

Dentitional surface features in snakes (Reptilia: Serpentes)

Bruce A. Young¹, Kenneth V. Kardong²

¹ Department of Biology, Lafayette College, Easton, PA 18042, USA

² Department of Zoology, Washington State University, Pullman, WA 99164-4236, USA

Abstract. The complexity of snake tooth morphology is more varied than has been recognized in functional, evolutionary, or taxonomic studies. We surveyed a broad sample of species across taxonomic groups to document and summarize the variation present. Our survey included a scoring of dentitional features of 1169 specimens representing 611 species of snakes on four dentiferous bones (dentary, pterygoid, palatine, maxilla). Besides presence or absence of teeth on these bones, we ranked the tooth type on each bone on the basis of a four category system: basic, furrowed, grooved, or hollow tooth. Basic teeth, without surface recesses or grooves, were the most common tooth type. Hollow teeth (fangs) were found most commonly on the maxilla and grooved teeth were often adjacent. Grooved teeth, when present, were found only on the maxilla although teeth with furrows, shallow creases in the surface enamel, were found in low numbers on the dentary, pterygoid, and palatine. Teeth exhibited further specializations, including multiple grooves, basal reinforcing ridges, development of a blade-like design, variation in the degree to which the secondary groove in hollow teeth might be in evidence, and variation in the position of the groove along the shaft of the tooth.

Introduction

The surface features of snake teeth have been used primarily in one of two contexts: evaluating the evolution of the ophidian feeding system, or as taxonomic characters. Workers exploring the evolution of the feeding system have typically focused on a presumed transitional sequence among the teeth: solid-grooved-caniculate (e.g., Boulenger, 1896; Sarkar, 1923; Smith, 1952; Anthony, 1955; Kroll, 1976; Kardong, 1980). Other workers (e.g., Van Denburgh and Thompson, 1908; Phisalix, 1912; Bogert, 1943; Underwood, 1967; Ernst, 1982) used surface features, or other aspects of selected teeth, as taxonomic characters to define, in part, groups of snakes.

These previous studies, whether the results were interpreted as taxonomic characters or as evidence of evolutionary transitions, often have two aspects in common. First, there has been a pronounced tendency to discuss only the dentitional features of the maxilla (Trauth, 1991). Little attention has been given to surface features of the teeth on the other dentition bearing bones of the ophidian skull (e.g., Peyer, 1968; Edmund, 1969). Second, the descriptions of the surface features have been based almost exclusively upon

a limited series of species. Our purpose therefore was to provide a broad survey of the dentitional surface features of snakes from a diverse group of specimens, and to survey all of the dentition bearing bones (except the premaxilla, see Smith et al., 1953; Schnabel and Herschel, 1955).

Materials and methods

Approach

Skeletal material from museums was examined following a three-step procedure. Initially, the specimens were examined at their respective museums by the first author (BAY) using available dissecting microscopes. Specimens were scored and any morphological variations noted. Secondly, selected museum specimens were taken out on loan and examined under a dissecting microscope by the second author (KVK) independently. Choice of these specimens was determined by any distinctive morphological variation, or scoring divergence among taxonomically related specimens. This double-scoring system enabled both authors to separately score most of the same specimens before comparing scores, resolving differences, and producing a composite score for all. Third, selected specimens illustrating the range of tooth variation were sputter coated with gold and examined under the scanning electron microscope.

Scoring System

The composite scores are based upon an examination of each tooth-bearing bone under a dissecting or electron microscope. Thus, for each specimen up to four pairs of bones were scored — dentary, pterygoid, palatine, and maxilla. Additionally, the maxilla was visually divided into equal thirds — anterior, middle, posterior — and the anterior and posterior thirds scored. The middle section of the maxilla was often transitional and too variable to score consistently. Therefore, the scored maxillary locations, anterior versus posterior, represent anatomical locations, cranial versus caudal, within the maxilla. For consistency of scoring, the functional fangs of Viperidae, Elapidae, and Hydrophiidae were considered to reside in the anterior region of the maxilla. The specific scoring system was based upon a graded series of morphological steps from 0 to 4 (see below). All teeth borne by a paired bone were examined and the highest score of any one of these teeth was the score assigned to that bone, or portion of the maxilla, for that particular specimen. Broken or missing teeth, or poor preparation of the museum specimen often reduced the number of teeth available for scoring in a particular specimen. The examined specimens were scored using the following series of categories with a common descriptor in parenthesis:

Type 0 Teeth - (edentulus). Type 0 was used to denote absence of tooth sockets.

Type 1 Teeth - (basic). Type 1 tooth lacked any surface depressions (fig. 1A).

Type 2 Teeth - (furrowed teeth). Type 2 teeth support a shallow primary furrow indented into the tooth's surface along at least a portion of the long axis of the tooth. This depression joined the surface of the tooth at a gradual angle and remained open to the surface of the tooth along its entire length (fig. 1B).

Type 3 Teeth - (grooved teeth). A depression, normally deep, was present in the surface of a Type 3 tooth for at least a portion of the middle third of the tooth. The lateral margin of the depression formed nearly a 90 degree angle with the outer surface of the tooth, and the entire length of the groove was open to the surface of the tooth (fig. 1C).

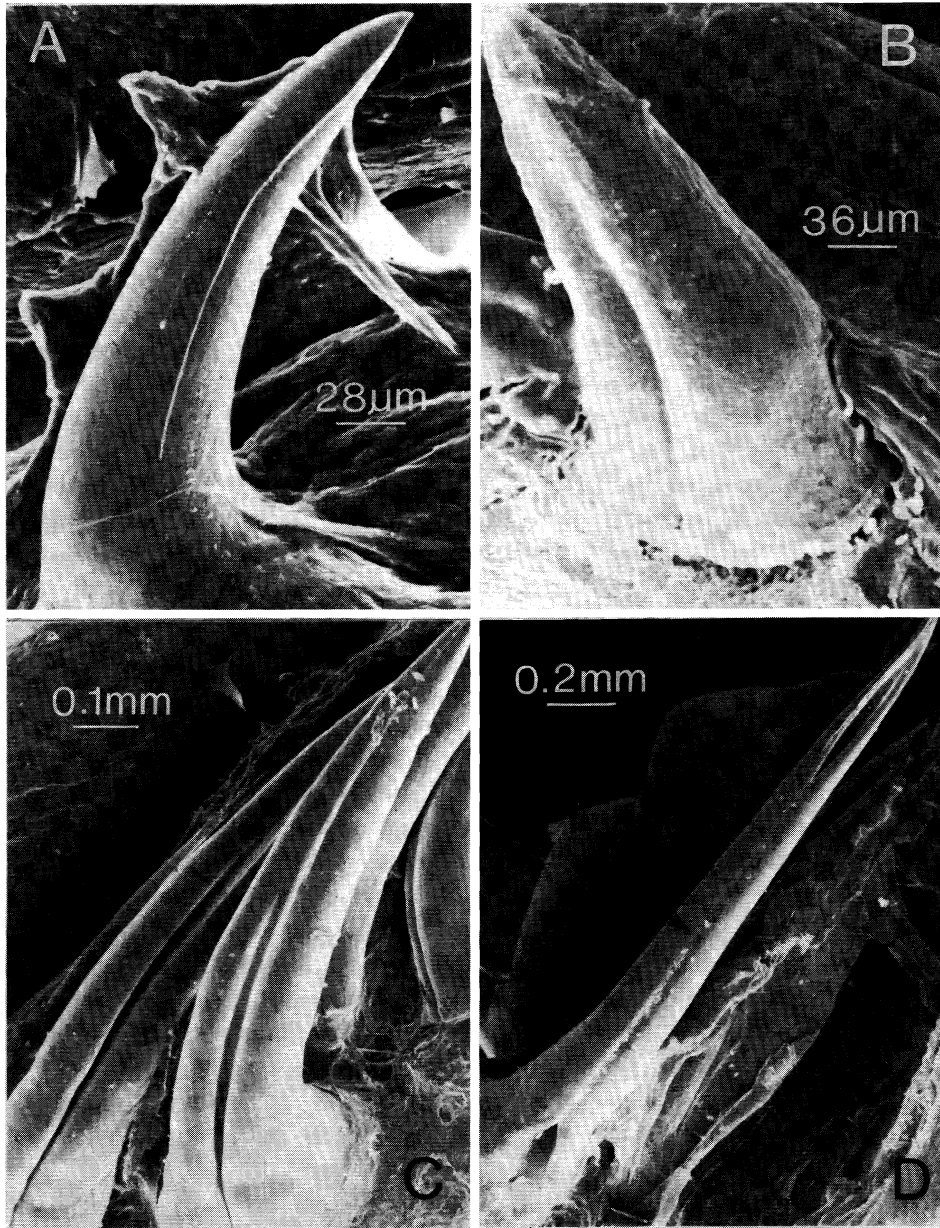
Type 4 Teeth - (hollow teeth). The Type 4 tooth was tubular, forming an enclosed channel within most or all of the middle third of the tooth. This internal channel was open at both ends, but in between, the tooth surface folded over this channel enclosing it and forming a secondary surface furrow where the contributing edges of the tooth folds met and fused (fig. 1D).

Several types of teeth examined fell outside of this scoring system. For example, Type 4 teeth from some viperid species exhibited complete fusion of the surface enamel over the venom channel, leaving no evidence of a secondary furrow. Such teeth lacking visual evidence of a secondary, surface furrow were scored as Type 5 teeth and entered in table 1 among subfamilies where they occurred. However, very few teeth fell outside our scoring system. Because of their infrequency and apparent unique character, these specialized teeth were therefore treated separately.

Dental terminology follows Edmund (1969) modified by Wright et al. (1979) wherein occlusal, middle, and basal thirds of each tooth are recognized; lingual and labial are used in preference to medial and lateral.

We examined a total of 1169 specimens representing 611 species. There is currently no universally accepted taxonomic scheme for ophidians and several issues remain contentious (e.g., the status of Hydrophiidae relative to the Elapidae; placement of Atractaspidae within the Caenophidia). The overall ophidian taxonomic scheme employed herein combines recent taxonomies of selected groups (Cadle and Gorman, 1981; Dowling et al., 1983; McDowell, 1987; Cadle, 1988; Cadle et al., 1990; Underwood and Stimson, 1990; Kluge, 1991; Underwood and Kochva, 1993; Cadle, 1994) together with thoughtful suggestions by Van Wallach.

In calculating the distribution of the different tooth types we always worked with scores from the individual specimens, not composite species scores. Bias resulting from variation in the number of specimens examined from each species is likely to be low since we rarely sampled more than three specimens from any species. Calculations using data from individual specimens, as opposed to species, enabled us to reflect the intraspecific variation we observed in tooth morphology. A tabulation of the dentitional scores for every specimen examined is available from the first author (BAY).



Results

Summary Percentages

The numerical scores for each tooth type were determined first within subfamilies then totaled for families. These numerical values (table 1) are expressed as the percentage of tooth types exhibited on each bone — dentary, pterygoid, palatine, anterior and posterior maxilla — for tooth types 0 to 4.

Morphological Variation

Type 1 Teeth. Three significant morphological variations were observed within this tooth type. First, low dental ridges (*sensu* Wright et al., 1979) were frequently present on the tooth's labial and lingual surfaces (fig. 1A). Second, several parallel ridges were present at the base of some teeth (fig. 2A); these ridges became pronounced enough in some species (e.g., *Achrochordus granulatus*) that the tooth's base had a distinctive "pleated" appearance (these ridges were described as accessory dental ridges by Vaeth et al., 1985). The gaps between the adjacent ridges of these pleated teeth differ from the grooves seen in Type 2 teeth in that they were not depressions in the surface of the teeth. Rather, the tooth surface was raised up into ridges leaving the lower tooth surface between. Third, the posterior face of some Type 1 teeth, was drawn out into a flat surface giving the tooth an overall blade-like shape (fig. 2B).

Type 2 Teeth. The furrow in Type 2 teeth varied considerably in terms of length, width, and angle of the defining wall. When present on the pterygoid or palatine, this furrow tended to be borne on the tooth's lingual surface; whereas when present on the dentary or maxilla, the furrow tended to be borne labially. The furrow also varied in the extent to which it was present along the length of the tooth. Where the furrow did not extend along the entire length, it was normally restricted to the basal third of the tooth (fig. 3A), although in *Elapsoidea sundevalli* the furrow resided in the distal third of the tooth.

Type 3 Teeth. Most of the variation observed in Type 3 teeth involved variation in the length and width of the groove. Most of the grooves that did not run the entire length of the tooth were restricted to the basal and middle portion (fig. 3B, C). In some species,

Figure 1. Tooth types. A: Type 1. Basic tooth type exhibiting no surface indentation. The raised dental ridge is indicated. Palatine tooth of the viperid, *Azemiops feae* (KVK 1135). B: Type 2. Furrowed tooth showing low depression characteristic of this tooth type. Dentary teeth of the colubrid, *Stenorrhina freminvillii* (AMNH 87382). C: Type 3. Grooved teeth wherein the depression along the tooth is deeply recessed but open its entire length. Posterior maxillary teeth of the colubrid, *Boiga irregularis* (KVK 1349). D: Type 4. The hollow tooth is produced by surface folds of the tooth that meet and fuse leaving a superficial secondary furrow (arrow) to enclose a channel within the tooth with entrance and exit openings at the ends. Fang of the viperid, *Azemiops feae* (KVK 1135).

Table 1. Summary of Tooth Types within Families and Subfamilies. Tooth types—0 to 4—are shown with the percentage occurrence within specimens in parenthesis. Where no parenthesis is indicated, the tooth type was present in 100% of specimens. The taxonomic groups are listed with the number of specimens examined indicated in brackets. Type 5 shown for a few groups is a hollow tooth like Type 4 except no secondary surface groove is present.

	Dentary	Pterygoid	Palatine	Maxilla Ant.	Post.
Typhlopidae [1]	0	0	0	1	1
Aniliidae [3]	1	1	1	1	1
Cylindrophiiidae [4]	1	1	1	1	1
Uropeltidae [1]	1	1	1	1	1
Boidae [54]	1	0 (2) 1 (98)	1	1	1
Pythonidae [45]	1	1	1	1	1
Xenopeltidae [7]	1	0 (14) 1 (86)	1	1	1
Bolyeriidae [1]	1	1	1	1	1
Tropidophiidae [9]	1	1	1	1	1
Acrochordidae [7]	1	1	1	1	1
Colubridae [739]	1 (95) 2 (5)	0 (1) 1 (98) 2 (1)	1 (99) 2 (1)	1 (99) 2 (0.5)	1 (71) 2 (1) 3 (28)
Colubrinae [261]	1 (95) 2 (5)	0 (2) 1 (96) 2 (2)	1 (98) 2 (2)	1 (99) 2 (1)	1 (77) 2 (1) 3 (22)
Lamprophiinae [23]	1	1	1	1	1 (74) 3 (26)
Lycodontinae [66]	1 (95) 2 (5)	1	1	1	1 (65) 3 (35)
Xenodermatinae [6]	1	1	1	1	1
Homalopsinae [26]	1	1	1	1	2 (12) 3 (88)
Natricinae [113]	1	1	1	1	1
Dipsadinae [206]	1 (91) 2 (9)	0 (0.5) 1 (99)	1	1	1 (55) 2 (0.5) 3 (45)
Xenodermatinae [4]	1	1	1	1	1
Xenodontinae [34]	1	1	1	1	1 (79) 3 (21)
Atractaspidae [22]	1 (95) 2 (5)	0 (5) 1 (95)	1 (95) 2 (5)	1 (64) 4/5 (36)	0 (36) 1 (5) 3 (59)
Atractaspinae [6]	1	0	1	4/5	0
Aparallactinae [16]	1 (94) 2 (6)	0 (6) 1 (94)	1 (94) 2 (6)	1 (87) 4 (13)	0 (13) 1 (6) 3 (81)
Elapidae [113]	1 (52) 2 (48)	0 (1) 1 (51) 2 (48)	0 (1) 1 (43) 2 (56)	4	0 (22) 1 (23) 2 (51) 3 (4)

Table 1. (Continued).

	Dentary	Pterygoid	Palatine	Maxilla	
				Ant.	Post.
Acanthophiinae [46]	1 (74)	1 (63)	0 (2)	4	0 (7)
	2 (26)	2 (37)	1 (61)		1 (23)
			2 (37)		2 (63)
					3 (7)
Elapinae [53]	1 (38)	0 (2)	1 (32)	4	0 (19)
	2 (62)	1 (43)	2 (68)		1 (17)
		2 (55)			2 (62)
					3 (2)
Micrurinae [14]	1 (36)	1 (43)	1 (29)	4	0 (86)
	2 (64)	2 (57)	2 (71)		1 (14)
Hydrophiidae [63]	0 (3)	1 (97)	0 (3)	4	0 (3)
	1 (91)	2 (3)	1 (76)		1 (38)
	2 (6)		2 (21)		2 (59)
Viperidae [100]	1	1 (98)	1 (98)	4	0
		2 (2)	2 (2)		
Causinae [5]	1	1 (60)	1 (60)	4	0
		2 (40)	2 (40)		
Azemiopinae [1]	1	1	1	4	0
Viperinae [29]	1	1	1	4	0
Crotalinae [65]	1	1	1	4	0

however, the groove was restricted to the occlusal portion of the tooth. Frequently, those grooves that did not run the length of the tooth were low and more poorly defined. A fascinating variation seen in several species with Type 3 teeth was the presence of multiple grooves running parallel along the long axis of the tooth (fig. 3D).

Type 4 Teeth. The Type 4 teeth exhibited less surface variation than either types 1, 2, or 3. Most of the variation was in the size of the entrance and exit orifices (figs 1D and 4A) which determined the length of the enclosed tube between them. The other major variation was in the presence of a superficial furrow over the enclosed tube. This superficial furrow presumably demarcates the line along which opposing tooth surfaces joined during embryonic development to define the hollow channel within the tooth. This secondary furrow varied in its definition from appearing almost incomplete (fig. 4A) to completely absent (thereby producing a Type 5 tooth, fig. 4B), although a complete absence of this secondary furrow was very rare.

Distribution of the Tooth Types on the Dentition Bearing Bones. The different tooth types had very different spatial distributions (table 2). Tooth Type 0 (edentulous) occurred in very low numbers on the dentary, palatine, and pterygoid, and most commonly on the posterior portion of the viperid maxilla. Type 1 teeth were the most common irrespective of the dentition bearing bone. Type 2 teeth (furrowed) were found on all the bones,

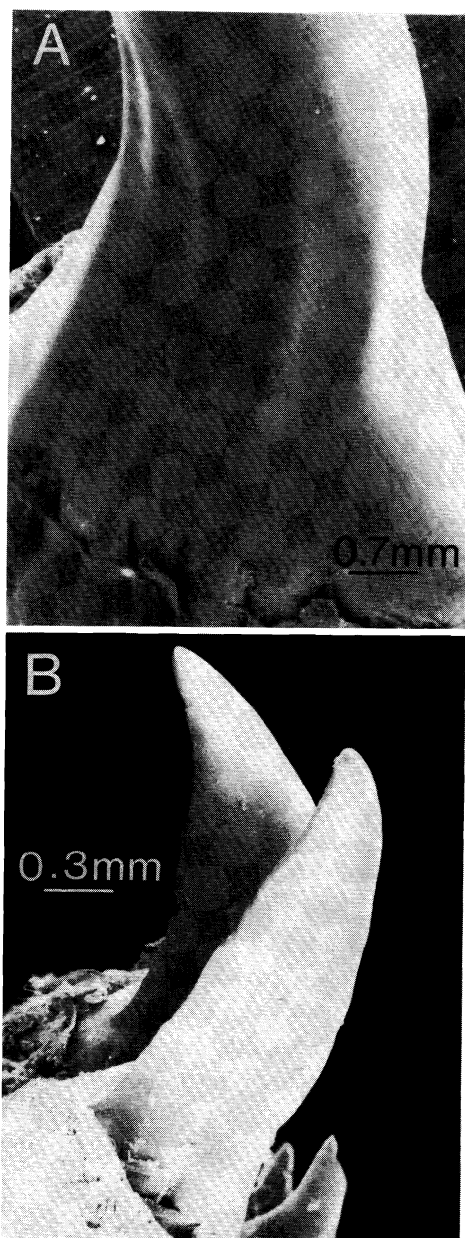


Figure 2. Morphological variation of tooth types. A: Parallel ridges along base of tooth. Fang of the viperid, *Lachesis muta* (USNM 247706). B: Blade-like teeth. Left, posterior maxillary tooth of the colubrid, *Heterodon platyrhinos* (MCZ 145874). The posterior face of these teeth area raised into a sharp ridge producing the knife-like shape to these teeth.

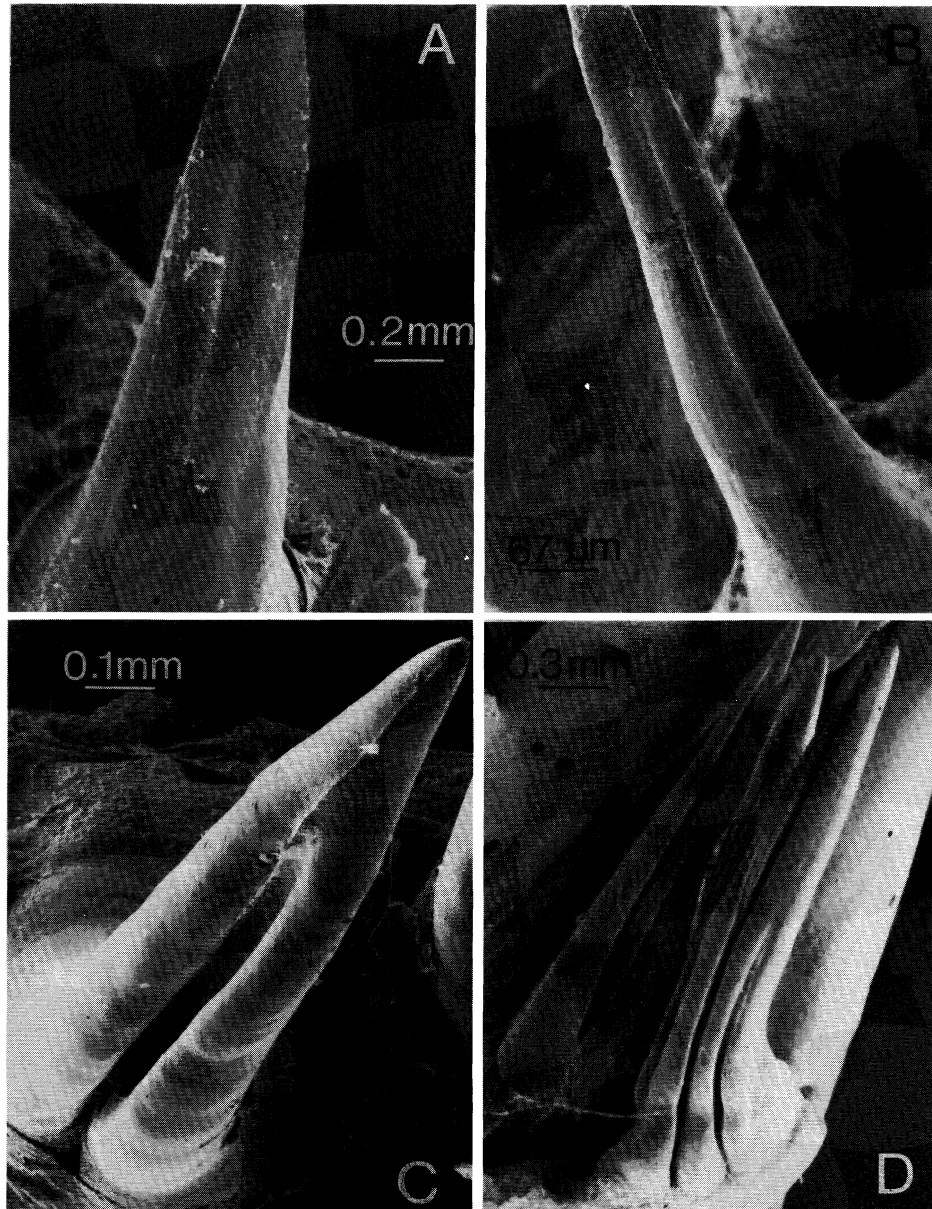


Figure 3. Morphological variations in tooth types 2 and 3. A: Basal furrow. Middle maxillary tooth of *Salomonelaps par* (MCZ 97310) showing a very shallow Type 2 furrow. B: Shallow groove. Middle maxillary tooth of *Holocephalus bungaroides* (MCZ 3642) showing a narrow, shallow, Type 3 groove. C: Occlusal groove. Posterior maxillary teeth of *Dispholidus typus* (KVK 416) showing a distinct Type 3 groove restricted to the basal portion of the tooth. D: Multiple grooves. Posterior maxillary teeth of *Psammophylax rhombeatus* (AMNH 8986) showing multiple Type 3 grooves.

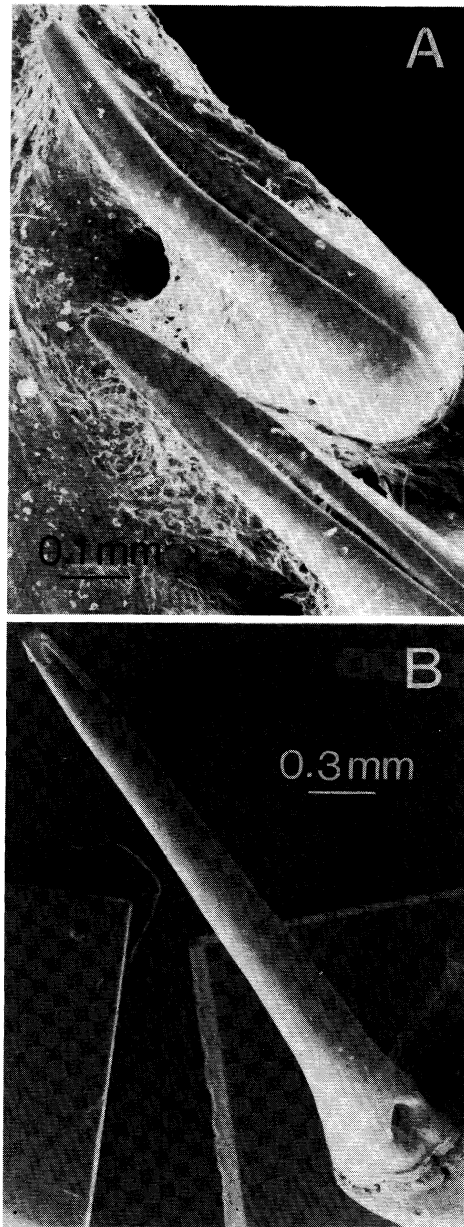


Figure 4. Morphological variation in Type 4 teeth. A: The fang of *Notechis scutatus* (AMNH 77589); note the length of the exit orifice and the presence of a distinct furrow. B: Fang of *Atractaspis irregularis* (FSM 52894); note the small size of the entrance and exit orifices, and the absence of a secondary furrow.

Table 2. Summary of tooth type distribution on the dentiferous bones for all sampled groups. Numbers are percentages of specimens examined.

Type	Dentary	Pterygoid	Palatine	Maxilla	
				Ant	Post
0	0.3	1.6	0.3	0	11.5
1	92.9	92.8	92.3	75.1	60.2
2	6.9	5.6	7.3	0.6	8.6
3	0	0	0	0	19.2
4	0	0	0	24.3	0.3

although this tooth type was extremely rare in the anterior portion of the maxilla. Type 3 (groove) and Type 4 (hollow) teeth had similar distributions in that they were found exclusively on the maxilla.

The dentary, pterygoid, and palatine had fairly similar dentitional types, each supporting predominantly Type 1 teeth (table 2). The only other tooth type found on these bones was Type 2. Among colubrids, if the pterygoid supported Type 2 teeth, then the palatine likely had Type 2 teeth in that specimen, and vice versa. Of the 36 colubrid specimens with dentaries exhibiting Type 2 teeth, five (14%) also had Type 2 teeth on the pterygoids and palatines. This correlation was pronounced in elapids. All (100%) elapid specimens with Type 2 teeth on the pterygoid also had Type 2 teeth on the palatine. The reverse, specimens with Type 2 teeth on the palatine, were also likely to have Type 2 teeth on their pterygoid (82%). Of the 54 elapid specimens with dentaries exhibiting Type 2 teeth, most also had pterygoids (76%) and palatines (88%) with similar Type 2 teeth.

The anterior portion of the colubrid maxilla is also easily characterized, with 99.5% of the species having Type 1 teeth. Only 0.5% of the species had an anterior maxilla scored as Type 2. The posterior third of the maxilla exhibited the greatest incidence of different types, but this variation was correlated with taxonomic status. The posterior maxilla bore exclusively Type 1 teeth in Typhlopoidea and Booidea, predominantly (71%) Type 1 in Colubridae, exclusively Type 0 in Viperidae and Atractaspidae, and predominantly (51/59%) Type 2 in Elapidae/Hydrophiidae.

Taxonomic Distribution of the Tooth Types. The distribution of each tooth type among the higher taxonomic categories is given in table 1. The Typhlopoidea and Booidea were characterized by the presence of only Type 1 teeth (or no teeth), although this same condition was found in many colubrid groups. Not surprisingly, the Atractaspidae, Elapidae, and Viperidae were characterized by the presence of a Type 4 tooth (hollow) on the maxilla. However, a large proportion (55%) of elapids bore furrowed or even grooved teeth posteriorly on the maxilla and a number of elapids (48-56%) had furrowed teeth on other jaw bones. There was a high correlation among elapids between furrowed (Type 2) posterior maxillary teeth and furrows on dentary or pterygoid/palatine teeth in

the same specimen. In viperids, the maxilla bore only a hollow tooth (Type 4); other dentiferous jaw bones carried predominantly Type 1 teeth, with only *Causus* (Causinae) showing some Type 2 pterygoid and palatine teeth.

The variation in tooth types was most pronounced among the Colubridae. Hollow teeth were absent in all examined colubrids. The maxilla carried a grooved tooth in 28% of our sample, this grooved tooth was always located in the posterior third of the maxilla. Only four of 736 colubrid specimens exhibited evidence of a furrow on the anterior maxillary teeth. One was a large specimen of *Boiga cynanea* (FMNH 180046), two were specimens of *Ahaetulla preocularis* (FSM 53434, 53610), and the other was *Rhachidelus brazili* (USNM 165573). Neither grooved (Type 3) nor hollow (Type 4) teeth were found outside the maxilla, but furrowed teeth (Type 2) constituted 5% (dentary) and 2% (pterygoid, palatine) in colubrids, the highest representation of Type 2 teeth on these bones within colubrids. We observed distinct Type 4 teeth on the anterior maxilla of the two specimens of *Homoroselaps lacteus* (Aparallactini) we examined (MCZ 6037, AMNH 90083).

The amount of variation in tooth type differed substantially among the taxonomic groups. For example, all Lampropeltini (7 genera, 17 species, and 50 specimens) had the same tooth types. By contrast, 15 different combinations of tooth types were present in Elapinae (13 genera, 26 species, and 53 specimens). Intraspecific variation in tooth type distribution was recorded in 37 of the species examined. In most of these intraspecific comparisons, the differences were attributable to differences of Type 1 or Type 2 teeth on a single dentiferous bone. Although beyond the scope of this study, it would seem that some, if not most, of this intraspecific variation is correlated with size differences between the specimens. Four specimens of *Naja nigricollis* were examined and each received a different score, the differences being the presence or absence of furrows on the teeth. The high level of variation within this species is noteworthy in that allometric changes do not account for the differences which are not a progressive amplification of surface features with increasing sizes.

Discussion

This survey documented considerable morphological variation among the dentitional surface features of snake teeth. This variation was evident in three aspects of the results presented herein; the variation observed within each tooth type, the variation in tooth type recorded from each dentition bearing bone (or portion), and the variation in tooth type observed among the taxonomic groups.

As commented on by others (e.g., Hoffstetter, 1939; Kroll, 1976), we also noted that initial scoring of teeth under a light microscope could produce mistaken scores. Low, dental ridges at quick, first glance can give the illusion of being grooves. For example, the reported "grooves" in the posterior maxillary teeth of *Heterodon* (Kroll, 1976) are in fact the result of the blade-like design of these teeth (Kardong, 1980). Further,

skulls in museum collections occasionally held teeth with artificial grooves, the result of shrinkage. *Enhydris* and other freshwater snakes seemed especially prone to such artifacts as confirmed by selected examination under a scanning electron microscope. Although conducting such a survey using a SEM is probably impractical, we found that being aware of such optical illusions, and carefully turning the specimen to many viewing angles, eliminated such scoring mistakes.

Lack of a standardized scoring system has also introduced inconsistencies in the literature. For example, in our sample of *Ahaetulla*, specimens exhibited low furrows (Type 2) on maxillary teeth near the middle of the bone, but no anterior grooved teeth (Type 3) were present. This differs from claims of anterior maxillary teeth of *Ahaetulla* with grooves (Underwood, 1967; Greene, 1989) which are based on an earlier report (Hoffstetter, 1939). These differences apparently arise from the different scoring system used. These earlier studies did not distinguish between distinctive tooth types, our Types 2 and 3, an understandable approach but one accounting for inconsistencies between investigators. In light of these difficulties, earlier literature claims about grooves on the teeth of colubrids must be taken cautiously.

Certainly our survey is not exhaustive. Improved taxonomic classifications or natural variation within genera might contribute to additional discoveries of tooth type distributions, and thereby also help to clarify inconsistencies within the literature. For example, we found no grooved, posterior maxillary teeth within *Rhabdophis*, a finding consistent with others (Sakai et al., 1983), but a view that perhaps will be modified with further work that might confirm contrary reports of grooves on teeth located here in this species (e.g., *Balanophis* [= *Rhabdophis*?], fig. 98A, Smith, 1943).

It has been hypothesized (Kardong, 1980; 1982) that proteroglyph and solenoglyph fangs arose from grooved posterior teeth within the maxilla, a view recently supported (Jackson and Fritts, 1995). As a corollary, it was predicted that colubrid intermediates should lack the presence of grooved teeth anteriorly placed on the maxilla (Kardong, 1980; 1982). In our study, all colubrid species examined lacked grooved, anterior maxillary teeth (Type 3). *Homoroselaps*, which has Type 4 teeth on its anterior maxilla, was placed within the tribe Aparallactinae of the Atractaspidae. The taxonomic position of this genus is controversial (see Underwood and Kochva, 1993), if placed within the Colubridae it would represent the only exception to the lack of grooved, anterior maxillary teeth within that family. Certainly, it must be noted that only about one-quarter of the described species were sampled, and our sample reflects the collection bias of the museums in which the specimens are held. Nevertheless, our study is based on a very large sample size, and includes the selective use of the higher resolution scanning electron microscope.

It is often claimed (e.g., Porter, 1972; Goin et al., 1978) that a superficial groove is normally lacking from the fangs of proteroglyphs. Certainly the rims of the primary groove meet and fuse during embryological development (Tomes, 1876; West, 1895), but usually leave a secondary shallow surface furrow at their point of union. As figure 1C

demonstrates, the higher resolution of the scanning electron microscope clearly shows this superficial groove. Occasionally fangs of large viperids (e.g., *Bitis*, *Lachesis*) or of some *Atractaspis* (fig. 4B) exhibit no trace of these secondary grooves, but these were unusual. In most (99%) proteroglyphs we examined, a shallow secondary groove was present.

Although a discussion of the functional significance of tooth form is beyond the scope of this paper, two points merit comment. The raised ridges in the basal third of some specialized teeth (fig. 2A) were evident in mostly large specimens. We take this as suggestive that these ridges are structural, contributing to the strengthening of the tooth base. The "grooves" between these ridges are quite unlike the recessed grooves which presumably convey secretions from oral glands (e.g., Kochva, 1978; Zalisko and Kardong, 1992), and should be distinguished from them in any descriptive terminology. We therefore agree with the suggestions of Vaeth et al. (1985), that such basal "fluting" might strengthen teeth and need not be seen as channels to convey venom or to aid tooth entry into prey. Similarly, the crease formed on blade-like teeth between the long, dental edge and shaft of the tooth should not be confused with a true groove recessed into the tooth shaft (fig. 2B).

The surface depressions on the teeth examined exhibited a wide range of morphological variation. Each category of tooth type (except category 0) included considerable variation. The four categories we used to classify the teeth appear to be a continuum of dental morphologies. Nevertheless, anatomical differences within this spectrum may reflect different functional properties. For instance, low furrows (fig. 1B) are quite distinct from deep grooves (fig. 1C), and both are anatomically distinct from hollow fangs (fig. 1D). Potentially fluids could move along/through these teeth under substantially different pressures, enabling snakes to employ different prey capture strategies (Kardong and Lavín-Murcio, 1993); other suites of dentitional characters have been linked to feeding specializations (e.g., Scanlon and Shine, 1988).

There are no combinations of tooth types that uniquely define a taxonomic group. Nor is there any correlation between the size of the taxonomic group (in terms of number of species included) and the amount of dentitional variation observed. Since each tooth type includes a great deal of morphological variation between species, even taxonomic groups characterized by a single tooth type (e.g., the natricini) may contain a considerable amount of dentitional variation.

Acknowledgements. We are indebted to the individuals and institutions that gave us access to the specimens examined as part of this study: G. Zug, National Museum of Natural History; J. Rosado and V. Wallach, Museum of Comparative Zoology (MCZ), Harvard University; C. Meyers, American Museum of Natural History (AMNH); J. Cadle, Academy of Natural Sciences (ANS), Philadelphia; W. Auffenberg, Florida State Museum (FSM); H. Voris, Field Museum of Natural History (FMNH); A. Kluge, University of Michigan Museum of Zoology (UMMZ); D. Wake, Museum of Vertebrate Zoology (MVZ), University of California, Berkeley; J. Vindum, California Academy of Sciences (CAS).

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Received: October 16, 1995. Accepted: April 19, 1996.