\pm$ 0.20	-1.49
Skull width (capsules)	0.73 $\pm$ 0.03	-0.22	0.67 $\pm$ 0.04	-0.12
Braincase width	0.83 $\pm$ 0.07	-0.67	0.79 $\pm$ 0.09	-0.58
Parietal length	0.90 $\pm$ 0.04	-0.47	0.82 $\pm$ 0.12	-0.35

width of the skull, and premaxilla length. The third component (PC 3) contrasts snout lengths (maxillary and premaxillary lengths: ML, PML) with the greatest length and width of the skull, and with braincase width.

Whereas the relationship between INDEX and TVL (Fig. 3) demonstrates a rough dichotomy in the proportions of the neuro- and viscerocrania in smaller cannibals and non-cannibals, dramatic morphological convergence occurred between the larger cannibals and non-cannibals. This convergence implies that the larger head and skulls of the cannibal morphs are not the result of an independent hypertrophy of the trophic apparatus. Rather, the entire head expands as a unit with each subcomponent increasing in size in pro-

portion with its contribution to the construction of the head as a whole.

DISCUSSION—*Ambystoma* larvae display intra-specific aggression at all body sizes. Even the stomach contents of “non-cannibals” (no evidence of the cannibal skull morphology) often reveal bits and pieces of conspecifics (Collins and Holomuzki, 1984). Consistent cannibal behavior in *Ambystoma tigrinum* seems to appear around 20 mm TVL when these animals shift from microphagy to macrophagy (Holomuzki and Collins, 1987). It is only at this size that a presumptive cannibal’s head and mouth are large enough to contain a conspecific and macrophagy becomes “cannibalism.” Lannoo and Bachmann (1984)

TABLE 4—Regression coefficients (slopes and intercepts) for log-transformed linear regression of head measures on TVL for large non-cannibals and cannibals.

Variable	Non-cannibal		Cannibal	
	Slope $\pm$ SE	Intercept	Slope $\pm$ SE	Intercept
Greatest skull length	0.88 $\pm$ 0.09	-0.32	0.65 $\pm$ 0.07	0.19
Greatest skull width	1.20 $\pm$ 0.11	-0.85	0.79 $\pm$ 0.07	0.00
Premaxilla width	1.00 $\pm$ 0.09	-0.83	0.73 $\pm$ 0.10	-0.26
Premaxilla length	1.46 $\pm$ 0.16	-1.92	0.57 $\pm$ 0.10	-0.16
Maxilla length	1.37 $\pm$ 0.14	-1.75	0.67 $\pm$ 0.11	-0.34
Frontal length	0.98 $\pm$ 0.08	-0.76	0.72 $\pm$ 0.13	-0.18
Vomer length	0.81 $\pm$ 0.10	-0.80	1.07 $\pm$ 0.25	-1.23
Vomer width	0.93 $\pm$ 0.15	-1.53	0.99 $\pm$ 0.22	-1.57
Skull width (capsules)	0.74 $\pm$ 0.06	-0.29	0.64 $\pm$ 0.06	-0.06
Braincase width	0.76 $\pm$ 0.07	-0.56	0.71 $\pm$ 0.10	-0.42
Parietal length	0.44 $\pm$ 0.07	0.30	0.62 $\pm$ 0.12	0.02

TABLE 5—ANCOVA comparisons of regression coefficients (slopes) among groups. Nonsignificant differences between slopes = ns (Bonferroni  $P = 0.0045$ ), other characters reflect the group with the statistically greater slope: small cannibals = "c," large cannibals = "C," small non-cannibals = "t," large non-cannibals = "T."

Variable	Comparison			
	Small vs. large non-cannibals	Small vs. large cannibals	Small vs. large non-cannibals	Small vs. large cannibals
Greatest skull length	ns	ns	t	ns
Greatest skull width	T	ns	t	ns
Premaxilla width	T	ns	ns	ns
Premaxilla length	T	ns	c	T
Maxilla length	T	ns	ns	T
Frontal length	T	ns	ns	ns
Vomer length	ns	ns	ns	ns
Vomer width	ns	ns	ns	ns
Skull width (capsules)	ns	ns	ns	ns
Braincase width	ns	ns	ns	ns
Parietal length	t	ns	ns	ns

and Pierce et al. (1983) have examined whether cannibals begin development with a bigger head, or whether they exhibit accelerated growth throughout development relative to non-cannibals. Lannoo and Bachmann (1984) showed that cannibals do not start with a larger head. Instead, the head of a cannibal simply grows more rapidly than that of a non-cannibal from the start.

Pierce et al. (1983) compared the heads of much larger cannibal and non-cannibal morphs on the basis of a variety of skull measurements and external head dimensions. The heads of cannibals were larger than those of non-cannibals, regression coefficients were smaller than those of non-cannibals, and the extrapolated regression lines intercepted the Y-axis at a higher point than did comparable non-cannibal regressions. Pierce et al. (1983) concluded that cannibals begin ontogeny with larger heads and then converge morphologically with non-cannibals later in development.

The apparent contradiction between the results obtained in the studies by Lannoo and Bachmann's (1984) and Pierce et al. (1983) is resolved by considering the different data bases: Pierce et

TABLE 6—Principal component analysis. Tabular values are loadings of the eleven log-transformed characters.

Variable	PC1	PC2	PC3
Greatest skull length	0.977	-0.163	-0.095
Greatest skull width	0.972	-0.187	-0.089
Premaxilla width	0.980	-0.122	-0.050
Premaxilla length	0.957	-0.171	0.206
Maxilla length	0.978	-0.029	0.125
Frontal length	0.987	0.002	0.046
Vomer length	0.964	0.203	0.014
Vomer width	0.942	0.271	0.031
Skull width (capsules)	0.986	0.019	-0.049
Braincase width	0.981	0.013	-0.084
Parietal length	0.964	0.174	-0.051
Eigenvalues	10.394	0.253	0.093
Proportion of original variance	0.945	0.023	0.008

al. (1983) used large (90–125 mm SVL) animals in comparison to the smaller (30–70 mm SVL) animals that were examined by Lannoo and Bachmann (1984). The present study complements both previous works by effectively combining the two size ranges, 28–131 mm SVL (19–102 mm TVL).

However, whereas my results generally support those of Lannoo and Bachmann (1984) that many structures associated with the trophic apparatus grow more rapidly in small cannibals,

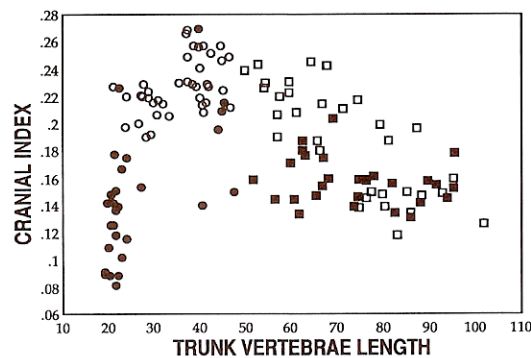


FIG. 3—Scatterplot of INDEX and TVL. Open circles = typical larvae < 50 mm TVL; closed circles = cannibal larvae < 50 mm TVL; open squares = typical branchiataes > 50 mm TVL; closed squares = cannibal branchiataes > 50 mm TVL. Note the convergence of large cannibals and non-cannibals (open and closed squares).

they are not supported statistically at the  $P = 0.0045$  level. The current regression analysis shows, if anything, that head growth in large non-cannibals is accelerated relative not only to small non-cannibals but also with respect to the growth rates exhibited by cannibals of all body sizes.

As convenient as it might be to consider each skeletal component as an independent unit (i.e., for cladistic analyses; Andrews, 1987), each structure is instead an integral part of the surrounding "functional matrix" (Moss, 1960). Changes in size, function, and shape of each cranial bone are effected by forces transmitted through the dura and periosteum from adjacent suture systems, synchondroses, muscles, and other adjacent organs (DuBrul and Laskin, 1961; Silver, 1962; Bosma, 1976; Blechschmidt, 1976a, 1976b; Hanken, 1983). Whereas Moss (1960, 1975, 1976) may exaggerate the role of soft tissues during development by stating that skull growth is compensatory and mechanically obligatory to head growth, the predominant role of soft tissues in skeletal morphogenesis has, nevertheless, been a recurring theme in theories concerning cranial evolution (Darwin, 1909; Blechschmidt, 1976a, 1976b; Hanken, 1983; Thorogood, 1988).

Accordingly, developing systems need to be most plastic when one developmental stage or functional demand gives way to another; e.g., metamorphosis in amphibians (Collins and Holomuzki, 1984) or, in the present case, when osteogenesis replaces chondrogenesis during skeletal development (Müller, 1990). Therefore, it is hardly surprising that cannibalistic behavior first appears at a stage where developmental plasticity is most capable of responding to the structural demands of cannibalism. This stage coincides with: 1) the shift from microphagy to macrophagy, 2) the ossification of the flimsy cartilaginous skull (adjacent cartilages do not contact each other) into a more robust form, and 3) the stage at which the head becomes large enough to contain conspecifics.

The enlarged vomerine bones of the cannibal morph exhibit a characteristic buckling, and extend down into the oral cavity (Lannoo and Bachmann, 1984). This buckling appears early in development, is retained by the large cannibals, and may be associated with the early hypertrophy of the vomerine teeth in cannibals (Pedersen, 1991). I interpret the early accelerated growth of the cannibal rostrum (VL, Fl, ML, PML) as a reflection of spatial (anatomical) competition and

compensatory growth of rostral elements adjacent to the expansive vomers. This prompts the following question: Could the hypertrophy of the cannibal's head be interpreted as the simple expansion of the existing functional matrix?

Expansion of the matrix needs only to engage the developmental mechanisms that are already in place to produce the compensatory growth necessary to respond to increased structural demands. With the advent of cannibalistic feeding behavior, cranial hypertrophy is an epigenetic amplification of a developmental system designed to maintain the functional relationships between affected subcomponents. If the conserved head composition of the larger aquatic morphs is any indication (INDEX; Fig. 3), the early acceleration in growth of the cannibal rostrum (though statistically insignificant) is absorbed by a well-integrated functional matrix, albeit a much larger one than that found in non-cannibals. This may also be reflected by the conserved allometry of most cranial characters within and between cannibals and non-cannibal trajectories. Of particular interest, this mechanism does not necessitate a morphological or functional dichotomy between cannibals and non-cannibals because it may generate an entire range of head sizes, the "cannibal morph" merely occupying one extreme.

The smallest individuals in the current study exhibited a "cannibal's" wider head, with recurved teeth and a mounded vomerine patch at 20 mm TVL, a body size at which, I assume, individuals are incapable of cannibalism. Although Pierce et al. (1981) found no consistent genetic differences between cannibals and non-cannibals, the appearance of this highly derived cannibal dentition at such a small size suggests a genetic predisposition for the cannibal morphology, as opposed to a structural response to durophagy. However, the appearance of recurved teeth in cannibals is spurious at best, with recurved teeth appearing on one side of the mouth but not the other, only on the vomer, or on all of the dentigerous bones; and recurved teeth may appear randomly within an arcade of typical straight teeth in non-cannibals (Pedersen, 1991).

Dissection of the cannibal carcasses revealed that the external shape of the head was greatly influenced by the deposition of large fat deposits along the lateral aspect of the head as well as around the base of the gills at the back of the skull. This fat deposition in cannibals rounded-out the dorsal head profile into the "U-shape"

noted by many authors. I also observed that cannibal gills are hypertrophied in kind with the head, their description is curiously absent from the literature. Certainly, the extent to which these enlarged respiratory surfaces effect changes in cannibal growth rates, physiology, or feeding mechanics deserves further investigation.

To summarize, it is difficult to characterize what constitutes a "cannibal morph." Indeed, the distinction between large and small heads at any one TVL is arbitrary; dental recurvature is a developmental mosaic (Pedersen, 1991), whereas feeding performance and head shape are apparently conserved (Reilly et al., 1992). I argue that the term "cannibal" can only refer to the ingestion of conspecifics. I strongly agree with Reilly et al. (1992) in that any attempt to "pigeon-hole" the extremes in dental and cranial morphology into an identifiable trophic subset of a polymorphic system would be, at the very least, misleading.

I wish to thank J. Hanken and S. Reilly for providing invaluable commentary on the project and on very early drafts of the manuscript. I also thank J. Collins, M. Lannoo, J. Mitton, B. Pierce, and S. Wu, for providing resource material. Additional thanks go to R. Wilkinson, D. Cundall, S. Nyman, P. Freeman, C. Lemen, R. Adams and an anonymous reviewer for their advice and patience. Supported by NIH grant 1 R23 DE07190 to J. Hanken.

#### LITERATURE CITED

- ANDREWS, P. 1987. Aspects of hominoid phylogeny. Pp. 23–54, in *Molecules and morphology: conflict or compromise* (C. Patterson, ed.). Cambridge Univ. Press, Cambridge.
- BLECHSCHMIDT, E. 1976a. Principles of biodynamic differentiation. Pp. 54–76, in *Development of the basicranium* (J. Bosma, ed.). Pub. No. (NIH) 76-989, U.S. Dept. Health, Education and Welfare, Washington, D.C.
- BLECHSCHMIDT, M. 1976b. Biokinetics of the developing basicranium. Pp. 44–53, in *Development of the basicranium* (J. Bosma, ed.). *Ibid.*
- BOSMA, J. 1976. Introduction to the symposium. Pp. 3–28, in *Development of the basicranium* (J. Bosma, ed.). *Ibid.*
- BRAGG, A. 1964. Further study of predation and cannibalism in spadefoot tadpoles. *Herpetologica*, 20:17–24.
- COLLINS, J. 1980. *Ambystoma tigrinum*: a multispecies conglomerate. *Copeia*, 1980:938–941.
- COLLINS, J., AND J. CHEEK. 1983. Effect of food density on development of typical and cannibalistic salamander larvae in *Ambystoma tigrinum nebulosum*. *Amer. Zool.*, 23:77–84.
- COLLINS, J., AND J. HOLOMUZKI. 1984. Intraspecific variation in diet within and between trophic morphs in larval tiger salamanders (*Ambystoma tigrinum nebulosum*) *Canadian J. Zool.*, 62:168–174.
- DARWIN, C. 1909. *The descent of man*. Second ed. Murray, London.
- DUBRUL, E., AND D. LASKIN. 1961. Preadaptive potentialities of the mammalian skull: an experiment in growth and form. *Amer. J. Anat.*, 109:117–132.
- FELDMAN, D., J. GAGNON, R. HOFMAN, AND J. SIMSON. 1988. *STATVIEW*, the solution for data analysis and presentation graphics. Abacus Concepts, Berkeley, California.
- GEHLBACH, F. 1967. *Ambystoma tigrinum* (Green). Tiger salamander. *Cat. Amer. Amphibians and Reptiles*, 52.1–52.4.
- HANKEN, J. 1983. Miniaturization and its effects on cranial morphology in plethodontid salamanders, genus *Thorius* (Amphibia, Plethodontidae): II. The fate of the brain and sense organs and their role in skull morphogenesis and evolution. *J. Morph.*, 177: 255–268.
- HANKEN, J., AND R. WASSERSUG. 1981. The visible skeleton. *Funct. Photog.*, 4:22–26.
- HOLOMUZKI, J., AND J. COLLINS. 1987. Trophic dynamics of a top predator, *Ambystoma tigrinum nebulosum* (Caudata: Ambystomatidae), in a lentic community. *Copeia*, 1987:949–957.
- LANNOO, M. 1985. Neuromast topography in *Ambystoma* larvae. *Copeia*, 1985:535–539.
- LANNOO, M., AND M. BACHMANN. 1984. Aspects of cannibalistic morphs in a population of *Ambystoma t. tigrinum* larvae. *Amer. Midland. Nat.*, 122:103–109.
- MOSS, M. 1960. Functional analysis of human mandibular growth. *J. Prosth. Dent.*, 10:1149–1159.
- . 1975. Functional anatomy of cranial synostosis. *Child's Brain*, 1:22–33.
- . 1976. Experimental alteration of basi-synchondrosal cartilage growth in rat and mouse. Pp. 541–569, in *Development of the basicranium* (J. Bosma, ed.). Publ. No. (NIH) 76-989, U.S. Dept. Health, Education and Welfare, Washington, D.C.
- MÜLLER, G. 1990. Developmental mechanisms: a side-effect hypothesis. Pp. 99–130, in *Evolutionary innovations* (M. Nitecki, ed.). Chicago Press, Chicago.
- PEDERSEN, S. 1991. Dental morphology of the cannibal morph in the tiger salamander, *Ambystoma tigrinum*. *Amphibia-Reptilia*, 12:1–14.
- PIERCE, B., J. MITTON, AND L. JACOBSON. 1983. Head shape and size in cannibal and non-cannibal larvae of the tiger salamanders from west Texas. *Copeia*, 1983:1006–1012.
- PIERCE, B., J. MITTON, AND F. ROSE. 1981. Allozyme variation among large, small and cannibal



- morphs of the tiger salamander inhabiting the Llano Estacado of West Texas. *Copeia*, 1981:590-595.
- POLIS, G. 1981. The evolution and dynamics of intraspecific predation. *Ann. Rev. Ecol. Syst.*, 12:225-251.
- POLIS, G., AND C. MYERS. 1985. A survey of intraspecific predation among reptiles and amphibians. *J. Herpetol.*, 19:99-107.
- POWERS, J. 1907. Morphological variation and its causes by *Ambystoma tigrinum*. *Stud. Zool. Lab. Univ. Nebraska, Lincoln* #71, 4:197-273.
- REILLY, S., G. LAUDER, AND J. COLLINS. 1992. Performance consequences of a trophic polymorphism: feeding behavior in typical and cannibal phenotypes of *Ambystoma tigrinum*. *Copeia*, 1992:672-679.
- ROSE, F., AND D. ARMENTROUT. 1976. Adaptive strategies of *Ambystoma tigrinum* Green inhabiting the Llano Estacado of West Texas. *J. Anim. Ecol.*, 45:713-729.
- SEMLITSCH, R., AND J. CALDWELL. 1982. Effects of density on growth, metamorphosis, and survivorship in tadpoles of *Scaphiopus holbrooki*. *Ecology*, 63:905-911.
- SILVER, P. 1962. *In ovo* experiments concerning the eye, the orbit and certain juxta-orbital structures in the chick embryo. *J. Emb. and Exp. Morph.*, 10:423-450.
- THOROGOOD, P. 1988. The developmental specification of the vertebrate skull. *Development (Supplement)*, 103:141-153.
- WILKINSON, L. 1990. SYSTAT: the system for statistics. Evanston, Illinois.