Mem. Inst. Butantan
Simp. Internac.
33(1):67-72, 1966

8. MODES OF EVOLUTION IN NEW WORLD OPISTHOGLYPH SNAKES

JOSEPH R. BAILEY

Department of Zoology, Duke University, Durham, U.S.A.

The area I have chosen to discuss this afternoon is the general phenomenon of opisthoglyphy and its evolutionary implications with emphasis on New World forms. Opisthoglyphy is the condition in colubrid snakes marked by the presence of grooved teeth on the posterior expanded portion of the maxillary bone immediately below its articulation with the ectopterygoid. These teeth are usually in pairs on either side, with one of each pair shed alternately, so that at least one is functional on a side at any given time. The grooves are on the anterior or outer face and serve as channels for the flow of venom by ducts from glands in the temporal region of the head. These glands, their histology, homology and biochemistry are currently being studied by my colleague, Aaron Taub, at Pennsylvania State University.

A half century ago the possession of grooved posterior maxillary teeth by a snake was thought to indicate subfamilial status among the COLUBRIDAE; i.e., all snakes with such dentition were considered to have been derived from a common ancestor. Since that time there has been a growing consensus among ophiologists that this opisthoglyph dentition has arisen many times in the course of snake evolution, and today systematists consider the grooved rear teeth to be useful taxonomically only at the generic and specific levels, and at times to vary even within a species. While being discredited, or at least demoted, as a useful character in classification, the morphological condition has, at the same time, been grossly neglected as a biological phenomenon. The fact that a considerable number of species of opisthoglyphs on three continents are known to be dangerous to man, and at times even fatal, indicates that the rear fangs as functional mechanisms are worthy subjects of investigation in their own right.

This paper examines opisthoglyphy from evolutionary, phylogenetic, geographical and ecological aspects in an attempt to discover any generalizations which might pertain to the condition, and which indicate promising avenues for further research.

In some species the grooves become subjective since their degree of development is sufficiently variable that one specimen may show it and another may not. This has been shown by Stickel (1943) in *Sonora*, *Erythrolamprus mimus* by Dunn and Bailey (1939) and it occurs in *Rhadinaea guntheri* according to verbal information from Charles Meyers who is making an intensive study of that genus and its relatives. This latter species currently resides in the literature under two names in two different genera.

Apparently any teeth may show a grooved condition. I have examined a skull of *Oxyrhopus formosus* which bears distinct grooves on the outer faces of the mandibular teeth. The type of *Calamodontophis* has them on the anterior maxillary teeth as well as the posterior, and a skull of *Tomodon dorsatus* has been examined in which the posterior fangs are deeply and doubly grooved. These rear fangs vary considerably from species to species as to their absolute length and as to their length relative to the more anterior teeth. In many these are scarcely differentiated. The most extreme condition I have observed is in *Tomodon dorsatus* in which the length of the fang may be nearly seventy per cent of the length of the maxillary bone. This species also illustrates what is probably the extreme of evolution towards functional dependence upon the fangs, since in some individuals the maxillary teeth are missing altogether or may be represented by one or two teeth only. In these individuals the dentigerous blade of the maxillary bone is thinned to much less than the basal diameter of a tooth. If only a single tooth is present the bone is thickened at that point only sufficiently to accommodate it, as if in development the tooth primordium had induced the deposition of the necessary bony base. Curiously and admittedly on an insufficiency of data, it appears that the fangs are relatively shorter when the anterior maxillary teeth are lacking. It is my belief that the anterior maxillary teeth are in the process of being lost and the fangs will take over as the whole maxillary dentition. This has perhaps reached the quantum stage (Simpson, 1953:389) and its evolutionary progression is currently very rapid. We know little of the functional aspects of this problem. No one to my knowledge has even described the feeding behavior of *Tomodon*, and until a careful analysis of the mechanical aspects of feeding in this species has been made I think it premature to speculate further.

How many different times the opisthoglyph condition has been derived in the course of evolution may never be determined. However its multiple origin would indicate that under certain ecological situations there is an adaptive advantage conferred on its possessors just as there is in the case of webbed feet in aquatic birds or mammals.

I am convinced from a long time intensive study of the relatives of *Drepanoides* that its flattened sabre-like posterior maxillary teeth, lacking grooves, have evolved from an opistoglyph *Clelia*-like ancestor. The only food record I have for it is reptile eggs which hardly require the injection of venom for subjugation.

Where, geographically, do we find opisthoglyphy? Table I makes it clear that the opisthoglyph condition is increasingly more prevalent as we move outward from a north polar center toward the tips of the three peninsulae of Austral-Asia, Africa and South America. Whether based on genera or species the percentages range from zero in the north to approximately fifty per cent in Australia, South Africa and Argentina. Fifty years ago it might have been tempting to invoke Mathew's (1915) then recently proposed thesis that the more primitive opisthoglyphous forms were forced out of more northern centers of origin by more progressive aglyphous forms. However, this interpretation would run counter to classical, and to my beliefs, of the true phylogenies. I think the answer is to be found in the ecological-behavioral area, possibly combined with recent invasions of northern geographical elements.

Habitudinally, without going into details and citing long lists of examples, opisthoglyps in the New World are well represented in arboreal, fossorial, and terrestrial habitats, and have only failed to establish themselves in the aquatic zone. In the Old World however, the opisthoglyph HOMOLOPSINAE are highly aquatic. A quantitative analysis of New World Snakes by habitats at this time is imprudent due to the dearth of reliable field knowledge of the snakes preferences. Many genera include species of diverse habitat selection, as for instance *Philodryas*, an opisthoglyph, and *Thammophis*, an aglyph. Tabulation then becomes necessary on a specific basis which is, of course, well beyond the scope of today's discussion.

Granted the supposition that an elliptical pupil indicates greater nocturnal activity, as interpreted from histological evidence by Gordon Walls (1932), we find a geographic analysis on this morphological basis revealing in the New World fauna. In Table 2 we see that among the aglyphous genera the round pupil greatly predominates in North and South America. Among ophisthoglyphous forms the elliptical pupil predominates when the continents are combined and they form 60% of the ophisthoglyph colubrid fauna of South America. The prevalence of nocturnal forms in the tropics is not all surprising among poekilotherms since cool nights of temperate regions are inhospitable to requisite nocturnal activity, but the hospitable tropic evening invites exploitation. The opisthoglyphs have apparently been better able to exploit nocturnal niches efficiently than the aglyphous groups. Whether this is due to the presence of a venom apparatus may be open to question. However, the more specialized dangerously venomous families are predominately night adapted. On the other hand the American opisthoglyph genera with elliptical pupils may be traced to not more than four phylogenetic stocks and two of these, comprising the relatives of *Pseudoboa* and those of *Tachymenis* contribute two thirds of the genera so that the success of these two lines in South America tips the balance in their favour. The phylogenetic stocks comprising the round pupil ophisthoglyph element are far more diverse.

In both groups the greater exploitation of the nocturnal environment in the tropics goes far to explain the greater diversity of colubrids in low latitudes.

Turning to the question of comparative food habits we are again confronted with a dearth of reliable knowledge of the animals in nature. Throughout my systematic studies of snake collections I have kept careful notes of food items, but these accumulate slowly, detailed literature reports are few and scattered, and the general ones are mostly repetitions of previous sketchy data.

Again, without going into detail, I suggest that on the average, and I emphasize average, the diet of opisthoglyphs is more narrowly circumscribed than that of aglyphous species. Perhaps it would be more accurate to say the diet of nocturnal forms is more restricted than that of diurnal species, because within my limited knowledge the nocturnal aglyphous species have as limited dietary selection as do the opisthoglyphs. I do not know any opisthoglyph which has the broad spectrum of food selection which is exhibited by *Coluber constrictor*, the elaphes, *Agkistrodon mokeson* and *A. piscivorous*. The mollusc eating DIPSADINAE are tropical, aglyphous, and nocturnal with very narrow dietary restriction. Most opisthoglyph species which are adequately known fit this pattern. For instance from my own work I find that adults of *Clelia* feed on other snakes and usually good sized venomous ones, perhaps, not because they are venomous but because they are more sedentary and available. *Erythrolamprus* is a snake feeder. Adults of *Oxyrhopus* and *Pseudoboa* are mammal eaters whereas *Rachidelus* is reputed to eat birds. *Phimophis* and *Siphlophis* are lizard feeders as are the juveniles of *Clelia*, *Oxyrhopus*, and *Pseudoboa*. *Tantilla*, with its curious short blunt maxillary teeth, is the only genus I know to specialize in centipedes, as indicated by the scattered half dozen or so records I have plus literature reports (Hamilton, 1956; Force, 1935). Our knowledge of this area of snake biology is too embryonic to justify conclusion at this time. Not only do we lack information on which food items are taken, but just as important, we do not know to what extent choice enters the picture. Are items taken simply because they are available at the time and place of snake activity and are of a suitable size, or does real choice and biological selection influence the results?

In conclusion I would like to briefly summarize the points suggested above; and then to point out other areas of insufficient knowledge:

1. Grooves may appear irregularly on teeth in several parts of the mouth.
2. Opisthoglyphy is polyphyletic in origin.
3. In *Tomodon dorsatus* the anterior maxillary teeth are in the process of being lost entirely and the large fangs will remain as the only maxillary dentition.
4. Aglyphy may be secondarily derived from an opisthoglyph condition, as in *Drepanoides*.
5. Opisthoglyphy is absent in the most northern colubrid faunas but is at least equally numerous with the aglyphous in the most southern faunas.
6. Opisthoglyphy is found in all habitats (except the aquatic in the New World).
7. Opisthoglyph genera predominate among nocturnal colubrids.
8. Opisthoglyph snakes take a wide variety of foods, but the diet of each species (or genera) is rather narrowly circumscribed.

Areas of future research:

1. Little has been done of an experimental nature on the activity patterns of snake species; at what hours are they active, at what temperatures, light intensities, humidities, etc.... This subject could best be approached on snakes in captivity.
2. We know far too little of the detailed food habits of all snakes in nature. I suggest these be kept and recorded in the literature in detailed and quantitative fashion including the size of the snake. Records in captivity should be noted as such, and food items rejected noted along with those accepted.
3. We need careful observation and analysis of the feeding behaviour and mechanics of nearly all snakes. Such analysis should utilize high speed photography when possible.
4. Virtually nothing is known of the pharmacology, immunology and biochemistry of opisthoglyph venoms. Will these disciplines help us in understanding opisthoglyph phylogenies or explain restricted food habits?

Literature

1. *Dun, E. R.* and *Bailey, J. R.* — Snakes from the uplands of the Canal Zone and Darien. *Bull. Mus. Comp. Zool.*, **86**(1):1-22, 1939.

2. *Force, Edith R.* — A local study of the opisthoglyph snake, *Tantilla gracilis* Baird and Girard. *Papers Mich. Acad. Sci., Arts and Letters*, **20**:645-659, 1935.

3. *Hamilton, William J.* — The food of some colubrid snakes from Fort Benning, Georgia. *Ecology*, **37**(3):519-526, 1956.

4. *Mathew, William D.* — Climate and evolution. *Ann. N. Y. Acad. Sci.*, **24**:171-318, 1915.

5. *Simpson, George G.* — *The Major Features of Evolution*. 434 pp. New York, 1953.

6. *Stickel, William H.* — The Mexican snakes of the genus *Sonora* and *Chionactis* with notes on the status of other colubrid genera. *Proc. Biol. Soc. Wash.*, **56**:109-128, 1943.

7. *Walls, Gordon* — Pupil shapes in reptilian eyes. *Bull. Antivenin Inst. Amer.*, 5(3):68-70, 1932.

TABLE 1 — LATITUDINAL TRENDS IN OPISTHOGLYPHY IN THE COLUBRIDAE

New World

	Genera	Percent Opisthoglyph	Species	Percent Opisthoglyph
Canada	9	0	13	0
North Carolina	20	5.0	37	2.7
Mexico	66	22.7	264	31.4
Costa Rica	45	28.9	115	27.8
Ecuador	42	35.7	117	27.4
Argentina	34	50.0	70	47.1

Europe-Africa

	Genera	Percent Opisthoglyph	Species	Percent Opisthoglyph
England	2	0	2	0
Europe	8	37.5	21	14.3
Africa	73	45.2		
South Africa	26	53.8	54	46.3

Asia-Australia

	Genera	Percent Opisthoglyph	Species	Percent Opisthoglyph
Japan	15	26.6	36	14.0
China	27	22.2	90	11.1
Thailand	33	33.3	72	30.0
Malaya	30	40.0	53	34.0
Australia	9	55.5	15	46.7

TABLE 2 — CORRELATION OF DENTAL TYPE WITH PUPIL SHAPE IN AMERICAN COLUBRIDAE

	Pupil Shape	Americas		South America	
		Number Genera	% Genera	Number Genera	% Genera
Aglyphous	Round	73	89.0	28	84.8
	Elliptical	9	11.0	5	15.2
Opisthoglyphous	Round	16	47.1	11	39.3
	Elliptical	18	52.9	17	60.7