

Why Snakes Have Forked Tongues

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The serpent's forked tongue has intrigued humankind for millennia, but its function has remained obscure. Theory, anatomy, neural circuitry, function, and behavior now support a hypothesis of the forked tongue as a chemosensory edge detector used to follow pheromone trails of prey and conspecifics. The ability to sample simultaneously two points along a chemical gradient provides the basis for instantaneous assessment of trail location. Forked tongues have evolved at least twice, possibly four times, among squamate reptiles, and at higher taxonomic levels, forked tongues are always associated with a wide searching mode of foraging. The evolutionary success of advanced snakes might be due, in part, to perfection of this mechanism and its role in reproduction.

Deeply embedded in the popular psyche, serpents' tongues have long been a part of the world's religious iconography (1) and in many cultures symbolize malevolence and deceit. Yet, despite this prominence, the function of forked tongues has eluded rational scrutiny for more than two millennia. A full understanding of this function and its significance to the evolution of snakes and lizards is only now emerging, yielding to a multilevel approach highlighting the need for analysis of the whole organism. Snake tongues, it turns out, tell us a great deal about snakes and about evolution as well.

Recorded inquiry into the functional significance of the forked tongue begins with Aristotle who, reasoning from the basis of his own tongue, thought that it would provide snakes "a twofold pleasure from savours, their gustatory sensation being as it were doubled" (2). Some 19 centuries later, Hodierna was not so charitable (3). He thought that snakes used their forked tongue "for picking the Dirt out of their Noses, which would be apt else to stuff them, since they are always grovelling on the Ground, or in Caverns of the Earth." A third theory has snakes catching flies "with wonderful nimbleness" between the tines of their forked tongues (4).

As it happens, Aristotle was close to the truth. We now know that snake tongues are, in fact, involved in chemoreception, but probably not gustation as Aristotle surmised. Rather, the tongue is a delivery mechanism for paired chemosensors in the snout, called the vomeronasal (Jacobson's) organs (VNO) (5). These organs communicate with the oral cavity through two tiny openings in the palate, the vomeronasal fenestrae. The tongue samples environmental chemicals by means of tongue flicking, a behavior in which the tongue is rapidly protruded, sometimes oscillated, and then

retracted into the mouth, usually after the tongue tip contacts the ground or some object (6). Odor molecules adherent to the tongue are delivered to the vomeronasal fenestrae where they make their way to the sensory epithelia of the VNO (vomero-faction) (7, 8). Tongue flicking, then, includes a sampling phase (protrusion, oscillation, and chemical pickup) and a delivery phase (deposition of the sampled chemical within the oral cavity for delivery to the VNO). For many species of squamate reptiles, particularly snakes, vomero-faction may be the dominant sensory mode underlying many complex behaviors (2, 5).

Chemical Delivery and Tongue Form: A Red Herring

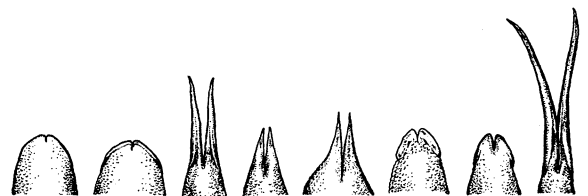
Despite Aristotle's early association of the snake's tongue with chemoreception, this concept was lost in a myriad of fanciful theories that were proposed over the centuries (4), two of which are noted above. By the 20th century, most scientists believed that the tongue was a tactile organ. Work in the 1920s and '30s then established chemical sampling and delivery to the VNO as the function of tongue flicking (9–11). These and later workers were seduced by the natural association between the paired VNO, their fenestrae in the palate, and the forked form of the tongue

tip. It was first suggested by Broman in 1920 that the attenuate tips of the forked tongue in snakes were inserted directly into the vomeronasal fenestrae to deliver odor molecules to the VNO (9). In so doing, Broman indelibly linked the forked tongue morphology with the delivery phase of tongue flicking, a link that has remained until nearly the present time.

Unfortunately, Broman's hypothesis of forked tongue function must be rejected on the basis of experimental and comparative evidence. First, cineradiographic (x-ray movie) studies of tongue flicks in snakes and varanid lizards (with a similar forked tongue morphology) have failed to reveal lingual movement within the oral cavity consistent with such a hypothesis (12). In addition, the tongue was seen to be fully retracted into its sheath before mouth closure (13), suggesting that sampled molecules are deposited by the tongue onto paired pads on the floor of the mouth (anterior processes of the sublingual plicae) and that these, not the tongue, are appressed to the vomeronasal fenestrae to effect delivery. Second, and ultimately damning to the Broman hypothesis, is the fact that vomeronasal function is highly developed in nearly all squamate reptiles (lizards, snakes, and amphisbaenians), and these share a similar, derived vomeronasal form, but only a few of them have forked, attenuate tongue tips (Fig. 1). In most lineages, the tongue is only slightly notched and is rather blunt; the tips could not possibly be inserted into the vomeronasal fenestrae. Despite this supposed mechanical limitation, such species have been shown to deliver chemicals effectively to the VNO (8). These findings refute Broman's hypothesis and call into question the role of the forked tongue tip in the delivery phase of tongue flicking.

Despite these observations, the idea that

Fig. 1. Variation in the form of the tongue tip in squamate reptiles including the plesiomorphic notched morphology and several forked forms. Shown are representatives of each of the four principal lineages of Squamata. The drawings are not to scale, but the approximate resting tongue length (RTL) for the specimens on which they are based is indicated here. From left to right: *Sceloporus* (Iguania) (RTL = 7 mm); *Coleonyx* (Gekkonidae) (RTL = 6.5 mm); *Cnemidophorus* (Teiidae) (RTL = 16 mm); *Lacerta* (Lacertidae) (RTL = 7 mm); *Bipes* (Amphisbaenia) (RTL = 3.5 mm); *Scincella* (Scincidae) (RTL = 5.5 mm); *Abronia* (Anguillidae) (RTL = 14 mm); and *Varanus* (Varanidae) (RTL = 50 mm). Most snake tongues would appear similar to that of *Varanus*.



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the forked tip morphology and the delivery phase of tongue flicking are linked has persisted in the notion that there is a correlation between the degree of lingual bifurcation (forkedness), sensitivity of the VNO, and importance of vomerolfaction in the life of the animal (7, 8, 14, 15). This erroneous notion has acted as a red herring in chemosensory studies because it has diverted attention away from the actual function of the forked tongue, namely, its mechanical role outside the oral cavity in sampling the chemical environment.

Chemical Sampling and Tongue Form: Evidence for Tropicaxis

The turn-of-the-century concept of animal tropisms was replaced by Fraenkel and Gunn (16) with several categories of movement they termed kinesis and taxes. For directed movement toward a stimulus source, they distinguished klinotaxis and tropotaxis. Both taxes involve repeated (or continuous) sensory assessment of the environment and the behavioral response of movement toward (or away from) the stimulus but are differentiated by their temporal nature: Klinotaxis involves comparison of successive stimulus intensities between disparate points, whereas tropotaxis involves simultaneous comparison of stimulus intensities on two sides of the body. Klinotaxis is common in chemoreception, but tropotaxis is theoretically possible only when the chemical gradient is steep enough for two parts of the animal's body to be stimulated with different intensities (16).

For a snake or lizard to use chemosensory tropotaxis, it must be able to sense simultaneously the chemical stimulus at two points. This requirement is met admirably by the forked tongue. The more deeply forked the tongue, the greater the potential distance between simultaneous sampling points. The distance between sampling points (the tip of each tine) is a function of absolute size, fork depth, tongue width, and the degree to which the tines of the fork are spread. A simple tongue fork score can be calculated (Table 1). In some species (snakes, varanid and teiid lizards, and amphisbaenians) the potential distance between the tips is considerable, exceeding the width of the head (Fig. 2) (17).

This mechanism requires that chemical stimuli on each tine be delivered to the ipsilateral VNO, which is the actual sensory organ. Although the mechanism of chemical delivery remains controversial (18), evidence indicates that same-side delivery would be possible either by the tongue itself or by the sublingual plicae.

The chemical source must exhibit a gradient sufficiently steep that a differential can be sensed within the distance available

between the separated tines of the forked tongue tip; in other words, the chemical source must be scaled to the receiver. This requirement is met, for example, by trails of pheromones left by passing conspecifics and prey. Such trails, a known target of tongue flicking by squamates (17, 19, 20), are of biological significance, are narrow, and not particularly volatile, and thus provide a steep chemical gradient of the appropriate physical dimension.

Does the forked tongue, in fact, function in tropotaxis? Auffenberg suggested this possibility with regard to prey trailing by the Komodo monitor (20), pointing out that each tine of the deeply forked tongue could deliver a different stimulus intensity to the VNO. However, the distinction between klino- and tropotaxis is a key factor in this discussion, because it is clear that virtually all squamates utilize tongue flicking and vomerolfaction for the former, but not necessarily the latter. In klinotaxis, gross movements of the head and body would allow sequential tongue flicks to sample disparate points along the ground. The stimulus strength of the temporally and spatially sequential points could then be compared by the central nervous system. Klinotaxis is characterized by wide-ranging, exploratory movements that sequentially define the chemical source (16). In contrast, tropotaxis mediated by a forked tongue would assess the gradient in a single tongue flick. It would be most effective once a circumscribed chemical source, such as a pheromone trail, was encountered. The forked tongue could then function as an edge detector to delimit the chemical zone and follow it with minimal deviation.

Although no single piece of evidence is, itself, definitive, a survey of the data leads to one ineluctable conclusion: forked tongues function during tropotaxis by providing a mechanism for instantaneous chemical edge detection that enhances a squamate's ability to follow pheromone trails, thus accomplishing the biologically critical activities of seeking both prey and mates. The evidence is of four general types.

1) *Behavior constitutes the richest source of support for the tropotaxis hypothesis.* The behavior most clearly implicated in the forked tongue mechanism is following of a pheromone trail. Therefore, there should be a rough correlation between depth of tongue bifurcation and ability to follow scent trails. Insufficient data exist to allow a quantitative comparison of trail-following ability among taxa, but those taxa with deeply forked tongues (snakes, amphisbaenians, teiids, varanids, and helodermatids) are highly proficient trail followers (2, 20–23). Iguanians and gekkonids, on the other hand, which have only slightly notched

tongues, appear not to follow scent trails.

Experimental removal of the forked portion of the tongue should eliminate the ability to follow scent trails but not delivery of stimulus particles to the VNO. Remarkably, these experiments were performed on snakes by Kahmann in the 1930s (11) and produced the predicted results: The only deficit found in the experimental animals was reduction or loss of the ability to follow scent trails. Kahmann, however, interpreted his results in light of the theory that the tongue tips deliver chemicals directly to the VNO. Waters (24) confirmed these results by blocking the vomeronasal fenestrae of garter snakes on one side. Treated snakes were unable to trail, but instead turned a circle toward the unblocked side.

Ford (17) observed male garter snakes following pheromone trails left by females

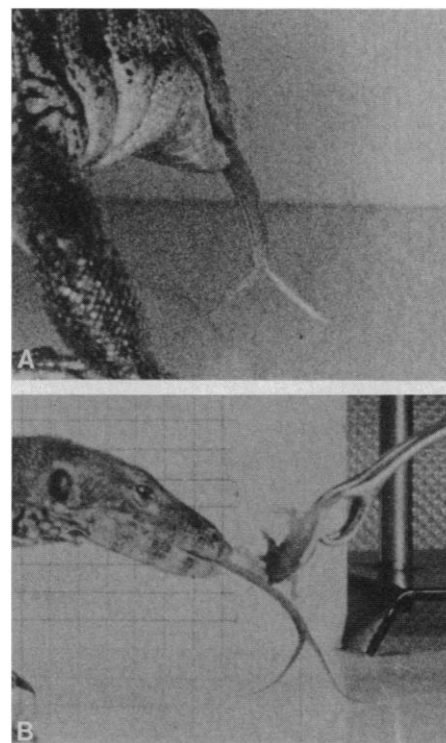


Fig. 2. Tongue flicks in a teiid (*Tupinambis nigropunctatus*) (A) and a varanid (*Varanus salvator*) (B) showing active separation of tongue fork tines at the moment of substrate contact (sampling). Photos are enlarged from individual 16-mm cine frames (64 frames per second) extracted from sequences of unrestrained animals tongue flicking the floor of the filming chamber. Sequences show that when the tongue is initially protruded, the tines are held together. They are progressively spread during the downward phase of the tongue flick and reach maximal spread during contact with the substrate. During retraction of the tongue into the mouth, the tines come closer together but remain separate until they disappear from sight. Photos were made from films taken by G. S. Throckmorton, with permission.

and suggested that the forked tongue functions as part of a tropotactic mechanism. He found that "When the edge of the trail was exceeded by one tongue tip during a tongue-flick, the snake reversed direction and swung his head back into the pheromone field during the period before the next tongue-flick." The tongue tips were widely spread during such trail-following behavior, as much as twice the width of the snake's head, and trail following was accurate and directed. Occasional loss of the trail only occurred when the male's head left the female's pheromone field between tongue flicks. Loss of the trail caused the male to stop for one or several tongue flicks and then swing the head from side to side between flicks until the trail was relocated. The latter behavior is consistent with klinotaxis, typical of all squamates, including those without forked tongues.

2) *A forked tongue tip morphology would be most significant during the sampling phase of tongue flicking and not the delivery phase.* Therefore, a forked tongue tip should not be necessary for chemical delivery to the VNO. This is supported by comparative analysis (above), as well as experimental evidence showing that removal of the forked portion of the tongue in snakes and lizards does not prevent stimulus delivery to the VNO after tongue flicking (7, 11, 25).

3) *The tips of the tongue should be spread laterally during a tongue flick when odor molecules are retrieved, because the greater the distance between sampling points, the greater the likelihood of sampling a chemical gradient in*

a single flick. Observations of lizards with forked tongues (teiids and varanids) (Fig. 2) and snakes (17) confirm that the tines are spread rapidly and widely just before contact with the substrate. Histology of the tongue tip in snakes suggests that muscle fiber architecture optimizes bending of the tines rather than elongation, in contrast to the remainder of the tongue (26).

4) *Central nervous system projections of the vomeronasal receptor cells must provide a neural substrate for comparing signal strength from each side of the tongue, that is, a mechanism that enables the animal to locate the signal in space.* Owl hearing offers an analogy, as owls use their paired ears to localize a sound source. They compare sound intensity (and the time of arrival of sound) at each ear (27). Similarly, squamates compare differential chemical signal strength delivered from each time to the paired VNO. In owls, each auditory pathway projects to a nucleus that communicates through commissural connections to the contralateral nucleus. Direct input to the nucleus is excitatory, whereas commissural input is inhibitory, thereby providing the basis for neural computation of interaural differences (28). In squamates the VNO projects to a nucleus (nucleus sphericus) (29), and in snakes the nucleus sphericus communicates with the contralateral nucleus through the anterior commissure (30), circuitry that is similar to the owl's (that is, central projection to a nucleus with commissural communication between contralateral nuclei). Although not conclusive, such circuitry is consistent

with the tropotaxis hypothesis. Physiological evidence of direct nucleus sphericus excitation and commissural inhibition would lend additional support.

The proposed mechanism of forked tongue function does not suggest that lizards and snakes use it to sense the direction taken by the prey or conspecific. This would require detection of some sort of polarized trail. Trail direction probably is determined by tongue flicking of objects in the environment against which the target has pushed during locomotion (31). During snake locomotion, chemical cues would be deposited only on the side facing the direction of travel, and therefore direction can be determined by tongue flicking both sides of the object. Some venomous snakes can differentiate between trails made by envenomated and nonenvenomated prey; hence they can follow a trail in the direction of the prey item once it has been struck (32). It remains unclear how directionality can be determined, if at all, for trails laid by limbed prey or conspecifics that do not push off against environmental objects.

Tongue Form and Ecology

The tropotaxis function of the forked tongue is indicated by a wide range of organismal data and suggests certain predictions. For example, if a forked tongue enhances the ability to follow prey trails, there may be a correlation between the presence of a forked tongue and foraging mode (33). Wide-ranging foragers should profit from a trail-following mechanism because they seek out prey by moving widely through the environment. The ability to follow a trail efficiently to its source would be an advantage to an animal that expends a great deal of its energy in search. Conversely, sit-and-wait foragers have no need to follow prey trails, because they wait for prey to come to them. Klinotaxis would be sufficient to locate a good ambush site.

The degree of tongue forkedness in lizards is, indeed, positively correlated with foraging mode ($P = 0.016$) (Table 1). Because phylogenetic relationships of two fork-tongued lineages (snakes and amphisbaenians) within Squamata remain unresolved (34), a test properly controlled for phylogenetic effects could not be made; however, when snakes and amphisbaenians are placed in the phylogeny at the nodes best supported by other data, the correlation is nearly perfect (Fig. 3). Foraging modes for amphisbaenians remain little known, but one species observed forages over large distances to locate prey trails leading to clumped prey sources (21). Scincids, the single exception to the generalization, may differ qualitatively in foraging mode (35), interposing long periods of stasis and observation between

Table 1. Tongue tip form and foraging ecology of lizards. Shown are families for which both tongue tip data and foraging mode data were available. Snakes were excluded from this analysis because data were not available to calculate tongue fork scores (TFS) by family. The presence of a forked tongue is positively correlated with wide foraging (Wilcoxon rank sum test, $P = 0.016$). Lizard families are ranked in order of increasing degree of tongue tip bifurcation. Numbers in parentheses after each taxon indicate [number of species used to calculate TFS, number of species used to calculate foraging mode score (FMS)]. TFS is the length of the lingual bifurcation (tine length) divided by the width of the tongue at the base of the bifurcation. Each score is given as a family mean followed by the standard error. Measurements are from photographs taken by the author. I calculated FMS from characterizations of foraging mode by species (43, 44). Sit-and-wait (SAW) species were scored 0 and wide foragers (WF) 1; FMS is the mean value for the family. For the dichotomous classifications, TFS > 1 is considered to be "forked" and FMS > 0.5 is considered to be "wide foraging." All snakes have forked tongues [TFSs range from 1.5 (Scolophoridae) to values comparable with varanids (6.0+) (Caenophidia)] and virtually all are wide foragers (43). The traditional families Iguanidae and Agamidae (Iguania) may be paraphyletic assemblages (45) but, in any case, are relatively uniform in terms of tongue tip form and foraging mode.

Taxon	Mean TFS	FMS	Dichotomous	
			TFS	FMS
Xantusiidae (1, 3)	0.10	0	—	SAW
Agamidae* (3, 6)	0.13 (0.06)	0	—	SAW
Iguanidae* (11, 68)	0.17 (0.02)	0	—	SAW
Scincidae (6, 3)	0.28 (0.02)	0.67	—	WF
Anguidae (3, 5)	0.53 (0.02)	0	—	SAW
Helodermatidae (1, 2)	1.08	1.00	+	WF
Lacertidae (3, 5)	1.70 (0.32)	0.80	+	WF
Teiidae (5, 19)	3.26 (0.25)	1.00	+	WF
Varanidae (2, 9)	6.43 (0.58)	1.00	+	WF

*Potentially paraphyletic taxa (45).

short bouts of foraging, as opposed to the intensive movement and investigation of typical wide foragers. Other aspects of squamate chemosensory biology, such as the ability to discriminate among prey odors, or the presence of postbite elevation in tongue-flick rate, might also correlate with foraging modes (36).

Macroevolutionary Patterns

Although the position of snakes and amphisbaenians within Squamata is not fully resolved, snakes probably evolved from within Anguimorpha (probably Varanoidea) and amphisbaenians from within Scincomorpha (14, 34, 37). Given these phylogenetic relationships, it is clear that forked tongues have evolved independently at least twice within Squamata and possibly four times, depending on placement of the aforementioned taxa (Fig. 3). As noted, wide foraging is tightly correlated with the evolution of forked tongues.

Forked tongues have evolved at least once in each of the major lineages, Anguimorpha and Scincomorpha. One family (the Pygopodidae) within a third lineage, Gekkota, exhibits more deeply cleft tongues than its sister taxon, the Gekkonidae (38). This tendency is interesting in light of the fact that pygopodids are elongated and nearly limbless, whereas geckos are rarely elongated and retain robust limbs. Among fork-tongued forms, snakes and amphisbaenians are elongate and limbless, many teiids and lacertids are elongate and some are nearly limbless, and lanthanotids are elongate with reduced limbs. Only helodermatids and varanids among these forms seem to retain robust limbs, but all are elongate, some varanids strikingly so. However, the corre-

lation between tongue forkedness and body form is a loose one because many squamate taxa lacking forked tongues (such as the scincids, cordylids, and anguids) also exhibit elongate, nearly limbless or limbless body forms. Body elongation and limb reduction, associated with locomotory mode, may also be associated with foraging mode, thus creating, in some lineages, a selective regime in which a tropotactic mechanism is favored. In other words, such changes in body form allow, but do not constrain, evolution in this direction.

Only among iguanians is there no tendency toward deeply bifid tongues, body elongation, or limb reduction, nor is there evidence of wide foraging. Nonetheless, tongue flicking and sensitive vomerolfaction are characteristic of many iguanians, features primitive for squamates (39). It is probable that use of the tongue to stimulate the VNO first evolved in squamates as a means to sample less volatile chemicals than those inhaled into the nasal chamber, and later, to increase the efficiency of source localization through klinotaxis. A bifurcate tongue tip is a synapomorphy of squamates, but the reason for its initial evolution remains obscure. Probably, inception of the notched tip was associated with the evolution of a direct VNO-oral connection (39), and it did initially confer a performance advantage in chemical delivery to the VNO. Subsequent selection for scent trail-following and a tropotactic mechanism may have caused the tongue to become increasingly forked in some lineages, a morphocline evident, for example, within the anguimorphan clade (14, 22).

Advanced snakes (comprising all colubroids, including venomous species) are an exceptionally diverse and speciose lineage

that might owe their success, in part, to vomeronasal specialization leading to their ability to detect and follow pheromonal trails, an important aspect of their reproductive biology (5, 17, 40).

Mechanisms for vertebrate chemosensory tropotaxis might be more diverse than recognized. For example, the proposed mechanism for VNO-mediated tropotaxis in squamates is probably analogous to the taste bud-laden barbels of catfish or the peculiar cranial morphology of hammerhead sharks which may use taste and nasal olfaction, respectively, in a similar manner (41).

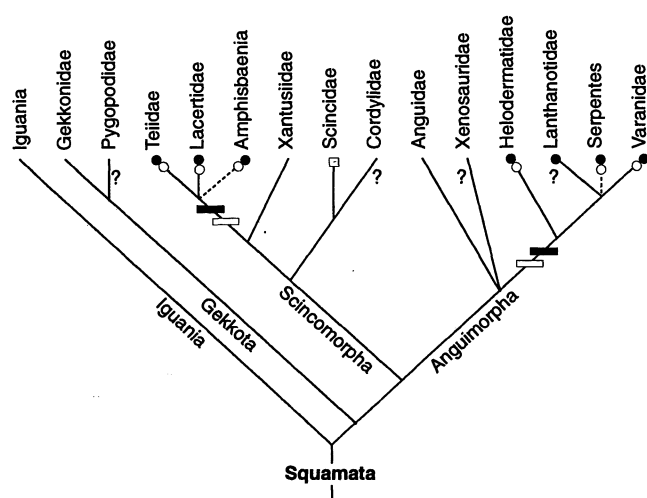
Evolutionary Integration

A trail-following function for forked tongues in squamates is compelling because of its explanatory power at several hierarchical levels. It provides an overarching theme for many disparate observations of theory, tongue anatomy, tongue function, sensory anatomy, neuroanatomy, behavior, and ecology. It clarifies previous attempts at generalization that assumed a connection between a forked tongue and vomeronasal sensitivity (7, 14, 15), despite the fact that vomerolfaction is highly developed in some iguanians, gekkotans, and scincids with only notched or slightly bifid tongues (5, 39, 42). By relating tongue tip form to the sampling phase of tongue flicking and decoupling it from the delivery phase (and therefore overall sensitivity of the VNO), these observations are reconciled. This study highlights the importance of organismal-level phenomena underlying macroevolutionary patterns and reminds us that organisms are integrated wholes whose atomized parts are frequently related in unforeseen ways.

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Fig. 3. A cladistic phylogeny of Squamata (34). Taxa with forked tongues (TFS > 1; Table 1) are indicated with black circles. Black horizontal bars show the most likely (most parsimonious) points of evolutionary origin for forked tongues. Forked tongues have evolved at least twice, at most four times, depending on the placement of snakes and amphisbaenians in the phylogeny (dotted lines indicate the tentative nature of their positions). Open circles indicate wide-foraging taxa (FMS > 0.5; Table 1). The open square indicates that scincid foraging might be qualitatively different from other wide foragers (35). Open horizontal bars show the most likely points of origin for wide-foraging behavior, which is tightly correlated with the presence of forked tongues. Question marks indicate taxa for which an FMS could not be calculated.



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