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A Review**

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**The Ecology and Behavior  
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(*Ahaetulla*, *Oxybelis*, *Thelotornis*, *Uromacer*):  
A Review\***

**Robert W. Henderson and Mary H. Binder**

\* Dedicated to Dr. Henry S. Fitch

**Abstract:** Vine snakes are members of four distantly related genera (*Ahaetulla*, *Oxybelis*, *Thelotornis* and *Uromacer*) and, as a group, are morphologically, ecologically and behaviorally unique. They are characterized by having a (1) head length/snout length ratio of  $< 3.0$ , (2) a snout base width/snout anterior width ratio  $> 1.76$  and (3) a head length/eye diameter ratio  $> 6.0$ . They show significant differences ( $P < .05$ ) from every other group they were tested against for at least two (#1 and #2) of the three ratios, and they differed from other arboreal lizard predators for all three characters. *Ahaetulla prasina* and three species of *Oxybelis* show no ontogenetic change for ratios #1 and #2, but all did for ratio #3.

All vine snakes are primarily arboreal, diurnal and feed on active prey—usually lizards. They may very well be the only arboreal snakes that routinely feed on potentially fast moving prey and they are visually oriented predators cued by prey movement. They have acute vision and the widest binocular fields of vision known for any snake. Prey stalking is initiated with lateral head swaying (which invokes parallax) or rigid tongue extension. Movement by the vine snake toward prey is correlated with type and duration of prey movement.

*Thelotornis* is morphologically, ecologically and behaviorally divergent from the other three genera. Although it feeds on lizards, they are primarily slow-moving members of the genus *Chameleo*. They also feed on snakes, a prey item essentially absent from the diet of other vine snakes. *Thelotornis* has the shortest, broadest snout of the vine snake genera. *Oxybelis brevirostris* is morphologically the most divergent species in the remaining three genera, and it may feed more frequently on frogs than do other vine snakes.

Vine snakes probably evolved from diurnal, semi-arboreal ancestors. Competition among closely related species in the arboreal adaptive zone resulted in character divergence whereby competing forms adapted ecologically and morphologically to different aspects of the biotic environment. "Proto-vine snakes" specialized in lizard prey, possibly for competitive reasons, and evolved morphological adaptations to saurophagy. Behavioral modifications followed. Vine snakes exhibit morphological, ecological and behavioral similarities due to convergent evolution rather than common ancestry.

Vine snakes are slender arboreal snakes with attenuated snouts. They are members of four distantly related colubrid genera that are geographically widely dispersed: *Ahaetulla* is found in tropical Asia, *Oxybelis* is primarily a neotropical mainland genus, *Thelotornis* is African, and *Uromacer* is endemic to Hispaniola in the West Indies. As a group, they are behaviorally and morphologically unique and for over a century biologists have written about their singular appearance and curious habits.

The purpose of this paper is to summarize what is currently known of the ecology and behavior of vine snakes. We will summarize the important literature, present the results of previously unpublished research and provide preliminary results of currently ongoing research. Hopefully, this summary and update will provide an overview of the morphology, ecology and behavior of these convergent genera of highly specialized snakes that will stimulate and focus future research.

### MATERIALS AND METHODS

A variety of live vine snakes representing all four genera have been kept alive for various lengths of time during the last two years: *Ahaetulla prasina*, *Oxybelis aeneus*, *O. fulgidus*, *Thelotornis kirtlandi*, *Uromacer catesbyi*, *U. oxyrhynchus* and *U. wetmorei*. In addition, the senior author has had field experience with *O. aeneus* in México, Belize and Nicaragua; *O. fulgidus* in Belize; and *O. argenteus* in Peru. We have both had field experience with three species of *Uromacer* in the Republica Dominicana (*catesbyi*, *oxyrhynchus*, and *wetmorei*). Live animals were maintained in 71 x 31 x 41 cm high glass enclosures with branches on a newspaper substrate and with a constant water supply. For detailed observations, snakes were transferred to larger glass enclosures (183 x 46.5 x 48 cm high) with branches clustered at opposite ends, a water source and a substrate of newspaper, pea gravel, or indoor-outdoor carpeting. Vine snakes were usually fed anoles (*Anolis carolinensis*), but sometimes fish, frogs, other lizards, snakes, birds and laboratory mice were offered. Some observations were also made in a small greenhouse on the roof of the Milwaukee Public Museum (see the description in Henderson and Nickerson, 1976).

Observations were made by a single observer or, when specific reactions to prey behavior were studied, by two observers recording data simultaneously. A tape recorder was used and one observer described the snake's behavior while the other described the anole's behavior. By simultaneously describing these behaviors it was possible to determine what kinds of prey movements elicited what kinds of snake behavior.

Some feeding sequences were filmed with a Photosonics camera (16mm), equipped with a Bell and Howell 52 mm (f 1.6) lens and a

timing light generator. Two 750 watt tungsten-halogen lamps with reflectors provided light during filming. Filming was done at 250 frames per second using Kodak 4X black and white reversal film (Henderson and Binder, *in prep.*).

### COLORATION AND MORPHOLOGY

**Coloration.**—Live vine snakes are dorsally colored a shade of green, brown or grey and frequently some combination of those colors. Some species are essentially patternless (e.g., *Oxybelis fulgidus*) while one genus is mottled in grey, brown and green (*Thelotornis*). *Oxybelis argenteus* has dull green and tan stripes dorsally and green and white stripes ventrally. Several green species have ventrolateral white or yellow stripes (e.g., *Ahaetulla prasina*, *Oxybelis fulgidus* and *Uromacer oxyrhynchus*). There is a dichromatic population of *O. fulgidus* on Isla Roatán and Isla Elena of the Islas de la Bahía, off the Caribbean coast of Honduras. The typical green color phase occurs (at least on Roatan) along with a population that is mustard yellow dorsally (Keiser, 1969; Wilson and Hahn, 1973). Some ontogenetic changes in color and pattern occur in at least two genera. According to de Silva (1955), the young of *Ahaetulla nasutus* differ "from the parent in having the head (except the snout) and the tail bright olive green, a distinct bright yellow stripe on the canthus rostralis, the color of the ventrals varying from bluish green to light brown with the bounding lateral stripes distinctly pale yellow." McCann (1928) noted that newborn *A. mycterizans* (possibly *A. nasutus*) have "a distinct white line over the upperside of the orbit which travels forward along the angle of the snout to the tip." Similar markings were absent in adults. Leviton (1968) pointed out that the red color phase of *A. prasina preocularis* is restricted to young animals and that adults are green. *Uromacer catesbyi* (which we consider to be a "marginal" vine snake; see below), undergoes an ontogenetic change in color and pattern, at least on Isla Saona (which lies off the southeastern coast of the República Dominicana). A juvenile collected in June had a green head, typical of adults, and the neck was greenish but blending into a pale chocolate brown. From the neck on, the snake was pale chocolate brown with a green tinge. The venter was also pale brown. After shedding, the greenish tinge was more obvious and it seems apparent that, with each progressive shed, the adult color and pattern will emerge. Interestingly, a similar ontogenetic change occurs in snakes of the neotropical genus *Leptophis* (Dundee and Liner, 1974; Nickerson et al., 1978; Rand, 1969) which is ecologically and behaviorally similar to *U. catesbyi*.

Species of *Oxybelis* and *Uromacer* have horizontal eye marks extending from a point posterior to the eye to the tip of the snout (Fig. 1). *Thelotornis* has markings that are more of an eye mask (Fig. 2). Ficken et al. (1971) suggested that the so-called eye lines are aids to vision for

species which feed on moving prey. Eye lines seem to be more prevalent in arboreal snakes than in terrestrial ones (Henderson, *pers. obs.*).

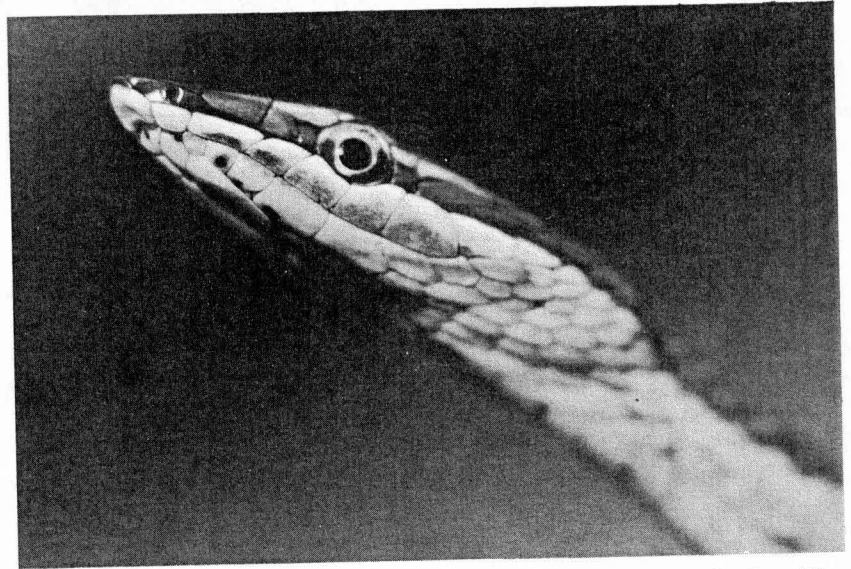


Fig. 1.—*Uromacer wetmorei* from Oviedo Viejo, Barahona Peninsula, Republica Dominicana, illustrating the eye-line from eye to snout tip.

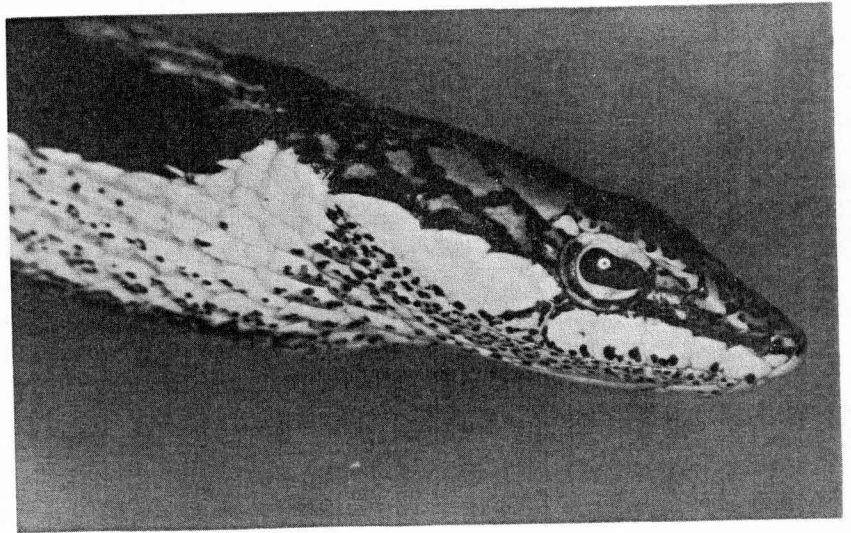


Fig. 2.—*Thelotornis kirtlandi* depicting eye mask.

**Eye.**—*Oxybelis* and *Uromacer* have eyes with round pupils, typical of most diurnal colubrids. *Ahaetulla* and *Thelotornis*, however, have horizontal, "keyhole" pupils (Fig. 3), a condition found in only one

other genus, *Dryophiops* of southeastern Asia. *Dryophiops* is comprised of two arboreal, diurnal species that apparently prey primarily

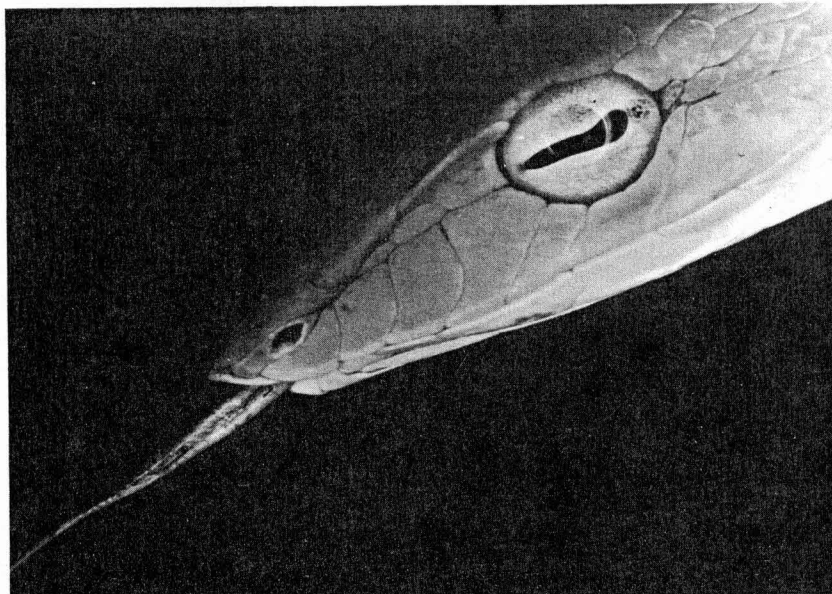


Fig. 3.—*Ahaetulla prasina* depicting the horizontal "keyhole" pupil and rigid tongue extension.

on lizards (Brongersma, 1947; Leviton, 1964; Taylor, 1922). *Ahaetulla* and *Thelotornis* (and possibly *Dryophiops*) are the only snakes known to have fovea. "The fovea in *Dryophis* [= *Ahaetulla*] is at the outer rim of the retina on the temporal or caudal side of the eye, and a line from it through the center of the lens passes out through the slot in the keyhole pupil, along a groove on the cheek in front of the eye, and straight forward parallel to the axis of the body." (Walls, 1942: 185). The keyhole-shaped pupil has the slot of the keyhole pointing forward well beyond the lens, thereby creating an extensive aphakic (lenseless) space. During accommodation in *Ahaetulla*, the lens moves not only forward but also more strongly nasally than in other snakes (Walls, 1942). Also, in *Ahaetulla* the cones are slenderized to increase visual acuity (Walls, 1942).

**Head morphology.**—Head shape is the most distinctive feature of vine snakes. Their long, attenuated snouts make them, as a group, unique from all other snakes. We took a series of head measurements from vine snakes and 17 other colubrid genera in order to 1) define vine snakes on the basis of head shape and 2) to determine if there was a relationship between head shape and a species' life style (*i.e.*, what it eats, where it lives, when it is active). Snout-vent lengths (SVL) of pre-

served specimens were measured on a meter stick and head measurements were taken with a dial caliper and always from the specimen's right side. Measurements taken were: 1) SVL; 2) head length (HL), measured from the posterior edges of the mandibles to the tip of the rostral; 3) eye diameter (ED); 4) snout length (SL), measured from the anterior border of the eye to the tip of the rostral; 5) snout base width (SBW), the breadth of the snout at the anterior edges of the eyes; and 6) snout anterior width (SAW), the breadth of the snout measured at the nares.

Usually ten large (adult) specimens of each species were measured. Large specimens were used in order to avoid variation caused by ontogenetic changes in proportions (Werner, 1969). Species examined were: *Ahaetulla nasuta*, *A. prasina*, *Alsophis vudii*, *Boiga dendrophila*, *Chrysopelea ornata*, *Conophis lineatus*, *C. vittatus*, *Dendrelaphis formosus*, *Dispholidus typus*, *Drymarchon corais*, *Drymobius margaritiferus*, *Dryophiops rubescens*, *Imantodes cenchoa*, *Leptodeira septentrionalis*, *Leptophis ahaetulla*, *L. mexicanus*, *Ninia sebae*, *Opheodrys aestivus*, *O. vernalis*, *Oxybelis aeneus*, *O. argenteus*, *O. brevirostris*, *O. fulgidus*, *Scaphiodontophis annulatus*, *Sibon sanniola*, *Thelotornis capensis*, *T. kirtlandi*, *Uromacer catesbyi*, *U. frenatus*, *U. oxyrhynchus* and *U. wetmorei*.

Each species was designated diurnal or nocturnal, arboreal or terrestrial and by what its primary prey was (e.g., lizards or anurans). We worked with three ratios: HL/SL, SBW/SAW, and HL/ED. These ratios were calculated for each species and then a mean was calculated for each ratio for every species. Species were grouped together (e.g., arboreal frog predators, nocturnal lizard predators, etc.) and t tests were performed comparing various groups for each of the three ratios. Values of  $P < .05$  were considered significant. Figures 4 and 5 illustrate various head shapes and Table 1 summarizes the relationships between head proportions and various pairs of ecological parameters.

Vine snakes are characterized by having a HL/SL ratio  $< 3.0$  (with one exception: *T. capensis* in which HL/SL = 3.25), an SBW/SAW ratio  $> 1.76$  (although all species except *O. brevirostris* and both species of *Thelotornis* have SBW/SAW ratios  $> 2.0$ ) and a HL/ED ratio  $> 6.0$  (with three exceptions: *O. brevirostris* and both *Thelotornis*). The combination of these characters makes vine snakes, as a group, morphologically unique in our sample, but probably among all snake species as well. *Thelotornis* is the most divergent of the four genera, and among the other three genera, *O. brevirostris* is the most divergent species. This divergence will be addressed from an ecological and behavioral viewpoint below.

Vine snakes show significant differences ( $P < .05$ ) from every



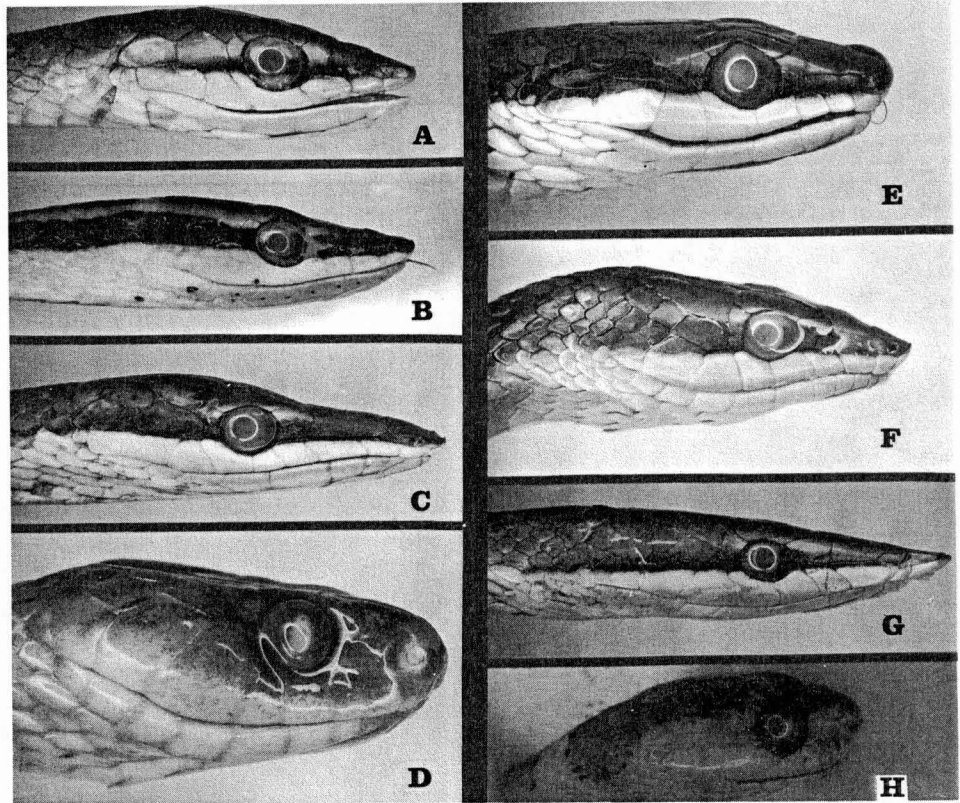


Fig. 4.-Lateral views of heads of a variety of arboreal snakes. A. *Oxybelis brevirostris*; B. *O. argenteus*; C. *O. aeneus*; D. *Leptodeira septentrionalis*, a nocturnal frog predator; E. *Leptophis mexicanus*, a diurnal frog and lizard predator; F. *Uromacer catesbyi*; G. *U. oxyrhynchus*; H. *Imantodes cenchoa*, a nocturnal lizard and frog predator.

group they were tested against for at least two (HL/SL, SBW/SAW) of the three ratios, and they differed from other arboreal lizard predators for all three characters (Table 2). Arboreal lizard predators differed from arboreal frog predators in all three ratios, but arboreal, blunt-snouted lizard eaters did not differ significantly from terrestrial lizard predators for any of the characters. Vine snakes showed significant differences from all other diurnal lizard predators tested and from diurnal frog predators for all characters. Whereas vine snakes had significant differences in HL/SL and SBW/SAW from diurnal terrestrial species, the arboreal, diurnal blunt-snouted snakes showed no differences.

The two most distinctive characteristics of the vine snakes are HL/SL and, primarily, SBW/SAW. *Chrysopelea ornata* and *Conophis vittatus* approach vine snakes in HL/SL. *Chrysopelea* is arboreal, diurnal and feeds primarily on frogs (Inger and Colwell, 1977) and lizards (Pope,

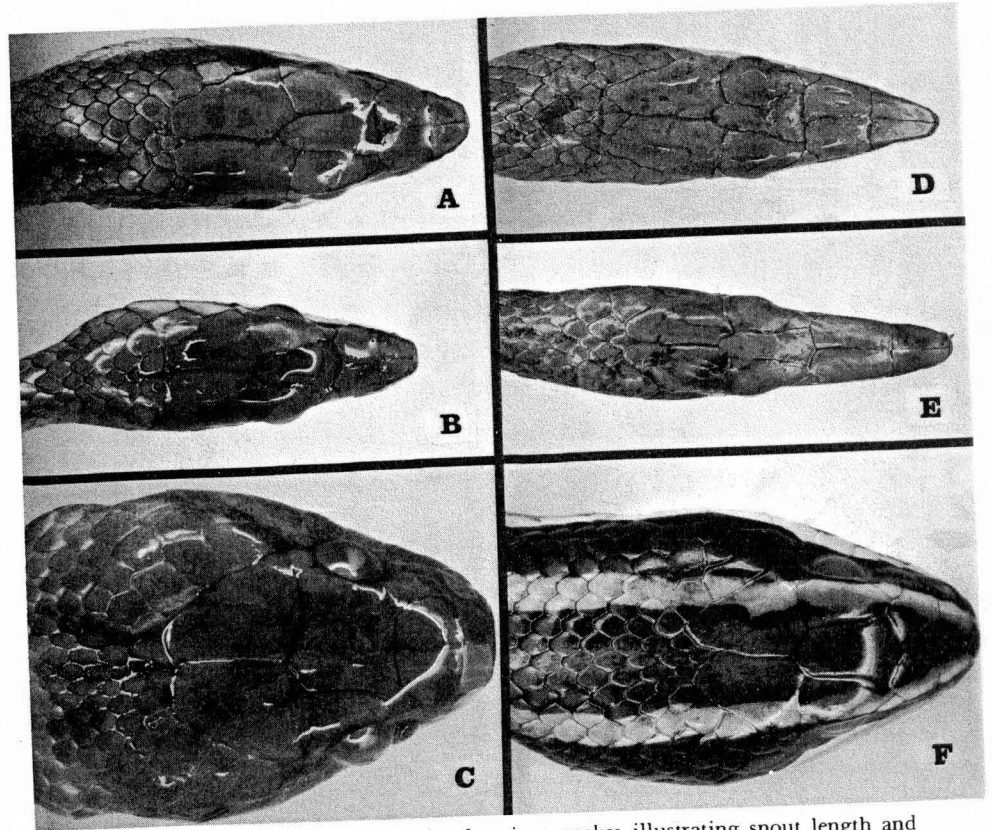


Fig. 5.-Dorsal views of the heads of various snakes illustrating snout length and attenuation. A. *Uromacer catesbyi*; B. *Oxybelis brevirostris*; C. *Leptodeira septentrionalis*; D. *U. oxyrhynchus*; E. *O. aeneus*; F. *Conophis lineatus*, a diurnal, terrestrial, lizard predator.

1935; Taylor, 1965; Wall, 1907); *Conophis vittatus* is a diurnal, terrestrial snake that feeds on the highly active lizards of the teiid genus *Cnemidophorus* (Wellman, 1963). Only *Uromacer catesbyi* approaches the vine snakes (and surpasses some) for SBW/SAW. *U. catesbyi* is a frog and lizard predator (Henderson, Binder and Sajdak, *in prep.*) and is a "marginal" vine snake.

Two additional taxa deserve some mention. Snakes of the Madagascan genus *Langaha* (two species) have bizarre, sexually dimorphic nasal appendages (Guibe, 1948) (Fig. 6). Exclusive of these appendages, however, at least one of the two species (*L. nasuta*) does have a vine snake-like head shape. A sample size of two provided a mean HL/SL of 3.00 (2.91-3.08) and a mean SBW/SAW of 1.84 (1.75-1.92). Unfortunately, nothing is known of the natural history of *Langaha* and we are reluctant, at this time, to include it with the vine snakes. *Philodryas*

Table 1.—Summary of relationships between head proportions and various pairs of ecological parameters.

	N genera/species	HL/SL $\bar{x} \pm SE$ (range)	SBW/SAW $\bar{x} \pm SE$ (range)	HL/ED $\bar{x} \pm SE$ (range)
vine snakes	4/11	2.79 ± .0669 (2.47-3.25)	2.09 ± .0657 (1.76-2.44)	6.81 ± .3329 (5.06-8.41)
vine snakes exclusive of <i>Thelotornis</i>	3/9	2.72 ± .0545 (2.47-2.96)	2.14 ± .0656 (1.76-2.44)	7.10 ± .3296 (5.06-8.41)
northern species (exclusive of vine snakes) frog predators	4/5	3.35 ± .1612 (2.93-3.92)	1.47 ± .0496 (1.36-1.63)	5.12 ± .3360 (3.99-5.83)
lizard predators	5/5	3.31 ± .1517 (2.93-3.83)	1.59 ± .1150 (1.38-2.03)	5.35 ± .6911 (3.93-7.96)
terrestrial species				
lizard predators	3/4	3.42 ± .1060 (3.17-3.62)	1.49 ± .0359 (1.42-1.58)	5.79 ± .3523 (4.78-6.29)
northern species (exclusive of vine snakes) frog predators	4/5	3.27 ± .0977 (2.93-3.51)	1.49 ± 0.513 (1.36-1.63)	5.05 ± .3076 (3.99-5.75)
lizard predators	7/8	3.30 ± .0815 (2.93-3.62)	1.56 ± .0723 (1.38-2.03)	5.74 ± .3912 (4.55-7.96)
northern	7/8	3.24 ± .0544 (2.93-3.40)	2.40 ± .2207 (1.36-2.03)	5.41 ± .4240 (4.55-7.96)
terrestrial	7/8	3.41 ± .0609 (3.17-3.61)	1.51 ± .0234 (1.42-1.58)	6.02 ± .2728 (4.78-7.32)
northern species				
lizard predators	2/2	3.48 ± .3500 (3.13-3.83)	1.34 ± .1250 (1.21-1.46)	4.58 ± .6450 (3.93-5.22)
northern	5/5	3.76 ± .2124 (3.12-4.41)	1.36 ± .0524 (1.21-1.47)	4.96 ± .4148 (3.93-5.83)

**Table 2.**—Results of t-tests comparing head proportions in various ecological groupings. A number 1, 2, or 3 indicates a significant difference ( $P < .05$ ) between the two sets of variables for 1) HL/SL, 2) SBW/SAW, and 3) HL/ED, respectively. An x in place of a number indicates that the difference was not significant. A = arboreal, B = blunt-snouted snake (as opposed to vine snakes which are attenuate-snouted), D = diurnal, F = frog predator, L = lizard predator, N = nocturnal, T = terrestrial, and VS = vine snakes.

	ABL	AF	AN	BD	BDL	DF	DT	LT	NL
VS	123		123	123	123	123	12x	12x	123
ABD		1xx				xxx			
AL		123							
BDL						xxx			xxx
LT	xxx								

*baroni* is a South American colubrid possessing a fragmented rostral (Marx and Rabb, 1972) and it looks superficially like a vine snake, and mean HL/SL = 2.59 (2.41-2.89) and mean SBW/SAW = 1.59 (1.49-1.67) ( $n = 5$ ). Thus, although long-snouted, except for the peculiar rostral, it does not have a particularly attenuated snout. Nothing is known of its food habits in nature (Thomas, 1976).

We examined *Ahaetulla prasina* (Fig. 7) and *Oxybelis argenteus*, *O. brevirostris* and *O. fulgidus* (Fig. 8) for ontogenetic changes in each of the three ratios. Only HL/ED shows ontogenetic change and it is positively correlated with an increase in SVL. If extreme snout length and attenuation are adaptations to lizard predation, and if there is not an ontogenetic shift in diet in vine snakes (as we believe there is not) as there is in some snakes (e.g., *Bothrops atrox* [Dixon and Soini, 1977; Sexton, 1957]), then an ontogenetic change in these ratios is not anticipated. On the other hand, HL/ED is a less distinctive character in vine snakes and large eye size is common in many species of young vertebrates; an ontogenetic shift in this character is not surprising.

Nocturnal animals, in general, tend to possess larger eyes than do diurnal species (Walls, 1942), and Werner (1969) found this to be true in gekkonid and sphaerodactylid lizards. Pianka and Pianka (1976) and Werner (1969) also found that terrestrial geckos have larger eyes than do arboreal ones and Werner related this to the difficulties of visual hunting on level ground as opposed to scouting from perches. Oliver (1948) believed that a proportionally large eye was indicative of arboreal habits, applied this to snakes of the colubrid genus *Leptophis*, and found it to be true. Marx and Rabb (1972) also found that arboreal

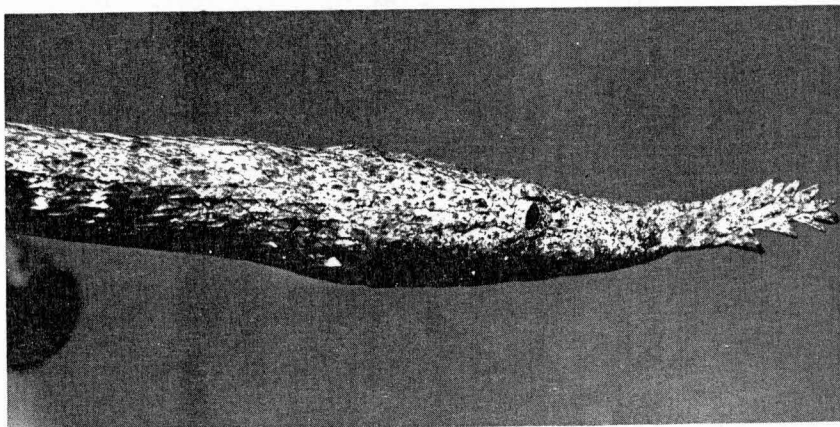


Fig. 6.—*Langaha nasuta* from an unknown locality in Madagascar. © New York Zoological Society.

snakes tend to have large eyes. We have found that, among arboreal snakes, diurnal species (even excluding vine snakes) have longer, more attenuate snouts and smaller eyes than do nocturnal species. Terrestrial diurnal species have shorter, less attenuated snouts and smaller eyes than do arboreal diurnal snakes (exclusive of vine snakes). Among lizard predators, terrestrial species have shorter, less attenuated snouts and smaller eyes than to arboreal species (exclusive of vine snakes).

**Other characters.**—Marx and Rabb (1972), in their phyletic analysis of 50 characters of advanced snakes, frequently used vine snakes as part of their working sample. State III of Character 22, number of subcaudals, is the maximal number of subcaudals and, in Marx and Rabb's working sample, it only occurred among vine snakes (*A. prasina*, *O. aeneus*, *O. brevirostris*, *O. fulgidus*, *U. oxyrhynchus*) and a marginal vine snake (*U. catesbyi*). In Character 26, the width of the skull relative to the length of the skull, *Ahaetulla nasuta* had the narrowest skull and *A. prasina*, *O. aeneus*, *O. argenteus* and *U. oxyrhynchus* were also in State IV (a relatively narrow skull) along with two other colubrid genera (*Enhydris* and *Malpolon*).

According to Johnson (1955), on the basis of vertebral form, "The arboreal snakes emerged from the analysis as the most distinctive of the mode-of-life groups." Vine snakes (*Ahaetulla* and *Oxybelis*) possess elongated vertebrae (Gasc, 1971; Johnson, 1955). Auffenberg (1963) described a Miocene colubrid snake, *Paraoxybelis floridanus*, on the basis of a fragmentary precaudal vertebrae. In centrum length, *P. floridanus* "is approached only by *Oxybelis*, *Leptophis*, and *Uromacer* among New World colubrid snakes," and among Old World colubrids, only *Ahaetulla* has a longer centrum (Auffenberg, 1963).

Parsons (1959) found no differences between *Thamnophis* and

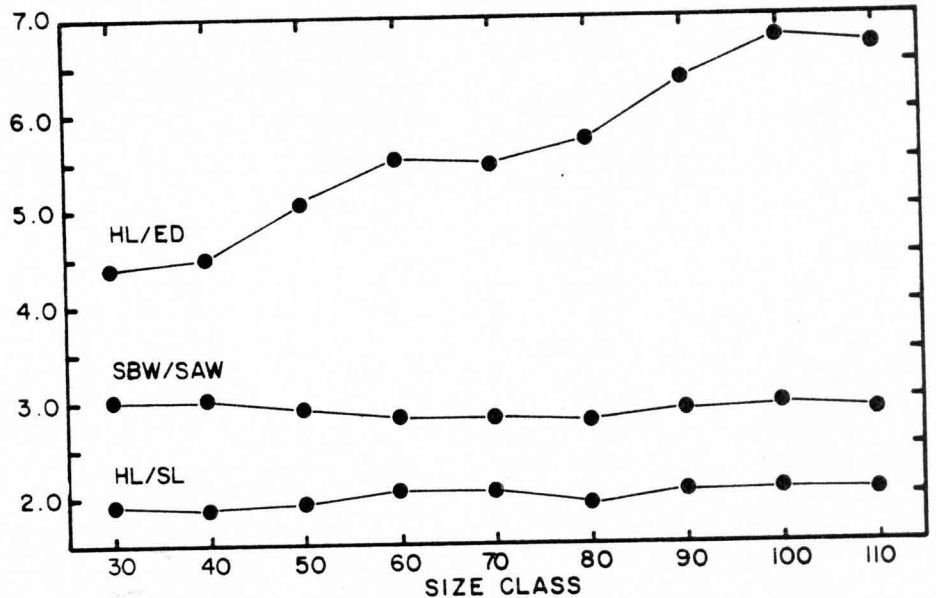


Fig. 7.—Ontogenetic change in three head proportions in *Ahaetulla prasina*. Size classes are in centimeters; size class 30 = snakes that are 30.0-39.9 cm SVL, size class 40 = snakes that are 40.0-49.9 cm SVL, etc. See text for abbreviations.

*Oxybelis* in young embryological stages of the nose. Kahmann (1954), however, found that Jacobson's organ is less developed in *Ahaetulla nasutus* than in other snakes studied.

## BEHAVIOR AND ECOLOGY

### *Ahaetulla* Link

**Range and habitat.**—The genus includes 8 species and ranges from India and Sri Lanka through southeastern Asia, the Malay Peninsula, and islands of the Indo-Australian Archipelago. Species of *Ahaetulla* are found in varied habitat including "low bushes and trees on the plains" of India (Whitaker, 1978) to deciduous and evergreen forests (R.F. Inger, *in litt.*), rainforests (R.F. Inger, *in litt.*; Lim, 1955; Whitaker, 1978), submontane forests (Brown and Alcalá, 1961), and coconut, tea and rubber plantations, gardens and other disturbed situations (de Haas, 1941; Tweedie, 1957; Wall, 1905). They have been observed on bare soil, leaf litter, low seedlings, tall grass, herbaceous plants, lianas, bushes and tall rainforest trees and coconut palms (R.F. Inger, *in litt.*; Wall, 1905; Whitaker, 1978).

Rieppel (1970) has noted that new born *Ahaetulla nasutus* wrap themselves around branches whereas adults lay across branches.

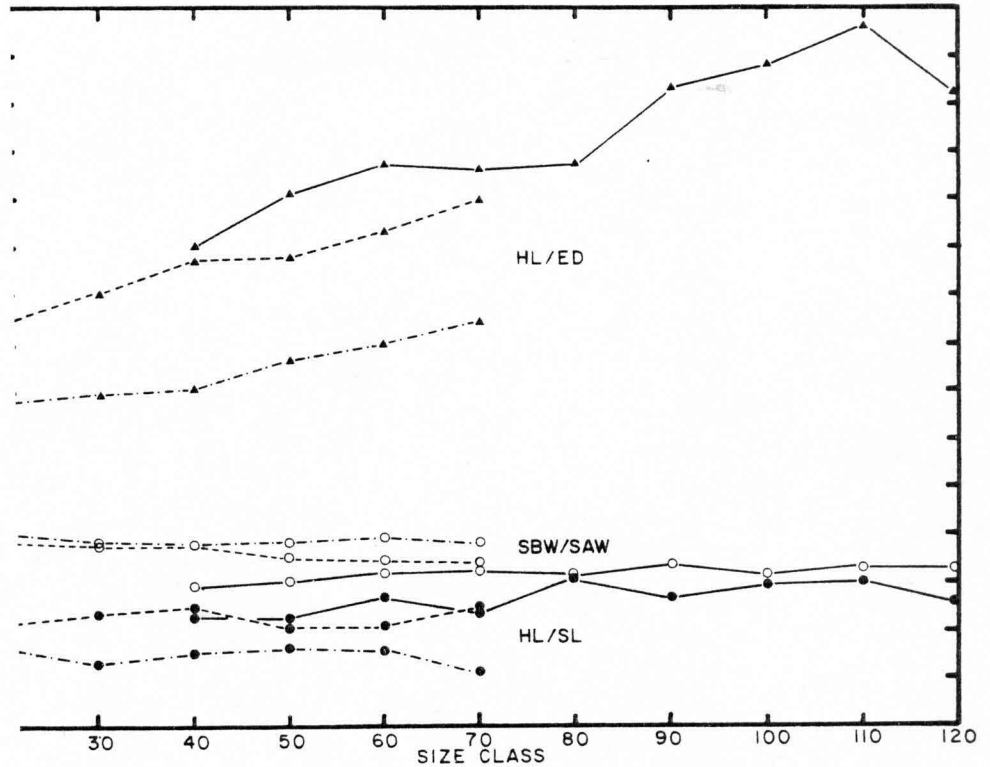


Fig. 8.—Ontogenetic change in three head proportions for three species of *Oxybelis*: dash-dot line = *O. argenteus*, dashed line = *O. brevirostris* and solid line = *O. fulgidus*. See Fig. 7 for additional information.

**Food.**—Wall (1905) considered *A. nasutus* to prefer lizards to the agamid genus *Calotes* “to any other creature” based on field observation, but found a gecko in the stomach of one (Wall, 1910). Whitaker (1978) also considered lizards a main food item, but has observed *A. nasutus* feeding on fish and a shieldtail snake (Uropeltidae) in the field. Leviton (1968) found the scincid lizard *Mabuya* in *A. prasina* and Wall (1921) found a *Mabuya* tail in the stomach of an *A. pulverulentus*. A number of authors have given more generalized food habits: Bergman (1956) found frogs and lizards in the stomachs of *A. prasina*; Boulenger (1912) states that *A. prasina* eats frogs and lizards; on two occasions Drieberg (1903) observed *A. nasutus* (or possibly *A. mycterizans*) capture birds in the field; Gharpurey (1954) states that *Ahaetulla* feeds on mice, birds, lizards, other snakes, and frogs. Presumably on the basis of stomach contents, Gunther (1864) wrote that *A. prasina* preys on birds, lizards, frogs and, when young, insects, and that *A. mycterizans* feeds on birds and lizards. Leviton (1968) reported geckos

and skinks from the stomachs of Philippine *A. prasina*. Mertens (1930) has suggested that *A. prasina* prefers frogs to lizards. Soderberg (1972) has observed captive *A. nasutus* capture adult sparrows (*Passer montanus*). Rieppel (1970) observed a captive female eat the fetal membranes of some of her newborn young.

**Feeding behavior.**—Wall (1905) reported observations on *A. nasutus*: “Its manner of capturing prey is invariable. When a lizard is introduced into the cage, the snake . . . coils itself in a zigzag fashion. Then, suddenly darting forward, it seizes the victim unerringly just behind the head . . .” R.K. Gratz (*in litt.*) observed captive *A. prasina* feed on *Hemidactylus* and *Mabuya*. One snake remained motionless with the anterior 5-6 in. in an S-coil and when the lizard moved away from the snake, “the snake drew about 10 more inches of body into the coil . . . Each move of the lizard brought a new move of the snake. However, when the lizard moved several feet swiftly, the snake merely turned his head and began the slow stalking process over again.”

We have had opportunity to observe two *A. prasina* in several dozen feeding sequences. Our observations are similar to Wall and Gratz but, interestingly, neither of them mentions prolonged, rigid tongue protrusion, an almost invariable component of prey stalking in sequences we have observed. Once aware of prey, stalking is preceded by lateral head swaying (Gans, 1974 and 1978; pers. observ.), and then slow forward movements by the snake are correlated with prey movement (Henderson and Binder, *in prep.*). Tongue protrusion may be continuous or sporadic during a stalking sequence or, if a prey item is less than approximately 30 cm from the snake at the initiation of stalking, it may be entirely absent.

If rigid tongue protrusion is used, the tongue usually remains extended until immediately prior to the strike. Lizards are usually seized in the nuchal region (Green, 1903; Sights, 1949; pers. observ.) and swallowing commences after all or most prey movement ceases. We have observed *A. prasina* rotate the anterior portion of its body 90° during a strike in order that it may seize behind the head an anole resting on a vertical perch (see *Oxybelis* “Feeding behavior” below).

**Defensive behavior.**—Wall (1905) described defensive behavior in *A. nasutus*: “When moderately alarmed it emits the tongue . . . with closed jaws, keeping it out for a second or two or longer . . . Whilst the tongue is maintained rigidly protruded in a forward direction the snake rears its head and forebody, and dilates the body so that the black and white interstitial skin becomes plainly apparent. If further excited it opens the jaws widely, . . . even so much as to double the lateral expanse of the floor of the mouth and make it shovel-shaped . . . Even a small specimen will not hesitate to bite viciously.” Whitaker (1978) remarks that *A. nasutus* will “open the mouth very wide and swell



the body menacingly" when provoked. Similar behavior has been noted in *A. prasina* (Mell, 1929) and *A. mycterizans* (Gharpurey, 1954). Soderberg (1971) has also noted hissing and tail vibrating during defensive displays, and Rieppel (1970) has observed newborn *A. nasutus* display rigid tongue extension in a defensive context.

We introduced an injured Ovenbird (*Seiurus aurocapillus*) into a large enclosure containing two *A. prasinus*. Both snakes were immediately aware of the bird and watched it closely. As soon as the bird hopped toward one of the snakes, it repeatedly struck at it defensively and then went into a high-intensity display which included prolonged, rigid tongue protrusion, exposure of the black and white interstitial skin and a series of S-shaped contours of the forepart of the body. The second snake performed a similar display when the bird approached it, but did not strike at it.

**Seasonal incidence.**—De Haas (1941) presented data on the monthly incidence of snakes collected at Bandjarwangi in West Java, and Henderson *et al.* (1978) analyzed these data in terms of monthly rainfall. For all species, there was a significant negative correlation between rainfall and the 2444 snakes collected.

Using only de Haas' monthly incidence of *Ahaetulla prasina* (total N=64), we analyzed seasonal incidence in terms of rainfall. Using Spearman's rank correlation procedure, we found no correlation ( $r=.08$ ) between monthly rainfall and incidence of these vine snakes. This is not surprising in light of Bandjarwangi being one of the wettest areas of West Java with 4143 mm of rain falling during the year (43-583 mm/month) the snakes were collected (1938).

#### *Oxybelis* Wagler

**Range and habitat.**—Snakes of the genus *Oxybelis* (four species) range from southern Arizona in the U.S.A., south along the eastern and western coasts of México, across the Isthmus of Tehuantepec, throughout most of Central America and into South America. There it ranges throughout most of northern South America east and west of the Andes and southward to Bolivia, southeastern Brasil and it may occur in Paraguay and northern Argentina (Keiser, 1974). They also occur on the Tres Marias Islands west of Nayarit, México and on a number of islands along the Caribbean coasts of México, Central America and off the northern coast of Venezuela. They occur in habitat ranging from dry, low, open scrub to primary rainforest and, although occasionally observed on the ground (Neill, 1965; Neill and Allen, 1959; *pers. observ.*), they are usually found above the ground in tall grass, sedges, bushes, saplings and sometimes tall trees (Duellman, 1963; Fowlie, 1965; Ruthven, 1922; Stuart, 1958; Wilson and Hahn, 1973; Wright and Wright, 1957; *pers. observ.*).

**Food.**—Keiser (1967) summarized natural prey for *O. aeneus* from the literature. Accounts have recorded lizards of the iguanid genera *Anolis* (Alvarez del Toro, 1960; Beebe, 1946; R.W. Henderson, *pers. observ.*), *Basiliscus* (Greene *et al.*, 1978; Netting, 1936), *Ctenosaura* (Stebbins, 1954), *Holbrookia* (Stebbins, 1954), *Iguana* (Greene *et al.*, 1978), *Sceloporus* (Barbour and Amaral, 1926; Schmidt, 1928), and *Uta* (Bogert and Oliver, 1945). Lizards of the teiid genus *Cnemidophorus* are also preyed upon (Hoogmoed, 1973; Smith and Grant, 1958; Stuart, 1954). In addition, insects (Keiser, 1967), fish (G.M. Burghardt, *in litt.*), frogs (Beebe, 1946; Mole, 1924; Wehekind, 1955), birds (Beebe, 1946; Mole, 1924; Wehekind, 1955) and rodents (Villa, 1962) have been recorded. Keiser (1967) examined the stomachs of 32 preserved *O. aeneus* that had noticeable bulges and 30 proved to be lizards, one a leptodactylid frog and one the remains of roaches (perhaps secondarily ingested?).

We examined the stomachs of 80 *O. aeneus* from the Mexican states of Quintana Roo and Yucatan and 21 of them (26.3%) had identifiable remains. Sixteen (74.2%) of the stomachs contained *Anolis* (one anole/snake), three contained hatchling size *Basiliscus vittatus* and two contained teiids.

Duellman (1978) examined stomach contents of *O. argenteus* from Amazonian Ecuador and found, in 10 stomachs, five lizards (*Anolis* and *Prionodactylus*) and five frogs (*Dendrophryniscus* and *Eleutherodactylus*). Although some of these prey items are largely terrestrial, they do, on occasion, ascend into the vegetation. *O. argenteus* may, of course, descend to the ground to feed on occasion, but vine snakes are also known to be capable of finding and capturing terrestrial prey from arboreal perches (Henderson and Nickerson, 1977).

Little is known of the food habits of *O. brevirostris*. We examined the stomachs of 33 *O. brevirostris* from Costa Rica, Panama, Colombia and Ecuador and only four had remains: two iguanid lizards and two frogs. *Oxybelis brevirostris* is known to descend to the ground, at least to oviposit (Sexton and Heatwole, 1965).

*O. fulgidus* is by far the largest member of the genus and this is reflected in its diet. Ditmars (1928) considered lizards to be the primary prey, but Alvarez del Toro (1960) states that the food consists of birds and small rodents, while Beebe (1946) recorded three *Anolis* and a small bird from the stomachs of three specimens. Dixon and Soini (1977) recorded two passerine birds from the stomach of a Peruvian specimen. Smith (1943) found a bird in a Mexican specimen, and Stuart (1948) found a fringillid bird (*Spinus notatus*) in an *O. fulgidus* from Alta Verapaz, Guatemala.

A specimen we examined from northern Belize had a passerine bird. Ten of 27 stomachs (37.0%) of *O. fulgidus* from the Mexican states of

Quintana Roo and Yucatan that we examined had identifiable remains: 3 *Anolis*, 1 *Basiliscus vittatus*, 1 *Ctenosaura similis*, 2 *Sceloporus*, 2 teiids, and 3 birds. Two of the snakes that had lizards in their stomachs also had birds.

**Feeding behavior.**—Feeding behavior is essentially as described above for *Ahaetulla*. A number of qualitative descriptions have been published, including Emsley (1977), Keiser (1975), Kho (1975), Mole (1924), Mole and Urich (1894), and Rabb (1972). Analysis of movie film shot at 250 fps has shown us that *O. aeneus* will at times rotate the anterior portion of its body 90° in order to seize an anole on a vertical perch (Fig. 9). Rotation brings the snake's upper jaw between the lizard and

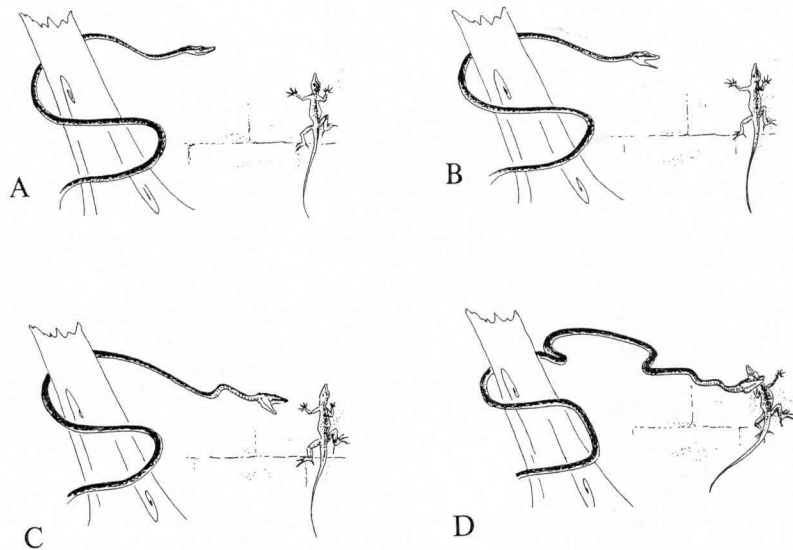


Fig. 9.—Feeding strike of *Oxybelis aeneus* illustrating 90° rotation of the neck.

the vertical substrate and allows the snake to remain in visual contact with the prey longer than if no rotation occurred. It may also facilitate seizing the lizard behind the head and avoiding the lizard's forelimb. Frazzetta (1966) observed "adjustments" during the strike of *Python sebae*, but we are not aware of previous observations in which snakes apparently "planned" a strike which would require mid-air maneuvering for it to be successful. We have observed similar behavior in *A. prasina*.

**Defensive behavior.**—This behavior in *Oxybelis* is also similar to *Ahaetulla*. In *O. aeneus* the mouth is widely gaped (Fowlie, 1965; Gasc, 1971; Mertens, 1946; Stebbins, 1954), thus presenting the potential predator with a dark blue mouth lining (see Henderson, 1974:

Fig. 5). This may or may not be followed by a strike (*pers. observ.*). We also observed rigid, prolonged tongue extension in defensive situations in *O. aeneus*, *argenteus* and *O. fulgidus*; we have not observed *O. brevirostris*. (See Kennedy, 1965, for a photographic sequence of tongue extension in *O. aeneus*.) Tail vibrating has been observed in *O. aeneus* (Henderson, 1974).

**Seasonal incidence.**—We examined seasonal incidence in *O. aeneus* at Belize City, Belize utilizing data collected by Henderson in 1970-71. Monthly rainfall and mean maximum and minimum temperatures for October and November 1970 and January-July 1971 were compared against the mean number of snakes captured or observed/session in the study area during which at least one snake was caught/observed. Using Spearman's rank correlation procedure we found no correlation with rainfall ( $r=.321$ ), but incidence of snakes was positively correlated ( $P < .05$ ) with maximum ( $r=.600$ ) and minimum temperature ( $r=.667$ ).

Zug et al. (1979) used Henderson's (1974: Table 1) growth data to try to determine seasonal activity in *O. aeneus* on the basis of growth. They did find seasonal differences and attributed depressed or accelerated growth rates to dry season or wet season condition, respectively. Interestingly, they considered April and May to be wet season months. They were actually the two driest months during Henderson's study! There is much more likelihood of a positive correlation between Zug et al.'s (1979) growth period and temperature, since mean minimum and maximum temperatures average 3.4-4.5°F higher during their season of growth. Henderson's collection effort was not uniform and virtually

We utilized Henderson *et al.*'s (1979) data for seasonal incidence of snakes of the Iquitos, Peru region. Comparing monthly incidence of two species of *Oxybelis* (*argenteus*, *fulgidus*) (N=34) and just *O. argenteus* (total N=25) to monthly rainfall and maximum temperature, we found no correlation with rainfall, but weak positive correlations ( $P < .10$ ) for incidence of both *Oxybelis* ( $r=.41$ ) and *O. argenteus* ( $r=.43$ ) with mean monthly maximum temperature.

**Activity range and movements.**—*O. aeneus* is the only vine snake that has been studied to any extent in the field (Henderson, 1974). The mean activity range (measured as a convex polygon) for eight snakes (4 males and 4 females) recaptured two or more times was 4.4 ares (3.7 ares for males and 5.0 ares for females).

The mean movement between captures for males (10 individuals) was 42 m (0-135) and 42.5 (0-103) for females (7 individuals).

**Growth.**—Growth slows with advanced age in *O. aeneus* and, although females grow to a larger size, males tend to grow faster (Henderson, 1974). Zug *et al.* (1979) found seasonal differences in growth

rate in *O. aeneus* and this could be related either to seasonal differences in snake or prey activity, or prey abundance.

#### *Thelotornis* Hallowell

**Range and habitat.**—*Thelotornis* is comprised of two species (*T. capensis* and *T. kirtlandi*) and it ranges over most of tropical (central) and southern Africa. Like other vine snakes, *Thelotornis* is almost exclusively arboreal and inhabits bushes and the low branches of trees (L.G. Hoevers, *in litt.*; Isemonger, 1962 and 1968; Wilson, 1965).

**Food.**—Prey is primarily arboreal lizards, and chameleons are taken more often than other kinds (Broadley, 1957; FitzSimons, 1970; L.G. Hoevers, *in litt.*; Isemonger, 1968; Loveridge, 1955 and 1957; Pienaar, 1966; Pitman, 1974; Sweeney, 1971; Wakeman, 1966). Other lizards taken include geckos and agamids (FitzSimons, 1970; Leston and Hughes, 1968; Sweeney, 1971). Other prey taken includes anurans, other snakes, and birds and bird eggs (Broadley, 1957 and 1959; Broadley and Cock, 1975; Cansdale, 1949; L.G. Hoevers, *in litt.*; Isemonger, 1955 and 1968; Pienaar, 1966; Pitman, 1962 and 1974; and Sweeney, 1971).

The most thorough food analysis for *Thelotornis* was done by Sweeney (1971) in Nyasaland. In the Lower River region the chief food of *Thelotornis* was *Philothamnus*, immature *Dispholidus* and *Psammophis*, and other *Thelotornis* among snake prey. Among lizards, *Chameleo dilepis*, arboreal agamids and geckos were the most frequent prey. Birds were also preyed upon. Anurans were occasionally preyed upon and these included *Chiromantis*, *Hylambates* and, rarely, *Hyperolius*.

**Feeding behavior.**—When stalking prey, *Thelotornis* exhibits some of the distinctive movements and postures of *Ahaetulla* and *Oxybelis*. Stalking sequences begin with a lateral head sway (Broadley, 1957; Broadley and Cock, 1975; Wilson, 1965; *pers. observ.*) and stalking is slow and cued by prey movement. Most noticeably absent is prolonged, rigid tongue protrusion. We have not observed it and it is not mentioned in the literature except in Barbour (1926), but J.D. Groves (*pers. comm.*) assures us that he has observed it in captive animals.

In the field *Thelotornis* holds the anterior 1/4-1/3 of its body rigidly straight, motionless, and unsupported while the rest of the body lies along a branch (Broadley and Cock, 1975; FitzSimons, 1970; Isemonger, 1955 and 1968; Pienaar, 1966; Pitman, 1974; Rose, 1962). Goodman and Goodman (1976) observed *Thelotornis* in this position for over an hour with the only noticeable movement being slow extensions and retractions of the tongue, and Broadley and Cock (1975) have seen it remain in this position "for hours." Apparently it is employing a sit-and-wait foraging strategy. FitzSimons (1970), Isemonger (1968) and

Sweeney (1971) commented on the ability of *Thelotornis* to recognize and stalk motionless prey at 4-5 ft, and Sweeney observed one stalk and capture an immobile *Chameleo* from an initial distance of 11 ft. Broadley and Cock (1975) state that *T. capensis* will notice prey within 5 m and stalk it.

Head swaying has been frequently observed, apparently in and out of the context of stalking prey (FitzSimons, 1962; L.G. Hoervers, *in litt.*; Pitman, 1974; Rose, 1962; Sweeney, 1971). Prey is seized in the neck region (Hoervers, *in litt.*; pers. observ.). A number of authors (FitzSimons, 1970; Isemonger, 1968; Pitman, 1974; Sweeney, 1971) have made reference to the habit of *Thelotornis* to sometimes swallow prey while hanging downward from a branch. Although this may be unusual behavior in African tree snakes, we have observed similar behavior in all genera of vine snakes.

**Defensive behavior.**—When excited, *Thelotornis* inflates its throat and the anterior part of its body which noticeably increases its size and also reveals a series of contrasting colors along the side of the neck (Broadley, 1957; Cansdale, 1949; Goodman and Goodman, 1976; Isemonger, 1962; Lambiris, 1965; Mertens, 1946; *pers. observ.*). Goodman and Goodman (1976) have suggested that, in addition to serving as a threat display, neck inflation may mimic a begging, fledgling bird and thus make some bird species vulnerable to predation when harassing *Thelotornis* (see Fig. 1 in Goodman and Goodman, 1976).

**Movements.**—Sweeney (1971) found that *Thelotornis* remains in one tree for several days and may "wander" in a limited area on a number of trees. He also concluded that the occurrence of *Thelotornis* was dependent on climatic conditions and that they were rare at seasonally dry times of the year. Wilson (1965) found they were most active "just after the first rains have fallen, when they are often found on the road."

**Social behavior.**—Mangili (1966) observed combat between captive male *T. kirtlandi*.

#### *Uromacer* Dumeril and Bibron

**Range and habitat.**—*Uromacer*, comprised of four species, ranges over much of Haiti and the República Dominicana (which comprise the Greater Antillean island of Hispaniola) and associated islets. It occurs in relatively dry, scrub habitat and is primarily arboreal, but all species apparently descend to the ground, at least in order to cross roads and trails (R.I. Crombie, *in litt.*; Mertens, 1939; Schwartz, 1970), and possibly to forage for prey (R.I. Crombie, *in litt.*; Schwartz, 1970). They occur in disturbed areas such as banana, cocoanut, cacao and lime groves, and cultivated gardens (Curtiss, 1947; Mertens, 1939; Schwartz, 1970). Figure 10 illustrates typical habitat of *U. catesbyi* and *U. oxyrhynchus* on Isla Saona, República Dominicana.



Fig. 10.—Habitat of *Uromacer catesbyi* and *Uromacer oxyrhynchus* on Isla Saona, República Dominicana.

**Food.**—Horn (1969) analyzed stomach contents of *Uromacer* and presented startling results: the blunt-snouted, heavier bodied *U. catesbyi* took primarily arboreal food, while the more slender-bodied, long snouted species took more terrestrial prey. Since then, a number of taxonomic changes have occurred (Schwartz, 1979b) to somewhat confuse his findings. Even more importantly, many or most of Horn's specimens were native-caught and *Uromacer* is famous for consuming its companions in collecting bags. Even though Horn disregarded stomach contents in which no digestion had occurred, it has been suggested to us by Albert Schwartz that Horn's food data be completely disregarded. We agree, and we will only make occasional reference to them.

*Uromacer catesbyi* is the heaviest bodied, shortest and broadest snouted *Uromacer* (Fig. 11) and we consider it only a "marginal" vine snake, but for the purpose of future discussion (below) we present food data here. *U. catesbyi* is the only *Uromacer* known to prey on frogs (*Hyla* and *Osteopilus*) (Henderson, Binder and Sajdak, *in prep.*; Horn, 1969; Mertens, 1939; Werner, 1909), but they also prey on *Anolis* (R.I. Crombie, *in litt.*; Henderson, Binder, and Sajdak, *in prep.*; Mertens, 1939; Schwartz, 1970) and, more rarely, *Leiocephalus melanochlorus* (Schwartz, 1970).

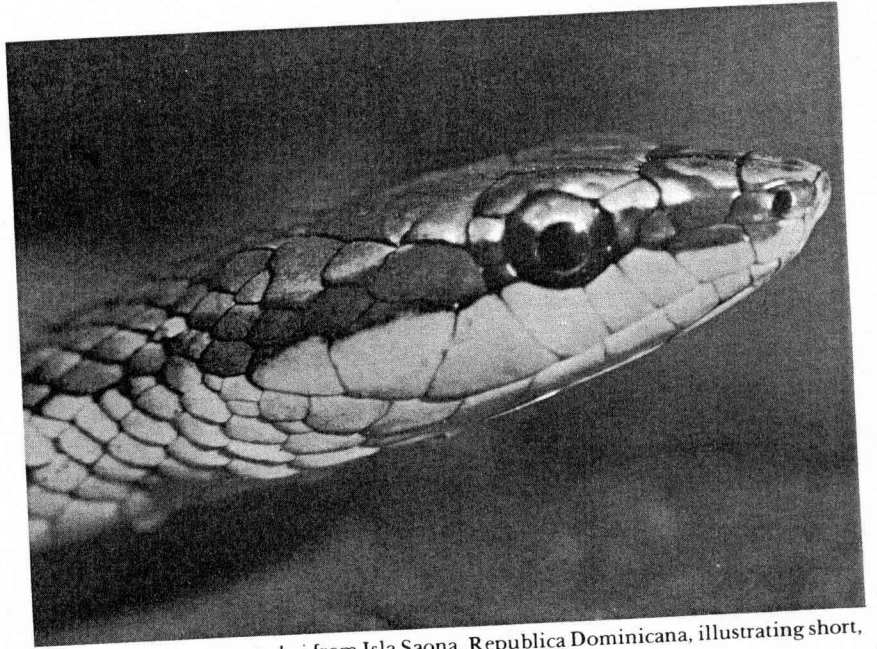


Fig. 11.—*Uromacer catesbyi* from Isla Saona, Republica Dominicana, illustrating short, rounded snout.

*Uromacer frenatus* feeds on *Anolis* (Schwartz, *in litt.*) and R.I. Crombie (*in litt.*) found the tail of a gecko (*Aristelligella*) in one.

*Anolis* are the primary food of *U. oxyrhynchus* (Henderson, Binder and Sajdak, *in prep.*; Mertens, 1939; Schwartz, *in litt.*), but R.I. Crombie (*in litt.*) saw one strike at a *Leiocephalus lunatus* on Isla Saona. Mertens (1939) observed *U. oxyrhynchus* drinking water from leaves in the field. Groves and Altimari (1977) have observed keratophagy in captive *U. oxyrhynchus*.

*Uromacer wetmorei* until recently was considered a subspecies of *U. frenatus* (Schwartz, 1979b). We presume it preys primarily on *Anolis*.

**Feeding behavior.**—Stomach content analysis suggest that all *Uromacer*, except *U. catesbyi*, employ a sit-and-wait foraging strategy. The frequency of hylid frogs taken by the diurnal *U. catesbyi* at least implies active foraging (Henderson *et al.*, 1977). R.I. Crombie (*in litt.*) saw one foraging in cocoanut trash in which *Anolis* and *Sphaerodactylus* were common. It was observed active on leaf litter and crawling across a termitarium at 4.5 m (Schwartz, 1970) and Schwartz (1979a) observed one actively foraging on a roadcut face occupied by *Anolis strahmi*.

We observed feeding behavior in captive *U. catesbyi*, *oxyrhynchus*



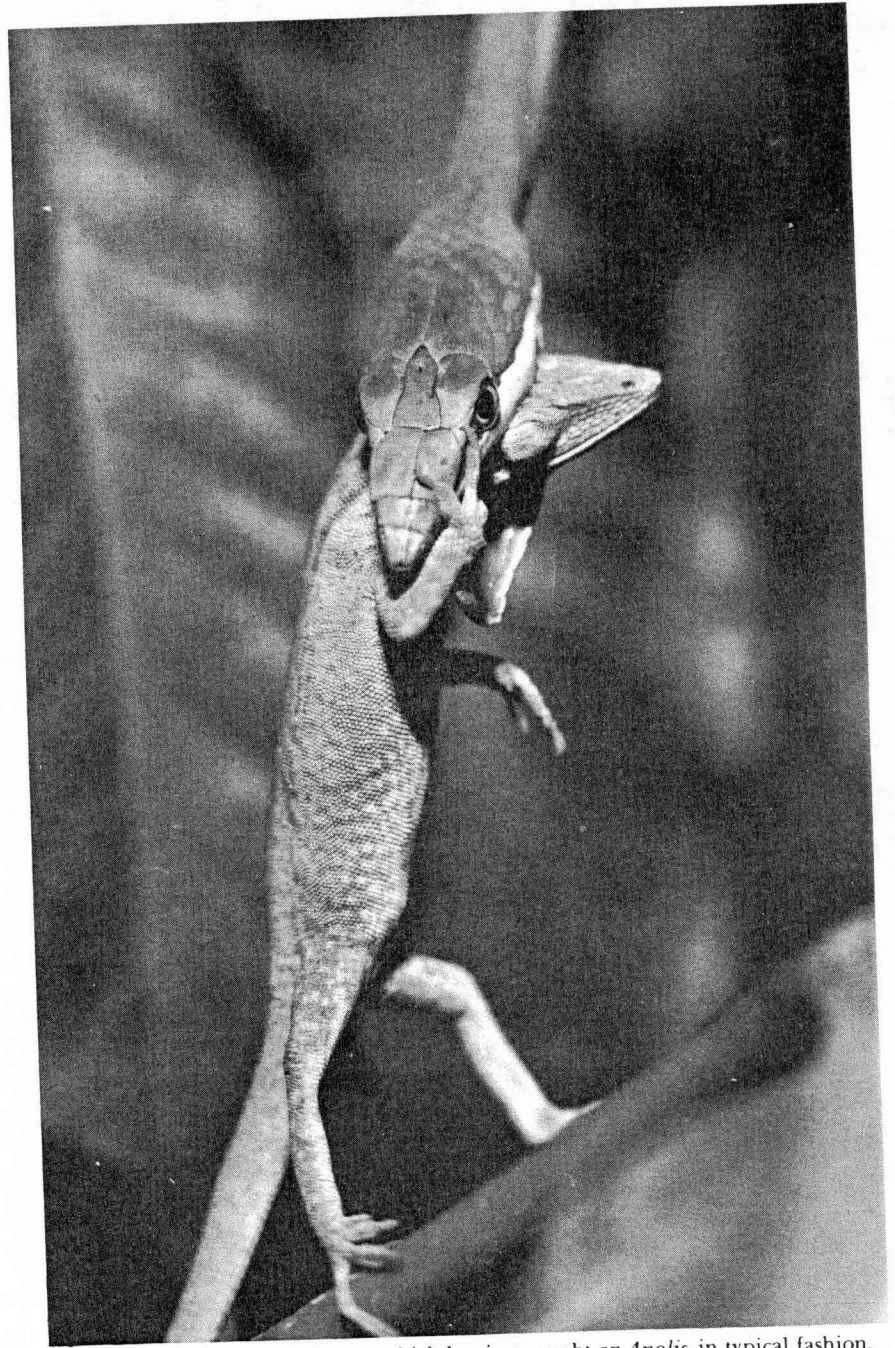


Fig. 12.-*Uromacer oxyrhynchus* which has just caught an *Anolis* in typical fashion.

and *wetmorei*. As in other genera of vine snakes, vision appears to be acute and stalking is initiated with lateral head sways and is cued by prey movement. Most of our observations were made on individuals of *U. catesbyi* and *U. oxyrhynchus* from Isla Soana, located off the southeastern coast of the República Dominicana, and these snakes do not exhibit rigid tongue extension to the degree displayed by *Ahaetulla prasina* and *Oxybelis* spp. we have observed. J.K. Bowler (*in litt.*) and J.D. Groves (*pers. comm.*) observed *U. oxyrhynchus* (probably from the vicinity of Santo Domingo) and noted evident rigid tongue extension.

Stalking is slow and deliberate and correlated with prey movement in *U. oxyrhynchus* and *U. wetmorei* (Henderson and Binder, *in prep.*). Prey is seized behind the head (Fig. 12), worked quickly to the back of the mouth and ingestion does not start until all or most prey movement has ceased. *Uromacer* that were disturbed after seizing prey carried the prey to higher arboreal sites before continuing prey immobilization and ingestion.

When an unsuccessful strike is made at a lizard, long-snouted *Uromacer*, like *Ahaetulla* and *Oxybelis*, do not pursue it. They seem disoriented, usually looking at the place the lizard was immediately before the strike, occasionally performing tongue flick volleys. Not until the lizard provides another visual cue does the snake again orient towards it. *Uromacer catesbyi*, on the other hand, although acting like a vine snake in some ways (prolonged, rigid tongue extension for short periods) (Henderson and Binder, *in prep.*), acts like a *Leptophis* when prey is missed and actively pursues it and quickly attacks again (Burghardt, 1977; *pers. observ.*).

**Defensive behavior.**—*U. catesbyi*, *U. oxyrhynchus* and *U. wetmorei* gape their mouth when excited, and this may or may not be followed by a strike (*pers. observ.*). Similar displays are found in many arboreal snake taxa (Greene, 1979).

**Social behavior.**—Schwartz (1970) reported what was probably male combat in *U. catesbyi*.

**Origin and evolution.**—Maglio (1970) and Horn (1969) discussed the origin and evolution of *Uromacer*, respectively.

*Uromacer* forms a subassemblage of Maglio's (1970) *cantherigerus* species assemblage. According to Maglio, "The assemblage appears to have been derived from an ancestral species probably not unlike *Alsophis cantherigerus* in its osteological, hemipenial, and external morphology." *Hypsirhynchus ferox*, a terrestrial, diurnal lizard predator, is close to the Jamaican *Alsophis ater*. *Uromacer* may have been "derived from an early form of *H. ferox* before the latter achieved its peculiar specializations." *Hypsirhynchus ferox* is suggestive of

*U. catesbyi* in skull structure, and *catesbyi* is the least specialized of the *Uromacer* subassemblage (Maglio, 1970). *Uromacer frenatus dorsalis* and *U. oxyrhynchus* are the most specialized forms based on cranial characters. Maglio (1970) suggested that *Alsophis anomalus*, *Hypsirhynchus* and *Uromacer* "may have differentiated as a means of dividing up the habitat more efficiently." Figure 13 illustrates the possible evolution of head shape from a blunt-snouted, semi-arboreal generalist to an attenuate-snouted specialist.

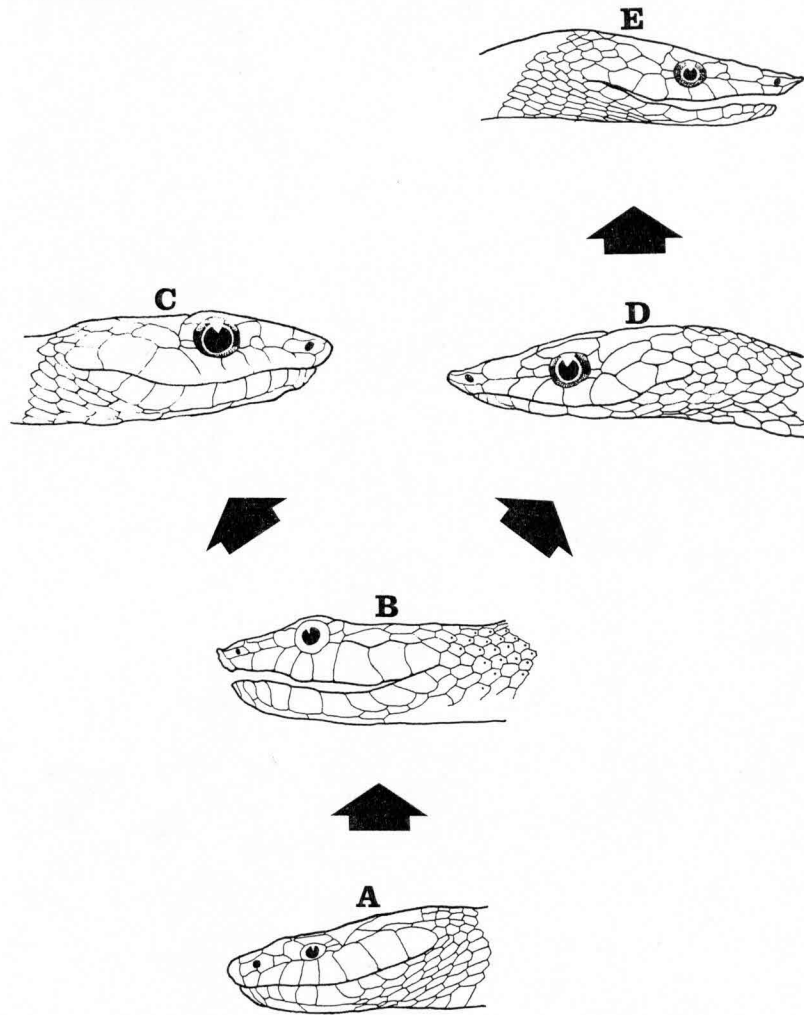


Fig. 13.—Possible evolution of head shape in *Uromacer*, using extant species and based on Horn (1969) and Maglio (1970). A. *Alsophis anomalus*; B. *Hypsirhynchus ferox*; C. *Uromacer catesbyi*; D. *Uromacer frenatus*; E. *Uromacer oxyrhynchus*.

On the basis of morphology, diet, distribution, physiographic history of Hispaniola and the "mechanisms of geographic speciation," Horn (1969) suggested "that *catesbyi* is the most primitive of the *Uromacer*, *oxyrhynchus* and *dorsalis* [= *U.f. dorsalis*] the most recently derived, and that [*U.f.*] *frenatus* represents an intermediate step."

#### DISCUSSION AND A SUMMARY OF FEEDING BEHAVIOR

Vine snakes are morphologically and behaviorally adapted to capture active prey on a physically unstable substrate (i.e., leaves, twigs and branches). Indeed, they may very well be the only diurnal, arboreal snakes that routinely feed on fast-moving prey.

A slender body, high number of subcaudals and cryptic coloration are adaptations to living in trees and bushes. This allows most vine snakes to move among slender branches without weighing them down and therefore making it easier to bridge gaps between them.

Elongation and narrowing of the head, and attenuation of the snout are undoubtedly aids to vision (Walls, 1942). Besides snout attenuation, vine snakes have grooves between the eye and snout tip and this increases straight-ahead vision (Fig. 14). Of snakes tested for binocular

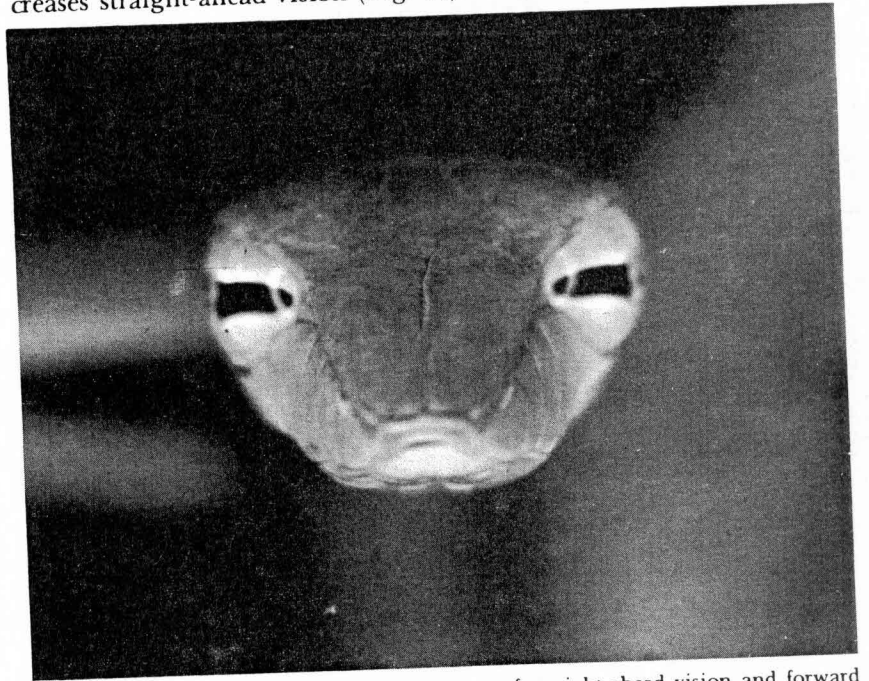


Fig. 14.-*Ahaetulla prasina* illustrating extent of straight-ahead vision and forward position of the pupil.

field of vision, *Ahaetulla prasina* has the widest field known ( $46^\circ$ ) and *Uromacer oxyrhynchus* has one of the widest ( $40^\circ$ ); the binocular angle in most snakes is less than  $40^\circ$  (Walls, 1942). Presence of an eyelid in the nasal groove of some vine snakes may be an additional visual aid for capturing active prey (Ficken *et al.*, 1971).

The ratios for HL/SL and SBW/SAW make most vine snakes, as a group, morphologically unique from all other snakes. No other snakes feed on active prey on an unstable substrate and therefore they do not need similar morphological requirements. The snakes that most closely approach vine snakes in these characters are also diurnal lizard predators, with the possible exception of *Langaha*.

*Thelotornis* is the most divergent of the vine snake genera for HL/SL and SBW/SAW in not having as long or as attenuated a snout, but it also diverges in other ways. It does not prey on active lizards to the degree *Ahaetulla*, *Oxybelis* and *Uromacer* do. Chameleons are the principal lizard prey of *Thelotornis* and they are essentially immobile or, when they do move, it can hardly be compared to, for example, most species of *Anolis*. But *Thelotornis* is also a frequent predator of other snakes, a prey group which is essentially ignored by the other three genera, and it apparently feeds more often on endotherms. The venom of *Thelotornis* is far more toxic than that of any of the other vine snakes, even capable of causing human fatalities (Visser and Chapman, 1978). This alone suggests a difference in prey preference. The most obvious behavioral difference is lack of prolonged, rigid tongue extension by *Thelotornis* during prey stalking and during defensive displays. Thus, *Thelotornis* is not as specialized morphologically or behaviorally for preying on potentially fast-moving lizards and this is borne out by prey preference.

Of the other vine snakes, *Oxybelis brevirostris* is the most morphologically divergent. Unfortunately, little is known of its behavior or ecology, but our scant data on prey preference, based on the contents of only four stomachs, suggest that it may not be as stenophagous for lizards as most other vine snakes.

Vine snakes employ a sit-and-wait foraging strategy. That is, a vine snake will remain in one location for a period of time waiting for prey to approach. Once it is seen, the snake will stalk it. *Oxybelis aeneus* has been observed in the field in the same tree or bush for over two days (Henderson, 1974; Henderson and Nickerson, 1977). If prey does not approach within several days, the vine snake probably moves to another arboreal site, possibly ascending to the ground to get to it.

Once a vine snake is aware of the nearby presence of prey, stalking begins with either lateral head swaying or rigid tongue extension. Head swaying causes parallax and it occurs in a number of lateral-eyed

vertebrates. By invoking parallax, snakes can "obtain a perception of solidity and relief - a sort of monocular stereopsis" (Walls, 1942:341). The prominence of an object can be evaluated when seen from more than one angle simultaneously (i.e., binocular vision) or in rapid succession (by head swaying or "rapid peering") (Walls, 1942). It is interesting that vine snakes, which already have the widest binocular fields of any snakes, also use head swaying to gain additional parallax.

A number of hypotheses have been proffered to explain rigid tongue protrusion. These were reviewed by Keiser (1975) and he offered two additional hypotheses. Prior to Keiser (1975), the peculiar lingual movements of vine snakes (and *Oxybelis* in particular) were considered fascinating to prey (e.g. Proctor, 1924) or as a lure for prey (Curran and Kauffeld, 1937). Keiser (1975) suggested (1) that the extended tongue has a "disruptive" and "potentially confusing influence" on prey, and (2) "that the immobility of the extended tongue functions for maintaining continuous olfactory contact with the environment without attracting undue attention." According to Gove (1979), "This rigid extension tongue-flick is most certainly a behavioral pattern which helps the snake remain cryptic." Gove (1978) found that when *Oxybelis aeneus* used rigid tongue extension, it was successful in stalking prey, but when a more typical tongue-flick volley was used, the lizards became wary and escaped.

We (Henderson and Binder, 1979) offered an alternative hypothesis: The rigidly extended tongue acts as an extension of the eye line and vine snakes use it for sighting prey or as a point of reference during prey stalking. Since vine snakes will sometimes extend the tongue at the beginning of a stalking sequence and not retract it until immediately prior to the strike, we are dubious of Keiser's (1975) second hypothesis. If the tongue is not retracted into the mouth, the snake is receiving no, or minimal, chemical cues during prey stalking. The function of prolonged, rigid tongue extension will be addressed in detail elsewhere (Henderson and Binder, *in prep.*).

Once prey stalking begins, vine snakes are cued by prey movement, and length and duration of a snake's movement toward a prey item is correlated with the duration and type of movement performed by the prey (Henderson and Binder, *in prep.*). Amazingly subtle prey movements (e.g. respiratory movements of the thorax, raising and lowering of a toe) are all that are necessary to cue stalking movement. If a lizard walks or jumps, the snake will move farther toward the lizard than if it merely turns its head or shifts a limb; then the snake's forward movement may be almost imperceptibly short. Stalking, at least from distances greater than 30-45 cm, is usually accompanied by rigid tongue extension. During an unusually long stalking sequence we observed, an *O. aeneus* had at least the tips of its tongue, and frequently the entire tongue, extended for over 17 minutes.

The strike begins when the snake is 10-15 cm from the lizard, and the lizard is almost invariably grasped at, or anterior to, the pectoral girdle. In a series of 100 routine feedings of vine snakes representing all four genera, 92% of the lizards were seized in that part of the body. By doing so, vine snakes reduce or eliminate the possibility of a lizard turning and biting them and are able to more quickly subdue the prey. There is then less likelihood of the prey escaping.

Once seized, the snake's hold on prey is never released for an obvious reason: it would most likely drop to the ground and be lost if the snake relinquished its hold while on an arboreal perch. Prey is quickly worked to the back of the jaws and once immobilized is swallowed head first.

Four apparently unrelated genera, representing two subfamilies and three tribes, show morphological, ecological and behavioral similarities. In light of the taxonomic and geographic diversity represented by the four genera, we assume the similarities are due to convergence rather than to a common ancestry. Like *Uromacer*, the other three genera probably evolved from diurnal, semi-arboreal ancestors that were euryphagic, having taken to the trees, possibly, to avoid competition with terrestrial relatives. Competition among closely related and overlapping species in the arboreal adaptive zone resulted in character divergence whereby competing forms adapted ecologically and then morphologically to different aspects of the biotic environment. "Proto-vine snakes" began specializing in lizard prey, became more and more stenophagous and evolved morphological adaptations to saurophagy. Behavioral modifications followed.

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