Dentitional specialisations for durophagy
in the Common Wolf snake, *Lycodon aulicus capucinus*

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Abstract. The Common Wolf snake, *Lycodon aulicus capucinus*, is a species known to feed on durophagous prey such as skinks. Here we examine in detail the dentitional morphology of *L. aulicus capucinus* to see whether it possesses morphological specialisations for durophagy comparable to those found in other squamates. We find that *L. aulicus capucinus* has greatly enlarged anterior maxillary teeth, followed by a large diastema. At the diastema, the maxilla is significantly arched. The diastema is followed by a row of small, closely-packed teeth. Finally, after a short second diastema are enlarged, but ungrooved posterior maxillary fangs, with the posterior surfaces modified into blades. We propose that this dentition helps *L. aulicus capucinus* to ingest hard-bodied skinks in several ways: The enlarged anterior teeth and arched maxilla encircle the prey during biting, preventing it from being squeezed out of the mouth anteriorly, the short, spatulate teeth may catch under the scales of the prey, preventing escape during swallowing, and the bladelike posterior fang may slice through the hard, cycloid scales of the prey.

Introduction

Squamates have evolved many morphological adaptations to overcome the challenge of feeding on hard-bodied prey, such as skinks, calcareous eggs, shelled gastropod mollusks, and arthropods (Savitzky, 1983). Durophagy presents several problems. During biting, the mouth closes starting at the posterior end, and bringing the upper and lower jaws together from the posterior corner of the jaw forwards. With soft-bodied prey, the prey is crushed as the mouth closes on it. However, a squamate biting down on a hard prey item such as a skink is likely to have the prey pushed anteriorly and out of the jaws as they close, rather like trying to cut a pencil in half with a pair of scissors.

In many lizards, this problem is solved by cranial kinesis, specifically mesokinesis, in which the upper jaw moves independently of the braincase, allowing the upper jaw to bend downward (the snout pointing down), thus preventing a prey item from being squeezed out

of the mouth anteriorly as the jaws close (Frazzetta, 1986). Schwenk (2000) proposes that there is an evolutionary trend toward cranial kinetism in lepidosaurs.

In snakes, other strategies are used. Bolyerids, sister group to the Caenophidia, have an intramaxillary joint. This allows the anterior half of the maxilla to bend downward independently of the posterior half, allowing cylindrical prey to be encircled as the snake bites down (Cundall and Irish, 1989). Savitzky (1983) proposes that the maxillary dentition of the colubroid, *Psammodynastes*, may represent an adaptation for durophagy. The maxillary morphology of *Psammodynastes pulverulentus* is described in detail by Jackson and Fritts (1996). The anteriormost maxillary teeth of *Psammodynastes* are greatly enlarged relative to other teeth, followed posteriorly by a diastema, then a series of small teeth, and finally a grooved fang, approximately equal in length to the enlarged anterior teeth. Savitzky (1983) and Greene (1989) report an arched maxillary bone as an additional specialisation for durophagy in the genus *Psammodynastes*, but Jackson and Fritts (1996) find no evidence of arching in the maxilla of *Psammodynastes pulverulentus*. Savitzky (1983) proposes that the diastema encircles hard-bodied prey, which are prevented from slipping out of the mouth anteriorly by the enlarged anterior teeth. The prey is then subdued by Duvernoy's secretions channeled into the prey by the grooved posterior fangs.

Another problem faced by durophagous squamates is that their prey is often covered in hard, overlapping, cycloid scales. These have the potential to catch on the predator's teeth during ingestion and possibly pull them out. A second type of adaptation to scincivory (or to durophagy in general), is hinged teeth, as described by Savitzky (1981), which have evolved at least three times and are found in *Xenopeltis*, *Liophidium*, *Scaphiodontophis*, *Sibynophis*, *Lycophidion*, and *Mehelya*, in addition to *Iguanognathus* (Jackson et al., 1999). In these genera, the maxillary teeth are short and stout, with their distal ends compressed and spatulate, so that they slide under the scales of the prey without penetrating the skin. Instead of being firmly ankylosed to the bone, these teeth are hinged along their posterior basal edge, so that they are able to fold backward against the jaw, thereby avoiding breakage by struggling prey, and functioning as a ratchet to prevent prey movements that could allow escape.

The purpose of the following study was to thoroughly investigate the dentitional morphology of a known skink-eating snake, to see if it possessed morphological adaptations consistent with its specialised diet.

The Common Wolf snake, *L. aulicus capucinus*, is widely distributed in Southeast Asia, the Philippines, and Indonesia. It is a nocturnal, semi-arboreal snake, with a slender neck, wide head relative to the width of the neck, a vertically elliptical pupil, and ungrooved posterior fangs. Its diet consists largely of geckos and skinks, but it is also reported to consume mice and frogs as well as birds (Fritts, 1993). N. Arnold (pers. comm.) reports that in the Mascarene Islands introduced *L. aulicus capucinus* have had a devastating effect on the native population of skinks of the genus *Gonglyomorphus*.

We have examined in detail the morphology of the dentition of *L. aulicus capucinus*, to elucidate possible morphological specialisations concordant with a durophagous diet.

Methods

The species

The genus *Lycodon* is a speciose and almost certainly polyphyletic genus widespread in Southeast Asia. In the past decade several new species have been added to the existing 25 or so (Ota and Ross, 1994; Lanza, 1999; Slowinski et al., 2001; Daltry and Wuster, 2002; Gaulke, 2002). We describe the dentitional morphology of *Lycodon aulicus capucinus*. *L. aulicus* and *L. capucinus* have been recognized as separate species in the past, but here, in the text, we follow the nomenclature of Ota (2000), in referring to both as the single species, *Lycodon aulicus capucinus*. Our study involves examination of museum specimens which have been variously catalogued as *L. aulicus* or *L. capucinus*. We refer to all these as *L. aulicus capucinus* in the text, but provide a list (Appendices I and II) of museum names and catalogue numbers so that systematists in the future may confirm or refute the identity of the specimens.

Methodology

The right maxillary bones of four specimens of *L. aulicus capucinus* were dissected out of fluid-preserved specimens and examined using scanning electron microscopy (SEM). The specimens were prepared for the SEM by removing all soft tissue manually, and mounting the entire maxilla on the SEM stub so as to preserve positional data, and to minimise damage to tooth surfaces during extraction and cleaning. Tissue was removed manually because soaking in trypsin had been found to loosen the teeth in some specimens. The mounted specimens were coated with an evaporated coating of carbon followed by a sputter coating of gold/palladium, and examined using a Cambridge 100 SEM at an acceleration voltage of 10 kV.

In addition, twenty fluid-preserved specimens of *L. aulicus capucinus* were examined under a dissecting microscope. The maxillary, dentary, palatine, and pterygoid teeth were probed with a pin against their anterior surface, to determine the nature of their attachment to the tooth-bearing bones.

Results

In three maxillae examined using SEM, the maxillary dentition was found to consist of three distinct types of tooth (fig. 1): The longest of the one to three anteriormost teeth (usually the third) is twice the length of the teeth immediately posterior to it, and separated from the teeth posterior to it by a diastema equal or greater in length to the longest anterior maxillary tooth. Of the anterior maxillary teeth, the posteriormost is the longest, being almost twice the length of the smallest. On the labial surface of each of these teeth, a single prominent ridge extends from the distal end of the tooth to the base. There is a slightly less

3mm
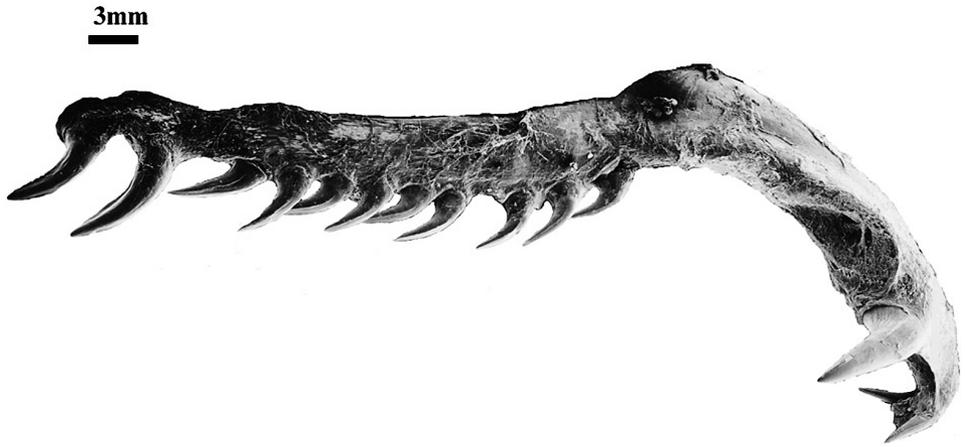
Figure 1. Scanning electron micrograph of right maxilla of *L. aulicus capucinus* (USNM 165063).

prominent ridge on the lingual surface of each of these teeth, extending along the distal 2/3 of each tooth, and in some cases reaching all the way to the base.

The maxillary teeth immediately posterior to the diastema, are small, uniform in shape, and positioned close together. Like the teeth anterior to the diastema, each one has a prominent ridge along its labial surface, extending from the distal end at least 2/3 the length of the tooth, and in most cases to the base. There is a less prominent ridge along the lingual surface of the tooth from its distal end to at least half the length of the tooth, and in many cases extending to the base.

At the posterior end of the maxilla there are one or two enlarged posterior teeth, slightly smaller than the largest anterior maxillary tooth, and separated by a short diastema from the teeth in the middle of the maxilla. These posterior teeth are different in shape from the anterior maxillary teeth in being more elongate and somewhat laterally compressed, with a short ridge on the anterior surface, and with the entire posterior edge of the tooth extended into a flat blade. The labial and lingual surfaces are smooth. The short ridge on the anterior surface extends along the distal third of the tooth, and the posterior edge of the tooth has a definite edge, possibly representing a ridge.

But the most striking characteristic of the maxilla of *L. aulicus capucinus* is that it is strongly arched, with the longitudinal axis of the maxilla anterior to the diastema approximately 120° downward from the rest of the maxilla.

The fourth maxilla examined using SEM was found to lack this arch. In addition the diastema was less and the distinction between the three types of teeth less clear. However, this specimen has subsequently been reidentified as belonging to *Lycodon solivagus* (see Appendix I), thus documenting intrageneric variation in the maxillary structure.

The teeth of fluid-preserved specimens were probed with a pin to investigate the possibility that they might be hinged. The first ten specimens examined were MCZ
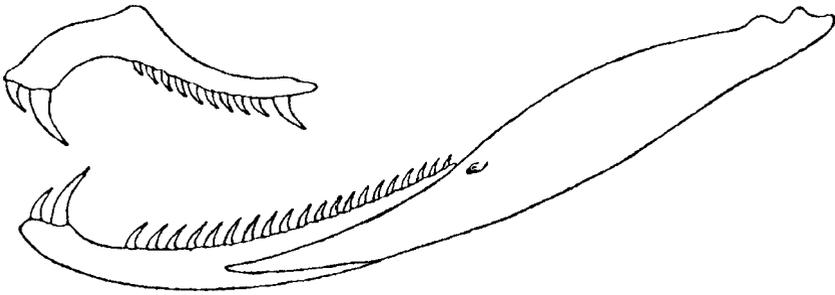
Figure 2. Illustration of the dentition of "*Lycodon aulicus*" from Boulenger (1893).

specimens (Appendix I) all collected at the same time, in the same locality in Hong Kong (SVL = 32.5 to 58 cm, mean = 46 cm). In 50% of the specimens, the small maxillary, palatine, pterygoid, and dentary teeth moved when a pin was pushed against their anterior surface, suggesting the possibility that some of the teeth might be hinged. However, as it seemed unlikely that tooth hingeing would be a variable character among such a homogeneous collection of snakes, a further ten specimens were examined from the collection of the USNM (Appendix I). These specimens came from four different localities: four in the Philippines and one in the Maldives, and ranged in SVL from 32 to 61 cm (mean = 46.7 cm). None of these specimens had teeth that moved in response to pressure from a pin.

Discussion

Our study is not the first description of the dentition of *L. aulicus capucinus*, but it is the first detailed one involving SEM and gross morphology, and the first to correlate dentitional morphology with diet. Boulenger (1893) provides a beautiful drawing of the dentition of *L. aulicus capucinus* (fig. 2), but with no comment on the functional significance of this unusual dentitional morphology. Anthony (1955) discusses the possible functional role of the dentition of *Lycodon*, but his main emphasis is on his interpretation of the enlarged anterior "fangs" on *L. aulicus capucinus* as evidence of an intermediate evolutionary step between usual colubrid dentition and proteroglyphy.

The maxillary dentition of *L. aulicus capucinus* resembles that of *Psammodynastes* more closely than that of any previously described durophagous snake. It has an enlarged anterior maxillary tooth, followed by a diastema, a series of small teeth, and finally an enlarged posterior tooth or fang. It has an arched maxilla, which may be present in some *Psammodynastes* (Savitzky, 1983; Greene, 1989). *Psammodynastes* has grooved posterior fangs thought to help subdue prey by channeling Duvernoy's secretions into the bite wound, but the enlarged posterior maxillary teeth of *L. aulicus capucinus* are ungrooved.

We consider the arched maxilla, and enlarged anterior teeth of *L. aulicus capucinus* to be adaptations for durophagy. We considered the possibility that the small maxillary, palatine,

and dentary teeth might be hinged, as their morphology closely resembled that of the teeth of other hinge-toothed snakes (Savitzky, 1981, 1983; Jackson et al., 1999), in being short, stout, spatulate, and arranged in a closely-packed row. Also, we found that the teeth of some of the fluid-preserved specimens moved when pushed with a pin. In addition, during preparation for SEM study, the teeth seemed to detach more easily from the dentigerous bones than from those of other colubrid specimens (e.g. *Coluber*, *Lampropeltis*, and *Boiga*). However, the solidly-attached nature of further specimens examined, from a variety of localities (USNM specimens in Appendix I) convince us that what we were potentially observing was an artifact of preservation rather than true hinged teeth.

The ridges along the labial and, to a slightly lesser extent, lingual sides of the anterior (anterior to the enlarged posterior teeth) maxillary teeth are typical of most colubrid maxillary teeth. Vaeth et al. (1985) refer to these as LMD (lateral medial dental) ridges. Savitzky (1981) interprets these ridges as the edge of the smooth coating of enamel covering the anterior but not the posterior surfaces of the teeth. The presence of such ridges on the anterior maxillary teeth of *L. aulicus capucinus* is therefore a characteristic shared by most colubrid snakes, but the absence of ridges from the labial and lingual surfaces of the enlarged posterior maxillary teeth is noteworthy.

The posteriormost maxillary teeth of *L. aulicus capucinus* differ from the anterior maxillary teeth, and from the anterior maxillary teeth of most colubrids in being laterally compressed, with a short ridge along their anterior surface and with a posterior edge extended into a flat blade. This morphology is distinct from that of the enlarged maxillary tooth found in many other colubrids, and described in *Thamnophis elegans*, by Wright et al. (1979), which has a short ridge on the anterior surface and a somewhat more pronounced ridge on the posterior surface, but the tooth is not laterally compressed. Jackson and Fritts (1995) propose that the prominent ridge on the posterior surface of some posterior maxillary teeth, and the lesser ridge on the anterior surfaces, may represent a 90° rotation of the pattern seen in anterior maxillary teeth in which there is a prominent ridge on the labial side of the tooth and a lesser ridge on the lingual surface.

The posterior maxillary tooth of *Thamnophis* is not extended posteriorly to form a blade like that of *L. aulicus capucinus*. The maxillary teeth of *Python* spp. have prominent ridges on their anterior surfaces and lesser ridges on their posterior surfaces (Frazzetta, 1966), the converse of what we found in *Lycodon* and other colubroids (Jackson, pers. obs.). Frazzetta suggests that these prominent ridges may serve to disengage the prey more easily after biting, by acting like the blood ridge on a bayonet, to prevent suction during withdrawal of the tooth from the wound. Wright et al. (1979) propose that in the case of the posteriormost maxillary tooth of *T. elegans*, in which the prominent ridge is on the posterior surface of the tooth, and the lesser ridge on the anterior surface, the function of the ridges is more likely to aid in engaging rather than disengaging prey, and may perhaps be an adaptation for feeding on slippery prey such as frogs.

This type of enlarged posterior maxillary tooth in which the ridge on the posterior surface is more prominent than that on the anterior surface of the tooth is typical among

colubrids (Jackson and Fritts, 1995). The posteriormost tooth of *L. aulicus capucinus*, in which the posterior ridge is extended into a blade, is therefore an exaggerated version of this morphology, and a potential adaptation for durophagy. This tapered edge may serve to cut through or pry apart the hard, cycloid scales of the prey, as the teeth are engaged.

By contrast, the anterior maxillary teeth, in which the distal ends of the teeth are dorsoventrally rather than laterally compressed, are more likely to slide under the overlapping scales without piercing the dermal armour, thereby preventing escape (Savitzky, 1981). Is it possible that these two different types of teeth compliment each other, with the anterior teeth allowing the snake to gain purchase on the prey item, and the laterally compressed posterior teeth cutting into it?

Noting our experience with the misidentified *L. solivagus*, which turned out to have a maxillary dentition quite different from those of the *L. aulicus capucinus* we examined, it will be interesting to see how much diet-related morphological variation can exist within a single genus, when the systematics of *Lycodon* are better understood, and when ecological data such as diet exist for many species.

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Appendix I: Fluid-preserved specimens examined

L. capucinus MCZ R-176511, *L. capucinus* MCZ R-177134, *L. capucinus* MCZ R-177131, *L. capucinus* MCZ R-177132, *L. capucinus* MCZ R-175965, *L. capucinus* MCZ R-177129, *L. capucinus* MCZ R-176512, *L. capucinus* MCZ R-173294, *L. capucinus* MCZ R-177130, *L. capucinus* MCZ R-181768, *L. capucinus* MCZ R-179504, *L. capucinus* MCZ R-181379, *L. capucinus* MCZ R-179505, *L. capucinus* MCZ R-181378, *L. capucinus* USNM 228310, *L. capucinus* USNM 228746, *L. capucinus* USNM 228283, *L. capucinus* USNM 228282, *L. capucinus* USNM 212631, *L. capucinus* USNM 140875, *L. capucinus* USNM 140864, *L. capucinus* USNM 140887, *L. aulicus* USNM 306660, *L. aulicus* USNM 306662.

Appendix II: SEM specimens examined

L. capucinus USNM 55902, *L. capucinus* USNM 165063, *L. capucinus* USNM 212631, *L. solivagus* USNM 449014.