THE SERPENT'S TONGUE

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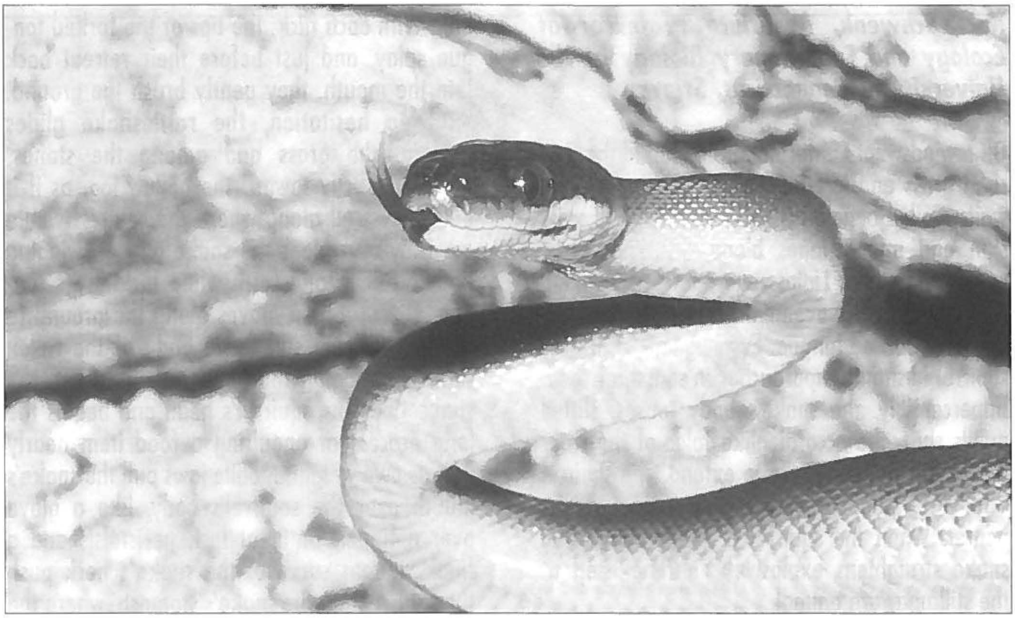
On a windswept California hillside, amid the parched grass and live oak, a western rattlesnake waits. Coiled beneath a rock overhang, its scaly skin and muted tones blend with the grass, earth, and stone. Lidless eyes stare, transfixed; the snake's only movement is the occasional flicker of its forked tongue. Ever vigilant, a ground squirrel hesitantly approaches in search of food. Imperceptibly, the snake's body tenses, slitted pupils shift, the accordionlike folds of the front third of its body prepare to extend. The squirrel - moving, stopping, moving, stopping - draws nearer. When the squirrel is within reach, the snake straightens explosively, hurling itself at the still unaware animal.

As it traverses the short distance between itself and the prey, the snake opens its mouth and erects its formidable fangs. Too late, the squirrel sees the snake and stares death in the mouth. It is thrown backward by the impact of the snake's head, impaled by the fangs, and poisoned deep within its core. The rattlesnake releases the squirrel and, after the concentrated fury of its attack, seems strangely unconcerned as the squirrel runs off in panicked flight. The squirrel soon slows, for each bound has pumped the poison farther and farther through its system. A witches' brew of enzymes and other compounds, the venom has already begun the process of digestion within the body of the squirrel. Now, fifty yards away, the doomed animal seeks refuge within the hollow of a log, where its labored breathing soon ceases. Slowly at first, the snake moves off. Its tongue extends and retracts constantly, its oscillations a blur. With each flick, the tips of the forked tongue splay, and just before their retreat back into the mouth. they gently brush the ground. With no hesitation, the rattlesnake glides through the grass and among the stones, moving directly toward the hollow log, as if it had known all along where the squirrel would go. Only once does the snake pause, swinging its head back and forth while flicking its tongue. Then it again moves along the ground to the log and the still warm body of the fallen squirrel. Nudging the body with its snout, the snake finds the squirrel's head and begins the long process of engulfing a food item nearly half its own weight. Mobile jaws pull the snake's mouth over the squirrel's body, like a glove over a finger, until, at last, peristalsis and a final, sinuous curve of the snake's neck push the squirrel into the snake's stomach, where the process of digestion will continue. Activity of the venom insures that the squirrel will be digested before it can putrefy and poison the snake. Safe within the log, its modest energy demands satisfied, the snake will not hunt again for several weeks or months.

This drama is enacted daily, in one form or another, around the world by almost 3.000 species of snakes. And while we may be predisposed toward sympathy with our hapless mammalian cousin, we must admire, however grudgingly, a snake's amazing ability to locate, identify, dispatch, and then relocate its furry victim. Pitted against the prey are the snakes' diverse sensory systems: acute vision in most species and color vision in some; hearing that is particularly sensitive to low-frequency sounds, such as groundborne vibrations; the chemical sense of smell; and in some species, such as rattlesnakes and large constrictors,



Liasis fuscus. Defensive posture with tongue flicking. Foto by Brian Barnett

heat receptors. However, by far the most important and exquisitely sensitive sensory mode employed by all snakes is another and less familiar chemical sense akin to smell, known as the vomeronasal system. Snakes inhabit a world richly textured in chemical cues that guide the animals in the most fundamental activities of life, from finding food to locating potential mates.

At center stage in this drama is a remarkable little organ as mysterious as it is feared - the serpent's forked tongue, a symbol of malevolence and deceit. Images of forked tongues appear in ancient pictographic scripts of Mesopotamia and China, petroglyphs of East Africa, and the religious iconography of cultures as diverse as the Aztecs, the Siberian Altai, and the Sumerians of Babylonia. Early naturalists, such as Aristotle, discussed the forked ophidian tongue. Indeed, snakes and their forked tongues are so deeply embedded in our collective psyche that I was surprised to learn that an obvious question had not been fully answered - why are snakes' tongues forked? Such questions are the bread and butter of evolutionary morphologists like me, and as someone who specializes (I hesitate to admit) in the anatomy, function and evolution of tongues, I thought that I should know the answer. In finding it, I learned not only about snakes but also something about the nature of scientific progress.

Unlike the rather obscure bits of anatomy that I usually ponder, the conspicuousness of snake tongues has made them a source of speculation over the years. Recorded inquiry into their function begins as for most things scientific, with Aristotle, who reasoned from the basis of his

own tongue that the fork provided snakes 'a twofold pleasure from savors, their gustatory sensation being as it were doubled.' Hodierna, a seventeenth-century Italian naturalist, thought that snakes used the tips of the tongue 'for picking the dirt out of their noses, which would be apt else to stuff them, since they are always groveling on the ground, or in caverns of the earth.' Many are convinced that the tongue is a stinger, particularly in venomous species, and others claim to have witnessed the capture of flies between the tongue tips.

The reigning scientific view during the firstpart of this century was that tongue flicking and the delicately forked tongue were part of a tactile mechanism, giving snakes a sense of fine touch. Unfortunately, these colorful, and even plausible, explanations of forked tongue function can no longer be accepted. Aristotle's idea, like our sympathy for the squirrel, is based less on science than on anthropomorphism. But unlike us and even their lizard kin, snakes lack taste buds on their tongues and are singularly depauperate in gustatory pleasure. And although I appreciate the symmetry expressed in Hodierna's hypothesis (two nostrils, two tongue tips), I have spent a lot of time watching snakes, and I have never seen one with its nostrils blocked with dirt nor with its tongue in its nose. Likewise, the stinger and flycatcher ideas are without basis, and the frequent flicking of the tongue into the air, contacting neither ground nor object, belies its role as a tactile organ.

In a series of elegant experiments conducted in Germany and the United States during the 1920s and 1930s, the first scientific clues to the function of tongue flicking in snakes were revealed and led directly to new ideas on the function of the forked tongue. Experimenters showed that the key to tongue flicking is found in two tiny organs that lie side-by-side in the snake's snout just above the roof of the mouth. Named Jacobson's organs after their discoverer, they are now usually referred to as the vomeronasal organs, or VNO. These small, bulb-shaped structures develop as an offshoot of the nasal cavity, becoming isolated from it and forming separate connections to the mouth through openings in the palate.

Each VNO contains its own small patch of sensory cells. These cells have nerves that connect them to the olfactory bulb of the brain, although not to the same part of the bulb that is connected to the sensory cells of the snake's nose. What the experimenters discovered was that tongue flicks deliver chemical particles into the mouth that make their way up through the openings and into the VNO, stimulating the sensory cells. This equips snakes (and their close cousins, the lizards) with a chemical sense similar to smell, but different and distinct. Although many mammals and other vertebrates also have a VNO that they stimulate through various means, we humans are as lacking in this vomeronasal sense as snakes are in taste. Although it was established that the tongue delivered odor panicles into the mouth, the mechanism of particle transfer to the VNO remained unknown. In the 1920s, some German researchers suggested that the slender tips of the forked tongue must be inserted into the openings of the VNO, delivering scent particles directly. This hypothesis was so elegant that it was almost immediately accepted and eventually became dogma.

The only problem with the theory is that it is contradicted by the evidence. Some of the earliest experiments, performed by German workers in the 1930s, demonstrated that snakes could deliver particles to the VNO even when their tongue tips had been surgically removed. Later that same decade, German and American researchers pointed out that most lizards have only notched tongues with blunt tips, hardly capable of being inserted into the tiny openings of the VNO, yet they too flick their tongues and stimulate the VNO as effectively as snakes. Recently, Brent Graves, of Northern Michigan University, and Mimi Halpern, of the Downstate Medical Center in Brooklyn, have experimentally verified these findings.

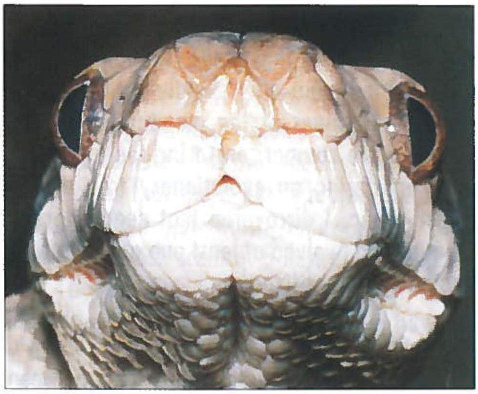
Film and X-ray studies have provided further evidence, showing that the tongue tips are not inserted into the VNO and . that - at least in snakes - pads on the floor of the mouth, and not the tongue directly, probably deliver the scent particles to the openings in the palate. As the tongue is retracted into its sheath, its tips brush along pads in the floor of the mouth. These pads are then elevated and pushed against the palate and VNO openings.

As strong as the evidence against it has been, the tongue-in-VNO explanation of forked tongues has had a significant impact on modern studies of snake and lizard chemoreception and can still be found in some textbooks. Such is the power of dogma.

A firm believer in the fruits of the unconscious mind and nonlinear thought, I was treated to one of the creative high points of my professional career one day when a colleague asked me why snakes have forked tongues. In that moment, years of miscellaneous thought on tongues and the VNO suddenly seemed to gel and the answer to his question became clear. What I realized was that the years of concentrating on how forked tongues deliver scent particles to the VNO had distracted us, like the proverbial red herring, from their true function: namely, sampling those scent particles from the air or the ground in the first place.

Like paired ears or paired eyes, a forked tongue could provide a kind of 'stereo smell' that would give snakes the ability to sense not only the presence of some chemical but also its location. If this were true, the snake would have to be able to sample scent particles from two different points (via its two tongue tips) and assess whether there was a difference in the strength of that chemical on the left side versus the right side. This ability would be particularly useful for following pheromone trails left by other animals. I ran to my office, where I set about the painstaking task of supporting or refuting my new idea.

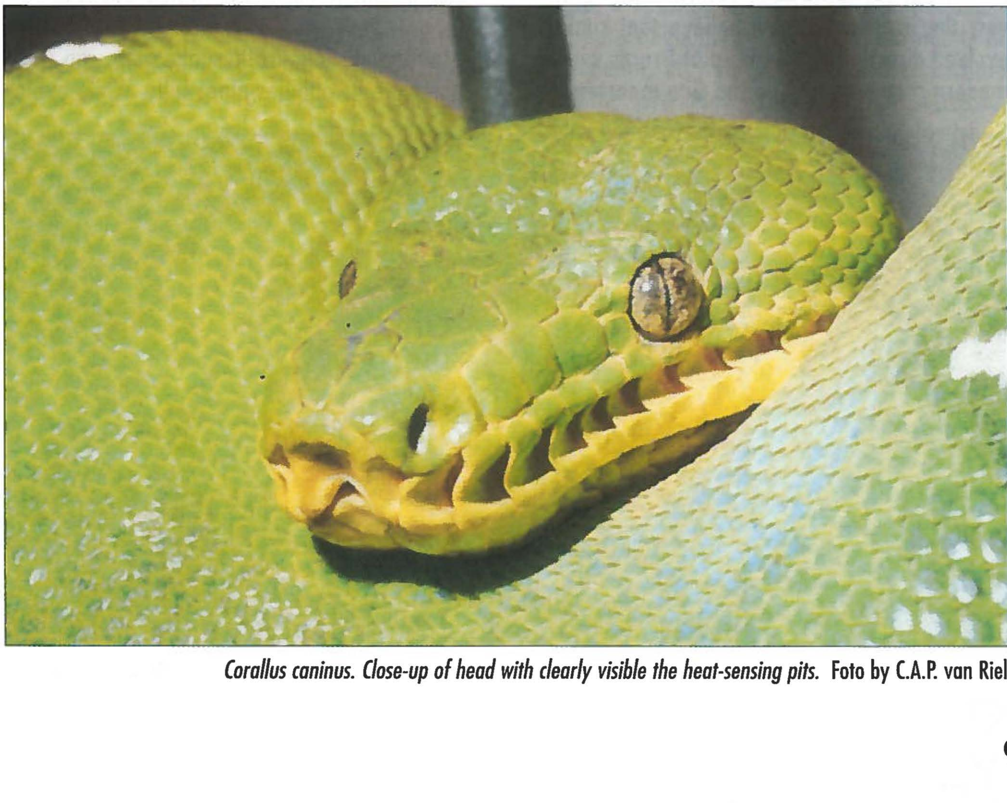
What I discovered shocked me: I was not the first to have this idea. Indeed, it had been proposed independently two times in the previous thirteen years. In the first case Walter Auffenberg, of the University of Florida (now emeritus), had intuited the theory during the course of his classic study of the Komodo dragons of Indonesia, fork-tongued lizards related to snakes. He observed the lizards' remarkable ability to follow invisible scent trails of prey animals, all the while flicking their deeply forked tongues. Similarly, Neil Ford, of the University of Texas at Tyler, had studied how male snakes follow pheromone trails left by passing females. He noted that the tips of the forked tongue would spread far apart and brush the ground before being retracted. As long as the tips stayed within the confines of the trail, the snake moved directly along it. When one tip overstep-



Morelia amethistina. Close-up of head. Mind the heat-sensing pits in the lower jaw. Foto by C.A.P. van Riel

ped the edge of the trail, the snake turned back. When both tips left the trail, the snake stopped, swung its head back and forth, and tongue flicked until it relocated the trail and resumed its travel. Both Auffenberg and Ford proposed that following scent trails was the function of the forked tongue for finding both food and mates. Mimi Halpern and her colleagues had already shown that the ability to follow scent trails is a hallmark of snake chemosensorv biology.

When I tested these ideas, I found that virtually all observations were consistent with the trail-following function of forked tongues. Indeed, the earliest experiments involving surgical removal of the forked tongue tips had shown only one behavioral deficit in the treated animals: loss ot the ability to follow trails. The brain circuitry of the the vomeronasal system in snakes is set up to provide the ability to compare chemical signal strength from left and

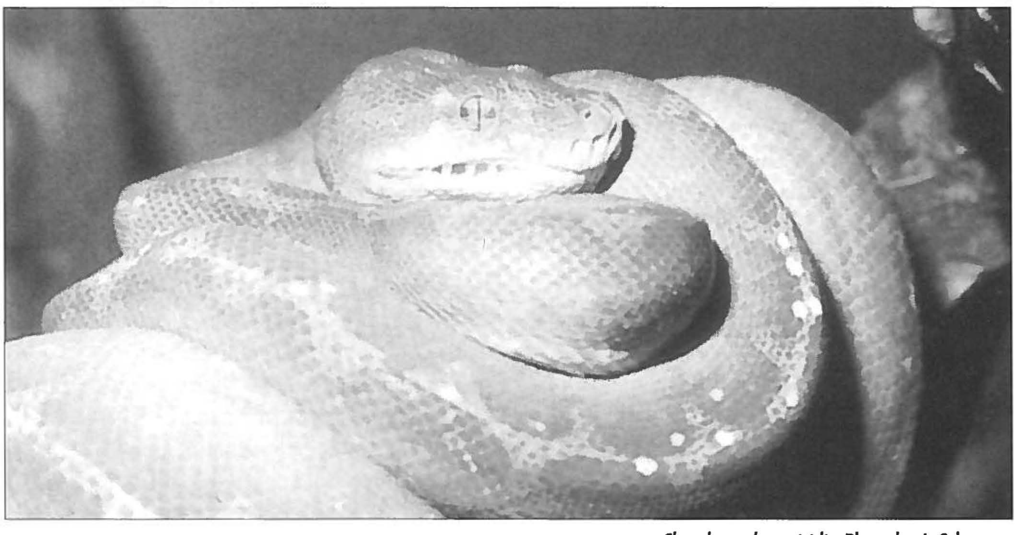


Corallus caninus. Close-up of head with clearly visible the heat-sensing pits. Foto by C.A.P. van Riel right sides. Slow-motion films revealed that both snakes and fork-tongued lizards spread their tongue tips far apart just as they touch the ground, apparently to maximize the likelihood of picking up a difference in chemical strength between sides. When access to the VNO on one side was blocked, a snake attempting to follow an odor trail turned consistently toward the strong, unblocked side - and as a result, simply made a circle.

How might this remarkable organ have evolved? Tongues are composed of soft tissue, so fossils are of little help. Comparisons among living species, however, can provide indirect clues to evolutionary history. Since all living snakes have forked tongues, little can be learned by examining them alone, so I began by comparing snakes to their closest living relatives, the lizards. We now believe that snakes evolved directly from a group of lizards whose modern members include the Gila monsters of the Southwest and the monitor lizards of the Old World. Within that group, I found that tongues ranged from only slightly forked to the snakelike tongues of the monitor lizards. By widening the comparison to include all lizards and considering an evolutionary tree of this larger group, I discovered that deeply forked tongues had evolved at least one other time, in another group of lizards.

Adding information from behavior and ecology to the analysis, I found a tight correlation between the presence of a forked tongue and the ability to follow scent trails, and that each time forked tongues evolved in lizard/snake history, so did the behavior of searching widely through the environment for food or appropriate ambush sites. Lizards that do little searching, simply waiting for food to come to them, lack forked tongues.

Returning to our rattlesnake, we can now appreciate its abilities more fully. While explo-



Chondropython viridis Photo by J. Schouten

ring its environment, the snake frequently flicks its tongue. At some point, it crosses a pathway used by small mammals and other animals. Among the many scents it detects is the odor of a female of its own species, but the rattler discerns that she is not in mating condition and therefore not worth following. It next detects the fresh scent of a desirable prey species. (Gordon Burghardt, of the University of Tennessee, has shown that most snakes have an innate ability to discriminate prey from nonprey.) Its search ended, the snake chooses a hidden spot within striking distance of the trail and awaits its next meal. The passage of a hiker and then a fence lizard elicits little interest other than a flick or two of the tongue, but the arrival of a squirrel triggers its predatory instincts. The rattlesnake's strike results from the complex interplay of visual, chemosensory, and thermal cues emanating from the squirrel. At the moment of impact and envenomation, the rattlesnake learns the scent of this individual animal, which it will then prefer over all others, as discovered by David Chiszar and his students at the University of Colorado. Hence, the snake is unconcerned about letting the squirrel go. By releasing the squirrel, it needn't fear any retaliatory bite, and it can let the squirrel's own muscle contractions and circulatory system distribute the digestive venom. Now, with the use of its forked tongue to monitor the chemical trail left by the squirrel, the snake easily tracks the animal to its final resting place within the log. There, tactile cues from the squirrel's fur direct the snake to the head for easier swallowing of so large an animal. Being ectothermic (cold-blooded), the snake needn't squander calories on generating body heat, and having eaten so large a meal, it will not have to feed again for many weeks.

These skills are applied by venomous and nonvenomous snakes. In each case the forked tongue plays an essential role. In many ways, the tongue and the tremendously sensitive vomeronasal system it serves are the essence of being a snake. The forked tongue symbolizes, not duplicity, but evolutionary success, for this marvel of engineering may have helped snakes become what they are today - one of the most successful radiations of land vertebrates alive on Earth.

First published in Natural History, no.4, 1995, 48-55 and republished in Litteratura Serpentium with the permission of the editorial staff of Natural History.