Evolutionary Patterns in Advanced Snakes[1]

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SYNOPSIS. One prevalent view of phylogenetic events in advanced snakes holds that the fangs evolved along at least two pathways, one (*e.g.*, elapids) from ancestors with enlarged anterior and the other (*e.g.*, viperids) from ancestors with enlarged posterior maxillary teeth. Selective forces driving these changes are presumed to arise from the increasing advantages of teeth and glands in venom injection. In this paper, another plausible view of these events is proposed.

First, fangs of both elapids and viperids likely evolved from rear maxillary teeth. In non-venomous snakes, differences in tooth morphology and function suggest that there may be some division of labor among anterior and posterior maxillary teeth. Anterior maxillary teeth, residing forward in the mouth, likely serve the biological role of snaring and impaling prey during the strike. They are also conical, frequently recurved, and lack a secretion groove. On the other hand, posterior teeth, because of their geometric position on the maxilla and mechanical advantages, tend to serve as aids in preingestion manipulation and swallowing of prey. They are often blade-shaped and occasionally bear a secretion groove along their sides. Although both front and rear maxillary teeth of non-venomous snakes may be elongated, this is likely to serve these different functional roles and hence they evolved under different selective pressures. When fangs evolved, they did so several times independently, but from rear maxillary teeth. In support, one notes a) the similar position, postorbital, of venom and Duvernoy's glands, b) similar embryonic development of fangs and rear maxillary teeth, c) secretion groove, when present, is found only on rear teeth, and d) similar biological roles of some rear teeth and fangs. For ease in clearance of the prey during the strike, the fangs are positioned forward in the mouth, accomplished in viperid snakes by forward rotation of the maxilla and elapids by rostral anatomical migration to the front of the maxilla.

Second, the adaptive advantage first favoring initial rear tooth enlargement likely centered not on their role in venom injection, but rather on their role in preingestion manipulation and swallowing. However, once enlarged, teeth would be preadapted for later modification into fangs under selection pressures arising from advantages of venom introduction.

This has implications for the function and evolution of associated structures. Besides possibly subduing or even killing of prey, the secretion of Duvernoy's gland may be involved in digestion or in neutralizing noxious or fouling products of the prey. The presence or absence of constriction need not be functionally tied to absence or presence of venom injection. The phylogenetic pathways outlined herein were likely traveled several times independently in advanced snakes.

INTRODUCTION

Perhaps because the head has been a major active site of phylogenetic change in snakes (Gans, 1962), much discussion of evolutionary events has focused on cranial features (*e.g.*, Marx and Rabb, 1972). Advanced snakes (=Caenophidia) contain from harmless to venomous varieties and include the families Colubridae, Elapidae (cobras, kraits, coral snakes, sea snakes, etc.), and Viperidae (vipers and pit-vipers). Most speculation as to evolu-

tionary events within this large and diverse group has centered on the development of the venom apparatus from non-venomous ancestry through a series of morphological intermediates. The adaptive advantages, implied or stated, driving these changes usually involve the growing functional role of the teeth and glands in venom injection.

The purpose of this paper is to review the functions and biological roles (*sensu* Bock, 1980) of snake dentition, maxilla, and of the associated oral glands. This will be the basis for analysis of related morphological and behavioral characteristics and for assessment of major evolutionary pathways within advanced snakes.
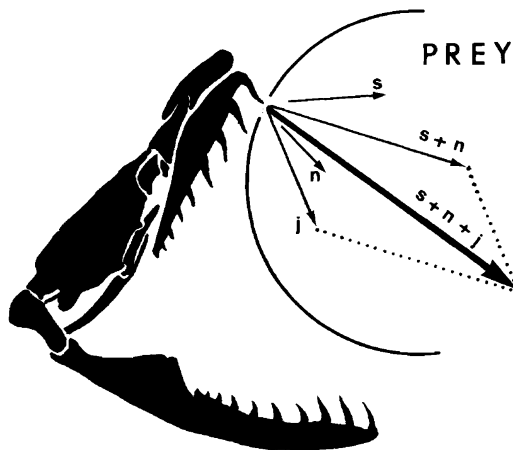
FIG. 1. Forces and their resultant for an anterior maxillary tooth. In recurved teeth, the cusp is inclined forward so as to bring the tip into closer coincidence with the resultant force at time of impact. At least three separate forces are present at time of impact due to forward momentum of strike (s), lowering of the jaws (n), and retraction of jaw apparatus (j) which have the single resultant force (s + n + j). After Frazzetta, 1966.

FUNCTION OF MAXILLARY TEETH

Form and function of snake dentition is less well studied than many other aspects of head anatomy such as myology and osteology despite an early impetus provided by a general survey in comparative odontology (Owen, 1840–1845). In snakes, attention has focused on the venom delivery fangs of elapid and viperid snakes both for their taxonomic (Bogert, 1943; Brattstrom, 1964) and functional (Klauber, 1956; Schaefer, 1976) interest. Less is known about the function of teeth in nonvenomous snakes. Certainly teeth have at least a dual role—prey capture and swallowing. But there may be some division of labor especially among teeth borne by the maxilla.

Anterior maxillary teeth

As a snake strikes, anteriorly placed teeth are first to come into the vicinity of the intended victim. If the strike was slightly in error or if the prey begins evasive action, these front teeth may bear primary responsibility for snagging the prey and preventing its escape until body coils

are thrown around or the remainder of the jaws are brought over the victim. In large *Python sebae* and *P. molurus,* anterior maxillary teeth are long and recurved. Their biological role is to snare and impale the prey (Frazzetta, 1966). In recurved teeth, the cusp is inclined forward so as to bring the tip into closer coincidence with the resultant force at time of impact. At least three separate forces are presumed to be present at time of impact due to forward momentum of strike (s), lowering of jaws (n), and retraction of jaw apparatus (j) which have the single resultant force (s + n + j) in Figure 1. The reverse curvature of the tooth tip brings it into closer alignment with the resultant force and so increases the chances that it will stab the prey at an angle aiding penetration. The basal part of the tooth slants posteriorly so that if a victim pulls back attempting to escape, the teeth that have made initial penetration only sink more deeply and securely. Further, from high-speed film analysis, Frazzetta concludes that at least for large prey, anterior teeth are the most important in prey-capture. In fact, it is here (anteriorly) that long recurved teeth are located.

Long maxillary teeth positioned anteriorly are commonly found in colubrid snakes. In the garter snake, *Thamnophis elegans,* long recurved teeth tend to be located anteriorly on upper jaw bones (Wright *et al.,* 1979). However, teeth at the posterior end of the maxilla are also commonly found to be long. In fact, over half of the colubrid snakes examined by Marx and Rabb (1972) had enlarged posterior teeth. The biological roles for these teeth are quite different than for anterior teeth.

Posterior maxillary teeth

In "rear-fanged" poisonous snakes, posterior teeth of the maxilla serve as instruments for venom injection to bring on rapid prey death. However, in many colubrid snakes these teeth instead serve as aids in swallowing prey. In these colubrid species, the rear teeth serve the biological role of providing a secure purchase on prey during preingestion manipulation and during swallowing. In the garter snake, *Thamno-*

phis elegans, the posterior maxillary teeth are quite unlike other teeth of the maxilla and, in fact, quite unlike other teeth in the mouth. Wright *et al.* (1979) observe that the rear teeth are curved and bear a blade-like posterior ridge. When prey is seized, alternating left and right side-stepping motions of the jaws begin until the head of the snake reaches a favorable position and then swallowing commences. During this preingestion and swallowing behavior, motion of the maxilla is such that on each closure, posterior teeth are the first of its teeth to engage the prey. The prey is often alive during this preingestion and swallowing behavior. Enlarged posterior maxillary teeth pressed firmly into the victim increase the security of the snake's grip. The holding and manipulative role of these large teeth has been reported in other snakes as well (Minton, 1944; Platt, 1969; Kroll, 1976; Kardong, 1979).

The mechanical advantages for long, posterior maxillary teeth are severalfold. Since the posterior maxillary teeth are the first maxillary teeth to engage the prey, the snake is able to take full advantage of the entire sweep of the retraction motion; posterior teeth are positioned farther from the point of rotation, sweep through a longer arc, and hence move the prey farther than more forward positioned teeth; elongation of teeth permits deeper, more certain penetration and hence increases purchase of the jaws on the prey (Kardong, 1979).

Like anterior teeth, posterior teeth are designed for penetration but unlike them experience two separate sequential forces. Jaw closure followed by retraction imparts two motions to the posterior teeth—first, downward toward the prey; and second, posteriorly after the teeth are engaged (Fig. 2). The first motion results in tooth puncture and the second in a cutting stroke. The tooth design reflects both actions. The long pointed shape facilitates initial tooth entrance. But, with the retraction motion, the broad side of the tooth is pressed against the tissue and the resistance increases. However, the presence of a blade-like ridge on this leading edge reduces this resistance and permits the tooth
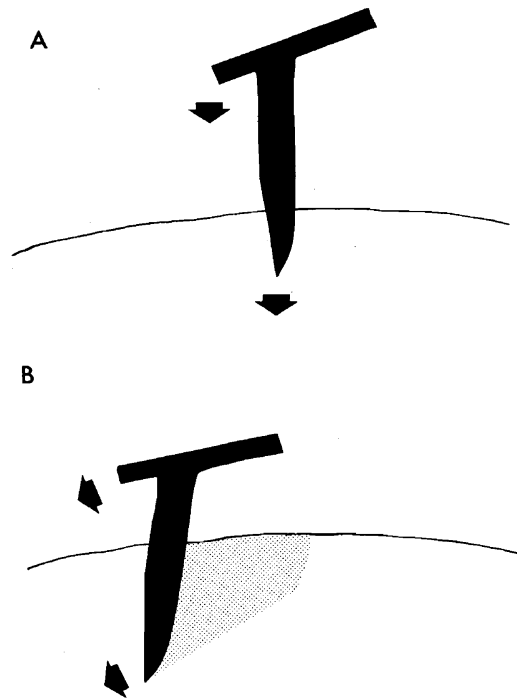

FIG. 2. Two step motion of posterior maxillary tooth common during swallowing by colubrid snakes. Ventrally directed motion of closing upper jaw carries the elongated tooth into contact with the prey where first penetration occurs (*A*). Next, retraction of the maxilla draws the engaged tooth posteriorly where its blade-like edge encourages further penetration into tissues of the prey (*B*).

to cut its way deeper. Cundal and Gans (1979) describe the temporal sequence of muscle activity that allows closure to occur independently of retraction.

Such elongation of posterior maxillary teeth seems to be of special advantage when prey is slippery (frogs), uncertain (puffy toads), or offers resistance (non-constricting snakes). Certainly other adaptations are conceivable (*e.g.,* increase in tooth number). But, the prominent use of enlarged posterior maxillary teeth in preingestion and swallowing is one solution. This adaptation would also facilitate the entrance of oral gland secretions into a victim. And in fact, many colubrid snakes have grooves in these long teeth that could channel secretory products.

Turning this sequence around, a plausible argument could be made that intro-
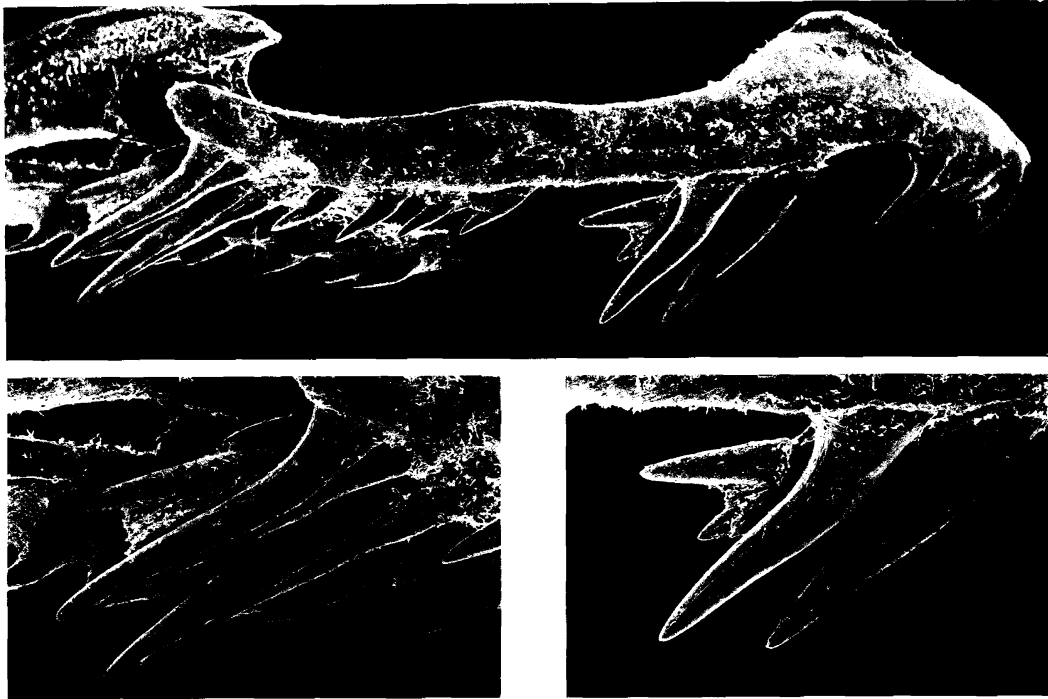
FIG. 3. Right maxilla of the colubrid, *Psammaphylax rhombeatus* (KVK 252). Enlargement of the posterior maxillary teeth at left showing lateral, open secre·ion grooves. Anterior enlarged teeth shown at right lack such grooves and tend to be slightly recurved.

duction of oral gland secretion evolutionarily preceded tooth enlargement, and actually made such modifications of the denition of selective advantage. Even an ungrooved, but elongated tooth could inoculate significant quantities of secretion beneath the skin (Stejneger, 1893). The posterior maxillary teeth, already strategically positioned for the reasons mentioned above, would be the ones most likely to be modified.

Although both anterior and posterior maxillary teeth may be elongated, sometimes even within the same species, the selective pressures acting on each are different. In *Psammophylax* (Fig. 3), enlarged teeth are present on both ends of the maxilla. However, the anterior tooth is slightly recurved and lacks any secretion canal. The posterior tooth is slightly curved and has a secretion groove. The angle each makes with the maxilla is different. My interpretation is that in *Psammophylax*, both conditions are simultaneously present be-

cause both types of selective pressure exist—anterior teeth involved in snaring prey, posterior teeth in preingestion/swallowing manipulation (and here additionally introduction of secretion). However, the evolutionary events that lead to development of fangs likely centered around changes in posterior maxillary teeth.

MAXILLA EVOLUTION

Fangs from opisthoglyph ancestors

The term fang is restricted to long, hollow or grooved teeth that ride upon an often erectile maxilla (Edmund, 1969). They are found in elapid (including hydrophiid), viperid, and many colubrid (*e.g., Dispholidus*) snakes. Although traditional descriptive terminology discriminates between front- and rear-fanged forms (proteroglyph *vs.* opisthoglyph), it seems likely that all fangs evolved from *rear* maxillary teeth (for contrary views see Anthony, 1955 or Marx and Rabb, 1972). The reasons are severalfold.
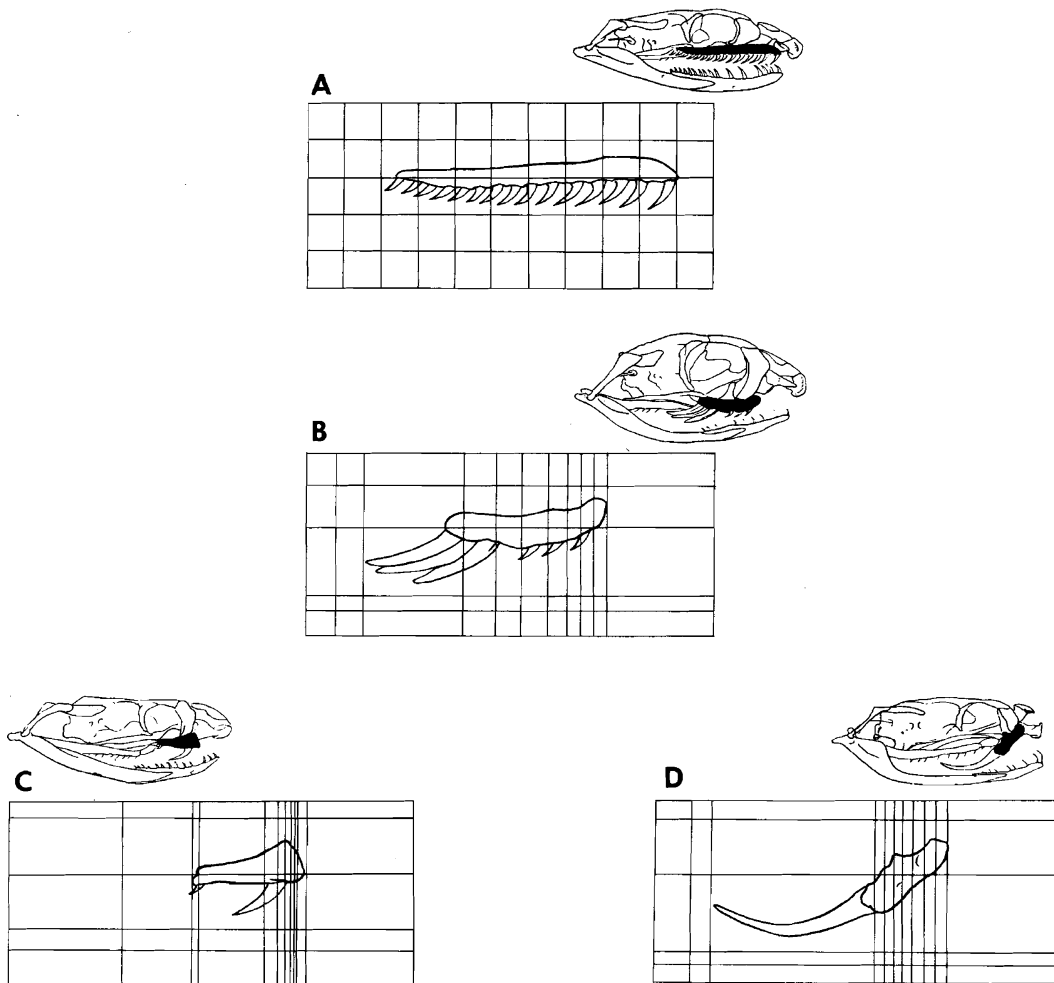
FIG. 4. Rectangular coordinate grids diagramatically showing hypothetical transformation of the maxilla from aglyph to opisthoglyph colubrid (*A* to *B*) and from here to elapids (*C*) and viperid (*D*) snakes. Within the transformation series, the maxilla shortens. The rear maxillary teeth lengthen and develop secretion grooves to form fangs. The fang of elapid snakes migrates forward on the shaft of the maxilla. Specific genera selected A–D, respectively, include *Pituophis, Dispholidus, Naja,* and *Vipera.*

First, if elapid front-fangs were derived from anterior maxillary teeth, it might be expected that the associated venom gland would also lie nearby in an anterior position in the snout. This, in fact, is not the case. Even though elapid fangs are at the front of the mouth, the venom gland resides behind the eye in the same location as the Duvernoy's gland of rear-fanged snakes (McDowell, 1968).

Second, the embryonic development suggests an origin of fangs from posterior maxillary teeth. The venom gland of vi-perid and elapid snakes and the Duvernoy's gland of colubrids form from a common embryonic rudiment associated with teeth at the rear of the dental lamina (Kochva, 1963, 1965).

Third, when both an enlarged anterior and posterior tooth are simultaneously present in the maxilla, only the rear tooth bears a secretion groove. If fangs evolved from front teeth, then one might expect to see this anticipated in a colubrid interme-diate. It would be a mistake to build a case for front tooth origin of fangs on the basis

of the existence of some elapid snakes with front fangs. Such a view would fail to take into consideration the argument, made here, that such fangs were originally rear fangs that subsequently migrated forward to the front of the mouth. However, in a few colubrid species (e.g., Psammophis, Psammophylax) both ends of the maxilla bear enlarged teeth thus removing doubt about relative position of teeth and ruling out the possibility that migration of teeth could obscure interpretation. In these forms, only the rear teeth carry a secretion groove. So far as I am aware, there are no colubrid snakes with such a dual presence of front and rear enlarged teeth where the secretion groove is borne on any teeth but the rear.

Fourth, derivation of fangs from rear maxillary teeth would be more in keeping with and closer to the biological role rear teeth serve. As mentioned above, they serve for prey manipulation during swallowing. If these swallowing motions begin before the prey has been dispatched, then these enlarged posterior maxillary teeth that penetrate the integument would be especially suited for the timely introduction of oral gland secretions. The close association of Duvernoy's gland with enlarged posterior maxillary teeth and the presence in some species of a secretion canal in the tooth suggest that, if not initially, then very soon in their evolution these posterior teeth became instruments to introduce substances on and below the integument of the prey. On the other hand, anterior maxillary teeth serve a quite different biological role, namely, that of snaring prey. Because anterior maxillary teeth do penetrate the prey upon impact, they could conceivably introduce killing or tranquilizing secretions. In colubrids, however, they do not show any evidence (e.g., secretion canals, enlarged associated glands) of being modified for such secretion delivery below the integument.

The rectangular coordinate grids in Figure 4 summarize the hypothetical evolutionary changes of the maxilla in advanced snakes. In advanced colubrids, the shaft of the maxilla shortens with accompanying reduction in number of front maxillary teeth. The rear tooth enlarges. In most elapids, remaining anterior teeth are lost and the enlarged "rear" tooth migrates forward. Often a small rear tooth holds its position and persists, possibly serving to stabilize the posterior maxilla while the struck prey is still struggling within the snake's jaws. Similar changes occur in viperid snakes with additional loss of the posterior shaft of the maxilla and the development of a prominent dorsal process that articulates with the prefrontal (not shown).

Fang evolution

The maxilla of viperid snakes undergoes extensive forward rotation during the strike carrying the fang into an erect position to plunge into the prey (van Riper, 1953 and others). Although less extensive, the maxilla in elapid and colubrid snakes also undergoes excursions relative to its point of suspension from the braincase. McDowell (1969b) described several groups of elapid snakes in which the maxilla slides forward relative to the prefrontal and other species where it actually rotates about its articulation with the prefrontal. In colubrids, the maxilla has been reported to experience motion in various planes relative to its point of suspension (Cowen and Hick, 1951; Albright and Nelson, 1959; Kardong, 1979; Cundall and Gans, 1979). Thus, maxilla rotation in viperids that dramatically erects the fang is not a "new" innovation but only represents a more extensive excursion in a parasagittal plane. What has been a major change from colubrid to viperid and, to a lesser extent, elapid snakes is the shift in biological role of these enlarged teeth from a role in swallowing to that of rapid prey killing.

In most colubrids, enlarged posterior maxillary teeth serve to manipulate prey during swallowing. Any oral gland secretion these teeth might introduce occurs not at the moment of the strike but later as the jaws are worked over the prey during swallowing. Although they may secondarily play a mechanical role in swallowing, in elapid and certainly viperid snakes their principal biological role is to deliver venom to promote the rapid death of the prey. A

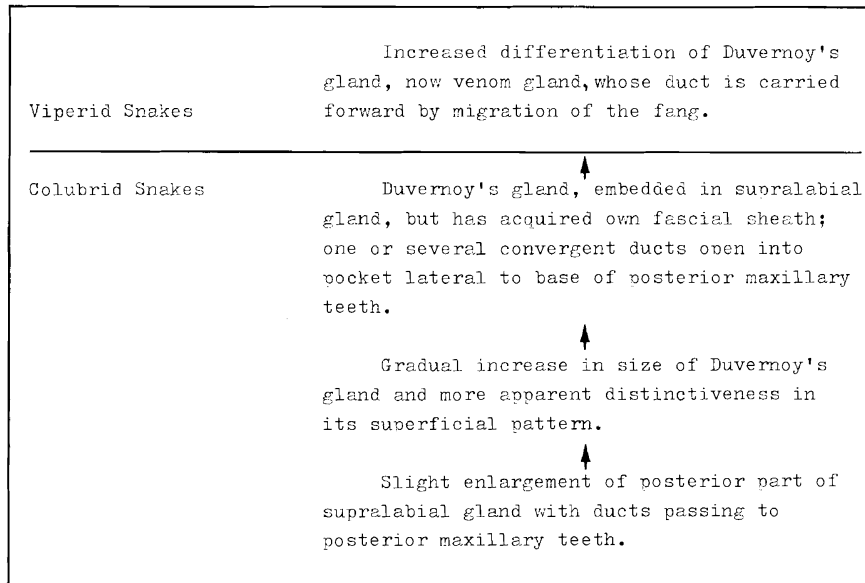| Viperid Snakes	Increased differentiation of Duvernoy's gland, now venom gland, whose duct is carried forward by migration of the fang.
Colubrid Snakes	↑ Duvernoy's gland, embedded in supralabial gland, but has acquired own fascial sheath; one or several convergent ducts open into pocket lateral to base of posterior maxillary teeth. ↑ Gradual increase in size of Duvernoy's gland and more apparent distinctiveness in its superficial pattern. ↑ Slight enlargement of posterior part of supralabial gland with ducts passing to posterior maxillary teeth.

FIG. 5. Scheme of venom gland evolution from Duvernoy's gland in turn from region of supralabial gland proposed by Smith and Bellairs (1947).

forward location of fangs in the mouth facilitates this role by positioning them at the point of widest gape and so ensures their clearance of the prey as these long fangs pass over it just before closing. In viperid snakes, the forward position of the fangs is accomplished by the extensive forward rotation of the maxilla that erects them into an anterior position. A few highly venomous colubrid species, that use fangs similarly to deliver a quick acting venom, have fangs that also ride on an erectile maxilla (*e.g., Dispholidus*). In elapid snakes, it seems likely that this forward position has been achieved by the rostral migration of the fangs in the maxilla (relative to the ectopterygoid-maxilla articulation). In a few forms, this migration is extreme (*e.g., Dendroaspis*).

EVOLUTION OF ASSOCIATED FEATURES

Venom, Duvernoy's and supralabial glands

Venom glands evolved from Duvernoy's glands of colubrid snakes (Gans and Elliott, 1968; Kochva and Gans, 1970; Kochva, 1978). The similar embryonic development (Martin, 1899a, b, c; Kochva, 1963, 1965; Gygax, 1971) of venom glands,

fangs, and Duvernoy's glands from the dental lamina of the maxilla in colubrid, elapid, and viperid snakes supports this general evolutionary association, even though venom glands may have arisen several times independently (Kochva *et al.*, 1967; Nickerson, 1969).

The first attempts to trace gland evolution centered around matching of tooth morphology to presumed changes in associated gland. Based in part upon Boulenger's (1896) proposed association of Aglypha to Opisthoglypha, Phisalix (1912) sought to construct an ascending morphological series of tooth evolution. Sarker (1923) carried this farther emphasizing the relationship between the duct of Duvernoy's gland and the evolving fang. His morphological series showed a gradual enlargement of the gland with "in pace" changes in tooth form (peg, cutting edge, lance, open groove, closed groove) and duct exit. Based upon gross morphology of the gland, Smith and Bellairs (1947) proposed a scheme of gland evolution (Fig. 5) that was similar to that of Sarker (1923). However, they were first to note that while teeth in representative species did enlarge and acquire a groove, this was not neces-

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                              Elapid, viperid and other more advanced
                           snakes.
                                              ↑
                           Duvernoy's gland present, tubuloacinous,
                           large, distinct from supralabial glands,
                           purely serous, tubule walls highly folded
                           with increased storage in lumen.
                                              ↑
                           Duvernoy's gland present, tubuloacinous,
                           large, distinct from supralabial glands,
                           purely serous.
                                              ↑
Duvernoy's gland present,
tubuloacinous, well-            Duvernoy's gland present, tubuloacinous,
developed,                  small, distinct from supralabial glands.
mostly serous with some                       ↑
mucous cells.                  Duvernoy's gland present, characterized
                            by cords of serous cells but not anatomically
                            distinct from mucous supralabial glands.
                                              ↑
Duvernoy's gland absent,                      (mucous and serous cells)
serous and mucous cell cords    Duvernoy's gland absent, mixed supralabial
alternate in supra-         glands.
labial glands.                                ↑
                               Divernoy's gland absent, supralabial gland
                            purely mucous.
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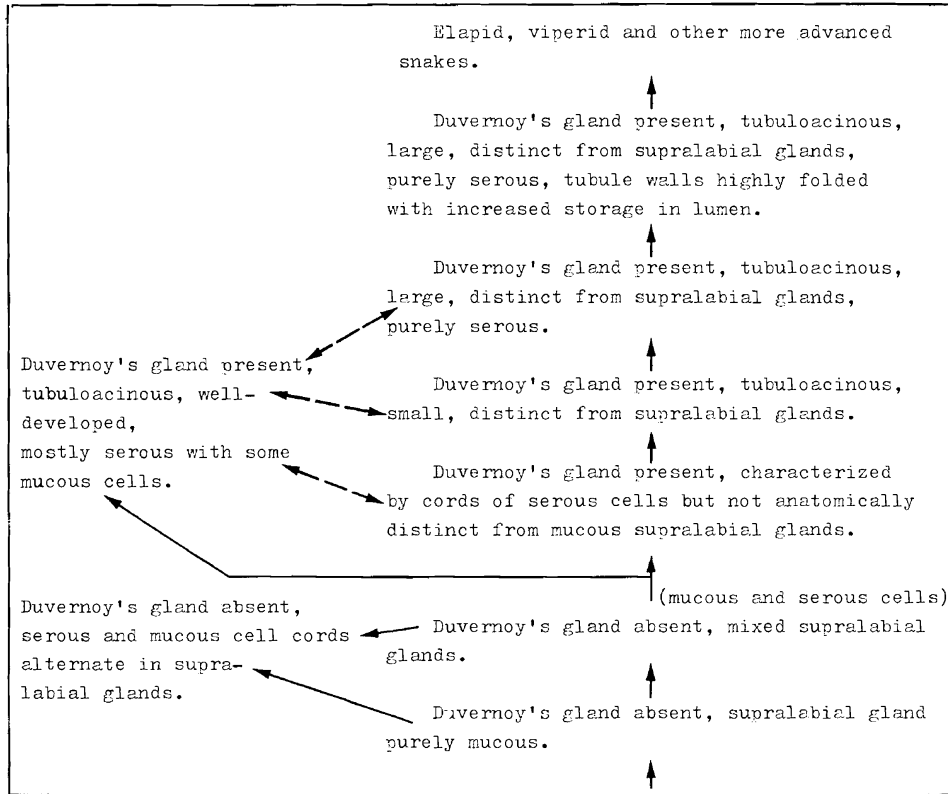
FIG. 6. Scheme of Duvernoy's gland evolution within colubrid snakes adapted from Taub (1967).

sarily "in step" with the corresponding stage of the development of Duvernoy's glands. They also observed that the differentiation of the gland (macroscopically) often preceded the appearance of a groove in the tooth. But, *enlargement* of the posterior maxillary teeth commonly preceded the differentiation of the gland (macroscopically).

Taub's study (1967) of gland evolution was the first to be based upon microscopic characteristics. He noted trends toward reduction in cell height, increased storage capacity, and tendency for serous cells to separate from the supralabial gland into the special Duvernoy's gland. He emphasized the variable nature of Duvernoy's gland and the divergent pathways of its development (Fig. 6). He also urged caution in interpretation of the relationship between glands and posterior maxillary teeth.

Table 1 compares the two studies. In closely related species, Taub, unlike Smith and Bellairs, did find a Duvernoy's gland present. This probably reflects inconsistencies in taxonomy (Savage, 1952). It may also reflect the fact that Taub examined the microscopic but Smith and Bellairs the macroscopic character of glands. Although gross differentiation may reflect a gland's relative prominence, this is not a reliable way to test for its presence or absence. Taub also found no evidence that development of Duvernoy's gland was in any way parallel to evolution of grooved fangs. However, he points out that two or more enlarged teeth in the region of the posterior maxilla could form between them a functional equivalent to a groove in a single tooth. Even a single enlarged but ungrooved tooth could introduce a significant amount of secretion into a prey animal (Stejneger, 1893).

TABLE 1. *Comparison of observations made on supralabial and Duvernoy's gland gross structure (Smith and Bellairs, 1947) and microscopic structure (Taub, 1967).*

| | | Duvernoy's gland | |
| | | Smith and Bellairs | Taub |
Species	Posterior maxillary teeth		
Ptyas	no enlargement	present	present
Dendrelaphis caudolineata	no enlargement	absent	
Ahaetulla fasciolata	?		present
Ahaetulla mycterizens	?		present
Ahaetulla prasina	?		present
Oligodon cyclurus	considerable enlargement	absent	
Oligodon ornatus musyi	?		present
Macropisthodon rhodomelas	enormous enlargement	absent	
Macropisthodon rudis	?		present
Malpolon monspessulana	?		present

Thus, establishing a functional relationship between posterior maxillary teeth and Duvernoy's gland cannot be easily accomplished by simple matching of their respective anatomies alone.

One of the relatively easiest functions to demonstrate of the venom and Duvernoy's gland secretions is toxicity. This directly concerns human well-being and much pharmacological literature has been devoted to characterizing constitutents of the secretion in terms of their contribution to the toxic function. This toxic function of the secretion has also been at the center of theories about the course of evolutionary events in advanced snakes (*e.g.*, Gans and Elliott, 1968; Kochva and Gans, 1970). Reduced to its simplest, a prevalent view has been that the adaptive advantages accruing from introduction of toxic secretions favored the evolution of a venom apparatus and fangs and this, in turn, a still more potent toxin and efficient delivery system. The eventual result of these snowballing events was the development of the complex venom systems of elapid and viperid snakes. Various characteristics of colubrids could, in light of this theory, be taken as circumstantial support; many, if not most colubrids (Marx and Rabb, 1972) have enlarged posterior maxillary teeth (incipient fangs?); some of the most venomous snakes are colubrids (*Dispholidus, Thelotornis*); and even some species once considered harmless show evidence of possessing

a toxic oral secretion (Heatwole and Banuchi, 1966; Willard, 1967; Goellner, 1975; Philpot *et. al.*, 1977).

Certainly the oral secretion in some species is toxic; in viperid and elapid snakes it serves the biological role of quickly killing prey and with this brings economy in prey capture effort and reduces the snake's risk of injury from the thrashing of a struck victim. However, evolving next to supralabial glands (Kochva, 1978), the venom-producing glands did and perhaps still do function directly in digestive processes. The presence of proteolytic enzymes in venom have been known for sometime (de Lacerda, 1881). And agents in poisons similar to enzymes of digestive juices have been expected (Phisalix, 1922) and discussed (Kellaway, 1939). But Zeller (1948) was one of the first to consider a biological role for these enzymes other than for promoting rapid prey death. He argued that many enzymes (proteases, peptidases, phosphatases, esterases) found in snake venoms also occur in digestive juices of other, non-venomous animals; "spreading factors" (*e.g.*, hyaluronidase) could promote spread of digestive enzymes; heavy necrosis *at the bite* site does not itself contribute to prey death but is attributable to "primitive digestive properties of snake poison" (p. 488). Anecdotal observations of Reichert (1936) and Stimnler-Morath (in Zeller, 1948) support this suggested digestive role of venoms. Re-

cently, Thomas and Pough (1979) added experimental evidence that viperid venom, in fact, increases digestion rate.

Snakes are specialized to ingest large prey relative to their size (Gans, 1961), yet possess no masticatory dentition to break down the prey that is swallowed whole. Digestive enzymes would have to work from the surface inward, often first passing matted hair or feathers. If there was strong competition or if prey were only seasonally available, a slow digestive rate could put an individual at a comparative disadvantage in processing the bolus and releasing the energy to metabolic requirements. But, if digestive enzymes could be introduced beneath the skin of still-living prey by enlarged, penetrating teeth, the circulation could spread them and digestion be promoted (Parker, 1963; Minton and Minton, 1969). In fact, rapid prey death may be disadvantageous to the action of these introduced oral secretions by stopping their distribution via the prey's own vascular system. In this regard, it may be significant that the heart is often still beating after other functions (e.g., respiration) have ceased following envenomation (McAlister, 1963).

Additionally, secretion of oral glands may serve the biological role of neutralizing noxious products of the prey. Amphibian integument contains individual flask-shaped microscopic serous and large, raised paratoid glands that release a "poison" that, depending upon the species, can be irritating to actually fatal for the predator (Habermehl, 1971; Lutz, 1971). Snakes feeding upon amphibians that release such noxious secretions would be under selective pressure to neuturalize their effects. Oral gland secretions, applied as a prey enters the esophagus, may provide an antidote to the effects of these skin secretions.

Prey secretions need not be toxic to present problems for a snake predator. For instance, the copious, sticky mucus of snails could interfere with swallowing action. Snail-eating specialists, e.g., Dipsas, possess distinct Duvernoy's glands (Taub, 1967) that may be involved in preventing the fouling of the jaws by such substances during swallowing. Gans (1978) speculates that an initial function for oral gland secretions in terrestrial vertebrates may, in fact, have been to condition teeth surfaces and clear them of adhering substances.

Musculature

Striated muscle plays a direct role in the discharge of secretion from venom glands of elapid and viperid snakes (Dullemeijer, 1956, 1959; Kochva, 1962; Rosenberg, 1967; McDowell, 1972). In elapids, a divided derivative of the M. adductor manibulae superficialis lateral jaw musculature attaches to the thick capsule of the venom gland. Contraction of the muscle deforms the gland causing intraglandular pressure to rise and venom residing in abundant storage space of the tubular lumena is expelled (Rosenberg, 1967). In most viperid snakes, M. compressor glandulae, a derivative of M. adductor mandibulae profundus (Haas, 1962; Kochva, 1963) wraps around the venom gland and attaches to its dorsoanterior edge. Upon contraction it compresses the gland, forcing expulsion of stored venom. A few species possess elongate venom glands (e.g., Causus rhombeatus) with strips of striated muscle running along their sides causing venom extrusion by a presumed "wringing" action (Haas, 1952).

However, in colubrid snakes, with only few exceptions, there is commonly no striated muscle associated with Duvernoy's gland in such a way that it could directly act upon the gland to expel "venom." Conceivably, nearby ligaments (1. quadratomaxillare) or integument may be drawn taut or deeper muscles bulge and press upon the gland raising intraglandular pressure. But, certainly there is no striated muscle adapted specifically for the task. Compared to viperid and elapid, colubrid Duvernoy's glands lack comparable storage space in the tubules. Because they lack large secretion stores and muscular action for its quick expulsion, the biological role of Duvernoy's glands is likely different from that of more advanced poisonous snakes that rely upon a tactic of rapid prey death. A few colubrids (e.g., Dispholidus) are exceptions in that they do possess large

storage lumena (Taub, 1967) and striated muscle that mechanically impinges directly upon the gland. But, these also deploy a rapid-kill tactic of prey capture.

Constriction

Constriction, as a prey-killing tactic, arose very early in the history of snakes being present in most (all?) of the primitive booids (Greene and Burghardt, 1978). The uncertain phylogenetic ancestry of colubrids makes it difficult to determine whether the presence of constriction in this family is derived directly from primitive snakes or evolved independently. However, the absence (loss?) of constriction in some colubrids can be attributed to several possible factors. First, non-constriction may be a primitive and constriction a derived colubrid characteristic. This implies that colubrids arose from ancestors lacking constriction. Though possible, the probably widespread occurrence of constriction in early snakes makes this less likely. Second, with the advent of venom injection, constriction was replaced as the primary method of prey-killing perhaps for reasons of economy or reduced chance of injury to the snake. In this regard, Gans (1978) has observed that, in general, the best constricting snakes lack venom and the highly venomous snakes lack serious constriction.

Third, non-constriction may be a consequence of anatomical compromises with other needs of the organism. For instance, Ruben (1977) argued that in fast moving snakes, rapid lateral undulation of the vertebral column is based upon design and attachments of the axial musculature that are incompatible with the use of these same structures in constriction. If correct, this would provide a form-function basis for the loss of constriction ability independent of selection pressures resulting from the biological role of venom injection.

CONCLUSIONS

Within colubrid snakes the maxillary dentition tends toward heterodonty. Posterior teeth often bear a secretion groove and are often blade-shaped, whereas anterior teeth lack these characteristics and are basically conical in form. These anatomical differences reflect differences in emphasis in the biological role of front and rear teeth. Anterior teeth are most important during prehension of prey. Being forward in the mouth, they are the first of the upper jaw dentition to be brought into the vicinity of the prey during the strike and at that moment serve the biological role of snaring the prey. Their long and often recurved design contributes to successful engagement during impact with the prey.

Posterior maxillary teeth serve different biological roles. They contribute to efficient prey manipulation and swallowing and they serve to introduce oral gland secretions into the prey. These roles are often complementary and simultaneous. The long, blade-like teeth common in most colubrids improve the snake's purchase and facility for prey manipulation during preingestion and swallowing. At present, a plausible case can be made for either the role in swallowing or role in introduction of oral secretion evolving first. However, the widespread presence of enlarged rear teeth with some accompanying degree of Duvernoy's gland differentiation suggests that whichever role came first the other soon followed although, as both Taub (1967) and Smith and Bellairs (1947) emphasize, the degree of tooth enlargement and Duvernoy's gland development are not directly parallel or proportionate.

The role of secretions from oral glands are severalfold. They come to coat the prey surface and so lubricate its passage into the esophagus; they perhaps have a role in promoting oral hygiene (Gans, 1978); some are tranquilizing or toxic and result in abatement of prey resistance or in death. Tonic immobility or just quieting prey struggle by oral secretions would be of advantage by increasing the ease of prey handling and by reducing the possible risk of damage to slender elements of the skull (Kochva and Gans, 1970; Gans, 1978). However, except for a few colubrid species (e.g., Dispholidus), prey capture does not include rapid killing from injection of toxins. Even though some colubrids apparently have toxic oral secretions (Alcock and Rogers, 1902), rapid killing is not part of their

prey capture behavior; some colubrids (*e.g.,* *Boiga*) possess grooved teeth presumably for delivery of secretions into the prey but are also constrictors; the large lumenal storage area and musculature used to quickly empty the gland, characteristic of venomous snakes, are absent in most colubrids. Besides prey lubrication, tooth hygiene, and prey quieting, the secretion of Duvernoy's gland may also be involved in biological roles not related to rapid prey death. One such role could be neutralizing of toxic or fouling products of the prey. For instance, snail-eating specialists (*e.g.,* *Dipsas*) encounter copious amounts of sticky mucus. The secretion of Duvernoy's glands may prevent binding of the jaws when the snail is being extracted and swallowed. The presence of digestive enzymes in (Zeller, 1948) and the demonstrated promotion of digestive rate by snake toxins (Thomas and Pough, 1979) suggest that another role for Duvernoy's gland secretion could be related to prey digestion. A rapid prey death could, in fact, be counterproductive to the spread of introduced digestive secretions via the prey's own circulation system. When, prehaps because of danger of injury to the snake, rapid prey death is required, constriction, *not* envenomation, is the common tactic in colubrids. Constriction leading to rapid prey death stops the general systemic spread of introduced secretions and reduces their digestive advantages. It may be for this reason that constricting snakes (*e.g., Lampropeltis, Elaphe, Pituophis*) lack enlarged posterior maxillary teeth and usually lack a well differentiated Duvernoy's gland. In viperid and elapid snakes a different style of prey capture is present. Here, in addition to digestive functions, venom contributes to rapid prey death which assumes a more prominent part of the prey capture strategy.

The fangs of proteroglyphs as well as solenoglyphs likely evolved from *rear* maxillary teeth although in different colubrid ancestors. During swallowing, the diagonal slant of the maxilla at jaw closure means that rear teeth are the first maxillary teeth to engage the prey. This plus the geometric position of these teeth place them in the most favorable mechanical position to introduce oral gland secretions and/or serve as instruments for prey manipulation. Both these functions are closer to that service performed by fangs of venomous snakes than is the apparent function of anterior teeth which serve to snare prey.

In the present paper, I assume that evolution in advanced snakes proceeded along two major pathways. This led to members of the family Elapidae on one course and Viperidae on the other, both independently derived from opisthoglyph members of the Colubridae (Fig. 4). Opisthoglyphs, in turn derived from aglyph members of the colubrids, show a shortening of the length of the maxilla and a lengthening of the posterior maxillary teeth with development of an open canal along the side of these teeth. In elapid snakes, the maxilla undergoes further shortening, the groove closes to form an internal venom channel and the fang migrates forward. In viperids, the maxilla is also further shortened, the rear grooved tooth becomes a solenoglyph fang and lengthens still further.

Evidence of polyphyletic origin is found in colubrids (Underwood, 1967; Kardong, 1979), elapids, (Nickerson, 1968; McDowell, 1969a; Voris, 1977), and viperid snakes (Kochva *et al.*, 1967; Marx and Rabb, 1972). Figure 4 is not meant to deny this, but rather is intended to summarize the major pathways of change that were traveled several times independently by evolving groups of advanced snakes. The form-function basis of this analysis invites tests of its mechanical analysis and evolutionary predictions.

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