

Are geckos olfactory specialists?

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(With 2 figures in the text)

Gekkonid lizards are shown to have well-developed nasal chemical senses. It is argued that they are unique among squamates so far studied in the degree of their olfactory (as opposed to vomeronasal) development. This contention is supported by evidence from the brain, nasal capsule, tongue, and experimental studies of behaviour. Limited evidence suggests that olfaction functions in food-finding and predator detection; vomerolfaction during investigation of novel stimuli and in reproduction. The conception of gekkonids as members of a 'visual Ascalabota' is not supported by these findings. Olfactory specialization makes geckos ideal subjects for tests of the Cowles and Phelan hypothesis of olfactory function and suggests that they might be better subjects than snakes for future studies of dual olfactory form, function and evolution in a non-mammalian lineage.

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Introduction

A burgeoning literature indicates that most squamate reptiles rely heavily on chemoreception to direct the fundamental activities of feeding, shelter location, aggregation, conspecific identification, predator avoidance, mate choice and reproduction (see Burghardt, 1970, 1980; Madison, 1977; Simon, 1983; Halpern, 1983; Halpern & Kubie, 1984; papers in Duvall, Muller-Schwarze & Silverstein, 1986; and Schwenk, 1993, for overviews). To achieve these ends, squamates possess at least three anatomically distinct chemosensory systems: gustation, olfaction and vomeronasal olfaction. Gustation refers to the sense of taste mediated by receptors (taste buds) located within the oral cavity and on the tongue of most terrestrial vertebrates. Olfaction and vomeronasal olfaction represent the so-called nasal chemical senses. Olfaction *sensu stricto* is associated with stimulation of the olfactory sensory epithelium within the nasal cavity by chemical-laden air inspired through the external nares. Vomeronasal olfaction results from stimulation of a separate sensory epithelium located within the paired vomeronasal or Jacobson's organ, developmentally a

diverticulum of the nasal cavity. The vomeronasal organ is located within the snout just above the palate and is a primitive feature of tetrapod vertebrates, though it is variously reduced or lost in adults of some groups (e.g. Bertmar, 1981). In squamates the vomeronasal organ communicates directly with the oral cavity and is stimulated by chemicals brought into the mouth by the tongue through a behaviour known as tongue-flicking (e.g. Graves & Halpern, 1989). Thus, tongue-flicking is linked to vomeronasal functioning, though other factors might also induce this behaviour in some instances (e.g. Greenberg, 1985; Schwenk, 1985).

Both nasal chemical senses are sometimes referred to simply as 'olfaction', but this usage obfuscates these two anatomically and functionally distinct senses (see below). To emphasize the distinctiveness of vomeronasal function relative to nasal olfaction, Cooper & Burghardt (1990b) recently suggested use of the term 'vomeroolfaction' for the former, restricting 'olfaction' to the latter. This usage is followed in the remainder of this paper.

Of the three chemical senses available to squamates, gustation remains virtually unstudied in a functional context (Schwenk, 1985). Olfaction and vomeroolfaction have been functionally linked through what has come to be known as the 'Cowles and Phelan hypothesis'. Based on observations of rattlesnakes, Cowles & Phelan (1958) suggested that olfaction is less discriminatory than vomeroolfaction, but operates over greater distances. They further suggested that olfactory stimulation acts as a 'trigger' that initiates tongue-flicking and, therefore, vomeroolfaction. These observations were extended to include the relative volatility and molecular weight of chemicals sampled by these two systems (Burghardt, 1980; Burghardt, Goss & Schell, 1988; Schell *et al.*, 1990); olfaction responds primarily to volatiles while vomeroolfaction is sensitive to nonvolatiles, including those of high molecular weight, and may require physical contact of the tongue with the substance in most cases. Halpern (1980) noted an additional distinction: in both mammals and squamates, the olfactory epithelium is a more or less passive recipient of airborne odorants, but odorant delivery to the vomeronasal organs is by voluntary action of the animal (through a variety of mechanisms in mammals and by tongue-flicking in squamates).

Surprisingly few data have been marshalled in support of the Cowles & Phelan hypothesis, despite its widespread acceptance. Cowles & Phelan (1958), themselves, arrived at their conclusion by noting that rattlesnake heart rates increased in the presence of potential predator odours even when the mouth was taped closed and tongue-flicking prevented. Duvall (1981) observed 'rapid nasal inhalation' and decreased time to initiation of tongue-flicking in *Sceloporus occidentalis*, an iguanid lizard, when individuals were exposed to odorants. Simon & Moakley (1985) noted a similar pattern in *S. jarrovi*. Halpern, Heller & Vagvolgyi (in Halpern & Kubie, 1983) showed that snake tongue-flick rates increased in the presence of airborne prey odours.

Given the putative importance of olfaction in activating tongue-flicking and vomeroolfaction, it is surprising that few studies exist which examine explicitly the function of olfaction in squamates. Noble & Kumpf (1936) found that olfaction alone was sufficient for a teiid, *Ameiva exsul*, to locate hidden food. However, their method of removing vomeronasal input by cauterizing the vomeronasal organs is questionable, as is their experimental design. Reliable data are available only for the natricine snake genus *Thamnophis* (Kubie, Vagvolgyi & Halpern, 1978; Halpern & Frumin, 1979; Kubie & Halpern, 1979; Heller & Halpern, 1982). These studies used vomeronasal and olfactory nerve lesions followed by histological confirmation. They concluded that olfaction is not necessary for normal function in courtship, prey attack and feeding, and aggregation behaviour in garter snakes. Halpern (1983), however, urged caution in the interpretation of these results, suggesting that the controlled, laboratory context of the studies may have obscured the true nature and ecological significance of olfaction in free-ranging snakes.

Finally, one additional factor has probably mitigated against a full understanding of olfaction in squamates. In most recent studies of squamate chemosensory behaviour, there has been an *a priori* assumption of vomeronasal dominance over other chemosensory modalities. Such an assumption is a curious reversal of the historical progress of chemosensory studies in mammals, in which the vomeronasal organ was assumed to be accessory to olfaction (this was also true of earlier studies on squamates, e.g. Noble & Kumpf, 1936). It was not until these systems were found to be anatomically distinct, not only peripherally, but also in their central nervous system projections, that the concept of a 'dual olfactory system' emerged (Raisman, 1972; Scalia & Winans, 1975; see Halpern, 1980, 1987 for discussion and comparisons of squamate and mammalian systems). Thereafter, many mammalian behaviours previously thought to be mediated by olfaction were shown to be associated with vomerolfaction. In contrast, the obvious and ubiquitous nature of tongue-flicking in squamates and its early connection to vomeronasal stimulation (Kahmann, 1932) have apparently led to a parallel, but opposite, neglect of olfaction in reptilian studies of the last 50 years. In these studies, it is olfaction that is assumed to be accessory to the vomeronasal system, as implicit in the Cowles & Phelan (1958) hypothesis. Furthermore, vomerolfaction offers the appeal of accessibility and quantification through observation of tongue-flicks (e.g. Burghardt, 1980; Cooper & Burghardt, 1990a). Experimental study of olfaction requires more invasive and time-consuming techniques, such as nerve lesions, histology, etc. (references above).

In this paper, circumstantial evidence is presented to argue that one family of squamates, the Gekkonidae, may be uniquely specialized in their use of olfaction. As the sister group of the highly derived Autarchoglossa (Estes, de Queiroz & Gauthier, 1988), data for Gekkonidae is essential in evaluating patterns of chemosensory evolution among squamates (Schwenk, 1993). Furthermore, such data are necessary for assessing the conceptual validity of Camp's (1923) classical 'Ascalabota'. Finally, identification of olfactory specialists among squamates underscores the need for investigators to consider the potential of olfaction as an equal, if not greater, partner in the dual olfactory system of some species.

Results

Evidence from the nasal capsule

In his classification of 1923, Camp allied gekkonids with the generally symplesiomorphic (primitive) Iguania by including them together in the paraphyletic taxon 'Ascalabota'. This taxonomy reflected the recognition by Camp (1923) that geckos retain many primitive characters, particularly in their osteology. Many workers since Camp (1923) asserted that the 'Ascalabota' were primarily visual animals and the remaining squamates (Autarchoglossa) primarily chemosensory (see discussion by Schwenk, 1993). It is therefore significant that early workers such as Malan (1946) found evidence from the gekkonid nasal capsule that disputed both Camp's (1923) classification and the conceptualization of geckos as members of a 'visual' group. Malan (1946) found that the gekkonid nasal organ is unlike that of iguanians and is similar to the chemosensory autarchoglossans. Indeed, she concluded that on the basis of nasal structure alone, gekkonids should be classified with Autarchoglossa. The significance of this conclusion is its implication that gekkonids have well-developed nasal chemical senses, on a par with those of the highly chemosensory Autarchoglossa, and that these senses are significantly better developed than those of most putatively visual iguanian ('ascalabotan') species. Since Malan's (1946) study,

additional qualitative and quantitative data have supported this conclusion and have suggested that olfaction, in particular, is well developed.

Pratt (1948) observed that the olfactory chamber in geckos is well developed and that the vomeronasal organ is very large. He also noted the large size of the olfactory bulb of the brain (see below). Stebbins (1948) noted the large nasal concha and extensive area of olfactory epithelium in *Coleonyx variegatus* and concluded that olfaction is well developed. He attributed this to the crepuscular and/or nocturnal behaviour of geckos and, based on comparative studies, suggested that a well-developed olfactory apparatus is characteristic of the family. Bellairs & Boyd (1950) had little to say about olfaction in the strict sense, but noted the large size of the vomeronasal organ in geckos.

The best data regarding nasal olfactory development come from Gabe & Saint Girons (1976), whose histological study provided quantitative data on olfactory structure. Based on the proportion of olfactory sensory cells to non-sensory cells, they ranked gekkonids in their highest category (along with *Xantusia*, Lacertidae and amphisbaenians), concluding that olfactory function in geckos is very highly developed. They also found that the gekkonid vomeronasal organ is well developed, but not to the same extent as in anguimorphs and most snakes.

A suggestive corollary to olfactory development has been observed by A. Bauer (pers. comm.). He has studied the circulatory system of geckos and other lizards by injecting the blood vessels with a plastic medium and clearing the surrounding tissue (see Russell, Walker & Bauer, 1988). He notes that the gekkonid nasal capsule is highly vascularized compared to other lizards and that the capillary beds are organized into a striking lamellar form. The functional significance of the nasal vascular form and hypertrophy is not apparent; however, it suggests an extensive and physiologically active nasal epithelium.

Evidence from the brain

Sensory neurons of the olfactory epithelium project to the main olfactory bulb (MOB) of the brain, an anterior extension of the telencephalon. Vomeronasal sensory cells project to the accessory olfactory bulb (AOB), adjacent to the MOB (e.g. Halpern, 1987). Relative size and volume of brain regions is considered to reflect in a general way the relative 'importance' of the functions mediated by the region; in particular, the size of the olfactory bulb is known to be correlated with the sense of smell (e.g. Northcutt, 1979). Given this general principle, size of the MOB and AOB relative to the brain as a whole and to each other can be used as a first approximation to the relative importance of olfaction and vomerolfaction, respectively, in different, related species.

Figure 1 illustrates the brains of four lizard species. In all except *Anolis*, the olfactory bulbs, as a whole, are well developed, indicating the importance of the nasal chemical senses generally. In *Anolis* (Iguania), olfaction and vomerolfaction are secondarily reduced (Armstrong, Gamble & Goldby, 1953; Gabe & Saint Girons, 1976). In contrast, the iguanine iguanid, *Dipsosaurus*, represents a moderately chemosensory species (e.g. Pedersen, 1988; Krekorian, 1989; Cooper & Alberts, 1990), and *Varanus* represents a highly chemosensory anguimorph (e.g. Auffenberg, 1981; Cooper, 1989). In *Dipsosaurus*, the AOB and MOB are approximately equal in size. In *Varanus*, the AOB is massively hypertrophied, suggesting the reliance of this species on vomerolfaction rather than olfaction, a conclusion supported by recent observations of tongue-flicking in this genus (Cooper, 1989). The absolute and relative size of the AOB and MOB in these species is concordant with sensory epithelial development in congeners studied by Gabe & Saint Girons (1976).

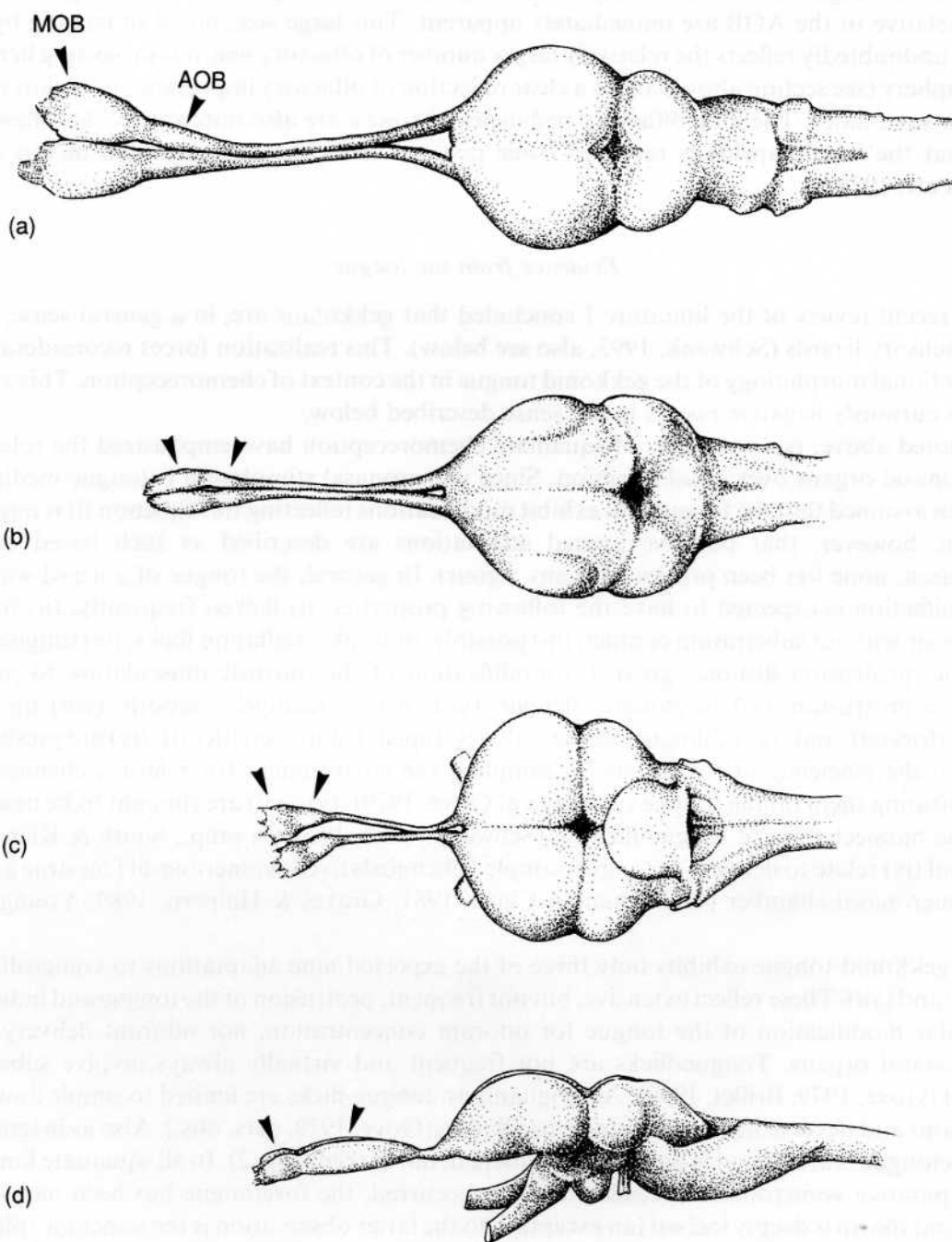


FIG. 1. Squamate brains showing relative sizes of main and accessory olfactory bulbs. See text for explanation. (a) *Gekko gecko* (Gekkonidae) (after Smeets *et al.*, 1986). (b) *Anolis garmani* (Iguanidae) (after Armstrong *et al.*, 1953). (c) *Diposaurus dorsalis* (Iguanidae) (after Ulinski & Peterson, 1981). (d) *Varanus flavescens* (Varanidae) (after Senn, 1966). (a-c) In dorsal view; (d) in lateral view. Anterior to the left. Drawn so that the cerebrium + optic tectum are approximately equal in length. Not to scale. AOB = accessory olfactory bulb. MOB = main olfactory bulb.

In *Gekko*, the large size of the olfactory bulb and, particularly, the pronounced enlargement of the MOB relative to the AOB are immediately apparent. This large size, noted in passing by Pratt (1948), undoubtedly reflects the relatively larger number of olfactory neurons projecting here from the periphery (see section above) and is a clear reflection of olfactory importance in geckos relative to other squamates. The long olfactory peduncles of *Gekko* are also noteworthy, but these show only that the nasal capsule is removed some distance from the neurocranium in this species (Northcutt, 1979).

Evidence from the tongue

In a recent review of the literature I concluded that gekkotans are, in a general sense, highly chemosensory lizards (Schwenk, 1993; also see below). This realization forces reconsideration of the functional morphology of the gekkonid tongue in the context of chemoreception. This analysis renders curiously negative results in the sense described below.

As noted above, recent studies of squamate chemoreception have emphasized the role of the vomeronasal organs over nasal olfaction. Since vomeronasal stimulation is tongue-mediated, it has been assumed that the tongue will exhibit modifications reflecting this function (it is important to note, however, that putative lingual adaptations are described as such based only on correlation; none has been proven with any rigour). In general, the tongue of a lizard with keen vomerolfaction is expected to have the following properties: (i) flicked frequently; (ii) frequent flicks in air without substratum contact; (iii) possibly, multiple oscillation flicks; (iv) tongue highly extensible, protrusion distance great; (v) modification of the intrinsic musculature to promote extensive protrusion; (vi) foretongue slender; (vii) surface relatively smooth; (viii) tip deeply incised (forked); and (ix) sublingual plicae well developed. Characteristics (i)–(iv) are presumed to relate to the efficiency of the tongue in sampling the environment for relevant chemicals and concentrating them on the tongue surface (e.g. Gove, 1979), (v)–(vii) are thought to be associated with the biomechanics of tongue-flicking (Schwenk, 1984, 1993, In prep.; Smith & Kier, 1989); (viii) and (ix) relate to delivery of tongue-sampled chemicals to the vomeronasal fenestrae and into the vomeronasal chamber (Gillingham & Clark, 1981; Graves & Halpern, 1989; Young, 1990, 1993).

The gekkonid tongue exhibits only three of the expected nine adaptations to vomerolfaction, (iv), (v) and (vii). These reflect extensive, but not frequent, protrusion of the tongue and indicate no particular modification of the tongue for odorant concentration, nor odorant delivery to the vomeronasal organs. Tongue-flicks are not frequent and virtually always involve substratum contact (Gove, 1979; Brillet, 1990). As in iguanians, tongue-flicks are limited to simple downward extensions and never exhibit even a single oscillation (Gove, 1979, pers. obs.). Also as in iguanians, the foretongue is broad and is only slightly notched, not forked (Fig. 2). In all squamate families in which putative vomeronasal specialization has occurred, the foretongue has been narrowed in width and the tip is deeply incised (an exception to the latter observation is the scincomorph family Scincidae, in which the tip remains notched only). The floor of the gekkonid mouth is unique among squamates in its total lack of sublingual plicae (ventrolateral ridges containing the sublingual glands, *sensu* McDowell, 1972). The sublingual glands of gekkonids are scattered diffusely beneath the free part of the tongue (Schwenk, 1988 and unpubl. data). Therefore, geckos have no recourse to a vomeronasal odorant delivery system mediated by apposition of the sublingual plicae to the vomeronasal fenestrae in the roof of the mouth, a mechanism implicated in snakes and presumed to occur in most lizards (e.g. Gillingham & Clark, 1981; Young, 1990, 1993).

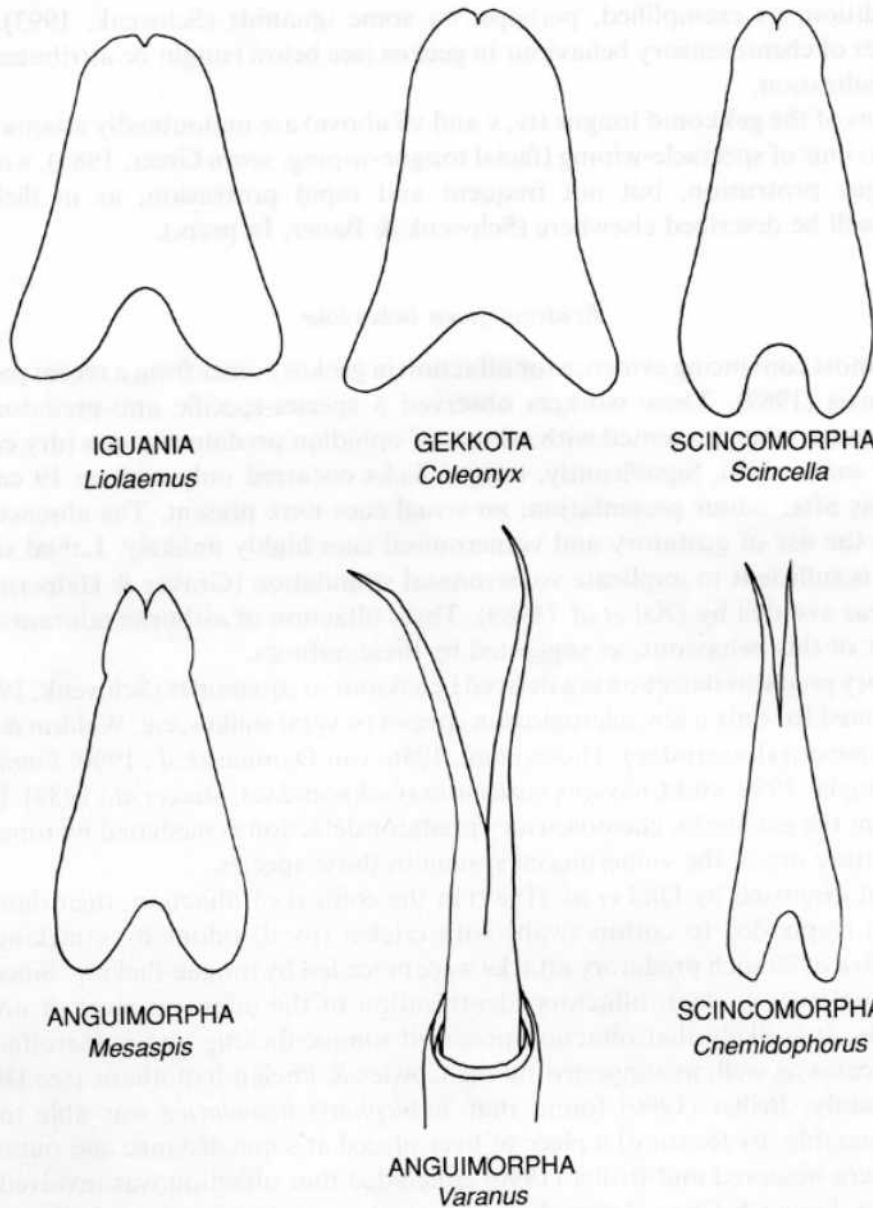


FIG. 2. Tongue shape in a variety of squamate reptiles. Note that in all except *Liolaemus* (Iguanidae) and *Coleonyx* (Gekkonidae) the foretongue has been narrowed, and in all except these and *Scincella* (Scincidae), the tongue tip is deeply incised. Geckos, like iguanians, show few lingual specializations for chemosensory tongue protrusion. Traced from photographs (Schwenk, unpubl.). Not to scale.

If gekkonids are highly chemosensory as seems clear (Schwenk, 1993 and below), it appears not to be the result of specialization in the tongue-vomer nasal system. By default, a greater role for olfaction is implicated in this group. However, this does not imply that vomerolfaction is poorly developed in geckos; indeed, evidence from the nasal capsule (above) indicates the contrary. The point is that the tongue-vomer nasal system is not remarkably advanced over the presumed

ancestral condition, as exemplified, perhaps, by some iguanids (Schwenk, 1993). Therefore, derived features of chemosensory behaviour in geckos (see below) might be attributed, in part, to olfactory specialization.

Modifications of the gekkonid tongue (iv, v and vii above) are undoubtedly adaptations for the gekkotan behaviour of spectacle-wiping (facial tongue-wiping, *sensu* Greer, 1985), which involves extensive tongue protrusion, but not frequent and rapid protrusion, as in flicking. These modifications will be described elsewhere (Schwenk & Bauer, In prep.).

Evidence from behaviour

Perhaps the most convincing evidence for olfaction in geckos comes from a recent paper by Dial, Weldon & Curtis (1989). These workers observed a species-specific anti-predator display in *Coleonyx variegatus* when presented with odours of ophidian predator species (dry cotton swabs rubbed across snake skin). Significantly, tongue-flicks occurred only once in 19 cases of anti-predator display after odour presentation; no visual cues were present. The absence of tongue-flicking makes the use of gustatory and vomeronasal cues highly unlikely. Labial scale contact with odorants is sufficient to implicate vomeronasal stimulation (Graves & Halpern, 1989), but such contact was avoided by Dial *et al.* (1989). Thus, olfaction of airborne odorants is the most likely mediator of this behaviour, as suggested by these authors.

Chemosensory predator detection is a derived behaviour in squamates (Schwenk, 1993) that has been demonstrated for only a few scleroglossan species (several snakes, e.g. Weldon & Burghardt, 1979; *Lacerta vivipara* (Lacertidae), Thoen *et al.*, 1986; van Damme *et al.*, 1990; *Eumeces laticeps* (Scincidae), Cooper, 1990; and *Coleonyx variegatus* (Gekkonidae), Dial *et al.*, 1989). However, in all species except the gekkonid, chemosensory predator detection is mediated by tongue-flicking, thereby implicating use of the vomeronasal system in those species.

Although not discussed by Dial *et al.* (1989) in the context of olfaction, their data show that *Coleonyx* often responded to cotton swabs with cricket (food) odour by attacking the swab; however, only five of 20 such predatory attacks were preceded by tongue-flicking. Since there were no relevant visual cues evident, olfactory identification of the odour in most, if not all of the attacks, is likely. It is likely that olfaction preceded tongue-flicking and vomerolfaction in the remaining five cases as well, as suggested by the Cowles & Phelan hypothesis (see **Discussion**).

In another study, Brillet (1990) found that *Eublepharis macularius* was able to detect (as indicated, presumably, by location) a piece of liver placed at some distance and out of sight. No tongue-flicks were observed and Brillet (1990) concluded that olfaction was involved.

Finally, Chou, Leong & Choo (1988) showed that experimental deletion of olfaction by nerve lesion resulted in significantly fewer prey captures in one of two gecko species studied (*Cosymbotus platyurus*). However, this study did not clearly distinguish between olfaction and vomerolfaction and it is possible that their 'olfactory nerve' lesion included the vomeronasal nerve. No data were presented on tongue-flicking, and several other problems with experimental design suggest that these results should be regarded cautiously.

Discussion

It is now well established that gekkonids utilize chemosensory cues in many aspects of their behaviour. Natural history, field and laboratory observations have long noted the frequent use of tongue-flicks by active geckos (e.g. Mahendra, 1936; Dial, 1978; Kingsbury, 1989). Controlled

observations and experiments have extended these reports, demonstrating the sensitivity of the gekkonid chemical senses and the variety of the contexts in which they act (Greenberg, 1943; Dial *et al.*, 1989; Mason & Gutzke, 1990; Brillet, 1990). These data and the morphological data discussed above refute the notion of a visual 'Ascalabota', as propounded by numerous workers since Camp's (1923) classification of lizards (e.g. Evans, 1961, 1967; Underwood, 1971; see Schwenk, 1993 for other references and discussion of this problem).

The obvious question remains: which of the chemical senses available to geckos is being exploited and in what context? Unfortunately, no studies have been designed to differentiate explicitly among the chemical senses. However, some clues exist.

I have presented evidence in this paper to argue that olfaction is not only present in gekkonids, but is highly developed. It is potentially more developed than in other squamates, even other species with generally well-developed chemical senses. Support for this contention comes from the peripheral sensory structures that receive and transduce chemical messages, from the central neural structures that integrate and process such messages, and from the behaviours that result from such neural processing. Given that olfaction is operating in these lizards, it is necessary to distinguish between this sense, vomerolfaction and gustation.

Both gustation and vomerolfaction are tongue-mediated and are therefore very difficult to differentiate without invasive techniques (Schwenk, 1985; see Graves & Halpern, 1990, for one possible approach). However, taste bud densities are quite low among the gekkonid species so far studied (Nonoyama, 1936; Schwenk, 1985), therefore gustation is unlikely to be a significant feature of gecko behaviour. Furthermore, evolutionary patterns of character origin and transformation in squamates suggest that tongue-flicking is causally linked to vomeronasal stimulation and is not associated with gustation (Schwenk, 1993). It is probably not unreasonable to assume, therefore, as previous investigators have done, that tongue-flicking in gekkonids mediates vomerolfaction only.

Given this conclusion, behaviours associated with tongue-flicking can be attributed to vomerolfaction and those that occur in the absence of tongue-flicking, to olfaction. The studies of Greenberg (1943), Mason & Gutzke (1990) and Brillet (1990) all clearly demonstrate the use of tongue-flicking (and therefore vomerolfaction) in reproductive behaviour. Vomerolfaction is used by males to identify females, even in the absence of visual cues (Greenberg, 1943; Mason & Gutzke, 1990). Mason & Gutzke (1990) showed that shedding female *Eublepharis* are temporarily rendered chemically 'invisible' to males and are attacked instead of courted. Brillet (1990) observed males of the same species to exhibit a courtship display (tail vibration) only in the presence of female chemical cues sampled by tongue-flicks. All behaviours (courtship or attacks) were preceded by tongue-flicking.

Eublepharis and *Paroedura* exhibited elevated tongue-flick rates when placed in a new, clean cage and *Eublepharis* showed 'marking' behaviour. These behaviours were not exhibited in home cages (Brillet, 1990) and undoubtedly reflect the typical and widespread squamate behaviour of tongue-flicking during general arousal and when confronted by novel stimuli, either visual or olfactory (e.g. de Fazio *et al.*, 1977; Chiszar *et al.*, 1980; Greenberg, 1985; Burghardt, Allen & Frank, 1986; Krekorian, 1989; Goosse & Bels, 1990). Vomerolfaction is implicated in these behaviours for gekkonids and other squamates. It is likely that gekkonids are more sensitive to airborne volatiles than other taxa and might therefore be alerted sooner to the need for further (vomeronasal) investigation with the tongue, *sensu* Cowles & Phelan (1958).

Brillet (1990) placed male *Eublepharis* in cages into which an airstream was directed that had passed through another cage (out of sight) containing a female. Males failed to exhibit their

vibratory (courtship) tail display as they had done after tongue-flicking female odorants. Brillet (1990) concluded that vomerolfaction was necessary for sex identification, olfaction alone being insufficient. This observation is not surprising in the light of the fact that integumentally-derived lipids and proteins are implicated in such chemical messages, and these are not very volatile (Alberts, 1990; Mason & Gutzke, 1990). Alternatively, it is conceivable that Brillet's (1990) technique simply did not deliver enough odorant to effect a response.

In contrast, the behavioural evidence cited previously (see **Results**) strongly implicates olfaction and not vomerolfaction in certain gecko behaviours, specifically, in predator identification (Dial *et al.*, 1989) and prey/food detection (Chou *et al.*, 1988; Dial *et al.*, 1989; Brillet, 1990). In these behaviours tongue-flicking was not necessary to elicit a response.

In summary, geckos are shown to be highly chemosensory and to have an especially well-developed olfactory system. Olfaction is implicated particularly in the detection of food and predators, vomerolfaction in the investigation of novel stimuli and in reproductive behaviour. Gustation is not well developed and is probably limited to assessment of palatability of food held within the mouth, but this is speculative. The role of olfaction in stimulating tongue-flicking and vomeronasal investigation (the Cowles & Phelan [1958] hypothesis) remains unclear and little-tested. Geckos, with their acute olfactory apparatus, are ideal candidates for study.

Speculating further, it is possible that low-light activity was the selective milieu driving the evolution of olfactory specialization in geckos, as suggested by Stebbins (1948). Vision is probably at least as important as olfaction in stimulating chemosensory investigation and initiating certain behaviours in diurnal species (see comments and references in Schwenk [1993]). Most geckos are nocturnal, and despite good visual acuity, are necessarily limited in their use of vision; olfaction is ideally suited to replace vision in such circumstances because it operates over comparable or greater distances, as opposed to the relatively short working distance of vomerolfaction. For example, several gecko species in New Zealand (and probably elsewhere) locate flowering plants at night and feed on nectar and fruit (Whitaker, 1987). Geckos were observed by Whitaker (1987) to congregate preferentially on plants in bloom, where they are found in remarkably high densities. The ability to locate and identify such transiently available and patchily distributed resources over some distance is of obvious selective advantage.

Using arguments parallel to those above, Marcellini (1977) suggested that nocturnality was responsible for the evolution of acoustic behaviour in gekkonids. Nocturnality has also been invoked as the selective regime promoting the evolution of increased olfactory and auditory senses in early mammals relative to their therapsid ancestors (Jerison, 1973; Crompton & Jenkins, 1978, 1979). These ideas could be tested in squamates, to some extent, by comparative studies of chemosensory development in other nocturnal or fossorial lineages. Xantusiidae and Amphisbaenia might be particularly fruitful taxa to consider in this light (note that both these taxa were found by Gabe & Saint Girons [1976] to have highly-developed olfactory epithelia).

Finally, I suggest that geckos are superb subjects for study of the dual olfactory system in a non-mammalian lineage. Nearly all such work to date has been with natricine snakes, especially the genus *Thamnophis* (work of Halpern and her colleagues, and Burghardt and his colleagues). Snakes, however, are extreme vomeronasal specialists. For example, the snake tongue meets all nine criteria for vomeronasal specialization noted above. No other squamates, not even the varanid lizards, have achieved this degree of modification. As such, advanced snakes have been the ideal group for establishing the independence of the vomeronasal system from the olfactory system and its importance in directing a great deal of vertebrate behaviour. But for the same reason, snakes are anything but typical of squamates and are probably quite different from mammals in

