

Of tongues and noses: chemoreception in lizards and snakes

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Anyone who has watched a snake for any length of time knows of its unusual propensity to protrude its tongue and flick it about. Lizards do something similar (Fig. 1). Knowledge of squamate tongue-flicks dates back to the time of ancient Greece and a variety of functions were proposed (e.g. stinger, nose cleaner, fly catcher). By the turn of the century, most scientists agreed that these delicate lingual ballets were tactile in nature, providing lizards and snakes with a sense of fine touch¹. However plausible, this explanation succumbed to the elegant experiments of several German and North American workers in the 1920s and 1930s, who demonstrated a connection between tongue-flicking and stimulation of chemosensory organs in the snout above the palate called the Jacobson's, or vomeronasal organs (VNO)² (see Box 1). The surprising role of the squamate tongue in chemoreception was thus established.

Curiously, the novel linkage of the tongue and the VNO in squamate reptiles – the vomeronasal system (VNS) – is not a substitute for, but rather a complement to, the usual set of vertebrate chemical senses, including, in most cases, well-developed nasal olfactory (NOS) and gustatory systems^{3,4} (Box 1). We still know little about how these senses interact (see below), but the depth and breadth of our knowledge of squamate chemical senses has mushroomed since Burghardt's pivotal 1970 synthesis², recently culminating in two important reviews^{3,5} and an international conference⁶. What is clearly established is the diversity of functions and behaviors in which the chemical senses play a critical role, and the overall importance of the chemical senses in the ecology of squamate reptiles. Chemoreception is known to mediate prey choice, prey location, foraging behavior, self and individual recognition, kin recognition, mate choice, mate location, shelter location, den location, trail-following, aggregation, predator identification, exploratory behavior, defensive behavior, courtship behavior, copulatory behavior and virtually all other aspects of social behavior in some, if not most, lineages^{2,3,5,6}. Given the fundamental nature of the chemical senses in the biology of squamate reptiles, it is no surprise that they are increasingly seen as central to answering ultimate questions of broader biological significance. Here, I consider six broadly construed and overlapping topics in squamate chemoreception that are currently receiving attention and which ought to receive more.

Sensory integration

There are two issues of sensory integration in squamates. The first concerns the three chemical senses and

Lizards and snakes inhabit a world so richly textured in chemical information that, as primates, we can only imagine it. Subtle nuances of chemical shading underlie nearly every fundamental activity of their lives, from finding food to finding mates. Recent work examines the nature of these chemical messages, mechanisms for their perception, the interplay of the chemical senses in the sociobiology of the group, and patterns of chemosensory evolution. Emerging is a new sense of lizard and snake behavioral complexity that belies the common notion of these animals as simple automata and points to a surprising capacity for plasticity and learning.

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the functional domain of each⁷. The second concerns how these are integrated with other sensory systems, including visual, auditory, tactile and thermal, to mediate specific behaviors.

Functional delineation of the chemical senses has proceeded slowly, probably because it requires invasive techniques and careful controls. Most convincing are a series of studies by Halpern and her colleagues in which the VNS and the NOS of garter snakes (*Thamnophis*) were separately blocked³. These studies show that, in advanced snakes, a functional VNS is critical to courtship and mating, prey attack and feeding, and aggregation. However, snakes are vomeronasal specialists and may not be typical of squamates as a whole⁸. Recent

work on two lizard species, nevertheless, confirms the precedence of vomerolfaction over olfaction and gustation (at least for feeding) in these more-generalized forms^{9,10}, tending to corroborate the classic notion of olfaction as a secondary sense that serves to trigger tongue-flicking and the VNS (the Cowles and Phelan hypothesis)¹¹. Still, this hypothesis has rarely been tested directly and circumstantial evidence indicates the dominance of olfaction in certain behaviors in some groups⁸. Furthermore, gustation remains wholly unexplored; we can therefore expect greater diversity in degree of VNS predominance than presently revealed.

Second, it has become clear that non-chemosensory systems interact with the chemical senses in complex and unpredictable ways. This complexity was hinted at by the early experimental work of Noble and his colleagues² and is especially clear in well-studied behaviors, such as the rattlesnake (*Crotalus*) strike. Visual and thermal cues override the VNS in eliciting the strike, but chemical signals predominate in pre- and poststrike behavior^{12,13}. In contrast, visual cues are insufficient to elicit a strike in some non-venomous species¹⁴. Lineage effects must be considered before generalizations are made (below).

Visual cues, including ultraviolet, are used by some lizards to locate sources of chemical signal for further investigation^{15,16}. Ultraviolet reflectance may be an important component of display behavior, particularly in species with reduced chemosensory sensitivity¹⁷. A complex interaction of vision (aposomatic coloration) and chemoreception promotes learned avoidance of unpalatable prey in garter snakes¹⁸. Likewise, visual and chemical signals from adult male iguanas (*Iguana iguana*) are mutually reinforcing in their physiological and behavioral effects on growing juvenile males¹⁹.

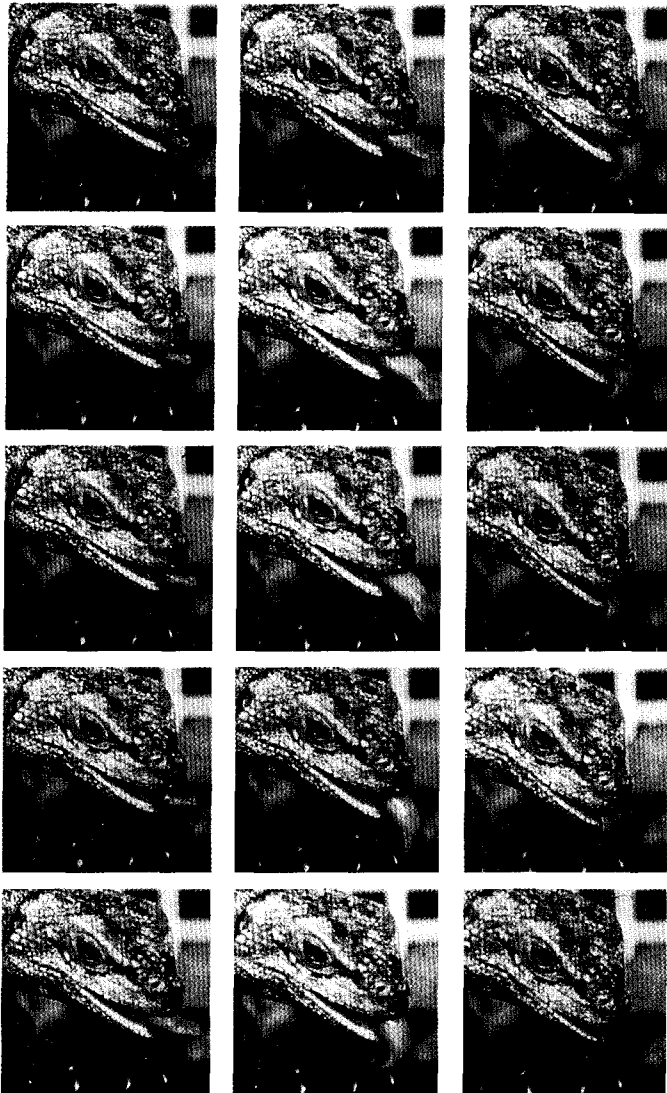


Fig. 1. A tongue-flick in a generalized squamate (Iguania, Iguanidae, *Sauromalus obesus*). Consecutive high-speed cine frames taken at 200 frames per second (5 ms between frames, total tongue-flick time = 0.075 s). Typically the tip of the tongue moves upward, then sweeps downward and curls as it is rapidly retracted. In most cases, the tongue tip contacts the substrate, or an object, but some tongue-flicks (including the one shown) sample the air, alone. In snakes and some lizard species, there can be multiple oscillations of the tongue before retraction. Kinematics of tongue-flicking vary among taxa²⁷.

Field studies have exploited the easily observed and quantified behavior of tongue-flicking to examine the actual context of putative VNS function in nature, documenting its ubiquity²⁰. These observations generally confirm laboratory findings indicating the role of chemoreception in most social and feeding behaviors. Particularly exciting are recent studies that combine observation with radiotelemetry and experimental intervention, such as nerve lesions, which selectively block either the VNS or NOS^{13,21}. These studies show a greater role for non-chemosensory systems than predicted by laboratory studies in behaviors such as prey attack and shelter location. They also indicate an unanticipated ability to compensate for chemosensory deficits (see below), at least in snakes. The need for further consideration of sensory integration at all levels and in many other lineages besides snakes is indicated.

Underlying these examples of complex integration is the central nervous system connectivity that makes it possible.

Recent work points to the amygdaloid formation, a group of nuclei at the base of the cerebrum in the squamate brain, as a major center of integration for the nasal chemical senses (VNS and NOS), and of these with other sensory systems and with motor output^{22,23}.

Functional morphology of the tongue–vomeronasal system

Few studies have considered the mechanistic basis of VNS function in squamates. Indeed, only two areas have received any attention at all. These are the functional morphology of tongue-flicking, and mechanisms for chemical delivery to the VNO.

The tongue is a complex, muscular structure that is astonishingly variable both superficially and histologically²⁴ (Fig. 2). It contains muscle fibers that originate and insert entirely within the tongue, and others that originate from skeletal elements of the hyobranchial apparatus (a skeletal framework that supports the tongue and throat musculature in most tetrapod vertebrates and which is derived from the ancestral gill skeleton) and the mandible. In most species, the muscular body of the tongue is supported by an anteromedial rod of the hyobranchial apparatus, but in snakes and some lizards it is free-floating. Its complex musculature and lack of hard, skeletal support give the tongue unique biomechanical properties. Such organs have been called ‘muscular hydrostats’ because they rely on muscle contraction and the incompressibility of cellular fluid in a constant volume structure to effect movement²⁵. Most tongue-flicking demonstrably involves such hydrostatic elongation rather than whole-tongue movement, and many derived features of the scleroglossan tongue reflect specialization of this mechanism for chemoreception²⁶.

Bels *et al.*²⁷ recently reviewed the functional morphology of squamate hyolingual movements, including tongue-flicking. They showed considerable diversity in tongue-flick kinematics, the evolutionary and functional bases of which remain poorly understood. Owing to hydrostatic elongation, chemosensory tongue protrusion is decoupled from hyobranchial movement, although the generality of this phenomenon remains to be tested. The precise mechanism of chemical pick-up by the tongue remains mysterious, but microscopic pores and facets on the tongue-tip surface are implicated²⁸. The deeply forked tongue of snakes and some lizards is used as a chemosensory edge-detector primarily to follow pheromone trails of prey and mates^{29,30}.

Young³¹ reviewed hypotheses for the mechanism by which chemicals are delivered into the VNO following a tongue-flick in snakes, and suggested that suction draws odorants into the VNO lumen. He speculated that dorsal movement of the mushroom body (see Box 1) collapses the lumen, which then expands by elastic recoil, creating, first, a positive pressure to flush the lumen and then a negative pressure to fill it. The precise effector of mushroom-body movement and luminal compression remains more controversial. Young argued for dorsal movement of the sublingual plicae (Box 1) caused by intermandibularis musculature, which would place pressure on the palate directly beneath the VNO. If the sublingual plicae are part of this mechanism, a comparative study is appropriate because the morphology of the sublingual plicae varies tremendously and in one lineage (Gekkota) they are lacking entirely²⁴. Gaping³² and ‘lip-licking’³³ also have been suggested as VNO ‘flushing’ mechanisms, but these behaviors are only intermittent and could not account for odorant delivery following individual tongue-flicks. Rather, they may indicate

occasional, deep VNO clearing that serves to 'reset' the system for the next round of tongue-flicking. 'Lip-licking', for example, occurs after completion of a feeding bout and might prepare the animal for the next foraging/feeding sequence.

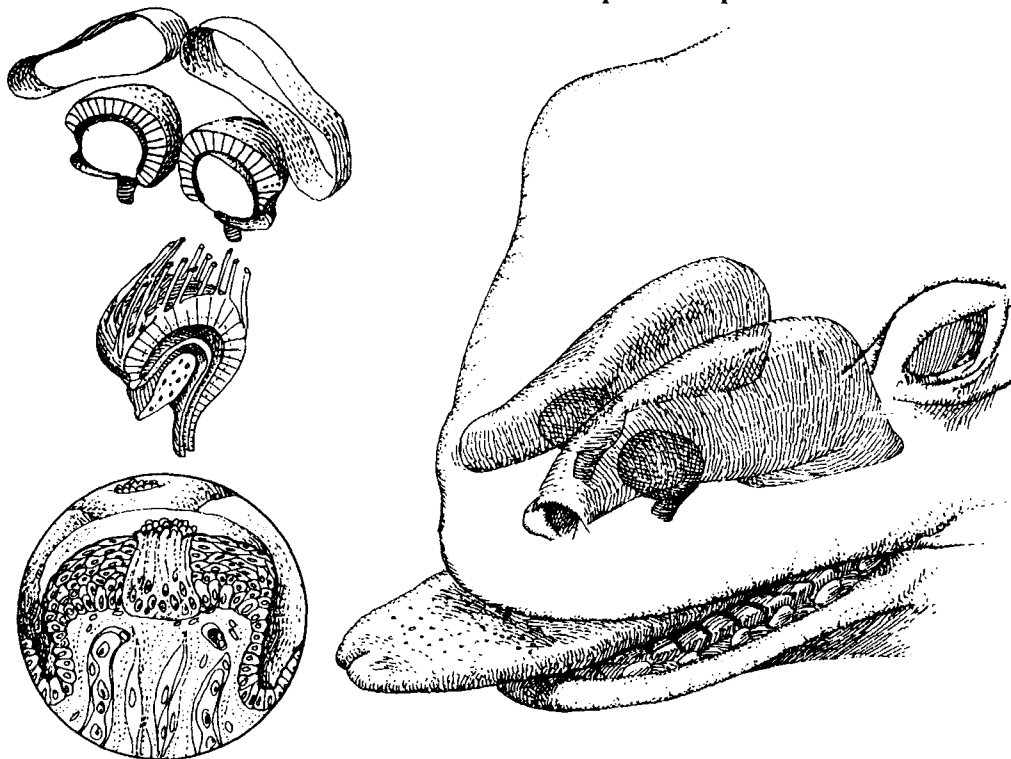
Nature of the chemical messages

Our knowledge of specific squamate pheromones is poor. However, mounting evidence points to integumentary lipids as a major source^{5,34,35}. Lipids are either broadly distributed in the skin or are restricted to secretion products of localized glands, such as the femoral and pre-cloacal glands of many lizards and amphisbaenians^{36,37}, or the cloacal glands of some³⁸. Molecular composition of glandular secretions can vary individually, seasonally and environmentally^{34,36} and therefore may be of sociobiological significance (see below). Femoral gland secretions of iguanas contain both a lipid and a protein fraction³⁶. These vary in volatility and, possibly, information content³⁹ (see below).

Sources of allomones (interspecific chemical messages) may be more variable than for pheromones. Integumentary lipids are, again, one likely source. Blood⁴⁰ and integumentary cues⁴¹ of rodent prey stimulate chemosensory behavior in rattlesnakes, and proteinaceous secretions of earthworms and frogs (natural prey items) stimulate the VNS of garter snakes^{42,43}.

The nature of a particular chemical message will determine the specific chemosensory system used. Messages potentially available to the gustatory system are chemically diverse, but probably limited to those brought into the mouth or sampled by the tongue directly⁴. There are no physiological data on gustatory function in squamates, so inferences must be drawn from the literature on other vertebrate groups. Volatile chemicals, on the other hand, diffuse through the air and will therefore be available to the NOS through nasal inspiration. Tongue-flicks directed into the air (e.g. Fig. 1) are thought to be necessary for such volatiles to reach the VNO. Conversely, non-volatile chemical signals can be sampled by direct lingual contact during tongue-flicking and sensed by the VNS without NOS stimulation⁴⁴. The temporal and spatial dispersion of volatile chemical signals depends on many factors, but when

Box 1. The chemical senses in squamate reptiles



There are at least three chemosensory systems available to squamate reptiles – illustrated here in a generalized lizard. Two nasal chemical senses reside within the snout³, including the **nasal olfactory system (NOS)** (often called the main olfactory system, or MOS) and the **vomerolateral system (VNS)**. The NOS is mediated by olfactory sensory epithelia within the paired nasal cavities, and the VNS is mediated by vomeronasal sensory epithelia within the paired **vomerolateral organs (VNO)**. The relationship between the nasal cavities and the VNO is shown in the right figure and in transverse section, top left. Air is inspired into the nasal cavities through the external nares (nostrils), exiting into the pharynx through the internal nares of the posterior palate. NOS sensory cells project via the **olfactory nerve** to the **main olfactory bulb** of the brain.

The VNO initially develops as a nasal diverticulum, but becomes isolated from the nasal cavity in squamates. Each organ lies ventromedial to the adjacent nasal cavity and forms a sphere with its anteromedial face invaginated by a cartilaginous structure called the **mushroom body** (shown in section, middle left). The lumen opens via a narrow **vomerolateral duct** directly to the oral cavity through a tiny opening in the palate, the **vomerolateral fenestra**, anterior to the internal nares. The thickened sensory epithelium lies dorsally and its nerve fibers project via the **accessory olfactory nerve** to the **accessory olfactory bulb**. Stimulus particles are delivered to the vomeronasal fenestrae during tongue-flicking (Fig. 1), either by the tongue directly, or by elevation and apposition of the **sublingual plicae** after being wiped by the tongue. The plicae (seen as ridges beneath the tongue in the right figure) are elevations of the mouth floor containing the sublingual salivary glands²⁴.

Many tetrapod vertebrates have a VNS, including amphibians and several mammalian lineages⁴⁸, but it is particularly well-developed in squamates where it is associated with the derived behavior of tongue-flicking. NOS function is referred to as **olfaction** (*sensu stricto*) and VNS function as **vomerolateral**⁵⁴, although some workers have used olfaction to mean both.

Taste, or **gustation**, mediated by lingual and oral **taste buds**, constitutes a third chemosensory system⁴. Taste buds (shown in the microscopic section, lower left) reach high densities in some species and are found primarily on papillae of the tongue tip. They are innervated by trigeminal and glossopharyngeal cranial nerves. It is unknown if other putative cranial nerve chemosensory systems (e.g. *nervus terminalis*) function in squamates. *Illustration by George Schwenk.*

there is air movement, volatiles should move through the environment faster and farther than non-volatiles and will therefore be sensible by the NOS and VNS at greater distances from the signal source.

Given the observations above, it is generally argued that the squamate tongue-vomerolateral system evolved to sample less-volatile chemicals than sampled by the NOS^{3,5}. This argument is complicated somewhat by the apparent redundancy of the VNS and NOS in sampling airborne volatiles. Alberts and Werner³⁹ have argued that air-flicks (and VNS stimulation) alert iguanas to the presence of a volatile lipid component of femoral gland secretions; this component indicates the presence of conspecifics but does not identify individuals. Localized secretion deposits could then be investigated by tongue-touches, which sample a non-volatile protein fraction of the secretion and provide information about individual identity.

Overall, it is probably useful to think of squamate chemosensory systems as a nested hierarchy of function and information: the NOS initially samples a volatile component of a chemical message, triggering the VNS (the Cowles and Phelan hypothesis, above). Air-flicks stimulate the VNS for finer-scale discrimination of the same or different volatile component; VNS processing probably increases information content of the chemical message relative to the NOS and determines whether additional investigation is necessary. Tongue-touches directed at the chemical source (once localized by means of klinotaxis or tropotaxis³⁰) detect non-volatile components for VNS processing and additional information about the message source, possibly including species identity, individual identity, social status, reproductive status, etc. (see below). Finally, if this is a predatory sequence, prey capture results in gustatory assessment of food palatability that might not have been communicated during tongue-flicking. Food is often rejected at this point. Vision (or thermal cues in some species) might substitute for or complement initial chemosensory (NOS and/or VNS) triggering of subsequent behavior, or might act synergistically with any chemical sense during particular behaviors.

Sociobiology and conservation

Many squamate species are capable of very fine-grained chemosensory discriminations, indeed, not only of food types⁴⁵, but of self, kin, sex and species^{3,5,34,36,38,45}. Such discriminatory ability is potentially very important in structuring communities and social hierarchies of squamate reptiles. For example, femoral gland activity (a source of lizard pheromones; see above) and androgen levels are correlated with dominance status in male iguanas³⁶, and adult male

chemical cues increase stress (elevated corticosteroid levels) in juveniles¹⁹. In conjunction with visual cues, such chemical signals also suppress growth and assertion displays in the juveniles¹⁹. These findings strongly implicate chemoreception as an arbiter of social structure in iguanas and other species^{19,36,39}.

The role of pheromones and the VNS in nearly every aspect of reproduction in squamates is now well established^{2,3,5,34}. Advanced snakes, in particular, seem to have a specialized tongue–vomeronasal system for purposes of reproduction³⁰. Non-volatile, integumentary lipids contain pheromones that are the target of tongue-flicking during species identification, conspecific trail-following and courtship leading to copulation. These fluctuate with skin-shed state and with season, and are correlated with hormonal state^{5,34}.

Taken together, these findings strongly indicate the necessity of considering the chemical ecology of rare species in captive propagation programs. Simple oversights, such as overcrowding, or the inadvertent exposure of hatchlings to chemical and/or visual cues of dominant males, could have a detrimental effect on growth, development and reproduction. Similarly, most components of feeding behavior are mediated by chemoreception, so this aspect of the chemical environment also could affect the health and reproductive success of captive species⁴⁶.

Evolutionary patterns

Although there is a dearth of comparative, evolutionary studies in squamate chemoreception²⁶, generalizations are beginning to emerge, the most important of which is that generalizations may not always be possible! Burghardt⁴⁷ has found unexpected inter- and sub-specific variation in a number of chemosensory parameters, so it will be difficult to generalize certain findings to higher taxa (e.g. 'snakes'). Proper attention to cladistic relationships and level of analysis is indicated.

Nonetheless, certain broad patterns are evident. Eisthen^{48,49} has considered the NOS and VNS in the context of vertebrate phylogeny and has clarified issues surrounding the origin and distribution of the VNS in tetrapods. Notably, she suggests that the VNS is not a terrestrial adaptation, as is usually assumed, but probably arose in aquatic ancestors of tetrapods. As such, the function of the VNS in sensing high molecular weight, non-volatile compounds must be seen as derived in tetrapods, including squamates. In Squamata, dominance of the VNS and its unique mechanism of lingual stimulation seem to be evolutionarily linked to the origin of a direct VNO–oral connection in a common ancestor²⁶ (Box 2). We lack direct evidence of this remarkable morphological transformation, but ontogenetic studies might eventually provide clues⁵⁰. Within squamates, individual clades express unique combinations of traits; some are considered in Box 2.

Various aspects of squamate chemosensory evolution have been linked to foraging mode. Wide- (as opposed to sit-and-wait) foraging is correlated with a postbite elevation in tongue-flicking rate (PETF), chemosensory prey discrimination⁴⁵, and the evolution of forked tongues³⁰.

Combined use of the hyolingual system for both chemoreception and feeding (and other behaviors) in most squamate lineages provides an interesting evolutionary dynamic^{24,26,27}. The necessity of lingual prey capture has constrained tongue (and therefore chemosensory) evolution in Iguania, but the origin of a novel prehension mechanism (use of the jaws) in Scleroglossa seems to have allowed diversification of the tongue and the VNS in this speciose clade²⁶.

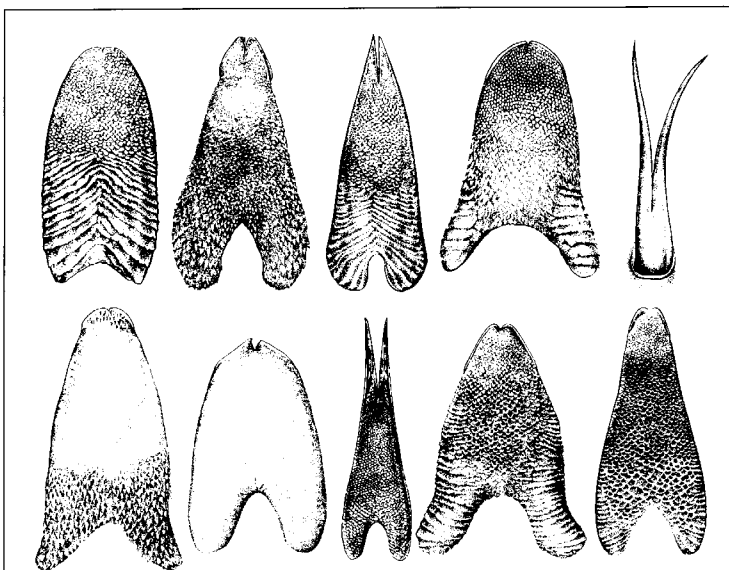
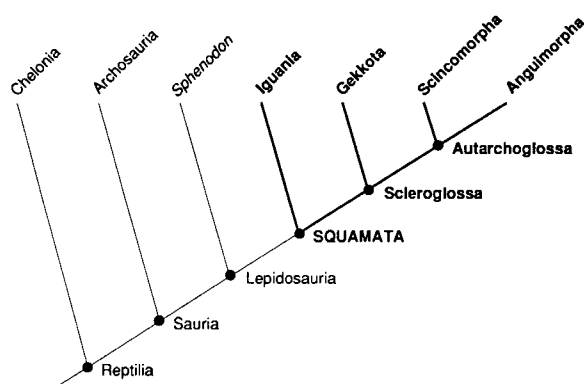


Fig. 2. Variation in the form of the squamate tongue. Tongues are shown in dorsal view, anterior at top. They differ in shape, surface morphology and tongue-tip form. Not shown is the equally variable microscopic anatomy of surface papillae and muscle fiber architecture²⁴. Most scleroglossans have shortened and smoothed the papillae of the foretongue, decreased its diameter laterally, dorsoventrally, or both, and have otherwise modified the tongue for hydrostatic elongation and chemosensory protrusion^{25,26}. From left to right, top to bottom: *Xantusia* (Xantusiidae, Scincomorpha); *Abronia* (Anguinae, Anguimorpha); *Podarcis* (Lacertidae, Scincomorpha); *Coleonyx* (Gekkonidae, Gekkota); *Varanus* (Varanidae, Anguimorpha); *Gonocephalus* (Agaminae, Iguania); *Crotaphytus* (Crotaphytidae, Iguania); *Cnemidophorus* (Teiidae, Scincomorpha); *Cordylus* (Cordylidae, Scincomorpha); *Dasia* (Scincidae, Scincomorpha). Illustration by Mary Jane Spring, based on unpublished photographs taken by K.S.

Box 2. Squamate phylogeny



Shown is a cladogram representing the major lineages of squamate reptiles (in bold) and the relationship of squamates to other reptiles. Snakes are probably members of the anguimorphan clade, and amphisbaenians (a mostly limbless, fossorial group) are probably scincocomorphans (references in Ref. 30). The sister group of Squamata is the tuatara, *Sphenodon*, sole surviving genus (two spp.) of the once speciose Rhynchocephalia. Sister group of Lepidosauria is Archosauria, comprising the living crocodilians and birds, the extinct dinosaurs, and other diapsid groups. Finally, the sister group of these is the Chelonia, or turtles. Reptiles, mammals and amphibians together constitute the Tetrapoda, or terrestrial vertebrates.

Within Squamata, certain lineage-specific combinations of chemosensory traits characterize individual clades. For example: (1) tongue-flicking, a bifurcated tongue tip, a VNO mushroom body, a direct VNO-oral connection, and modifications of the tongue associated with protrusion, are synapomorphies of Squamata²⁶; (2) phrynosomatid iguanians have very high taste-bud densities⁴; (3) iguanid iguanians have a well-developed VNS³⁶ that may reflect the primitive squamate condition²⁶; (4) chamaeleonid iguanians have secondarily reduced the chemical senses and true chameleons are almost completely visual²⁶; (5) evolution of a new prey capture system allowed scleroglossans to specialize the tongue-mediated VNS^{24,26}; (6) gekkotans have a particularly well-developed NOS⁸; (7) scincocomorphans are very diverse, but all groups seem to be highly chemosensory, relying primarily on the VNS^{26,45}; (8) anguimorphans have specialized VNS function^{26,45}, with snakes the most extreme expression of this trend^{2,3,5,8,26,30,45}; (9) forked tongues have evolved at least twice (once in Scincomorpha, once in Anguimorpha), but possibly four times, and are always associated with chemical trail-following and wide-foraging³⁰.

Final comments: behavioral complexity and human attitudes

Although Linnaeus' feelings about amphibians and reptiles ('These foul and loathsome creatures...') are no longer expressed in the scientific literature, they are subtly reflected in the pervasive sense that reptiles are little more than hard-wired automatons, incapable of higher cognition or behavioral plasticity (see Burghardt⁵¹ for an interesting explication). This perception has been useful, on the one hand, because it promotes the use of reptiles as 'model organisms' uncomplicated, unlike mammals, by the confounding effects of experience and learning. On the other hand, it is likely that this perception causes even those of us who work with reptiles to underestimate their abilities or, for lack of a better word, sophistication. Several very recent studies of snakes argue for a revised outlook. Graves *et al.*²¹ showed that, despite laboratory evidence indicating the necessity of a functional VNS for preferred shelter location, free-ranging garter snakes deprived of this sense could return to shelters perfectly well. This finding suggests that, far from being crippled by loss of their most important sensory mode, snakes were able to compensate behaviorally. Second, Burghardt⁵² and Terrick *et al.*¹⁸ have demonstrated a surprising ability of garter

snakes to learn from experience. Previous exposure to prey odors in naive neonates influences their subsequent chemosensory response to prey odor presentations⁵², and adult garter snakes used aposomatic coloration to enhance chemosensory learning and future avoidance of unpalatable prey¹⁸. Finally, results summarized by Chiszar *et al.*⁵³ indicate that, at the instant of the strike, rattlesnakes learn a chemosensory signature of an individual mouse, whose scent trail they prefer over others. Controls indicate that this preference is independent of envenomation and stems from chemical cues gleaned from the prey tissues themselves.

Taken together, these findings suggest that snakes, and probably other squamates as well, are capable of exceptionally subtle behavioral shifts and modulations that testify not only to their inherent complexity and sophistication, but to their ability to survive through behavioral plasticity, a characteristic usually reserved for endotherms. If nothing else, consideration of the chemical senses in lizards and snakes should leave us with new found respect for these remarkable animals.

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Something borrowed, something green: lateral transfer of chloroplasts by secondary endosymbiosis

Geoff McFadden and Paul Gilson

The obvious dichotomy between plants and animals has always been an attractive point at which to start ordering living things into categories. Indeed, the old question – ‘Animal, vegetable or mineral?’ – reinforces the concept that life forms can fit into either of two categories. Biologists of course recognize that a plant/animal dichotomy is untenable at the level of the protists, many of which are at once photosynthetic, mobile and phagotrophic. Yet even in protistology, there has been a tendency to assemble the organisms into groups based on the presence or absence of a chloroplast. Chloroplast-containing organisms were collectively known as the algae, but this is undoubtedly an artificial group, not least because recent findings reveal that certain ‘algae’ are technically protozoans and obtained their chloroplasts by taking them from ‘real’ algae.

When early life forms began photosynthesizing, the planet embarked on a new era¹. No longer dependent on scavenging organic nutrients from the environment, the photosynthesizers proliferated and ultimately became a

New molecular data confirm what electron microscopists long suspected – fusion of two different eukaryotic cells into a single more-complex cell created novel groups of protists. By engulfing an algal cell and putting it to work as a solar-powered food factory, heterotrophic protozoans became autotrophic. Drastically reduced, the engulfed cell now exists as an organelle in the host cell. Such blending of lineages was perhaps a driving force in early eukaryotic diversification.

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food supply for heterotrophs¹. Oxygen, the byproduct of a predominant form of photosynthesis, gradually accumulated in the atmosphere and provided a radiation shield that was probably essential to the colonization of the land. Eventually this oxygen began to be used as an electron acceptor for the oxidation of food molecules during aerobic respiration allowing vast increases in metabolic efficiency. Somewhere during these events, the eukaryotes arose. Apparently bereft of photosynthesis, the early eukaryotes probably made their living as phagotrophs. Eventually, one or

more of these eukaryotic lineages entered into symbiotic partnerships with photosynthetic prokaryotes and the chloroplast was born^{2,3}. This partnership, in which a photosynthetic prokaryote was engulfed and retained by a phagotrophic eukaryote, can be termed a ‘primary endosymbiosis’. The endosymbiont was gradually reduced, and relinquished its autonomy, including a large part of its genome, to the eukaryote host^{2,3}.

Plants and the green algae are the product of this primary endosymbiotic partnership, and the double membrane