

"PROTOVIPERS" AND THE EVOLUTION OF SNAKE FANGS

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Anthony (1955) argued in his summary report on the venom apparatus of snakes that the fang of viperid snakes evolved from a maxillary tooth, specifically a tooth at the posterior end of the maxilla. He identified specific colubrid snake genera which, when aligned into a morphocline (*sensu* Maslin, 1952), showed an increasing similarity in maxillary tooth form to the viperid solenoglyph fang. Since then, a search for plausible nacent "protovipers" among the colubrids has continued (Weaver, 1965; Kroll, 1976).

Certainly, colubrids are a promising group in which to search for clues to the evolution of the viperid fang and associated apparatus. Over half (51.5%) of the 309 species of colubrids examined by Marx and Rabb (1972) had enlarged teeth at the posterior end of the maxilla and of these over one-quarter (26.8%) even had grooves in these enlarged teeth. The family Colubridae includes many forms harmless to humans, as well as some of the most toxic (e.g., *Dispholidus*, boomslang; *Thelotornis*, bird snake). Toxicity, or at least mild-toxicity, may be more widespread in colubrids than is appreciated. For instance, some colubrids customarily considered non-venomous to humans occasionally deliver a painful bite (Heatwole and Banuchi, 1966; Willard, 1967; Johansson, 1974; Goellner, 1975). Since many colubrids have teeth similar in general appearance to viperid fangs, and because some of these are mildly to highly venomous, many investigators have looked to colubrids for viperid ancestors.

The changes leading to the evolution of the viperid fang have usually been attributed to the selective advantages accruing from a progressively more efficient injection system together with increasing ven-

om toxicity. Certainly, long teeth (fangs) are effective in delivering venom into a prey. It is possible however that injection may not have been the *initial* selective factor favoring fang development. Instead, enlarged teeth may have evolved initially to play a role in prey swallowing and were secondarily modified into instruments for venom injection (Kroll, 1976). It is my purpose here 1) to identify possible initial selective advantages of enlarged teeth and, 2) to follow the implications of enlargement in "protoviper" evolution.

MATERIALS AND METHODS

Swallowing events were observed directly and by cinematography followed by frame-by-frame analysis. Filming was done at speeds of 25, 50, or 200 frames per second with a Hycam 16 mm cinematic camera before two 1000 watt tungsten photoflood lamps. Over two hundred meters of usable swallowing sequences were obtained of adult snakes of *Pituophis melanoleucus*, *Crotaphopeltis hotamboeia*, and *Xenodon merremii*. *Pituophis* were fed mice and the two other species frogs. Additionally, single radiographs were taken of *Pituophis* and *Crotaphopeltis* at various points in the swallowing cycle and assembled into swallowing sequences much as described elsewhere (Kardong, 1977).

Dissections were performed under a dissection microscope and skulls drawn with the aid of a camera lucida attachment (Wild). Teeth (shown in Fig. 4) were removed from the posterior end of the maxilla from dried snake skulls, placed on mounting stubs, sputter coated with approximately 30 nm of gold, and examined with a scanning electron microscope

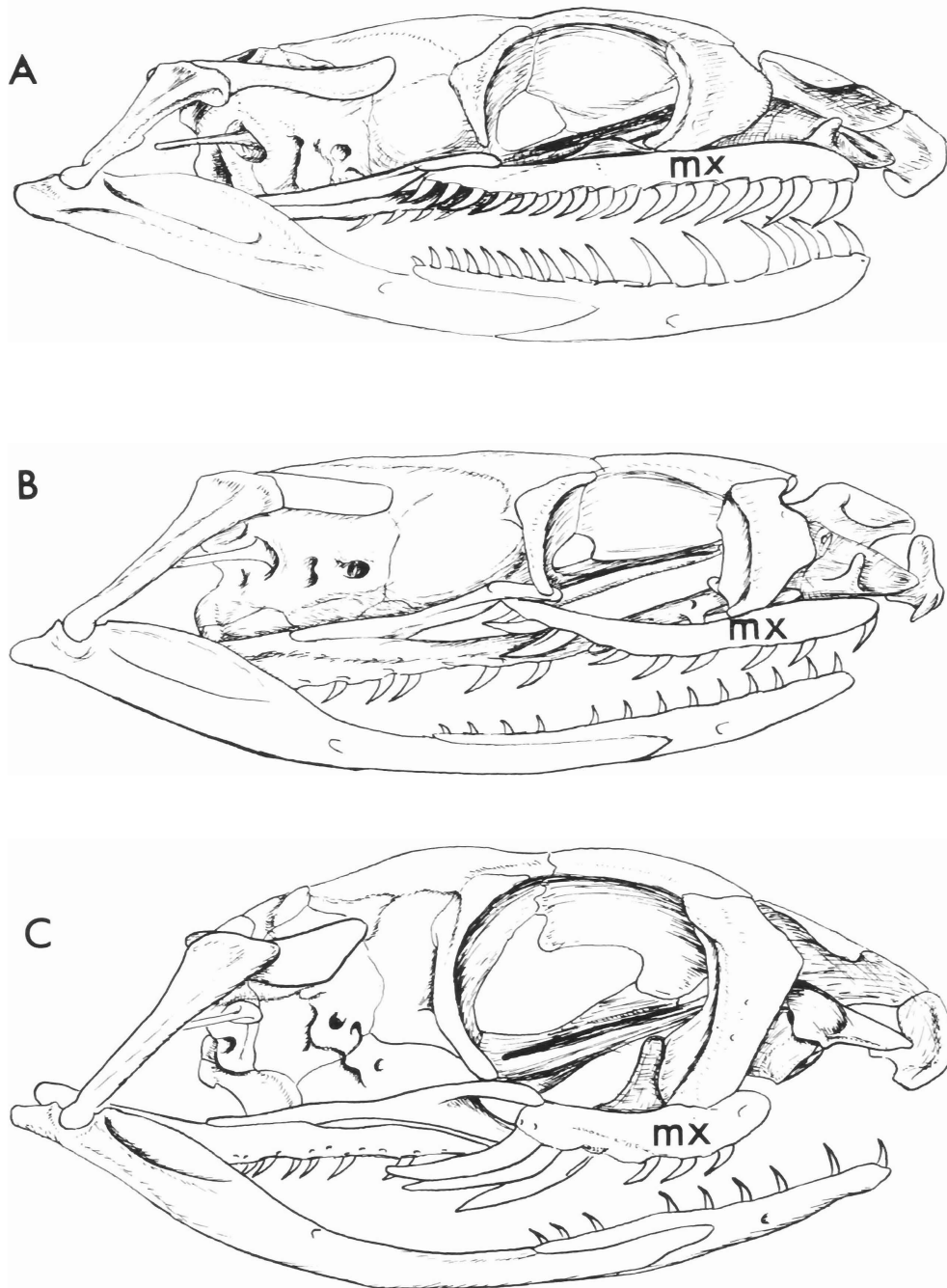


FIG. 1. Three species of colubrids showing three degrees of relative length of posterior maxillary teeth compared to other teeth borne by the maxilla (mx). A) *Pituophis melanoleucus*, B) *Crotaphopeltis hotamboeia*, C) *Dispholidus typus*.

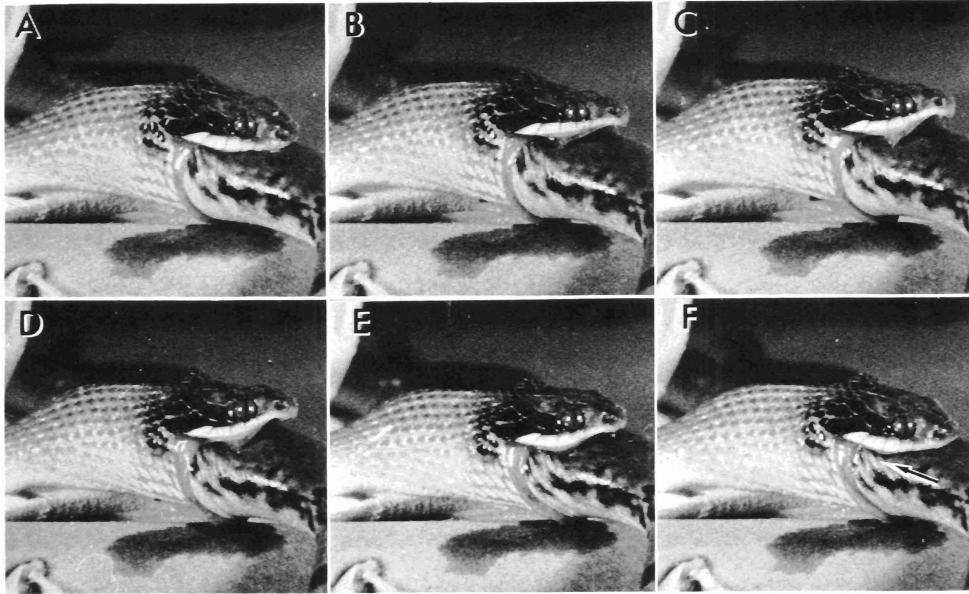


FIG. 2. Lateral view of *Crotaphopeltis hotamboeia* swallowing the severed hind leg of a frog. Events unfold left to right as the maxilla is carried forward and tilts. In C, the mouth closes bringing the large posterior maxillary teeth into the prey; in D the maxilla is retracted, pulling the prey into the mouth and, as it does, causing wringing (arrow) of the skin.

(ETEC Autoscan UI). Anatomical terminology follows Haas (1973).

TOOTH SIZE AND MAXILLARY DISPLACEMENT IN COLUBRIDS

Two aspects of the maxilla in colubrids deserve mention because of the special significance they have for interpretation of tooth evolution. First, varying degrees of posterior tooth enlargement can be found. For example, in Figure 1 all three are colubrid species yet among them there is considerable difference in relative size of teeth along the maxilla. In *Pituophis*, the posterior maxillary teeth are smaller than the anterior teeth. However, in *Crotaphopeltis*, and especially in *Dispholidus*, the posterior maxillary teeth are enlarged and the long posterior teeth bear a groove down which secretions from the oral glands can pass. Occasionally, the functional equivalent to such a secretion groove is provided by the channel formed between a pair of enlarged teeth (Taub, 1967). However, not all colubrids with

enlarged posterior maxillary teeth have these secretion grooves or functional equivalents. For instance, in *Thamnophis elegans vagrans* (western terrestrial garter snake) the posterior maxillary teeth are enlarged as in *Crotaphopeltis* but lack a secretion groove or its equal.

Second, the maxilla of colubrids is "rotatable" though much less so than in viperid snakes. In *Pituophis* the maxilla of one side advances horizontally over the prey during swallowing and is then brought downward, its posterior end swinging ventrally first so that rear teeth re-engage the prey slightly before more anterior teeth. This is similar to the swallowing motions of *Elaphe* described in greater detail by Albright and Nelson (1959a, b).

The maxilla of *Crotaphopeltis* describes a similar displacement pattern (Fig. 2) except that during jaw advance over the prey it experiences a greater degree of rotation about its articulation with the prefrontal. This causes the maxilla to tip

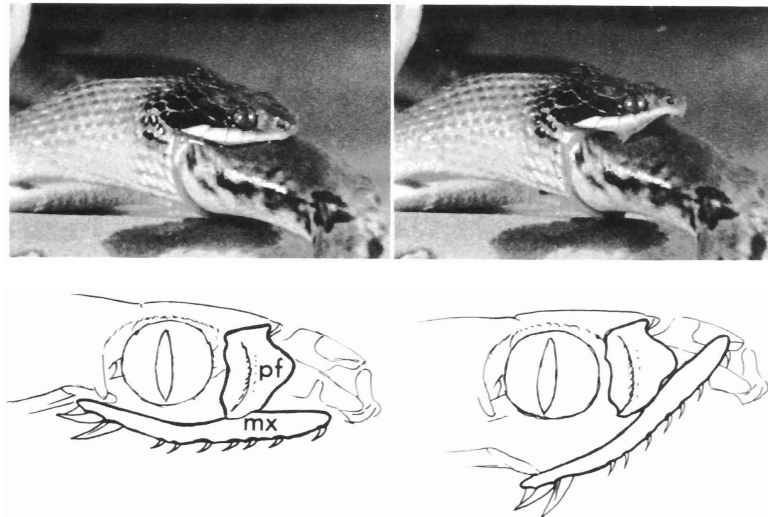


FIG. 3. Lateral photographs (top) of *Crotaphopeltis hotamboeia* showing the maxilla advancing forward (left) and during contact with prey (right) when mouth closes. Below each photograph is sketched the position of the maxilla (mx) relative to the prefrontal (pf) about which it rotates.

sharply out of a horizontal plane (Fig. 3), resulting in upward swing of its anterior end and downward swing of its posterior end. As the posterior end of the maxilla is rotated ventrally during closure of the jaws, the rear teeth are the first to penetrate into the prey and provide a firm purchase. Thus, in addition to whatever role they may play in prey capture, the enlarged posterior maxillary teeth of *Crotaphopeltis* also function during swallowing to engage the prey firmly and aid in moving it past the angle of the jaws during maxillary retraction.

SELECTIVE ADVANTAGES OF ENLARGED POSTERIOR MAXILLARY TEETH

Engage first.—As described above, the maxilla, during swallowing, experiences displacement such that teeth borne on its posterior end are first to engage and hence the first teeth to start moving the prey along. If the prey was not advanced until mid or anterior teeth engaged it, then much of the retraction motion of the maxilla would have passed before the prey began to move. Since the posterior teeth are the first teeth of the maxilla to engage the prey, the snake is able to take full ad-

vantage of the entire sweep of the retraction motion.

Long arc.—The posterior teeth are geometrically farther from the point of rotation about the prefrontal than are the middle maxillary teeth. This means that posterior teeth swing through a longer arc than teeth closer to the point of rotation. Any object engaged by the posterior teeth will likewise be advanced farther (longer arc) than if carried by more anterior maxillary teeth. The posterior teeth thus enjoy a geometric advantage over other teeth of the maxilla in that they ride through a longer arc and can thus advance the prey farther during each swing of the maxilla.

Spikes.—If the prey presents special mechanical problems in swallowing, then one design adaptation favored may be the elongation of the maxillary teeth. Certainly, other adaptive responses are conceivable (e.g., increase in tooth number, and/or change in tooth orientation). However, the lengthening of the teeth allows for deeper penetration. Further, with teeth of even length, the force of jaw closure is experienced approximately equally by each individual tooth. But, when a few teeth (e.g., posterior maxillary teeth) proj-

ect beyond the even tooth row, this permits the force of jaw closure to be locally concentrated upon these long teeth. Thus, a few long, projection teeth not only sink deeper but also concentrate forces to aid their penetration. As a consequence, the elongated projecting posterior maxillary teeth gain secure purchase on the prey.

The specific kinds of special mechanical problems favoring tooth enlargement are not known. Perhaps the prey may be moist (e.g., amphibians), smooth skinned (e.g., skinks), or inflated (e.g., toads) and thus offer only a slippery or uncertain surface to an even row of teeth. In non-constricting snakes, the prey may continue to struggle even as swallowing proceeds. This would also place a premium upon dental adaptations effective in retaining a firm purchase on a thrashing victim. Further analyses of feeding mechanics and prey type may in time eventually help to identify the specific mechanical problems. Whatever these may prove to be, it is apparent, at least in *Crotaphopeltis*, that the large posterior teeth are swung into a position so that they gain a firm purchase upon the prey and do transmit a force to the tissues during retraction. The long, projecting posterior teeth function like spikes to give the snake a better grasp upon the prey during swallowing.

IMPLICATIONS

General.—The rotation of the maxilla and geometric position of its rear teeth would emphasize the role of posterior teeth in swallowing; as I have argued above, tooth lengthening would be favored if the prey presents special mechanical problems during swallowing. If this line of reasoning is sound, then the initial enlargement of posterior maxillary teeth represents an adaptation not to venom injection, but to the requirements of swallowing. This hypothesis has special implications for the interpretation of viperid snake evolution.

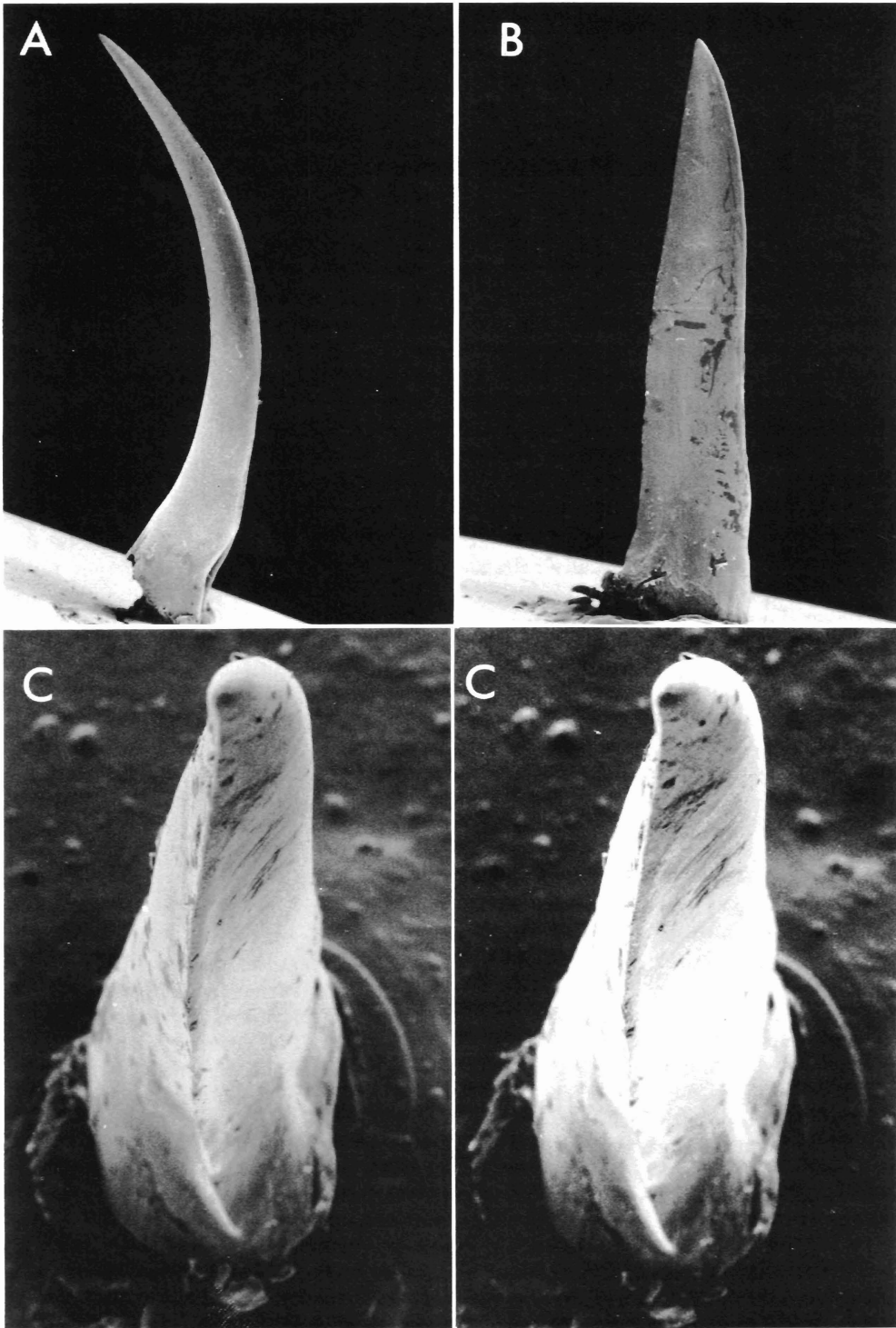
Protovipers.—A close phylogenetic relationship has been claimed between certain colubrid genera (*Heterodon* and *Xe-*

nodon) and viperid snakes. Ancestral to both these colubrid genera and to viperids is an hypothesized "protoviper" presumed very heterodon- or xenodon- like in jaw anatomy (Weaver, 1965). Some evidence in support of this phylogenetic relationship comes from serological work (Minton and Salanitro, 1972), but most of this proposed *Heterodon-Xenodon* to viperid affinity is based on the viper-like construction of the maxilla and associated features (Anthony, 1955; Mosauer, 1935; Weaver, 1965). However, many structures of *Xenodon* and *Heterodon* are likely special adaptations for swallowing, not venom injection, and upon closer look do not resemble viperid characters.

First, the posterior maxillary teeth are dissimilar. The posterior maxillary teeth of *Xenodon-Heterodon* and fangs of viperids though lengthened are structurally different and serve quite different functions. In viperids, the fangs function primarily during the strike to deliver venom and play only a very modest (Kardong, 1977) or no (Dullemeijer and Povel, 1972) role during swallowing. On the other hand, the posterior teeth are used not to deflate puffed-up toads as was once thought (Pope, 1947; Morris, 1944; Minton, 1944; Smith and White, 1955; McAlister, 1963), but to manipulate prey during swallowing in *Heterodon* (Kroll, 1976) and in *Xenodon* (personal observation).

Second, *Xenodon* and *Heterodon* have anatomical features of the skull that are quite different from those of viperids and even different from many other colubrids (Figs. 4, 5). The curving forward of the ventral end of the *M. adductor mandibulae externus superficialis* jaw muscle near its insertion has been claimed to be a primitive condition in vipers (Weaver, 1956). However, this character is not as useful for assessment of phylogenetic affinities as was earlier thought, because some very nonviper-like colubrids have been found to have a similar direction for this muscle (Varkey, 1973; Cundall, 1974).

Though some variations do exist among



colubrids and viperids (Varkey, 1973; Kardong, 1973), the *M. cervico-mandibularis* is generally a single muscle that inserts on the retroarticular process of the mandible and/or joint capsule formed between quadrate and mandible (Haas, 1973). In *Xenodon*, however, the *M. cervico-mandibularis* is divided, the posterior part inserts on the retroarticular process and nearby joint capsule, but the anterior part inserts extensively on the quadrato-maxillary ligament. In addition, dissimilarities occur in the quadrato-maxillary ligament itself. In viperids and most colubrids, this ligament attaches posteriorly on or near the retroarticular process of the mandible. However, in *X. merremii* it attaches not to the mandible but to *M. cervico-mandibularis* and in *Heterodon*, the ligament is absent (Fig. 5). Further, in both *Xenodon* and *Heterodon* the *M. pterygoideus* inserts over a much more extensive area of the posterior mandible than is common in other colubrids or viperid snakes.

The distinctiveness of the *ligamentum quadrato-mandibularis*, *M. cervico-mandibularis*, and *M. pterygoideus* may be especially noteworthy. It is these structures that attach in such a way as to influence directly the mobility, rotation, and deployment of the maxilla and its teeth. The distinctiveness of these structures may reflect the specialized role they play in controlling the maxilla. Whether specializations or not, however, they do represent unique anatomical features of *Xenodon* and *Heterodon* compared to other colubrids and compared to viperids.

Finally, the presence of toxicity in *Heterodon* (Bragg, 1960) has been presented as evidence of anticipation of the viperid venom system in *Heterodon* (Kroll, 1976).

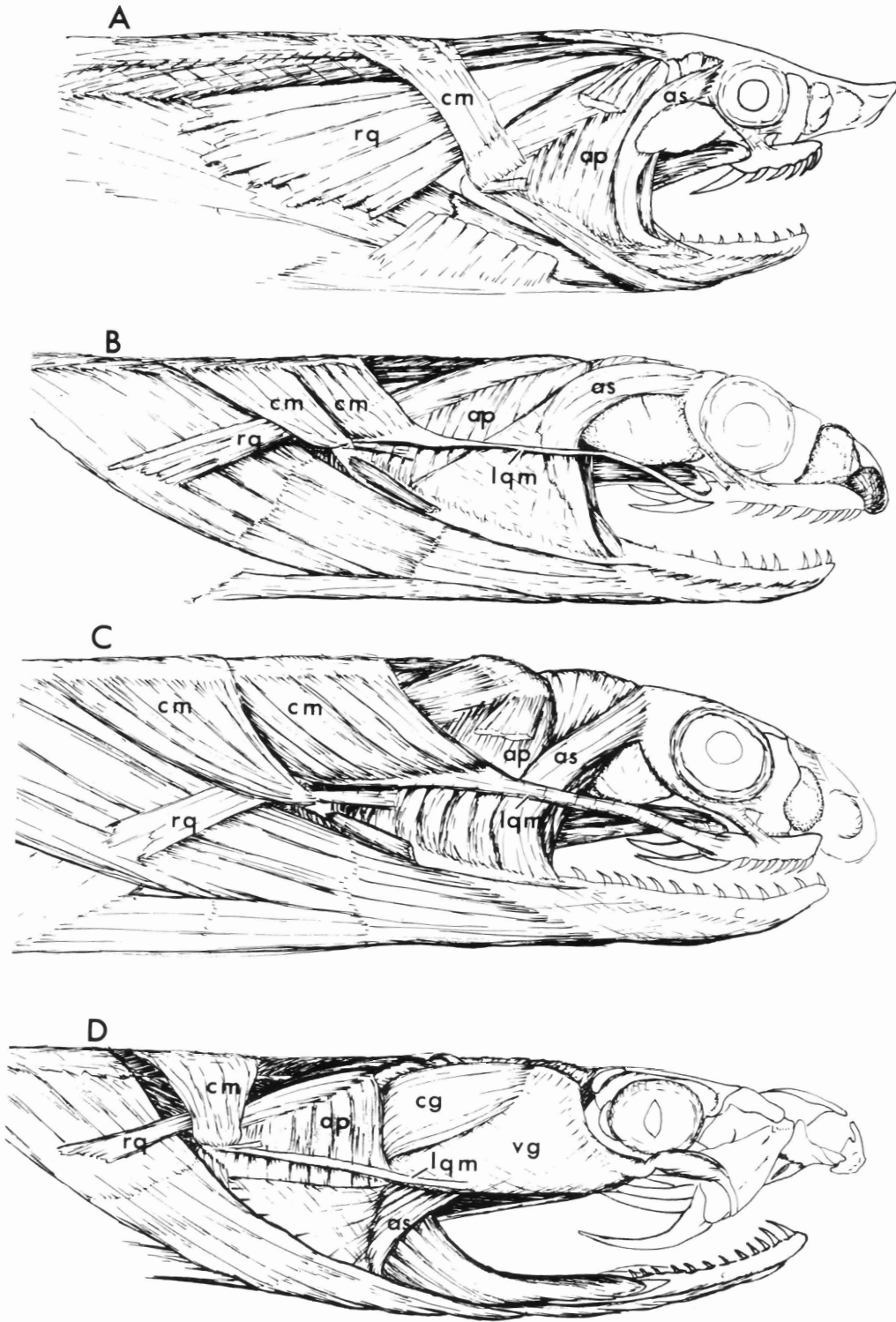
However, the presence of toxicity and even a separate gland (Duvernoy's) presumably for its secretion have been reported in a variety of colubrid species other than *Heterodon* and *Xenodon* (Taub, 1967).

The central role of enlarged maxillary teeth and maxillary rotation in swallowing and the differences in tooth structure all argue that *Heterodon-Xenodon* and viperids are not closely related. The dissimilarities of muscle anatomy not only distinguish *Heterodon-Xenodon* from viperids but also from other colubrids. These genera, both specialists on toads, then represent an evolutionary pathway not toward vipers, but towards a separate line of colubrids adapted for grasping and manipulating a unique prey item. Stated another way, *Xenodon* and *Heterodon* are unlikely "protovipers" in the sense of being evolutionary intermediates between colubrids and vipers.

Parallel evolution.—Selection pressure relating to their role in swallowing would favor an initial enlargement of posterior maxillary teeth. Such a state may then be the condition ancestral to at least two subsequent independent lines of evolution that both involve further enlargement of rear maxillary teeth. In one line, continued but increased involvement in the swallowing mechanics of prey manipulation would favor further enlargement perhaps with accompanying modification of the jaw musculature. The result would be a snake such as *Heterodon* or *Xenodon* and account for the presence of long maxillary teeth with specialized features of jaw musculature. In the second line, involvement in the introduction of oral gland secretion could favor further tooth enlargement and modification. Introduc-

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FIG. 4. Fang of a rattlesnake, *Crotalus viridis* (A) compared to the enlarged posterior maxillary tooth of *Heterodon simus* (B). Note that this tooth in *Heterodon* is blade-like, more-or-less straight, and has a long posterior knife-like edge seen to better advantage in the stereopair (C) from a posterior aspect looking directly at the pointed tip. The fang, by contrast, is round, curved, and does not possess a long edge down one side.



tion of any oral gland secretion that tranquilized the prey would facilitate prey capture and thus be of selective advantage. As a snake worked its jaws over a struggling prey, elongated teeth would be plunged and re-plunged into the tissues. This would open channels for entrance of oral gland secretion and even introduce any secretion flowing over or adhering to the dental surfaces. An enzyme or chemical of the oral gland secretion that tranquilized or hastened prey death would be of selective value by reducing the snake's efforts and risks in subduing the victim. In fact, any component of the oral gland secretion that enhanced evenomation would be favored once it could be introduced deeply enough to reach and be circulated by the vascular system of the prey (Gans and Elliott, 1968). Though any tooth in the mouth that breaks the prey's skin could conceivably carry oral gland secretions inward, the posterior maxillary teeth are the best suited for this because they are enlarged and thus would penetrate deeper than the shorter anterior teeth.

In both lines of evolution, enlargement of the posterior maxillary teeth would result and superficially appear to be an example of parallel evolution, but the functions (prey manipulation vs. injection) and hence selective pressures underlying these trends would be quite different.

Venom evolution.—If, as argued above, the selective pressure favoring initial tooth enlargement centered upon the use in swallowing and not injection, then the likely initial function of oral secretions was also different from that of killing prey. Gans (1978) has suggested that one initial function for oral gland secretions was that of conditioning teeth and promoting oral hygiene. To speculate with

this argument, the oral gland secretion may also initially function to promote digestion as seems to be true in rattlesnakes (Thomas and Pough, 1977). Like the initial selective forces favoring tooth enlargement, the selective forces acting upon the oral secretions may not have been related to their toxic properties but to their more immediate role in tooth health, swallowing, or digestion. Any assessment of oral gland function or evolution should look not only to its toxicity but also to possible other roles and properties.

SUMMARY

Changes leading to the evolution of the viperid fang involved lengthening of rear maxillary teeth and have usually been attributed to the adaptive value derived by providing for more effective venom injection. As an alternative interpretation, it is argued here that an *initial* factor favoring elongation was not venom injection but instead increased swallowing effectiveness. During swallowing, rear maxillary teeth are the first teeth of the maxilla to engage the prey upon each swallowing cycle. Further, they are geometrically positioned more favorably than other maxillary teeth so as to swing through a longer retraction arc and hence move the prey farther. Consequently, *rear* maxillary teeth might be expected to be the ones most likely modified in any dental adaptations that served swallowing. Elongation of a few teeth permits deeper penetration into the tissues and hence increases purchase of the jaws on the prey. These factors, it is argued, all favored the initial elongation of posterior maxillary teeth. However, once elongated to enhance swallowing effectiveness, they became a key feature preadapted for subsequent modification along several evolutionary

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FIG. 5. Lateral jaw muscles as seen in three colubrid snakes (first three) and viperid snake (bottom). A) *Heterodon simus* B) *Xenodon rabdocephalus* C) *Xenodon merremii* D) *Agkistrodon halys*. Abbreviations as, *M. adductor mandibulae externus superficialis*; ap, *M. adductor mandibulae externus profundus*; cg., *M. compressor glandulae*; cm, *M. cervicomandibularis*; lqm, *Ligamentum quadrato-mandibularis*; vg, venom gland.

pathways. One direction led toward the *Xenodon* and *Heterodon*-like snakes in which the manipulation function of the elongated teeth during swallowing was further enhanced. These snakes thus represent not "protovipers" but simply a specialized form of snake in which the teeth aid prey manipulation during swallowing. A second line of evolution led to viperid snakes in which the emphasis shifts so that the elongated teeth now play a greater role in venom injection. Although the superficial impression would be that of two parallel lines of evolution involving rear maxillary tooth elongation, the selective forces acting in each line would be quite different. In one, the adaptations would serve to improve prey manipulation during swallowing while in the other to improve envenomation.

Just as the mechanics of swallowing could have been the initial factor favoring tooth elongation, one might expect that oral gland secretions also served initially not a toxic function but as an aid in prey handling or swallowing.

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