The “DON’T TREAD ON ME” Phenomenon

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ABSTRACT: The evolution of venom and venom delivery systems in snakes has been viewed chiefly as a prey capture strategy. Consideration of the probable phylogeny of the elapids, viperids and crotalids suggests however that venom toxicity has been decreased as venom delivery systems have improved. This apparent paradox is resolved by considering the viperid and crotalid delivery system maximally effective which has allowed toxicity to be decreased thereby holding prey capture capability constant but increasing the defense value of the venom system through sublethal predator poisoning.

Regardless of the selective pressure precipitating the viperid and crotalid venom systems the potential for defense through conditioned avoidance by the predatory population is viewed as having significance for the suborder Serpentes as a whole. It is suggested that the mechanism of mimicry, both Batesian and Mullerian, accounts for the successful radiation of the majority of snakes without departing from a unique and homogeneous form. The hypothesis accounts for the apparently concurrent appearance of the venomous families with the Miocene period of major colubrid evolution. The hypothesis also accounts for both the behavioral and morphological warning signals seen in many venomous and non-venomous snakes throughout the world.

Snakes occupy a special place in the minds and hearts of the human race; a place inhabited by them alone. The snakes also occupy a special place in the evolutionary story of the reptiles. They appeared and radiated into all available major ecological niches as the mammals were overrunning the earth and supplanting the other reptiles as they came. The success of the snakes is also unique among the vertebrates which have assumed the elongated legless form. All others have remained restricted to the life-style which participated the form. In addition to success despite a traditionally disadvantageous morphology, their morphology has remained remarkably homogeneous throughout all members despite their vast range of habitats

The suggestion will be that these "peculiarities" of the snakes are linked together by a common denominator, the single and simple fact that contained within the snakes are a percentage of species which are the most noxious creatures on the face of thee art h , This situation , when viewed over the course of its development, appears to have come about in a progressive series of stages. This paper will attempt to outline the development and consequences of venom systems for the snakes that possess them and the ones that don't,

<u>Origin</u>

The snakes represent the extension of one lizard family which entered into a lifestyle which participated the characteristics typical of the snakes, i.e. (1) drastic reduction or complete absence of limbs, (2) absence of external ear openings, (3) reduction of one lung and elongation of the other, (4) shortened tail, (5) spectacles over eye as opposed to eyelids, and (6) regression of the pineal eye. Some discussion remains about what lizard family adopted which lifestyle, but the most frequently defended position is that some platynotid lizard, probably similar to today's monitors (Varandea) underwent the required morphological changes as the result of a burrowing lifestyle ((Bellairs and Underwood); Walls, 1940; Brock, 1941; Dowling, 1959)

The primary interest in the evolutionary development of the snakes, regardless of origin, has centered on the factors contributing to their startling success. There is unanimous agreement that the ability of snakes to ingest comparatively large prey has been an important factor (Schmidt, 1950; Gans, 1961). While the ingestion of large food items has advantages, more food for less effort, it also creates some difficulties .In particular the digestive system must be geared for a feast and famine feeding routine, and the entire snake must be geared for contending with the fact that no animal wants to be eaten and relatively large animals are relatively more capable of defending themselves. For some of the snakes part of the solution to the first problem of digestion seems to have fostered the solution to the second problem of prey capture. Presumably the ingestion of large prey created a selective pressure favoring elaborate and copious salivary secretion which has resulted in the wide array of oral glands found in all snakes. The advantages are clear of delivering these preliminary digestive enzymes into the prey’s body with elongated teeth modified to carry the enzymes. It is simple to visualize the course of events from this starting point. Improvements toward faster digestion were accomplished by an increase in enzyme strength and by administration of the enzymes into the body of the prey with specialized teeth. As these specialized teeth crept forward toward the front of the mouth and the effects of preliminary digestion became more severe on the prey, the initial bicarbonate status of the system changed into an offense of unprecedented force. With fangs to administer the venom, the selective pressure shifted to killing power and presented the world with poisonous snakes.

If only the delivery system is considered, a clear trend is apparent. The trend has been toward deeper and faster venom delivery. (Slide 1) The initiation of the fang appears to be represented by the rear fanged colubrids illustrated by skull A. In this condition the fangs are grooved, sometimes multiple in number, and set deep in the mouth so that the prey must be partially ingested before the fangs come into play. The rear fanged delivery gives rise to the front fang delivery by a shortening of the maxillary bone. The initial front fang mechanism possessed by the elapids is represented in skull B. In this condition the fang is rigid and short but is the most anterior tooth in the mouth. The fang is either deeply grooved or a hollow tube. The elapid delivery allows envenomation of the prey with brief chewing motions. The transition from the rear fanged colubrids to the front fanged elapids represents the transition of the venom system into primarily a prey capture apparatus. The viperids and crotalids, represented by skull C , have developed much longer fangs by a still greater shortening of the maxillary bone which has allowed the fangs to be folded up against the roof of the mouth when not in use, In these snakes the fang is always a hollow tube. This condition may well represent the ultimate system for the delivery of a fluid into the tissue of another animal.

This apparent trend in the venom delivery system led Bogert (1943) to the conclusion that a colubrid-like rear fang snake gave rise to the elapids and the elapids to the viperids with the crotalids the latest model in the viper line. Johnson (1955) argued convincingly for vertebral characteristics as time and life-style stable within the recognize ‘families of snakes. Johnson then turned to the venomous families and concluded that the elapid-viperid-crotalid sequence suggested by Bogert was correct.

The differences in venom composition and toxicity of the various venomous snake families has not received any evolutionary consideration beyond the decision that venom composition would probably represent questionable characteristic for taxonomic purposes. However, with phylogeny established by independent and osteological characters, it is possible to return to the venom and attempt to determine any trends. Minton (1969) has gathered together toxicity data for a wide variety of snakes belonging to the front-fanged families. Toxicity was represented as the amount of venom required to kill *50%* of the population of 20g mice when administered subcutaneously. It is possible from Minton's data to calculate the average toxicity for the front-fanged snakes in each family. (slide2) When this is done the elapids emerge as the most toxic with the viperids a distant second, and the crotalids lowest of all. The figure illustrates this trend in venom toxicity, expressed as $1/LD_{50}$ micrograms, across the developmental sequence of the front-fanged snakes ($p< 0.01$).

It has been the undisputed contention that the venom system of snakes was evolved primarily as a prey capture strategy. This contention is undoubtedly true. It is difficult, however, to explain an abrupt decline in venom toxicity with a concurrent improvement in delivery if offense, that is killing power, was the only objective.

It could be that the viperids and crotalids are unable to manufacture venom of the toxicity typically found in the elapids. This could have occurred through some mutation back toward the less toxic enzymes that were the initial origin and has been tolerated selectively by the better delivery. This possibility seems unlikely since within the crotalids individual species can be found which possess venoms well above the average toxicity for the elapids.

It could be that the overall killing power i.e. quality x quantity, has remained constant and the principle of "what you don't use you lose” has taken hold. Again, relying on Minton's data, the average venom capacity for the elapids, viperids, and crotalids listed is 109mg. 138 mg. and 92 mg. respectively. The average quantity of venom possessed by the families does not conform to the required pattern if killing power was held constant.

It could be that there are different patterns of food preferences between the three families and that venom changes have been directed at manufacturing more appropriate toxins for the prey. There are in fact differences. The elapids contain a relatively high percentage of members which feed upon other reptiles, while the viperids and crotalids tend toward mammalian prey. It should be noted, however, that the toxicity measures were taken against a mammal so that the trend in toxicity has been away from the chief prey animals.

It could be that the tissue destruction which frequently accompanies viperid and crotalid bites contributes importantly to prey digestion. However, when these snakes are deprived of their ability to inject venom they feed and grow normally. Furthermore, many nonvenomous species share identical diets with their venomous neighbors and are at no apparent digestive disadvantage.

While this apparent decline in toxicity with the appearance of improved delivery marks the most blatant turn toward lowered killing power, there is another trend which indicates a move in the same direction within the lifetime of an individual snake. (slide3) Minton (1967) studied venom toxicity as a function of age for two species of crotalids and one elapid. He observed that toxicity increased from birth through the first 6 to 9 months of life, reaching peak toxicity *3* times that of the adult snakes for Crotalus and Naja. The relatively constant toxicity for Agkistrodon was attributed to "the rather poor conditions of the juveniles between their fourth and ninth months." Minton felt that the toxicity increase might reflect changed feeding habits. This could well be the case since most species of snakes are born in early Fall with activity presumably reduced during the next 6 to 9 months at which time, Spring and Summer, the food supply materializes. The real question, however, is not why toxicity increases but why toxicity declines as the snake grows larger and presumably more capable of delivering his venom.

A venomous snake has one goal with respect to its prey. That goal is immediate incapacitation which is achieved through injection of a sufficient quantity of venom. If a snake possesses a modest delivery system, as with the elapids, or is small in size, as with young individuals, toxicity must remain high to insure efficient prey capture. As delivery is improved either through morphological adaptations or increased size of the individual, the toxicity of the venom need not remain as high to achieve the desired result.

A venomous snake has one goal with respect to its predators. That goal is to be left alone. There are in principal two ways to achieve this end. One is to adjust the reproductive probabilities of the predator; the other is to adjust the behavioral probabilities of the predators. While these two paths have the same end, the means are very different. It seems that the venomous snakes have been presented with a clear choice point. The simplest means to adjust the reproductive probabilities of the predatory population is to kill those individuals given to attacking snakes thereby creating a selective pressure favoring those individuals which do not. This route would have as its outcome an innate avoidance. The other possibility is to adjust the behavioral tendencies of the individual predators by administering a noxious or punishing stimulus, thereby reducing the probability of future attack on an individual basis. While the innate avoidance would be beneficial in the long run, natural selection gazes only at the moment. "In order to make it clear how, as I believe, natural selection acted, I must beg permission to give one imaginary illustration “(Darwin 1859). Consider two venomous snakes, A and B. Snake A possesses a highly toxic venom and snake B a less toxic venom. Both have equal deliveries. In dealing with their prey A and B both kill within a criterion time period. When dealing with the respective predators, however, A kills them all while B kills 15%, leaving 85% sick but surviving. Snake A has succeeded in opening a number of slots for the survival of new predators or the migration in of neighboring ones. Snake B, on the other hand, has left the predator population by and large intact, but now possessing individuals with rather bitter memories. Snake A will continue to face roughly as many aggressors as before, but snake B now has a percentage of the predator population avoiding him. Assuming only the territorial tendencies of the organisms involved and the capability of a predator to form an association between a previously neutral stimulus, the snake, and an inherently noxious event, the venom, it is suggested that snake B is at an immediate advantage over snake A. The proposal I wish to make is that the decline in venom toxicity seen both across the families of venomous snakes and within the lifetime of the individual is a move toward lowering the probability of killing a predator during defensive biting since in principle it would appear more effective to address a predator's CNS than his DNA.

Regardless of the selective pressures which have participated the toxicity declines mentioned, the outcome will still be a lowered incidence of predators killed or rather an increasing incidence of poisoned survivors. The only criterion for the venomous snakes to capitalize upon this situation is the acquisition of some warning stimuli either morphologically or behaviorally. This criterion appears to have been met chiefly through behavioral signals, i.e. the animal does something during defense interactions which renders him more detectable. Many examples are available. (Slides 4, 5, 6, 7) These are by no means exhaustive but represent some of the more notorious characters.

The mechanism of Batesian mimicry whereby one harmless organism gains a selective advantage by approximating the appearance of another noxious animal has been documented in many instances, primarily among insects. In Batesian mimicry the noxious animal is termed the model, the harmless animal the mimic, and the similarity in appearance between them the signal. It has been demonstrated that unpalatable stings, chemical sprays and a host of other stimuli will function as sufficiently effective deterrents to a predator to allow both model and mimic to enjoy reduced predation.

Consideration of both laboratory and field data indicates that the most important variable in a Batesian mimicry complex is the intensity of the noxious stimulus. Duncan and Sheppard (1965) explicitly demonstrated that if a mild and strong noxious event is associated with a particular signal, animals receiving the strong noxious stimulus will generalize their avoidance to a much wider range of similar stimuli. They translated this finding into the next SLIDE. These data, when translated into Batesian mimicry, indicate that if a model is mildly noxious then natural selection will insist upon a good signal match by the mimic. On the other hand, if a model is very noxious, then a mimic may achieve protection with only a modest approximation of the model signal.

Let us return now to the venomous snakes. As mentioned before, simple unpalatably, stings and a variety of other stimuli have been shown to support a host of mimicry complexes. We must now ask where the bite of a venomous snake would fall on a continuum of unfortunate outcomes which might befall a potential predator. The answer, I feel, is clear. There is probably no more noxious event that could befall a medium size carnivore during the course of his food getting.

Johnson (1956) suggested that the vertebral characters indicated that the elapids probably represent a more primitive family than today's nonvenomous Colubridae family, with the elapids springing from some pre-Colubrid. While the fossil record is scarce for snakes in general, Johnson noted that elapid fossils appeared slightly before the fossils of today's family Colubridae in the early Miocene. Tihen, at these meetings last year, suggested that the fossil record indicated that for all intents and purposes the appearance of most of our modern families was simultaneous in the Miocene. Johnson posed an interesting problem at the conclusion of his proposed phylogeny of the venomous families. He stated, "It is possible that venom and the venom apparatus were developed when competition for food was intense. As this condition was alleviated, the nonvenomous Colubrids had the opportunity to undergo their major radiation without the advantage of venom. Unless some such postulate of lessening competition between venomous and nonvenomous snakes is made, it seems difficult to understand why the venomous snakes have not completely dominated our present herpetofauna."

The proposition I wish to set forth is that the sudden expansion of the nonvenomous colubrids was the result of the appearance of venomous snakes. With the advent of these extremely noxious animals, apparently bent upon keeping the predatory population alive, the elongated legless form of the snake became a signal paired with an exceedingly noxious stimulus.

While the possibility exists that the snake form per se could mark the outer limits of a generalized avoidance, such a suggestion is insulting to the intelligence, i.e. discrimination ability, of the signal receivers. In all regions of the world save Australia the nonvenomous species out number the venomous which implies that by chance alone a significant proportion of predators will encounter nonvenomous snakes first. Furthermore, the nonvenomous snakes represent comparatively defenseless prey for their size. For the most part they are slow in escaping and incapable of inflicting a bite of any consequence. A one pound rat represents a much more favorable prey item than a one pound nonvenomous snake. These considerations strongly suggest that predatory signal receivers should have both opportunity and motivation to discriminate nonvenomous snakes from their venomous neighbors. Therefore the expectation would be that nonvenomous species should approximate, to some degree, the signal(s) of sympatric venomous species.

(a) Southeastern United States-The Southeastern United States represents a convenient "test area" since three genera from two families of venomous snakes are found there. The three genera will be addressed individually in an attempt to assess the signal(s) available to a potential predator. The remaining genera of snakes will then be reviewed to determine the extent to which these signals are approximated by nonvenomous species.

(1) The Moccasins (Agkistrodon, Family Crotalidae) - The moccasins are represented in two species, the cottonmouth (A. piscivorus) and the copperhead (A. contortrix). The cottonmouth inhabits the Gulf Coastal States and the copperhead has its stronghold in the interior regions. The two snakes have very similar patterns at birth. The copperhead retains its juvenile pattern while the cottonmouth becomes dark, almost black, by its second year. When alarmed both species rapidly vibrate their tails and the cottonmouth exposes the white interior of its mouth (hence the name).The classic distinguishing characteristics are the facial pit , thick body, triangular shaped head, vertical pupils, and single row of scales under tail (Conant, 1958). Of these characteristics only four seem useful signals, i.e. tail vibration, exposure of mouth interior, thick body, and triangular shaped head. The other characteristics would necessitate unduly close inspection.

(2) The rattlesnakes (Crotalus, Family Crotalidae)- Three species of rattlesnakes are found in the Southeastern United States. They differ markedly in pattern and size. The uniting character and unquestionable signal is the rattle borne on the tail. The rattlesnakes share all the morphological and behavioral characteristics of the moccasins

but greatly accentuate the audibility of the tail shaking with the rattle. Frequently they hiss when aroused.

(3) The coral snake (Mircrurus, Family Elapidae)- One species is found in the S.E. United States and possesses the triad ringed pattern(black-yellow-red). The coloration of the coral snake has been taken to be warning in its function (see Mertensian mimicry).

If attention is turned to the twelve open air (nonburrowing) genera of snakes found in the S.E. United States, the following defensive behaviors have been noted by Conant (1958): Flattening of the body 33% (Natrix, Stoseria, Thamnophis, Heterodon); hissing 50% (Heterodon, Drymarchon, Elaphe, Pituophis, Lampropeltis, Stilosoma); tail rattling 58% (Coluber, Masticophis, Drymarchon, Elaphe, Pituophis, Lampropeltis, Stilosoma). The only remaining genera is Cemophora and this snake possesses triad red-yellow-white banding, like the coral snake

Extensive personal field observation has also shown that a number of genera (Natrix,Thamnophis , Heterodon, Coluber, Masticophis, Elaphe) extend horizontally the posterior ends of the mandibles when assuming a defensive posture. This behavior is not seen when the snake is on the offense against a prey item. This behavior has the result of giving the head a decidedly triangular shape

(b) Worldwide - Similar situations appear to be the case in other parts of the world.

Australia and the Pacific Islands: “About the only way to identify a poisonous snake from this region is to kill it and look for fangs.” (Dowling et al, 1965).

Southeast Asia: “The hood identifies a living cobra. Although some nonpoisonous Asian snakes flatten the neck slightly when alarmed.”(Dowling et al, 1965).

Africa: “The various elapid and dangerous colubrid species.. .have no general characteristics that set them off from harmless snakes,..even some of the elapids without well-developed hoods will flatten the neck if disturbed and some which do not resemble cobras in any way will flatten the neck and raise the anterior part of the body in the familiar cobra stance.” (Dowling et al,1965).

The South Seas: "The sea snakes are naturally fish eaters with a strong predilection for eels, curiously enough for the banded eels of tropical seas, which many of the sea snakes greatly resemble.” (Schmidt 1950) In all probability it is the eels which resemble the sea snakes for reasons now obvious.

SLIDE 12

3. One signal receiver's opinion: man

Section I revealed that in general man was appreciative of the signal match between models and mimics in a variety of situations. Human opinions, however, were of no use in evaluating proposed mimicry systems since these were neutral with respect to Homo sapiens. Neither model nor mimic played any role in human affairs and vice versa.

Poisonous snakes, on the other hand, do interact with man on occasion. In fact snakes kill more people every year than all other vertebrates combined, about 40,000, This figure represents approximately a 15% death rate which moves the total venomous bites to at least 300,000. These estimates are probably too low with the total number of venomous bites running possibly up to one million annually (Milton,1969). Therefore it would seem reasonable to allow Homo sapiens' opinion to count as evidence for or against the proposition under consideration.

People don't like snakes. Minton (1969) puts it, "The primates that were to become men were indulging in a unique sort of cerebral activity, They were taking images that came into their brains by way of perfectly good mammalian sense organs, coloring them with emotions, and projecting them somewhat distorted upon a screen of inner consciousness,...The snake was one of these images,., the snake remains today the one animal that man universally respects and fears, covertly loves, and intensely hates." Minton however also suggests, "There is no good biological reason why this should be so. "

Many propositions have been suggested to account for man's attitude toward snakes. The kindest thing which can be said about most of these proposals is that they are imaginative. It rather seems, however, that the phenomena of snake avoidance may be accounted for without mention of inner consciousness screens, or phylaic symbols, or colored images. People avoid snakes for the sane reason that toads avoid yellow and black buzzing insects, and for the same reason that birds avoid butterflies of a particular color pattern, i.e. an indeterminant percentage of all these creatures are best left alone. Man is simply a signal receiver of the snakes' mimicry efforts. It seems likely that if

Homo sapiens is generally reluctant to bet his hand or his life on proper identification, the rest of earth's creatures may be equally reticent. And from the snakes' point of view nothing could be more useful than to be left alone by these creatures too large to be eaten, at that moment.

SLIDES

1. Skulls Opisthoglyphs, Proteroglyphs, Solenoglyphs

2. Venom toxicity as a function of family

3. Venom toxicity as a function of age (Milton, 1967)

4. Cobra

5. Eastern diamondback rattlesnake

6. Cottonmouth, open mouth display

7. Coral snake

8. Selective advantage as a function of similarity for two noxious models

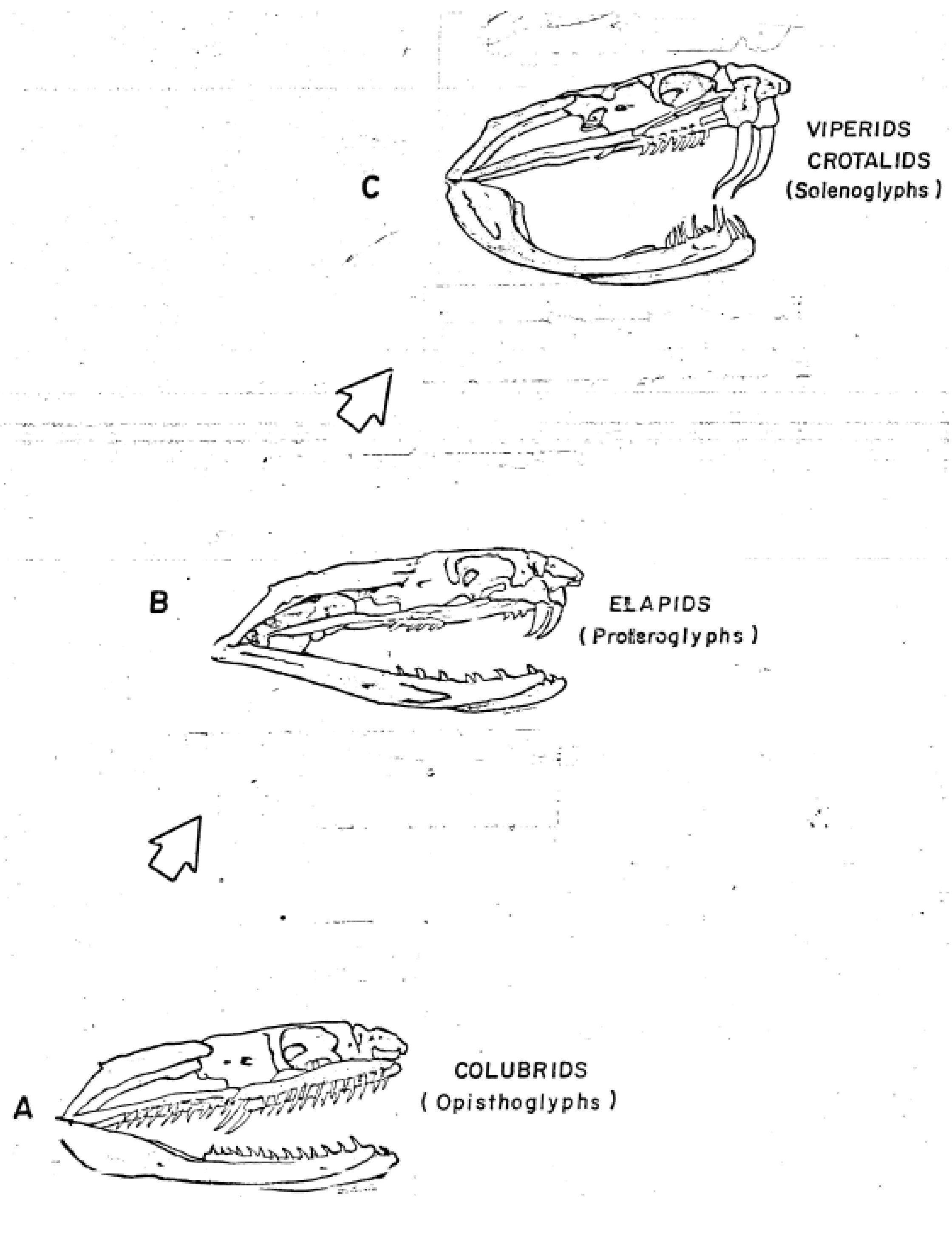
(Duncan & Sheppard, 1965 Fig. 5)

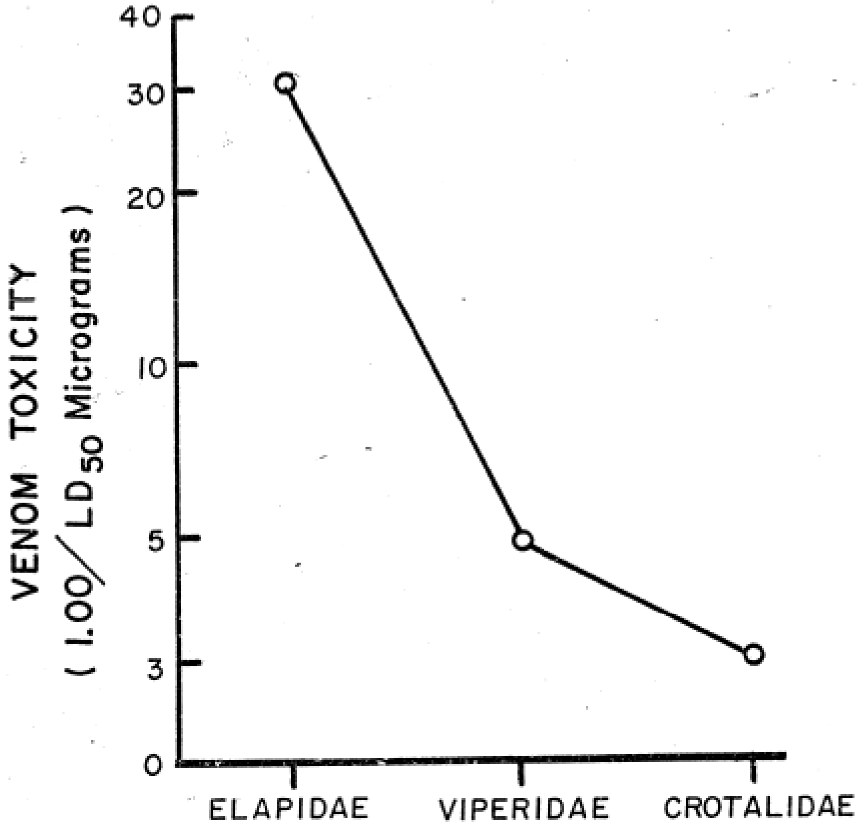
9. Hognose snake display

10. Cottonmouth

11. Banded water snake

12. Diamondback water snake head


C
VIPERIDS
CROTALIDS
(Solenoglyphs)
B
ELAPIDS
(Proteroglyphs)
A
COLUBRIDS
(Opisthoglyphs)



VENOM TOXICITY
(1.00/LD50 Micrograms)
40
30
20
10
5
3
0
ELAPIDAE
VIPERIDAE
CROTALIDAE

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