

Ecological and phylogenetic influences on maxillary dentition in snakes

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Abstract

Ecological and phylogenetic influences on maxillary dentition in snakes. The maxillary dentition of snakes was used as a system with which to investigate the relative importance of the interacting forces of ecological selective pressures and phylogenetic constraints in determining morphology. The maxillary morphology of three groups of snakes having different diets, with each group comprising two distinct lineages—boids and colubroids—was examined. Our results suggest that dietary selective pressures may be more significant than phylogenetic history in shaping maxillary morphology.

Keywords: Serpentes, dentition, diet, ecology, evolution, morphology.

Resumo

Influências ecológicas e filogenéticas sobre a dentição maxilar das serpentes. Usamos a dentição maxilar das serpentes como um sistema para investigar a importância relativa das pressões seletivas ecológicas e das restrições filogenéticas na determinação da morfologia. Examinamos a morfologia maxilar de três grupos de serpentes com diferentes dietas, com cada grupo compreendendo duas linhagens distintas—Boidae e Colubroidea. Nossos resultados sugerem que as pressões seletivas relacionadas à dieta podem ser mais significativas que a história filogenética na conformação da morfologia maxilar.

Keywords: Serpentes, dentição, dieta, ecologia, evolução, morfologia.

Introduction

Morphology is controlled by the interaction of phylogeny and selective pressure (Losos and Miles 1994). We hypothesized that in the case of snake maxillary dentition, form follows function,

and that dentitional morphology would be correlated with the type of prey favored by different species. Phylogeny constrains the “starting point” from which the morphology of a structure deviates in response to various selective pressures (i.e., natural selection). Therefore, we reasoned that the relative strength of selective pressures could be tested by examining the extent to which maxillary dentition in a species deviated from the plesiomorphic condition of the lineage. Our goal was to test the impact of selective

Received 14 September 2010.
Accepted 20 November 2010.
Distributed December 2010.

pressures attributable to different types of prey by observing the variation in the maxillary dentition in snakes.

Alethinophidian snakes have teeth on four or five bones—the palatine, pterygoid, dentary, maxilla, and sometimes, a premaxilla. However, many snakes have evolved specific dentitional patterns that affect their function. Because maxillary morphology is highly variable, it is an important taxonomic character; the dentition has been used as a character trait for describing and identifying snake taxa for more than a century (e.g., Boulenger 1896) and is still used today (e.g., Chippaux 2006). Because ophidian maxillary morphology varies interspecifically, it is useful for identifying and describing snakes, along with other features, such as scales, hemipenial morphology, and molecular characters. We used a collection of snake maxillae originally assembled for taxonomic studies to investigate the relationship between dentitional morphology and diet in a diversity of snakes.

Several studies have demonstrated apparent correlations between specific types of prey and the maxillary morphology of species of snakes (e.g., Savitzky 1981, Vaeth *et al.* 1985, Jackson *et al.* 1999, Jackson and Fritts 2004). For example, Savitzky (1981) addressed dentitional specialization for a specific prey type; he hypothesized that the occurrence of hinged teeth in some snake genera is associated with durophagy, and is an adaptation that prevents the teeth from breaking when it comes in contact with hard-bodied prey. Other studies (Savitzky 1983, Cundall and Irish 1989, Greene 1989, Jackson and Fritts 2004) elaborated this hypothesis to include other morphological modifications, such as the presence of a large diastema in the maxillary dentition and an arched maxillary bone for the purpose of encircling the hard-bodied prey as the snake bites it. Substantially lengthened teeth were reported in predators that prey on soft items such as slugs (Zweifel 1954), and piscivorous snakes typically have numerous, sharp, posteriorly curved teeth (Savitzky 1983). Snakes that are specialized for calcareous egg-eating

have few, small teeth thought to facilitate regurgitation of the egg shell after its contents have been consumed (Savitzky 1983). In contrast, snakes that prey on soft-shelled eggs have broad, bladelike teeth to slice open the eggs for digestion (Broadley 1979). Based on these studies documenting dentitional specializations in snakes, a comprehensive study can be undertaken to describe taxonomic and ecological patterns.

Comparison of the morphological variation of ophidian maxillae with the dietary habits of snakes may lead to a better understanding of the selective pressures acting on the morphology of the maxilla. An ecomorphological perspective allows us to explore whether diverse prey availability might have driven rapid evolution from a generalized plesiomorphic condition in the colubroid ancestor. If so, then we should observe a strong correlation between different types of maxillary dentition in snakes and their preferred type of prey.

To test the role of phylogenetic constraints in shaping morphology, we examined representatives of two lineages of snakes—the boids and the colubroids (excluding taxa with highly specialized maxillary dentition for the injection of venom). We recognize that this combination is far from ideal because Boidae comprises about 43 species, whereas Colubroidea contains some 2300 species (Jackson 2007). The colubroids in our study are a diverse assemblage belonging to the paraphyletic group traditionally referred to as “Colubridae.” However, the two lineages are reciprocally monophyletic and distantly related; nonetheless, many taxa from each lineage fill similar ecological niches. Potentially, analysis of the differences between boids and colubrids that share the same niche may provide insight into the operative selective pressures and the ways in which these pressures interact with phylogenetic constraints. It is important to note fundamental differences in the dentitional patterns of colubrids and boids—colubrids have a posterior fang, sometimes enlarged and/or grooved, which often conducts venom, whereas boids lack a posterior fang but usually have enlarged anterior teeth.

These are phylogenetically determined morphologies that may be modified by selective pressures. Thus, we are interested in determining whether the maxillae of boids more strongly resemble those of other boids or is their maxillary morphology more similar to that of colubroids that fill similar dietary niches.

Materials and Methods

We compiled dietary information from the literature for 45 species of snakes. We chose snakes that specialized on particular prey to investigate explicit selective pressure. A total of 45 colubroid and boid snake maxillae was photographed; snakes from Africa and South America were most numerous. Species were grouped according to their dietary preferences before their maxillae were examined. We focused on three dietary groupings—viz., species preferring (1) mammalian, (2) aquatic, or (3) arboreal prey.

Maxillae were stored in a 75% ethanol solution. All African specimens had been sputter-coated with a gold/palladium mixture for scanning electron microscopy as part of another study. Maxillae were secured to a contrasting color of construction paper with double-sided tape to photograph them. The camera was mounted to a photocopy stand and the photographed with an Olympus Evolt E-510 Digital SLR camera with accessory components (Zuiko 50-mm Macro Lens, Olympus Lens Hood LH-55, Olympus Ring Flash Set SRF-110, and Olympus Flash Adapter Ring SRF-11). The photos were taken by remote control from a nearby computer to eliminate vibration. Olympus Studio 2 photo software was used for this remote function and basic image editing.

Results

Snakes that Prey on Mammals

We examined maxillae of six species that prey primarily on mammals—*Python sebae* (African Rock Python), *Liasis mackloti* (Macklot's Py-

thon), *Pituophis catenifer deserticola* (Bull Snake), *Lamprophis lineatus* (Striped House Snake), *Psammophylax rhombeatus* (Rhombic Skaapstecker), and *Calabaria reinhardtii* (African Burrowing Python). Systematic and ecological information appears in Table 1 and maxillae are illustrated in Figure 1.

Despite the fact that these species eat mammals, their respective ranges of prey are at times diverse and may include other types of prey or have “generalist” qualities. *Python sebae* preys on antelope and other large mammals. *Lamprophis lineatus* is a generalist that feeds primarily on rodents. *Liasis mackloti* is a semi-aquatic generalist that consumes small mammals and some reptiles. *Calabaria reinhardtii* is fossorial and feeds on rodents by suffocating them. *Pituophis catenifer* eats small mammals and bird eggs, and *Psammophylax rhombeatus* consumes mostly mammals, in addition to lizards and amphibians.

Only one of these taxa has enlarged posterior dentition—*Psammophylax rhombeatus*, which has grooved posterior fangs. None of the maxillae is curved or contains diastemata. *Python sebae*, *Pituophis catenifer*, *Lamprophis lineatus*, and *Liasis mackloti* share many dentitional characteristics, including moderate intertooth spacing, the absence of striations, and anterior and posterior teeth that are angled posteriorly at approximately 45°, owing to moderate curvature of the teeth. *Lamprophis lineatus*, *P. sebae*, and *Liasis mackloti* have strikingly similar in dentitional patterns, with enlarged anterior teeth that protrude more posteriorly than the smaller and more numerous, posterior teeth. In contrast, in *Pituophis catenifer* and *Psammophylax rhombeatus*, all of the maxillary teeth are the same and each bears a prominent, lateral ridge. *Psammophylax rhombeatus* has grooved posterior maxillary dentition, which is not greatly enlarged relative to the anterior dentition. The dentition of *Calabaria reinhardtii* differs considerably from that of the other four species, because the many, heavily striated teeth are tightly packed and seem to bend posteriorly at only a small angle; the anterior teeth appear to be “twisted” (Figure 1f).

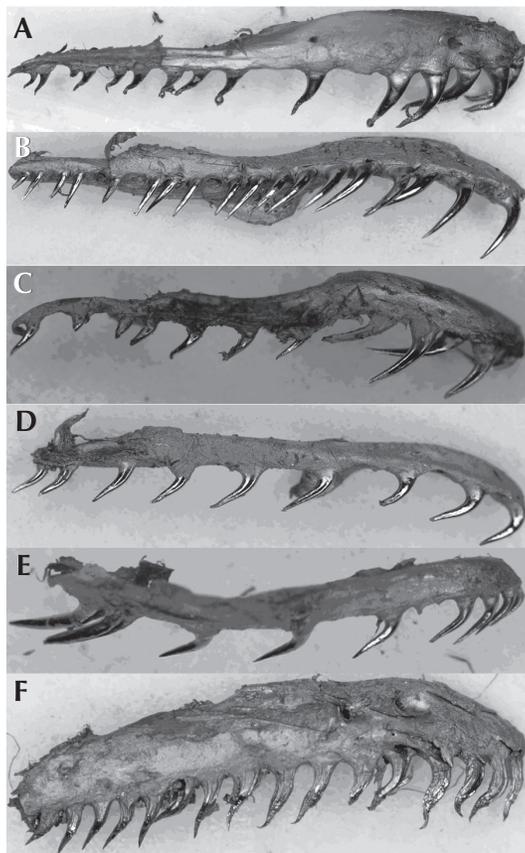


Figure 1. Photographs of maxillae in lateral view of snakes that prey on mammals; length in mm. (A) *Python sebae*: right maxilla, 10.1 mm. (B) *Liasis mackloti*: right maxilla, 11.5 mm. (C) *Lamprophis lineatus*: right maxilla, 5.8 mm. (D) *Pituophis catenifer deserticola*: right maxilla, 7.5 mm. (E) *Psammophylax rhombeatus*: right maxilla, 3 mm. (F) *Calabaria reinhardtii*: right maxilla, 6.5 mm.

Arboreal Snakes that Prey on Lizards, Birds, and Mammals

Seven of the snake species are arboreal and primarily consume lizards, birds, and mammals. As juveniles, these snakes primarily prey on lizards, whereas they eat birds and rodents as adults. Included are *Pseustes sulphureus* (Amazon Puffing Snake), *Spilotes pullatus* (Yellow Rat Snake), *Corallus cookii* (Emerald Tree Boa),

Boiga irregularis (Brown Tree Snake), *Oxybelis fulgidus* (Green Vine Snake), *Boiga blandingi* (Blanding's Tree Snake) and *Coelognathus flavolineatus* (Common Malayan Racer). Systematic and ecological information appears in Table 2 and maxillae are illustrated in Figure 2.

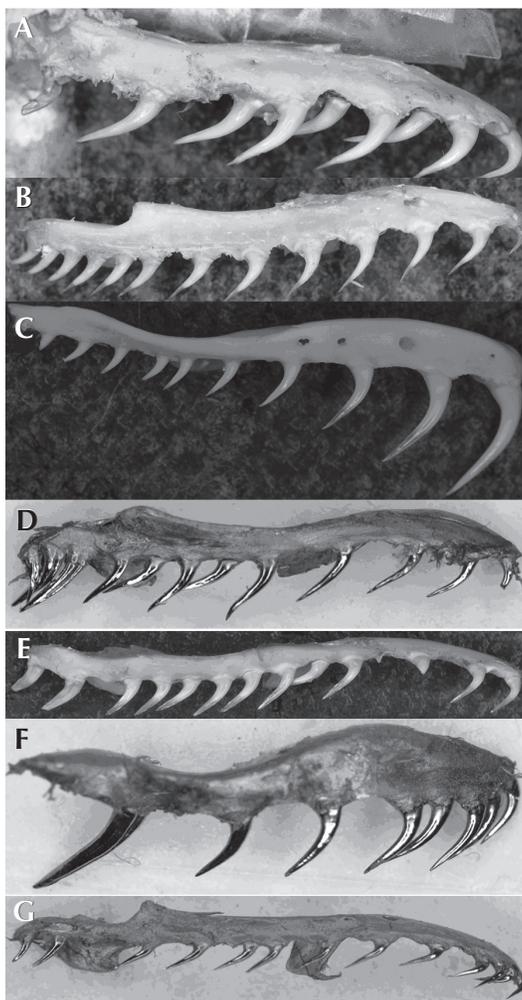


Figure 2. Photographs of maxillae in lateral view of arboreal snakes that prey on lizards, birds, and mammals; length in mm. (A) *Pseustes sulphureus*: right maxilla, 11 mm. (B) *Spilotes pullatus*: left maxilla, 12 mm. (C) *Corallus cookii*: right maxilla, 8 mm. (D) *Boiga irregularis*: right maxilla, 7.5 mm. (E) *Oxybelis fulgidus*: right maxilla, 11 mm. (F) *Boiga blandingi*: right maxilla, 9 mm. (G) *Coelognathus flavolineatus*: right maxilla, 6 mm.

Table 1. Phylogenetic and ecological information for snakes that prey on mammals.

Species	Family	Natural range	Diet	Authority
<i>Python sebae</i>	Boidae	Africa	Large mammals	Luiselli 2001
<i>Liasis mackloti</i>	Boidae	Australia	Rodents, reptiles	Madsen and Shine 1999
<i>Pituophis catenifer</i>	Colubridae	North America	Small mammals, birds, eggs	Rodriguez-Robles 1998
<i>Lamprophis lineatus</i>	Colubridae	Africa	Rodents	Akani 2008
<i>Calabaria reinhardtii</i>	Boidae	Africa	Rodents	Luiselli 1999
<i>Psammophylax rhombeatus</i>	Colubridae	Africa	Mammals, lizards	Van Wyke 1988

Table 2. Phylogenetic and ecological information for arboreal snakes.

Species	Family	Natural range	Diet	Authority
<i>Pseustes sulphureus</i>	Colubridae	South America	Rodents, birds	Rufino 1999
<i>Spilotes pullatus</i>	Colubridae	South America	Lizards, birds	Martins and Oliveira 1998
<i>Corallus cookii</i>	Boidae	South America	Lizards, rodents	Henderson 1993
<i>Boiga irregularis</i>	Colubridae	Australia	Lizards, birds, mammals	Savidge 1988
<i>Oxybelis fulgidus</i>	Colubridae	South America	Lizards, birds	Henderson 1982
<i>Boiga blandingi</i>	Colubridae	Africa	Lizards, birds, mammals	Luiselli 1998
<i>Coelognathus flavolineatus</i>	Colubridae	SE Asia, Indonesia	Rodents, birds	Lim and Lee 1989

Despite their wide geographic distribution, these species share many similar dentitional characteristics. The posterior fangs of the colubrids are about the same length as the anterior teeth (*Boiga blandingi* and *B. irregularis* being the two possible exceptions). However, the anterior teeth are more widely spaced than

the posterior teeth, and directed posteriorly at an angle that does not exceed 45°. The teeth are of a large, uniform size and fewer in number than other subgroups. They lack striations and diastemata.

The notable exception to these generalizations is the only boid, *Corallus cookii*, which possesses

anterior teeth that are 3–5 times the length of the posterior teeth. The teeth decrease in size posteriorly on the maxilla. Additionally, boids lack grooved posterior fangs.

Aquatic Snakes that Prey on Fish and Aquatic Amphibians

Seven species studied feed on aquatic prey, such as fish and amphibians. Included are *Liophis breviceps* (Short Ground Snake), *Helicops leopardinius* (Leopard Keelback), *Homalopsis buccata* (Masked Water Snake), *Hydrodynastes gigas* (False Water Cobra), *Afronatrix anoscopus* (African Brown Water Snake), *Grayia smithii* (Smith's African Water Snake) and *Natriciteres olivacea* (Olive Marsh Snake). Systematic and ecological information appears in Table 3 and maxillae are illustrated in Figure 3.

Members of this subgroup are characterized by having a single, enlarged posterior fang, and many smaller anterior teeth that are quite sharp and almost always oriented posteriorly at angles between 40° and 60°. These colubrids have either a single posterior fang or a pair of fangs located adjacent to one another that might represent a single functional unit. This is best exemplified in *Homalopsis buccata*, but also present in *Natriciteres olivacea* and *Afronatrix anoscopus*. In many species, the anterior teeth are notably slender and acuminate. The teeth of *H. buccata*, *Helicops leopardinius*, and *Grayia smithii* are striated. Three species (*Hydrodynastes gigas*, *Helicops leopardinius*, and *A. anoscopus*) possess several teeth located lingual to the main row of teeth; these teeth are bent at a more posterior-facing angle than the other teeth. All species seem to have a small diastema directly anterior to the posterior fangs, which creates a spatial distinction between the anterior and posterior teeth. All species have straight maxillary bones except *Natriciteres olivacea*, in which the maxilla is deflected ventrally at its anterior end.

There are several notable exceptions foregoing characterization. The anterior teeth are notably thicker in *Hydrodynastes gigas* than in other

specimens and there is a diastema (about 20% of the length of the maxilla) between the posterior fang and the anterior teeth. There is a large amount of residual tissue on the maxilla of *Liophis breviceps*; this artifact obscures many of the fine details of the snake's dentition. The specimen of *Grayia smithii* has many broken teeth and seems to be a missing posterior fang;

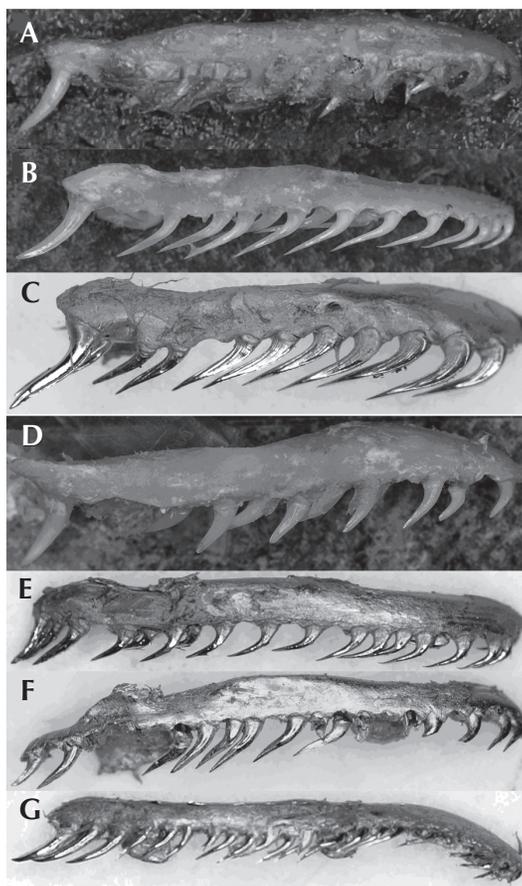


Figure 3. Photographs of maxillae in lateral view of aquatic snakes that prey on fish and aquatic amphibians; length in mm. (A) *Liophis breviceps*: left maxilla, 3.5 mm. (B) *Helicops leopardinius*: right maxilla, 6 mm. (C) *Homalopsis buccata*: right maxilla, 7.5 mm. (D) *Hydrodynastes gigas*: left maxilla, 15 mm. (E) *Afronatrix anoscopus*: right maxilla, 5.8 mm. (F) *Grayia smithii*: right maxilla, 14 mm. (G) *Natriciteres olivacea*: right maxilla, 4 mm.

Table 3. Phylogenetic and ecological information for snakes that prey on fish and amphibians.

Species	Family	Natural range	Diet	Authority
<i>Liophis breviceps</i>	Colubridae	South America	Fish, anurans	Martins and Oliveira 1998
<i>Helicops leopardinius</i>	Colubridae	South America	Fish, amphibians	Avila 2006
<i>Hydrodynastes gigas</i>	Colubridae	South America	Aquatic generalist	Lopez 2004
<i>Afronatrix anoscopus</i>	Colubridae	Africa	Tadpoles, fish	Luiselli 2003
<i>Grayia smithii</i>	Colubridae	Africa	Fish, anurans	Akani and Luiselli 2001
<i>Natriciteres olivacea</i>	Colubridae	Africa	Tadpoles, fish	Chippaux 2006
<i>Homalopsis buccata</i>	Colubridae	Southeast Asia	Fish, tadpoles	Murphy 2007

however, *G. smithii* is known to have an ungrooved posterior tooth that is not significantly larger than the anterior teeth and that is separated from the anterior teeth by a small diastema but (K. Jackson *pers. obs.*).

Discussion

Terrestrial Snakes that Prey on Mammals

Except for *Calabaria reinhardtii*, the maxillae of snakes that eat mammals are characterized by homoplastic features that occur in widely distributed taxa. The maxillae of this subgroup seem to lack specializations and the size of the prey consumed is proportional to the size of the snake. There is a general trend toward increased size of anterior teeth and decreased size of posterior teeth. The enlarged anterior maxillary dentition noted in *Liasis mackloti*, *Python sebae*, and *Lamprophis lineatus* may be advantageous for capturing and subduing mammalian prey,

which have a thick, furry integument. The posteriorly recurved anterior teeth may prevent the prey from escaping, because if the prey attempts to move out of the mouth, the teeth will penetrate deeper and securely impale the prey item (Frazetta 1966).

Liasis mackloti contains more numerous, slender maxillary teeth than do other species in this subgroup, and thus, bears some resemblance to snakes that consume aquatic prey items. The known diet of *L. mackloti* is based on examination of stomach contents recovered from museum specimens and an intensive population study of the species at one site in northern Australia (Madsen and Shine 1999, R. Shine *pers. comm.*). Possibly, *L. mackloti* is more piscivorous than previously thought; its diet is poorly known, especially in juveniles such as the specimen we examined. Conversely, the lack of dentitional specializations of other snakes that prey on mammals may reflect a recent change in the dietary preferences of *L. mackloti* (e.g., a recent

increase in population of small mammals), which is semi-aquatic. It would be informative to investigate if there have been recent changes in populations of available prey at Madsen and Shine's (1999) study site to see if mammalian prey have become more abundant than aquatic prey.

The small size of the posterior dentition of *Pituophis catenifer* and *Psammodromus rufus* produces nearly uniform tooth lengths on the maxilla. The absence of enlarged anterior teeth may be correlated with generalized dietary habits that permit these species to consume other prey, such as reptiles and eggs,

Calabaria reinhardtii has decidedly peculiar maxillary dentition. Its spiraled teeth are unlike anything other teeth observed in this study and may be an artifact of damage that occurred during preservation. *Calabaria reinhardtii* is the only species in this group that kills its prey by constriction. Possibly the condition of the maxillary teeth is irrelevant to prey consumption in this species and as such, have not been subject to selection. The condition of the dentition in *C. reinhardtii* should be verified by examination of other specimens.

Arboreal Snakes that Prey upon Lizards, Birds and Mammals

The colubroids in this group are distinguished from those of other groups by the small size of the posterior fang, which is equivalent in size to the anterior teeth. In this feature, the colubroids resemble the single boid (*Corallus cookii*) in the group. Generally, members of this group have large anterior teeth that are bent posteriorly at an angle less than 45°, which seems to increase the functionality of the anterior teeth in grasping prey. In all colubrid species, the longest and most pronounced teeth are located in the mid-length of the maxilla.

As juveniles, many arboreal snakes prey on lizards and shift to birds and mammals as they mature. Some dentitional features of arboreal snakes resemble those of the terrestrial group

that preys solely upon lizards; however, further specializations are evident. The larger, more substantial teeth of these groups may be correlated with the need to puncture the skin of birds and mammals after having first passed through heavily keratinized layers of feather and fur, respectively. Alternately, the nature of the dentition may be related to the fact that arboreal snakes often must manipulate their prey in the absence of a solid substrate, thereby implying that the entire weight of the prey item rests on the teeth (H. Greene *pers. comm.*). The thick teeth, as well as the sturdy, posteriorly angled anterior teeth observed in this group may be advantageous. The involvement of multiple teeth in the initial grasp may increase the success of prehension, thereby favoring selection for sturdy, angled anterior dentition. Owing to the widespread occurrence of this dentitional pattern, it would seem that this is a homoplastic feature associated with successful feeding in arboreal taxa of different lineages.

Aquatic Snakes that Prey on Fish and Aquatic Amphibians

Snakes that prey on aquatic vertebrates are distinguished from those in other subgroups by their possession of a single, enlarged posterior fang and highly acuminate, posteriorly angled teeth in many. The scales of fishes and the slimy mucous covering of fishes, and adult and larval anurans would render these aquatic prey difficult to grasp. The large fang may be used to puncture the skin of the prey and release venom and the anterior teeth may gain purchase under scales. Tooth engagement of the anterior teeth may be enhanced by dentitional striations. For example, the striated teeth of *Homalopsis buccata*, *Helicops leopardinus*, and *Grayia smithii* may facilitate penetration through the relatively hard, scaly integument of fish (Vaeth *et al.* 1985). It also is possible that the striations help the snake extract its teeth from a mucous-covered scale by reducing suction—in much the same way a blood groove acts in a bayonet (Vaeth *et al.* 1985).

Several taxa, notably *Helicops leopardinus* and *Afronatrix anascopus*, have a few teeth that are oriented medially and almost form an additional dentitional series. Perhaps this increases the number to teeth that are able to get under the scales of fishes.

Hydrodynastes gigas lacks several of the traits described above; however, it is a generalist that consumes fish, amphibians, mammals, and snakes. Although this species lacks many of the dentitional features associated with snakes that consume fish (e.g., striations and numerous slender teeth), *H. gigas* has enlarged anterior dentition like that of snakes that prey on mammals and birds.

Selective Pressures vs. Phylogenetic Constraints

We concluded that selective pressures play a greater role in determining maxillary dentition than phylogenetic constraints. Data support both hypotheses, but we think that examples such as the lack of a pronounced posterior fang and possession substantial anterior teeth in both *Lamprophis lineatus* and *Python sebae* support our view. Likewise, the similarity of the dentitional morphology of arboreal snakes and those that prey upon hard-bodied prey strengthen our conclusions.

The maxillary dentition of colubroids is much more variable than that of boids. Basal snakes such as boids require the use of all cranial tooth-bearing bones to swallow prey, whereas the colubroids do not use the maxilla to swallow (Cundall 1983). Thus, the colubrid maxilla could be adapted for other uses, whereas the boid maxilla is conserved. This doubtless explains the great range of adaptation observed in the colubrid maxillae, as well as the number and variety of different dietary niches that colubroids have utilized in contrast to the boids, which have a phylogenetically constrained morphology. The number of boids available for comparison with the colubrids is important limitation of this study. Our sample included far fewer boids than colubrids because there are only 43 boids in

contrast to the 1800 species of colubrids. One of the three subgroups lacked a boid for morphological comparison. Nonetheless, in the other groups the dentitional morphology of boids and colubroids converged.

Despite having reviewed the literature on the snake diets carefully, in most cases, we could not find a detailed accounts of their dietary preferences. This posed two problems. First, the study was based on grouping taxa into dietary subgroups; with incomplete dietary information, it is possible that some taxa were not categorized correctly, which would invalidate analyses. To minimize this risk, we omitted any species for which we had insufficient dietary information. Second, it is difficult to distinguish generalists from specialists in any particular dietary type without detailed dietary information. We assume that specialists will have evolved in response to the greatest selective pressure and thus, we would prefer to examine dietary specialists. However, there are many intermediate morphologies and it can be difficult to distinguish specialists from generalists (Rodriguez-Robles and Greene 1999). We discarded many species from the study because they seemed to be dietary generalists in an attempt concentrate on dietary specialists.

Acknowledgments

We thank J.-P. Chippaux for his donation of a collection of snake maxillae, and Whitman College for the use of its facilities and the Royal Museum of the Netherlands for on the loan of some of the specimens. Richard Shine and Harry Greene provided helpful comments and insights in the preparation of this manuscript. This study was funded by a Whitman College Start-up Grant to Kate Jackson. 

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