

## Dental Morphologies in Gartersnakes (*Thamnophis*) and Their Connection to Dietary Preferences

E. J. BRITT,<sup>1</sup> A. J. CLARK, AND A. F. BENNETT

Department of Ecology and Evolutionary Biology, University of California, 321 Steinhaus Hall,  
Irvine, California 92697 USA

**ABSTRACT.**—We examined morphological variation in tooth structure in four populations of garter snakes (genus *Thamnophis*) with diverse feeding habits and tested the hypothesis that morphological homoplasy evolved in the malacophagous predators *Thamnophis ordinoides* and *Thamnophis elegans terrestris*. Although long, slender teeth are typical in Neotropical colubrid snake species that prey on slugs and snails, this morphological feature did not occur in *T. ordinoides* and *T. e. terrestris* relative to closely related garter snakes (the diet generalist *Thamnophis elegans elegans* and piscivore *Thamnophis couchii*). However, we did find pronounced posterior ridges located on the posterior maxillary teeth in the two slug predators but not in the generalist feeders. The evolutionary origin and functional advantage of these ridges has yet to be identified. The fish specialist *T. couchii* has many morphological features characteristic of adaptations for piscivory, such as long, sharper teeth and elongated mandible bones.

Skull and dental morphologies in snakes are especially constrained by prey size and shape, making the head a considerably important site for evolutionary adaptation in this group (Gans, 1961; Greene, 1997). Malacophagy, an exclusive diet of gastropods, presents multiple challenges for prey capture and processing. Most malacophagous snakes prefer feeding on slugs rather than snails to circumvent the mechanical demands of extracting prey from hard shells (Kofron, 1982; Sazima, 1989). Although slugs are soft-bodied and slow-moving, they are of low nutritional value and are difficult to capture and digest (Arnold, 1993; Britt and Bennett, 2008). Despite these constraints, many malacophagous species of the Colubroidea are morphologically and behaviorally adapted for preying on terrestrial gastropods (Laporta-Ferreira and Salomao, 2004).

Malacophagy has arisen independently several times across distantly related families of colubroids. Among the most recognized gastropod specialists are the Asian pareatines and Neotropical dipsadines and xenodontines, all of which use slow, unilateral movements when feeding on slugs and snails (Sazima, 1989; Hoso, 2007). Long, slender teeth in slug-eating snakes have been hypothesized to be adaptations for properly gripping the slippery, mucus-secreting integument of prey (Zweifel, 1954; Laporta-Ferreira et al., 1986; do Amaral, 1999). Long teeth in malacophagous snakes typically occur

on the anterior dentary and posterior maxilla (Cundall and Greene, 2000; Laporta-Ferreira and Salomao, 2004).

Although slug specialization occurs in some North American snakes, the morphologies and functionalities associated with this dietary preference are unclear (Rossman and Myer, 1990). Slugs and earthworms are preyed on by the natricine genera *Storeria*, *Virginia*, and a few species of *Thamnophis* (*Thamnophis ordinoides*, *Thamnophis butleri*, and coastal populations of *Thamnophis elegans*) (Arnold, 1981). *Contia tenuis* (Sharp-Tailed Snake), a small secretive snake of the Pacific Coast region, also feeds heavily on slugs and possesses long needlelike teeth (Zweifel, 1954; Greene, 1997; Stebbins, 2003). Furthermore, two abundant species of *Storeria* that feed on snails, slugs, and earthworms in the eastern United States have been documented as having proportionately longer, slender teeth with a shallow maxilla (Rossman and Myer, 1990; do Amaral, 1999). Although these studies clearly describe tooth surface features and behavioral feeding habits in malacophagous species, quantitative descriptions of tooth length proportions are surprisingly minimal or absent (Rossman and Myer, 1990).

In this study, we used scanning electron microscopy (SEM) and principal components analysis (PCA) to assess the relationship between tooth morphology and diet from four populations of gartersnakes: *Thamnophis elegans terrestris*, *Thamnophis elegans elegans*, *Thamnophis couchii*, and *T. ordinoides*. *Thamnophis ordinoides*, the Northwestern Gartersnake, is a specialist on banana slugs (*Ariolimax* spp.) occurring in coastal areas of the Pacific Northwest (Rossman

<sup>1</sup> Corresponding Author. Present address: Archbold Biological Station, PO Box 2057, Lake Placid, Florida 33862 USA; E-mail: ebritt@cas.usf.edu

et al., 1996). *Thamnophis couchii*, the Sierra Gartersnake, is a piscivorous aquatic species occurring in riparian habitats throughout the Sierra Nevada mountain range in California (Rossman et al., 1996). *Thamnophis elegans*, the Terrestrial Gartersnake, is commonly regarded as a prey generalist, although populations in the Pacific Northwest specialize on the very abundant *Ariolimax* (Arnold, 1977). The trophic generalist inland populations (*T. e. elegans*) eat mostly fish and anurans, whereas the coastal populations (*T. e. terrestris*) are thought to be a model example of a vertebrate population in the process of niche contraction, in which geographically isolated populations specialize on slugs, leading to adaptations for slug predation (Arnold, 1981). Therefore, we expected an evolutionary divergence in tooth morphology in which the two slug predators in our study (*T. e. terrestris* and *T. ordinoides*) have longer, more slender teeth than the two other gartersnakes (*T. e. elegans* and *T. couchii*).

#### MATERIALS AND METHODS

Specimens of *T. ordinoides* (slug specialists) were collected near Ellmaker State Park, Lincoln County, Oregon. *Thamnophis couchii* (fish specialists) were collected near the Susan River, Lassen County, California. *Thamnophis elegans elegans* (inland generalist population of *T. elegans*) were collected near Eagle Lake, Lassen County, California. *Thamnophis elegans terrestris* (coastal slug specialist population of *T. elegans*) were collected near the mouth of the Mad River in northern California. All specimens were collected on California Department of Fish and Game Permit SC 006587 and were previously used in an energetic study (Britt and Bennett, 2008).

Skulls from 12 *T. ordinoides* (six male, six female), eight *T. couchii* (four male, four female), 11 *T. e. elegans* (six male, five female), and 11 *T. e. terrestris* (five male, six female) were cleared and stained (Dingerkus and Uhler, 1977). One mandible (dentary and compound) and one maxilla were removed from each snake and

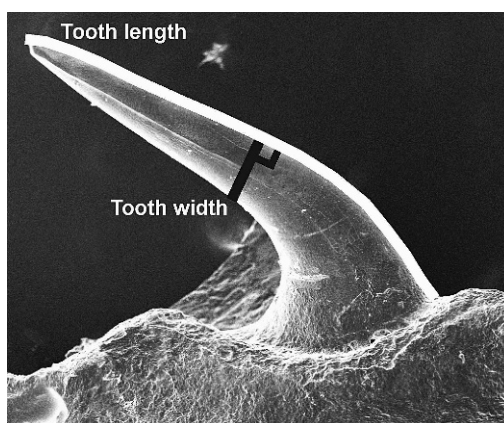


FIG. 1. Metrics for measuring tooth length (L) and tooth width (black line) (W). Tooth length is the distance along the anterior edge of the tooth between the base and tip. Tooth width is the perpendicular distance between the anterior edge at midlength and the posterior edge of the tooth.

rinsed with distilled water followed by reagent alcohol before examination with a scanning electron microscope. SEM analysis was performed at the Carl Zeiss Center of Excellence at the University of California, Irvine, using a Zeiss EVO 50 SEM. All imaging was in the secondary mode in dry, high vacuum conditions using an acceleration voltage of 10 kV.

Length measurements of tooth length, tooth width, mandible length and depth, and maxilla length and depth were performed with ImageJ® (Rasband, 1997). We used multiple (two or three) sequential SEM images for measuring mandible length. The length of the maxilla was measured in a single image. Tooth length and width were measured from the three anterior most teeth on the dentary bone and the three posterior most teeth on the maxilla. The teeth we measured in this study were selected because of their functional significance during swallowing and handling prey (Wright et al., 1979). Tooth length was measured as the distance along the anterior edge of the tooth between the base (attachment) and the tip of the

TABLE 1. Length (mm) and depth (mm) of mandible and maxilla bones of four garter snake populations. Entries are mean values  $\pm$  SE. For each variable, superscript letters that are shared denote nonsignificant ( $P > 0.05$ ) differences between means as determined from pairwise comparisons. Significance levels are from analysis of covariance of distance versus SVL between populations. *P*-values in bold indicate populations are significantly different.

Variable	<i>T. e. terrestris</i>	<i>T. e. elegans</i>	<i>T. couchii</i>	<i>T. ordinoides</i>	<i>P</i> -value
Mandible length	18.65 $\pm$ .95	19.28 $\pm$ .54	21.04 $\pm$ .97	15.91 $\pm$ .76	0.612
Mandible depth	0.97 $\pm$ .04 <sup>A</sup>	1.15 $\pm$ .05 <sup>B</sup>	1.24 $\pm$ .07 <sup>B</sup>	0.90 $\pm$ .04 <sup>A</sup>	<b>0.007</b>
Maxilla length	9.44 $\pm$ .42 <sup>A</sup>	9.33 $\pm$ .19 <sup>A</sup>	10.59 $\pm$ .42 <sup>A</sup>	7.40 $\pm$ .35 <sup>B</sup>	<b>0.009</b>
Maxilla depth	0.52 $\pm$ .04	0.63 $\pm$ .08	0.47 $\pm$ .04	0.40 $\pm$ .04	0.099

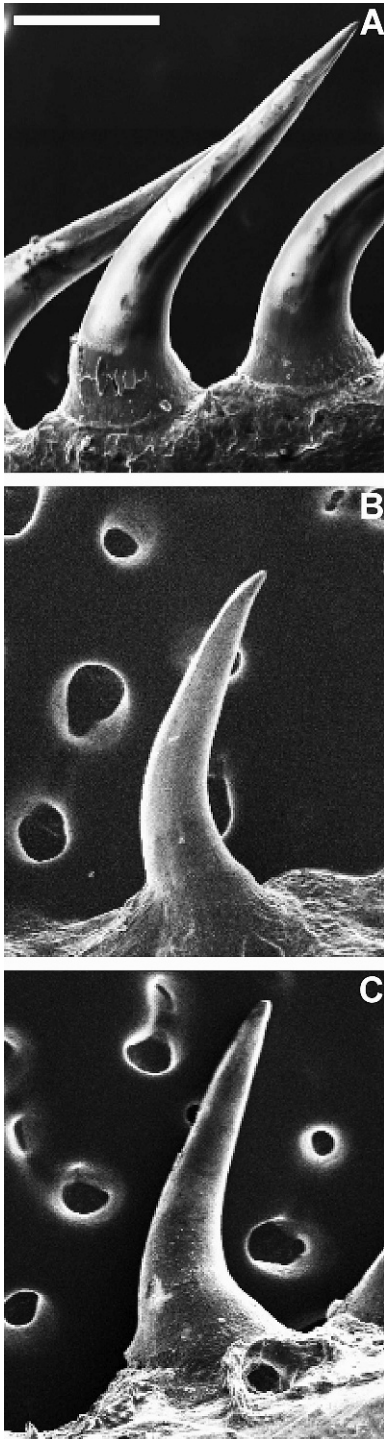


FIG. 2. The three main tooth types of *Thamnophis* populations in this study. (A) recurved, taken from middle maxilla of *Thamnophis couchii*; (B) curved, taken from anterior dentary of *Thamnophis elegans elegans*; and (C) linear, taken from posterior maxilla of *T. e. elegans*. Bar = 300  $\mu$ m.

tooth (Fig. 1). Tooth width was defined as the perpendicular distance between the anterior edge at midlength and the posterior edge of the tooth (Fig. 1). Each measurement of distance was the mean of three measurement trials. Images of all dentary teeth were taken from lingual view, and images of all maxillary teeth were taken from labial view. We also measured maxilla depth at the prefrontal articulation and mandible depth at the joint between dentary and compound. Maxilla and dentary depth were recorded because shallow bones may cause the teeth to appear longer and may be functionally important for malacophagous diets (Rossman and Myer, 1990). In addition to the gartersnakes, we obtained mandibles from a single specimen of the slug specialist *Contia tenuis* from the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ Herp 80921). Then, we compared dentary tooth size and structure with that of the gartersnakes.

Univariate ANCOVA tests were performed for measurements of both mandible and maxilla lengths and depths using population as the fixed factor and snout-vent length (SVL) as the covariate. Multivariate (MANCOVA) statistics were used for tooth length and width measurements from the gartersnakes, using population as the fixed factor and SVL as the covariate. Each *F*-test was based on the linearly independent pairwise comparisons among the estimated marginal means. PCA was performed using tooth length, tooth width, and SVL. PCA was carried out from the correlation matrix and used to separate taxonomic groups based on morphology. Then, we plotted the variation in tooth structure among snake populations in relation to the first three principal components. Analyses were performed with SPSS 12.0 for Windows; significance was assessed at  $P = 0.05$ .

## RESULTS

There was considerable variation in body mass among the four *Thamnophis* populations, ranging from  $13.6 \pm 1.43$  g (mean  $\pm$  SE, range 6.1–22) for *T. ordinoides* to  $22.6 \pm 2.95$  g (mean  $\pm$  SE, range 11.1–39.6) for *T. e. terrestris*, suggesting that the animals varied between relatively small and large adults. Snout-vent length correlates with body mass among the populations; however, *T. couchii* were longer and slimmer than the other species. Snout-vent length was used in our statistical procedures because it was a better indicator of size and less dependent on the health and dietary condition of the snake. We found significant variation in relative mandible depth and maxilla length (ANCOVA:  $F_{3,36} = 4.75$ ,  $P = 0.007$ ;  $F_{3,36} = 4.47$ ,  $P = 0.009$ ;

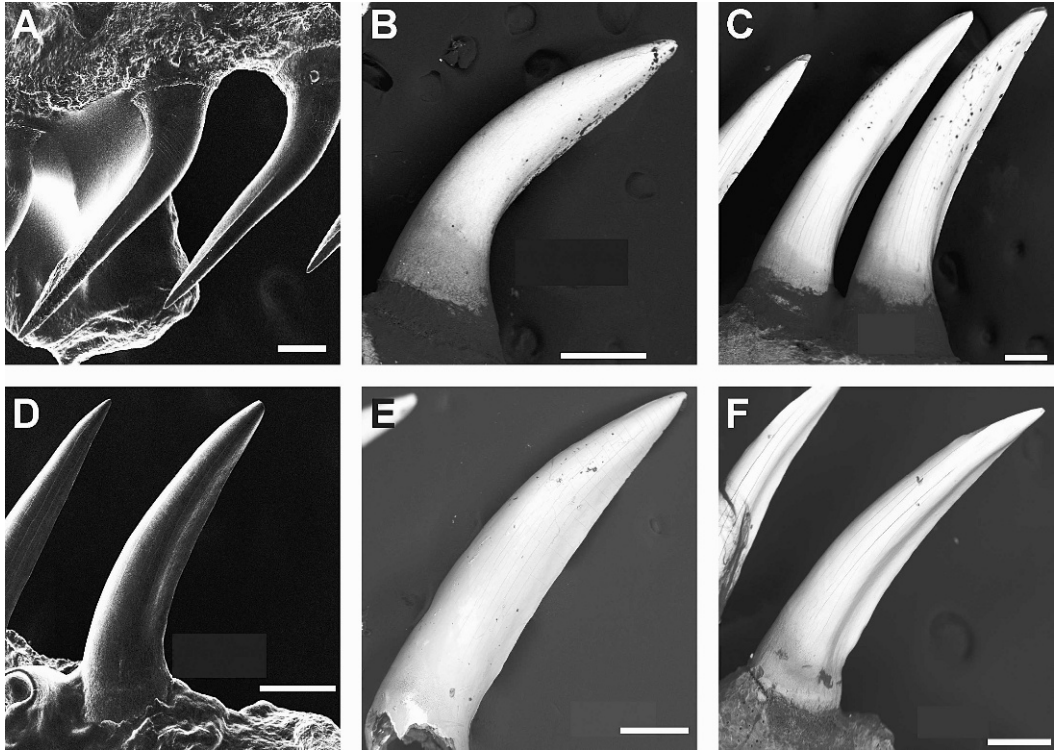


FIG. 3. (A) Dental ridges located on the labial side of the teeth, viewed from middle maxilla from *Thamnophis couchii*, also found in teeth occurring on both maxilla and dentary. (B–F) Labial view of posterior dental ridges found in most posterior maxilla teeth. *Thamnophis elegans elegans* (B–C); *Thamnophis ordinoides* (D); *Thamnophis elegans terrestris* (E); *T. couchii* (F). Bar = 200  $\mu$ m.

respectively), with *T. ordinoides* having thin, short mandibles (Table 1).

Surface features of the teeth in all populations were similar to those previously reported in *T. elegans* (Wright et al., 1979). Three basic tooth

types (linear, curved, and recurved) were observed in all four populations: dentary teeth were typically linear or curved, whereas maxillary teeth were curved at the anterior end, recurved, or curved in the middle and linear or

TABLE 2. Body mass, tooth length and width of the three most anterior teeth on the dentary, and the three most posterior teeth on the maxilla. The row just below each tooth length denotes the corresponding tooth width. All measurements of distance are in units of mm. Entries are mean values  $\pm$  SE. For each variable, superscript letters that are shared denote nonsignificant ( $P < 0.05$ ) differences between means as determined from planned pairwise comparisons after analysis of covariance.  $P$ -values in bold indicate populations are significantly different.

Population	Mass (g)	Dentary			Maxilla		
		Anterior	Middle	Posterior	Anterior	Middle	Posterior
<i>T. e. terrestris</i>	22.62 $\pm$ 2.94	1.00 $\pm$ 0.06	1.05 $\pm$ 0.06	1.07 $\pm$ 0.07	1.28 $\pm$ 0.06	1.53 $\pm$ 0.07 <sup>A</sup>	1.48 $\pm$ 0.08 <sup>A</sup>
		0.16 $\pm$ 0.01 <sup>A</sup>	0.16 $\pm$ 0.01 <sup>A</sup>	0.16 $\pm$ 0.01 <sup>AB</sup>	0.17 $\pm$ 0.01	0.22 $\pm$ 0.01 <sup>A</sup>	0.22 $\pm$ .01 <sup>A</sup>
<i>T. e. elegans</i>	22.26 $\pm$ 2.08	1.00 $\pm$ 0.03	1.05 $\pm$ 0.03	1.05 $\pm$ 0.03	1.32 $\pm$ 0.05	1.50 $\pm$ 0.06 <sup>A</sup>	1.60 $\pm$ 0.04 <sup>A</sup>
		0.17 $\pm$ 0.01 <sup>A</sup>	0.17 $\pm$ 0.01 <sup>A</sup>	0.17 $\pm$ 0.01 <sup>A</sup>	0.18 $\pm$ 0.01	0.22 $\pm$ 0.01 <sup>A</sup>	0.24 $\pm$ .01 <sup>A</sup>
<i>T. couchii</i>	18.6 $\pm$ 3.32	1.04 $\pm$ 0.06	1.08 $\pm$ 0.07	1.09 $\pm$ 0.06	1.19 $\pm$ 0.11	1.34 $\pm$ 0.12 <sup>B</sup>	1.34 $\pm$ 0.10 <sup>B</sup>
		0.13 $\pm$ 0.01 <sup>B</sup>	0.13 $\pm$ 0.01 <sup>B</sup>	0.13 $\pm$ 0.01 <sup>C</sup>	0.16 $\pm$ 0.02	0.19 $\pm$ 0.01 <sup>AB</sup>	0.18 $\pm$ 0.01 <sup>B</sup>
<i>T. ordinoides</i>	13.64 $\pm$ 1.43	0.889 $\pm$ 0.05	0.94 $\pm$ 0.05	0.94 $\pm$ 0.05	1.01 $\pm$ 0.07	1.05 $\pm$ 0.06 <sup>B</sup>	1.09 $\pm$ 0.06 <sup>B</sup>
		0.13 $\pm$ 0.01 <sup>A</sup>	0.14 $\pm$ 0.01 <sup>AB</sup>	0.14 $\pm$ 0.01 <sup>BC</sup>	0.13 $\pm$ 0.01	0.15 $\pm$ 0.01 <sup>B</sup>	0.16 $\pm$ 0.01 <sup>B</sup>
ANCOVA (Tooth L)		$P = 0.918$	$P = 0.853$	$P = 0.816$	$P = 0.056$	<b><math>P = 0.002</math></b>	<b><math>P = 0.001</math></b>
ANCOVA (Tooth W)		<b><math>P = 0.003</math></b>	<b><math>P = 0.008</math></b>	<b><math>P = 0.001</math></b>	$P = .053$	<b><math>P = 0.006</math></b>	<b><math>P = 0.001</math></b>

TABLE 3. The eigenvectors associated with the principal component loading of the six tooth lengths and widths, snout-vent length (SVL), and mandible length describing tooth structure and the amount of variation explained by the first two principal components. Morphological variables are listed in decreasing order of PC1 eigenvectors.

Variable	PC1	PC2	PC3
Posterior maxilla tooth L	0.914	-0.006	-0.237
Middle maxilla tooth L	0.902	0.016	-0.357
Anterior maxilla tooth L	0.89	0.135	-0.241
Posterior dentary tooth L	0.88	0.25	0.297
Anterior maxilla tooth W	0.877	0.006	-0.257
Middle dentary tooth L	0.87	0.279	0.301
Posterior maxilla tooth W	0.87	-0.214	-0.148
Anterior dentary tooth W	0.87	-0.277	0.292
Anterior dentary tooth L	0.856	0.277	0.312
Middle dentary tooth W	0.852	-0.374	0.255
Posterior dentary tooth W	0.851	-0.34	0.193
Middle maxilla tooth W	0.849	-0.21	-0.312
Snout-vent length	0.575	0.657	-0.093

curved at the posterior end (Fig. 2). In all four populations, the two most posterior maxilla teeth are the longest in the mouth and bear distinctive posterior ridges that give the teeth a bladelike appearance (Fig. 3). Posterior-most maxillary teeth from the malacophagous populations *T. ordinoides* and *T. e. terrestris* possessed prominent posterior dental ridges that were longer and deeper than those from the other populations. However, Figure 3F shows that *T. couchii* possessed long but shallow posterior ridges. In all species examined, the maxilla and dentary teeth contained two short dental ridges that extend along the labial and lingual distal third of the tooth (Fig. 3A).

There was no indication that the teeth of the slug eaters, *T. ordinoides* and *T. elegans terrestris*, were longer or more slender than those of the nonslug-eating populations. However, the piscivorous *T. couchii* exhibited a higher density of teeth per jaw bone and more curved teeth than other populations. On average, the posterior most maxilla teeth in both populations of *T. elegans* were longer than those in *T. couchii* and *T. ordinoides* (Table 2). *Thamnophis ordinoides* had significantly shorter middle and posterior maxilla teeth than did both *T. elegans* populations (MANCOVA:  $F_{3,36} = 6.09$ ,  $P = 0.002$ ;  $F_{3,36} = 7.30$ ,  $P = 0.001$ ; respectively; Table 2). Table 2 also shows that both *T. elegans* populations exhibited significantly larger teeth (measured as width at midlength) than did *T. ordinoides*. Both *T. elegans* populations also had wider posterior maxilla teeth (MANCOVA:  $F_{3,36} = 7.19$ ,  $P = 0.001$ ) did than *T. couchii* and larger middle and posterior maxilla teeth (width and length) than did *T. ordinoides* (Table 2).

The first principal component (PC1) for tooth length, tooth width, and snout-vent length explained 72.9% of the total variance (Table 3).

The second principal component (PC2) and third principal component (PC3) explained 8.4% and 6.9% of the total variance, respectively (Table 3). PC1 was an indicator of size variance, showed approximately equal positive loadings on all variables, and was most highly correlated with maxilla tooth length and moderately correlated with snout-vent length. The second and third principal components were indicative of shape variance. PC2 showed positive loadings for SVL and dentary tooth length and negative loadings for dentary and maxilla tooth width (Table 3). PC3 showed mostly weak positive loadings for dentary tooth width. The plot of principal components demonstrates that *T. couchii* has longer and more slender dentary teeth and marginally shorter maxilla teeth when rescaled to SVL did than the other populations (Fig. 4). The plot also shows that the two populations of *T. elegans* had longer maxilla teeth and were clustered with each other more than any other pair of populations. Individuals of *T. ordinoides* also tended to cluster in the PCA plots. SEM images show that our slug-eating populations do not have similar dental features and proportions as that of *C. tenuis* (Fig. 5); however, this comparison is based on one individual *C. tenuis* specimen and should be viewed only as a preliminary analysis. Unlike the garter snakes, *C. tenuis* displayed long, conical shaped anterior dentary teeth, as consistent with previous reports (Zweifel, 1954).

#### DISCUSSION

All four *Thamnophis* populations from this study show the typical surface features and tooth organizational patterns found in earlier accounts of *T. elegans* (Wright et al., 1979). All three basic tooth types were identified and were

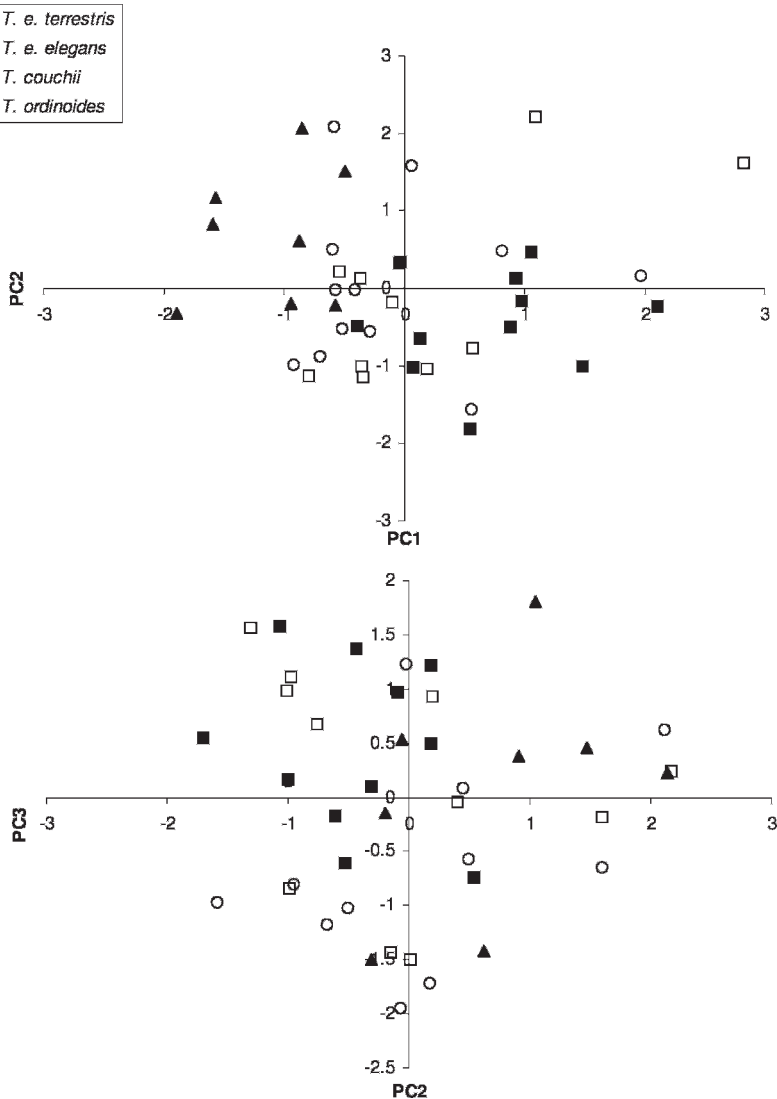


FIG. 4. Variation in tooth structure among garter snake populations in relation to the first three principal components of six tooth lengths, six tooth widths, and snout-vent length.

in similar positions along the maxilla and dentary. Despite the presence of three typical tooth shapes and overall similarities in their position, we found that the teeth from *T. couchii* were more numerous, narrower, and predominantly curved or recurved. The dental morphologies we observed in *T. couchii* are consistent with previous observations of fish specialists (Savitsky, 1983).

We did not find any evidence that relatively long, slender teeth occur in *T. ordinoides* and *T. e. terrestris*. The extensive accounts for relatively long, slender teeth in slug-eating colubrids are largely based on observations of Neotropical

species and other thanmophiine snakes (Laporta-Ferreira and Salomao, 2004). Although there has been no demonstration that long teeth are functionally advantageous in slug predation, most studies agree that long, thin teeth and thin, flexible jaws are well suited for snail extraction (Peters, 1960; Sazima, 1989; Rossman and Myer, 1990; do Amaral, 1999). None of the malacophagous species from our study is known to feed on snails and, therefore, would not be expected to have been selected for functional specializations involved with snail extraction. Although our gartersnakes, including the two malacophagous species in this

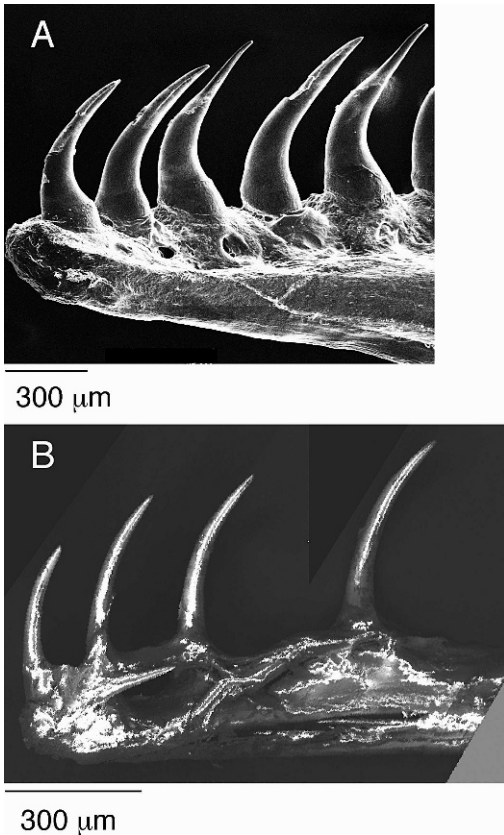


FIG. 5. SEM images of the anterior portion of the mandible from (A) *Thamnophis ordinoides* and (B) *Contia tenuis*. Similar to the other garter snake populations in this study, *T. ordinoides* has larger teeth at the base than the slender teeth of *C. tenuis*.

study, lacked noticeably long, slender teeth, both slug-eating species possessed a more pronounced ridge located on the trailing edge of the posterior maxillary tooth (Fig. 3).

All populations we observed had relatively long posterior maxillary teeth, which are the first teeth to contact prey during intraoral transport (Wright et al., 1979). The posterior ridge or fluting on the posterior maxilla teeth are common among colubrids (Jackson and Fritts, 1995) and have been attributed to both an advantage in disengagement of slippery, viscous prey during swallowing (Vaeth et al., 1985) and engagement of prey during capture (Jackson and Fritts, 2004). The ridge structure we observed could be advantageous in grasping and swallowing prey by facilitating deeper penetration, which in turn could aid in the delivery of saliva produced in the Duvernoy's gland (Wright et al., 1979; do Amaral, 1999). Ridges and grooves (depressions formed by two

ridges in close proximity to one another) on posterior maxilla teeth are thought to be associated with Duvernoy's glands, because few species bearing Duvernoy's glands lack ridged or grooved posterior maxilla teeth (Vest, 1981; Young and Kardong, 1996; Kardong, 2002). The functional roles of dental ridges in feeding may vary between species. For example, individuals of *Oligodon formosanus* (an egg-eating colubrid) use their enlarged and ridged posterior maxilla teeth for cutting slits on egg shells for extracting yolk (Coleman et al., 1993). It has been proposed that ridged surfaces increase surface area for enamel deposition, which in turn may increase tooth strength (Folinsbee et al., 2007); however this would be unlikely in the case of a slug predator.

Capturing and intraorally transporting extremely sticky prey are mechanically challenging aspects of slug foraging. *Thamnophis ordinoides* and *T. e. terrestris* may rely more on tooth surface features (prominent ridges) than tooth dimensions for handling slugs. Presumably the teeth in our slug specialists deviate from the Neotropical species because of prey differences—perhaps slug species preyed upon by the Neotropical predators are different in size, shape, mucus, integument strength, etc. The properties of mollusks may impose limits to how snake teeth can be developed. For example, Neotropical slug integument may have greater puncture resistance and, therefore, require predators with narrow teeth, which have smaller cross-sectional area for applying greater stress on tissue. Also, there is evidence that these species are physiologically adapted for digesting slug prey (Britt and Bennett, 2008). A potential avenue for assessing the functionalities associated with thamnophine dietary preference for slugs is to study cranial kinematic profiles during foraging, in as much as previous observations on feeding mechanics in *Thamnophis* have focused on axial kinematics (Drummond, 1983; Alfaro, 2002, 2003). Comparing Duvernoy's gland toxicity among species and studying puncture mechanics in ridged teeth may also provide some insight into possible selective pressures involved in malacophagy.

*Acknowledgments.*—We thank A. Summers and K. Jackson for suggestions with the manuscript. We also thank S. Arnold, A. Bronikowski, and their field assistants for help in locating and capturing our study animals. All our study animals were previously used in research projects reported by the first author. Also, we would like to thank C. Zeiss Center for Excellence for providing the use of their SEM equipment. This work was supported by National Science Foundation grant IBN 0091308 to AFB and J. W. Hicks.

## LITERATURE CITED

- ALFARO, M. E. 2002. Forward attack modes of aquatic feeding garter snakes. *Functional Ecology* 16:204–215.
- . 2003. Sweeping and striking: a kinematic study of the trunk during prey capture in three thamnophiine snakes. *Journal of Experimental Biology* 206:2381–2392.
- ARNOLD, S. J. 1977. Polymorphism and geographic variation in the feeding behavior of the garter snake *Thamnophis elegans*. *Science* 197:676–678.
- . 1981. The microevolution of foraging behavior. In A. Kamil and T. Sargent (eds.), *Foraging Behavior: Ecological, Ethological, and Psychological Approaches*, pp. 409–453. Garland Press, New York.
- . 1993. Foraging theory and prey size-predator size relations in snakes. In R. A. Seigel and J. T. Collins (eds.), *Snakes: Ecology and Behavior*, pp. 87–115. McGraw-Hill, New York.
- BRITT, E. J., AND A. F. BENNETT. 2008. The energetic advantages of slug specialization in garter snakes (genus *Thamnophis*). *Physiological and Biochemical Zoology* 81:247–254.
- COLEMAN, K., L. A. ROTHFUSS, H. OTA, AND K. V. KARDONG. 1993. Kinematics of egg-eating by the specialized Taiwan snake *Oligodon formosanus* (Colubridae). *Journal of Herpetology* 27:320–327.
- CUNDALL, D., AND H. W. GREENE. 2000. Feeding in snakes. In K. Schwenk (ed.), *Feeding—Form, Function and Evolution in Tetrapod Vertebrates*, pp. 293–333. Academic Press, San Diego, CA.
- DINGERKUS, G., AND L. D. UHLER. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. *Stain Technology* 52:229–231.
- DO AMARAL, J. P. S. 1999. Lip-curling in Redbelly Snakes (*Storeria occipitomaculata*): functional morphology and ecological significance. *Journal of Zoology*, London 248:289–293.
- DRUMMOND, H. 1983. Aquatic foraging in garter snakes: a comparison of specialists and generalists. *Behaviour* 86:1–30.
- FOLINSBEE, K. E., J. MULLER, AND R. R. REISZ. 2007. Canine grooves: morphology, function, and relevance to venom. *Journal of Vertebrate Paleontology* 27:547–551.
- GANS, C. 1961. The feeding mechanism of snakes and its possible evolution. *American Zoologist* 1:217–227.
- GREENE, H. W. 1997. *The Evolution of Mystery in Nature*. University of California Press, Berkeley.
- HOSO, M. 2007. Oviposition and hatchling diet of a snail-eating snake *Pareas iwasakii* (Colubridae: Pareatinae). *Current Herpetology* 26:41–43.
- JACKSON, K., AND T. H. FRITTS. 1995. Evidence from tooth surface morphology for a posterior maxillary origin of the proteroglyph fang. *Amphibia-Reptilia* 16:273–288.
- . 2004. Dentitional specializations for durophagy in the Common Wolf Snake, *Lycodon aulicus capucinus*. *Amphibia-Reptilia* 25:247–254.
- KARDONG, K. V. 2002. Colubrid snakes and Duvernoy's venom glands. *Journal of Toxicology: Toxin Reviews* 21:1–19.
- KOFRON, C. P. 1982. A review of the Mexican snail-eating snakes, *Dipsas brevifacies* and *Dipsas gaigeae*. *Journal of Herpetology* 16:270–286.
- LAPORTA-FERREIRA, I. L., AND M. G. SALOMAO. 2004. Reptilian predators of terrestrial gastropods. In G. M. Barker (ed.), *Natural Enemies of Terrestrial Gastropods*, pp. 427–481. CAB International, Oxfordshire, UK.
- LAPORTA-FERREIRA, I. L., M. G. SALOMAO, AND P. SAWAYA. 1986. *Biologia de Sibynomorphus* (Colubridae-Dipsadinae)-reproducao e habitos alimentares. *Brazilian Journal of Biology* 46:793–799.
- PETERS, J. A. 1960. *The Snakes of the Subfamily Dipsadinae*. Miscellaneous Publications of the Museum of Zoology, University of Michigan, Ann Arbor.
- RASBAND, W. S. 1997. ImageJ, U.S. National Institutes of Health, Bethesda, MD. Online data base available from <http://rsb.info.nih.gov/ij/>, 1997–2007.
- ROSSMAN, D. A., AND P. A. MYER. 1990. Behavioral and morphological adaptations for snail extraction in the North American brown snakes (Genus *Storeria*). *Journal of Herpetology* 24:434–438.
- ROSSMAN, D. A., N. B. FORD, AND R. A. SEIGEL. 1996. *The Garter Snakes: Evolution and Ecology*. University of Oklahoma Press, Norman.
- SAVITZKY, A. H. 1983. Coadapted character complexes among snakes: fossoriality, piscivory, and durophagy. *American Zoologist* 23:397–409.
- SAZIMA, I. 1989. Feeding behavior of the snail-eating snake, *Dipsas indica*. *Journal of Herpetology* 23:464–468.
- STEBBINS, R. C. 2003. *Peterson Field Guides, Western Reptiles and Amphibians*. 3rd ed. Houghton Mifflin Company, New York.
- VÆTH, R. H., D. A. ROSSMAN, AND W. SHOOP. 1985. Observations of tooth morphology in snakes. *Journal of Herpetology* 19:20–26.
- VEST, D. K. 1981. The toxic secretion of the Wandering Garter Snake, *Thamnophis elegans vagrans*. *Toxicon* 19:831–839.
- WRIGHT, D. L., K. V. KARDONG, AND D. L. BENTLEY. 1979. The functional anatomy of the teeth of the western Terrestrial Garter Snake, *Thamnophis elegans*. *Herpetologica* 35:223–228.
- YOUNG, B. A., AND K. V. KARDONG. 1996. Dentitional surface features in snakes (Reptilia: Serpentes). *Amphibia-Reptilia* 17:261–276.
- ZWEIFEL, R. G. 1954. Adaptation to feeding in the snake *Contia tenuis*. *Copeia* 1954:299–300.

Accepted: 19 September 2008.