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The Evolution of Chemoreception in Squamate Reptiles: A Phylogenetic Approach

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Abstract

Recent advances in the field of squamate reptile chemoreception have been paralleled by the growth and preeminence of cladistics in the field of systematics, but for the most part, workers in the former have failed to incorporate the conceptual and informational advances of the latter. In this paper, I attempt a preliminary rapprochement by combining the methods of phylogenetic systematics and current hypotheses of squamate relationships with an overview of squamate chemosensory biology. This purely phylogenetic approach leads to a number of falsifiable generalizations about the evolution of chemoreception in squamates: 1) Evolution of this system is conservative rather than plastic, reflecting to a large extent suprafamilial attributes rather than adaptation to local conditions; 2) Anguimorphs are highly chemosensory and teiids show convergence with this group; 3) Tongue-flicking, a bifurcated tongue tip, a vomeronasal (VNO) mushroom body, and a complete circular muscle system in the tongue are a correlated character complex associated with the attainment, in squamates, of a direct VNO-oral connection and the loss of a VNO-nasal connection; 4) There is little support for a visual-chemosensory dichotomy within Squamata; 5) Gekkotans are allied with Autarchoglossa, both phylogenetically and in terms of chemosensory biology; 6) Iguania are highly variable in chemosensory development; iguanids represent the primitive iguanian condition, while agamids and chamaeleonids have secondarily reduced or lost their chemosensory abilities; 7) Apparent contradictions in chemosensory behavior among iguanids probably represent intrafamilial divergence; 8) Ecological correlates within Iguanidae and other taxa might be spurious, resulting from historical factors unrelated to the adaptations in question; 9) The mechanical demands of lingual food prehension have constrained chemosensory evolution in Iguania; chemosensory evolution within Scleroglossa was permitted by the liberation of the tongue from this ancestral role.

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Introduction

Since Burghardt's [1970] review, there has been a virtual explosion of studies related to chemoreception in squamate reptiles. These have greatly expanded both our knowledge of the chemical senses and the number of taxa for which we know them to be important, but for the most part they are notable in their lack of an evolutionary perspective. When evolutionary generalizations have been attempted, most studies have relied on Camp's [1923] taxonomy of squamates, especially his dichotomous division of these into the Ascalabota and Autarchoglossa [e.g. Madison, 1977; Bissinger and Simon, 1979; Duvall, 1981; Simon, 1983; Nicoletto, 1985a; Cooper, 1989a, b]. Generalizations about squamate chemoreception have remained primarily ethological and ecological rather than phylogenetic [e.g. Burghardt, 1980; Cooper, 1989a, 1990a].

In nearly the same period of time, the field of systematics has undergone a revolution, stimulated in this country by the publication of Hennig's [1966] *Phylogenetic Systematics*. Phylogenetic systematics (also known as cladistics) differs from the schools of phenetics and evolutionary taxonomy in that it attempts to distinguish between similarities among organisms resulting from the retention of ancestral attributes (primitive characters) and similarities resulting from evolutionary novelties uniquely derived in a common ancestor (derived characters). Phylogeny can only be inferred from derived characters, and a phylogenetic classification must reflect exactly the phylogeny. Therefore, only monophyletic taxa (a common ancestor and *all* of its descendants) are named [Wiley, 1981]. Acceptance of cladistic principles has been nearly universal among systematists, but morphologists and ethologists have been slow to adopt its methods of historical analysis [Lauder, 1981, 1986].

Perhaps for this reason, there has arisen a gap between our burgeoning knowledge of squamate chemoreception and our current knowledge and interpretation of squamate phylogeny. This gap hinders our ability to understand patterns of morphological, functional and behavioral evolution of chemoreception within Squamata and may have led to incorrect evolutionary conclusions. In this paper, I attempt to bridge the gap by combining methods of phylogenetic analysis and current hypotheses of squamate relationships with an overview of chemoreception in squamate reptiles. Such an analysis leads to generalizations about the evolution of chemoreception in squamates that, because of their explicit phylogenetic context, are potentially falsifiable. Furthermore, this analysis points clearly to deficits in our current knowledge and suggests possible avenues of future research.

Squamate Phylogeny

The Squamata includes the lizards, snakes and amphisbaenians. Although relationships among squamates remain controversial, particularly as to the proper placement of snakes and amphisbaenians, the monophyly of the group is not questioned, nor is its sister relationship with the sole-surviving rhynchocephalian reptile, *Sphenodon,* with which it forms the Lepidosauria [Estes et al., 1988; Gauthier et al., 1988]. Camp's [1923] classic monograph has formed the basis for squamate classification and phylogeny for many years and, as noted above, has been used routinely by workers in squamate chemoreception. However, what is often not fully appreciated is that Camp's [1923] *classification* does not reflect *phylogeny*, even his own, in the modern sense. Thus, Camp's [1923] classification divides squamates into two formal 'Divisions', the Ascalabota and the Autarchoglossa, but only the Autarchoglossa is monophyletic and therefore representative of phylogeny (fig. 1A). Ascalabota is a group formed from two unrelated lineages that are similar only in their retention of many primitive morphological traits. As such, these lineages (iguanians and gekkotans) share no special relationship. In fact, the gekkotan lineage is more closely related to autarchoglossans than to iguanians, although the classification might suggest the opposite to the modern worker. Evans [1961] first suggested that ascalabotans are primarily visual, relying little on chemoreception, and that autarchoglossans are, conversely, primarily chemosensory. This dichotomous view was repeated by Evans [1967] and many workers since. As such, the concept of a 'visual Ascalabota' and a 'chemosensory Autarchoglossa' has become dogma, although some recent papers have begun, finally, to erode this artifice [e.g. Cooper and Alberts, 1990].

Recent work on squamate phylogeny and classification has utilized a strictly phylogenetic approach [e.g. Kluge, 1987; papers in Estes and Pregill, 1988; Frost and Etheridge, 1989]. Estes et al. [1988] have considered, once again, relationships within the Squamata and have proposed an updated, cladistic phylogeny for the group (fig. 1B). Notably, their phylogeny does not differ from Camp [1923] in its identification of several suprafamilial groups (Iguania, Gekkota, Scincomorpha, Anguimorpha), but it does differ in the placement of certain families and in relationships among families *within* groups. Furthermore, Estes et al. [1988] concluded that there were insufficient data to place reliably the Serpentes, Amphisbaenia and the enigmatic Dibamidae. Because theirs is a cladistic analysis, only monophyletic groups, reflecting the phylogeny, are named by Estes et al. [1988]. Hence, 'Ascalabota' is no longer valid as a formal taxon. The primary phylogenetic dichotomy identified by these workers is between the Iguania (Iguanidae, Agamidae, and Chamaeleonidae) and all remaining squamates, the Scleroglossa, a dichotomy corroborated by Schwenk [1988] using an independent data set. Hence the Gekkota (Gekkonidae and Pygopodidae), part of Camp's [1923] Ascalabota, are seen to be united with Autarchoglossa (Anguimorpha and Scincomorpha) to form the Scleroglossa, reflecting the phylogeny of the group.

Squamate Phylogeny and Chemoreception

What is the relevance of recent developments in systematics generally, and squamate phylogenetics specifically, to workers in the field of chemoreception? Perhaps most important is the way in which our conception of phylogeny, often conveyed by a classification, influences both the interpretation of our data and the direction of future research. Indeed, the very questions we ask are, to an extent, determined by our preconceived notions of phylogeny. One wonders, for example, if we would have appreciated many years sooner the richness of chemosensory behavior among iguanid and gekkonid lizards (see below and references cited therein), had we not been burdened by the notion of a 'visual Ascalabota'? As an example of this, I note the otherwise excellent work of Malan [1946: 124], who was so influenced by Camp's [1923] classification that she could ignore her own data and utterly contradict herself within the space of a few sentences: 'The general type of the nasal organ occurring in the Lacertilia *fully supports the division of the order into the two subdivisions of Camp [1923]:* the Ascalabota comprising the Geckonidae, Iguanidae, Agamidae and Chamaeleontidae, and the Autarchoglossa comprising all other families ... The Geckonid nasal organ represents an intermediate type which, though showing an approach to the Ascalabota condition in several characters, *is yet so similar to that of the Autarchoglossa, that, with respect to the nasal region alone, the Geckonidae would certainly have to be included in the latter subdivision. In the remaining Ascalabota a very different type of nasal organ is found'* (italics added). Surely data such as Malan's and a classification reflecting the close relationship of gekkonids to the autarchoglossans would have directed us sooner to consider geckos as highly chemosensory lizards, as they are now known to be [Greenberg, 1943; Dial, 1978; Dial et al., 1989; Brillet, 1990; Mason and Gutzke, 1990].

This study seeks to discern patterns of structural and functional evolution in the chemosensory apparatus of squamate reptiles. A consideration of this topic in a phylogenetic context leads to three complementary questions: What phylogenetically informative morphological, functional, and behavioral characters can be identified? What can these characters tell us about the phylogeny of squamates? Conversely, what can an independent phylogeny tell us about the evolution of the chemical senses in squamates?

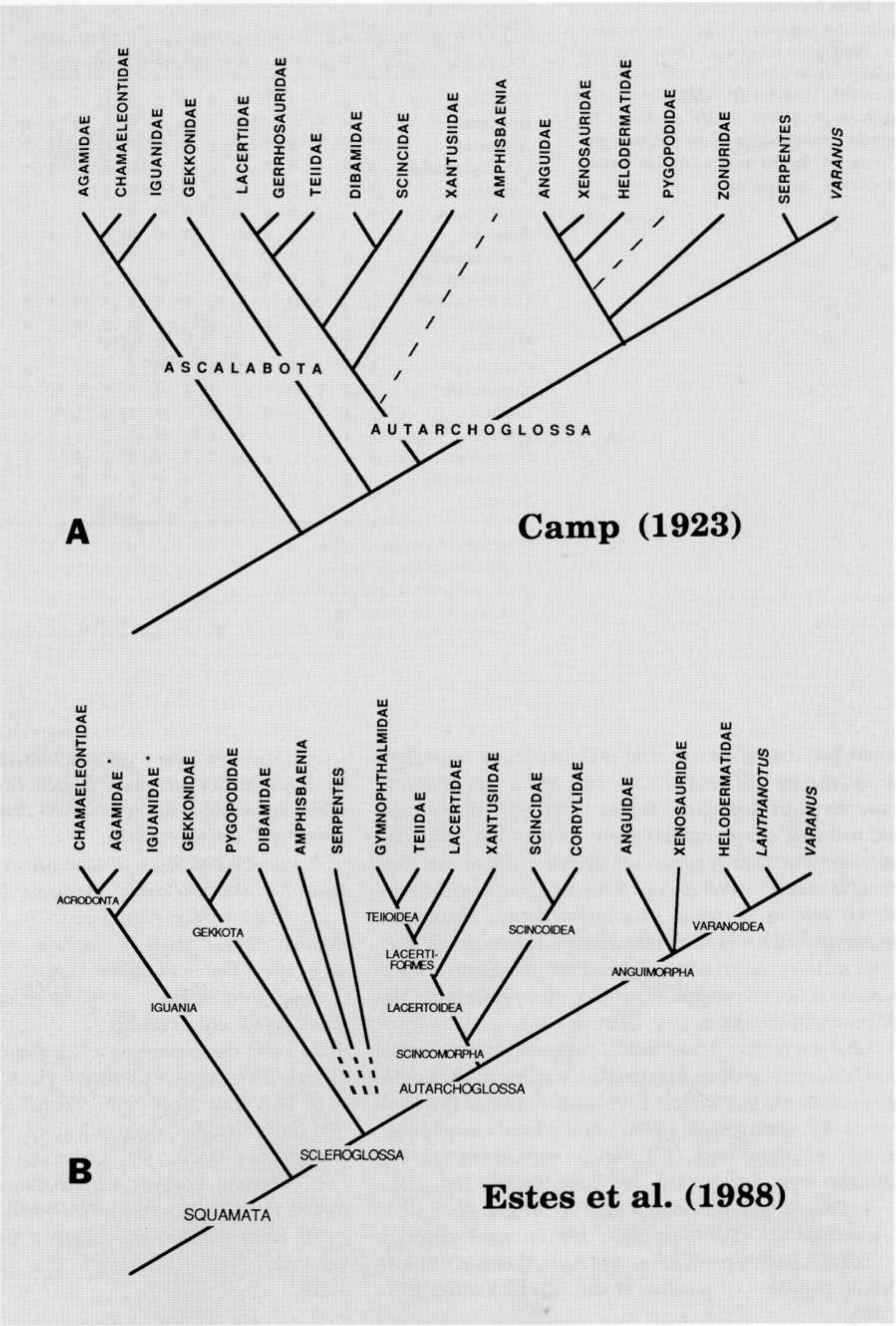
Chemosensory Characters and Character Analysis

A review of the literature on squamate chemosensory biology and behavior resulted in the identification of 21 characters with variable states among lepidosaurs (below). A more thorough search would undoubtedly have revealed more potential characters, but the purpose of this study is primarily heuristic; it is neither complete nor exhaustive.

I used outgroup comparison to determine which character states were primitive and which derived (polarization). More than one outgroup is necessary to polarize reliably a set of characters [Watrous and Wheeler, 1981; Maddison et al., 1984], but this is problematic for many aspects of behavior and soft anatomy in squamates, owing to loss and secondary modification in living archosaurs (birds and crocodilians), the outgroup for Lepidosauria [Schwenk, 1988]. Hence, it is not usually possible to use an outgroup other than *Sphenodon*. Therefore, for the purpose of this study, I have taken the condition of a character present in *Sphenodon* to be the primitive state. This may not be a poor assumption, since *Sphenodon* has retained primitive features in many of its systems, including some of direct relevance ot this study [Schwenk, 1986, 1988].

After identification of a character, the state of the character was determined for every squamate taxon for which I

Fig. 1. Phylogenetic hypotheses (cladograms) of squamate reptile relationships. **A** Cladogram from Camp [1923], based on his 'skiogram' showing his divisions Ascalabota and Autarchoglossa. Note that Ascalabota comprises two unrelated, monophyletic lineages, the Iguania (Iguanidae, Agamidae and Chamaeleonidae) and the Gekkonidae. **B** Cladogram of Estes et al. [1988] based on cladistic analysis of morphology. Note that only monophyletic lineages are named so that the taxonomy will accurately reflect the phylogeny; hence, 'Ascalabota' is no longer recognized as a valid group. Gekkota is grouped with Autarchoglossa, forming the Scleroglossa. The Autarchoglossa retains essentially the same constituents as in Camp [1923]. Also, suprafamilial clusters of families are only slightly changed from Camp [1923], including the Iguania, Gekkota, Scincomorpha, and Anguimorpha. Dibamidae, Amphisbaenia and Serpentes are placed within Squamata *incertae sedis*. Cladograms reprodued from Estes et al. [1988] with permission of Stanford Univ. Press.


AGAMIDAE
CHAMAELEONTIDAE
IGUANIDAE
GEKKONIDAE
LACERTIDAE
GERRHOSAURIDAE
TEIIDAE
DIBAMIDAE
SCINCIDAE
XANTUSIIDAE
AMPHISBAENIA
ANGUIDAE
XENOSAURIDAE
HELODERMATIDAE
PYGOPODIDAE
ZONURIDAE
SERPENTES
VARANUS
ASCALABOTA
AUTARCHOGLOSSA
A
Camp (1923)
CHAMAELEONTIDAE
AGAMIDAE *
IGUANIDAE *
GEKKONIDAE
PYGOPODIDAE
DIBAMIDAE
AMPHISBAENIA
SERPENTES
GYMNOPHTHALMIDAE
TEIIDAE
LACERTIDAE
XANTUSIIDAE
SCINCIDAE
CORDYLIDAE
ANGUIDAE
XENOSAURIDAE
HELODERMATIDAE
LANTHANOTUS
VARANUS
ACRODONTA
GEKKOTA
TEIIOIDEA
LACERTIFORMES
SCINCOIDEA
VARANOIDEA
ANGUIMORPHA
IGUANIA
LACERTOIDEA
SCINCOMORPHA
AUTARCHOGLOSSA
SCLEROGLOSSA
SQUAMATA
B
Estes et al. (1988)

1

Table 1. Taxon-by-character data matrix for squamate reptiles. *Sphenodon* is the designated outgroup. Those taxa indicated with an asterisk (*) were excluded from the computer (PAUP) analysis owing to incomplete data. PAUP generated 12 equally parsimonious trees; a representative tree is shown in fig. 2A. See text for characters and discussion

Taxon	Character																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Sphenodon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Iguanidae	1	0	1	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	1	1	?
Agamidae	1	0	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	?	?	?	?
Chamaeleonidae	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	?	?	?	?	?
Gekkonidae	1	1	2	0	1	1	1	0	0	0	1	1	1	0	0	1	1	?	1	1	1
Pygopodidae*	1	1	2	0	1	1	1	0	0	0	?	1	1	?	1	1	?	?	?	?	?
Anguidae	2	1	2	0	1	1	1	1	0	0	?	1	1	1	1	1	1	?	?	?	?
Xenosauridae*	2	1	2	0	?	?	?	?	?	?	?	?	1	?	0	?	?	?	?	?	?
Helodermatidae	2	1	2	0	?	?	?	?	?	0	2	1	1	1	0	1	1	1	?	?	?
Lanthanotidae*	2	2	2	0	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?
Varanidae	2	2	2	1	1	1	1	1	1	2	2	1	1	1	0	0	1	1	?	1	?
Scincidae	1	1	2	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1
Cordylidae*	1	1	2	0	1	1	1	?	0	1	?	1	1	1	0	1	?	?	?	?	?
Xantusiidae*	1	1	2	0	1	1	1	1	0	?	?	1	1	?	0	1	?	?	?	?	?
Lacertidae	2	1	2	0	1	1	1	1	0	1	1	1	1	1	0	1	1	?	?	1	1
Teiidae	2	1	2	0	1	1	1	1	0	1	2	1	1	1	0	1	1	1	?	?	?
Dibamidae*	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Amphisbaenia	2	1	2	0	1	1	1	1	0	1	?	1	1	1	0	1	1	1	?	?	?
Serpentes	2	2	2	1	1	1	1	1	1	?	2	1	1	1	1	1	1	1	1	1	1

0 = primitive character state.
1 = derived character state.
2 = second derived character state.
? = unknown character state.

could find data (table 1). The primitive character state is designated by a 0, derived states by 1 and 2, and unknown states by a question mark (?). Characters were then used in the two analyses described below. Initial trials with computer-generated phylogenies utilizing these characters (first analysis below) revealed that too many taxa are too incompletely known to obtain meaningful results. These taxa were removed for subsequent analyses. The complete character matrix given in table 1 is provided to indicate obvious lacunae in our knowledge as an aid to identification of fruitful research directions (see Discussion).

Characters were drawn from a variety of morphological and behavioral systems that putatively relate to chemosensory function in squamates. These include tongue morphology (1–4), vomeronasal (VNO) and palatal morphology (5–10), neuroanatomy (11), tongue movement (12–15), olfactory morphology (16), and behavior (17–21):

1. Tongue tip bifurcation absent (0); tongue tip notched (1); incised (2). [Schwenk, 1986, 1988, unpubl. observ.].

2. High-profile papillae present on foretongue (0); low-profile papillae (1); papillae absent (2). [Schwenk, 1986, 1988].

3. Intrinsic circular muscle system incomplete (0); weakly developed (1); well-developed (2). [Schwenk, 1986, 1988, unpubl. observ.; Smith, 1984, 1986, 1988; Bell, 1989; Smith and MacKay, 1990].

4. Lingual taste buds present (0); absent (1). [Schwenk, 1985; K. Schwenk and D. Bednarz, unpubl. observ.].

5. VNO weakly developed (0); well-developed (1). [Malan, 1946; Pratt, 1948; Bellairs and Boyd, 1950; Parsons, 1970; Gabe and Saint Girons, 1976].

6. Mushroom body of VNO absent (0); present (1). [Refs. as for character 5].

7. VNO duct opens to nasal chamber (0); duct opens directly into oral cavity only (1). [Refs. as for character 5].

8. VNO duct opens into choanal groove of soft palate (0); duct opening independent of choanal groove (1). [Bellairs and Boyd, 1950; Gabe and Saint Girons, 1976].

9. Choanal grooves well-developed (0); reduced or absent (1). [Bellairs and Boyd, 1950].

10. Bony palate 'paleochoanate' (0); 'incomplete neochoanate' (1); 'neochoanate' (2). [Bellairs and Boyd, 1950].

11. Nucleus sphericus of forebrain weakly developed (0); well-developed (1); hyper-developed (2). [Halpern, 1976, 1978; Northcutt, 1978].

12. Tongue used for prey/food prehension (0); not used for prehension (1). [Schwenk and Throckmorton, 1989; Schwenk, unpubl. observ.].

13. Chemosensory tongue protrusion (tongue-flicking) absent (0); present (1). [Parcher, 1974; Gove, 1979; Bissinger and Simon, 1979; Dawbin, 1982; Schwenk, unpubl. observ.].

14. Tongue-flicks predominantly with substrate contact (tongue-touch, substrate-lick); tongue-flicks without substrate contact (air-flick, air-lick) rare (0); air-flicks relatively common (1). [Gove, 1979; Greenberg, 1985; Schwenk, 1988, unpubl. observ.; Brillet, 1990].

15. Tongue-flicks always single (0); sometimes multiple oscillations (1). [Gove, 1979; Schwenk, unpubl. observ.].

16. Olfactory epithelium poorly developed (0); well-developed (1). [Gabe and Saint Girons, 1976].

17. Chemosensory discrimination of prey from nonprey odors absent (0); present (1). [Bogert and Cowles, 1947; Gans, 1960; Burghardt, 1967, 1973; Dial, 1978; Iverson, 1979; Chiszar et al., 1980; Simon et al., 1981; Auffenberg, 1982; Halpern and Kubie, 1983; von Achen and Rakestraw, 1984; Nicoletto, 1985a, b; Cooper, 1989a, b, 1990b, c, 1991; Cooper and Vitt, 1989; Krekorian, 1989; Cooper and Alberts, 1990, 1991; Graves and Halpern, 1990].

18. Unable to find food without aid of vision (0); able to locate food without vision, and/or find hidden food, and/or follow prey trails (1). [Berg, 1913, as cited in Noble and Mason, 1933; Noble and Kumpf, 1936; Lederer, 1942, as cited in Auffenberg, 1981; Bogert and Cowles, 1947; Bogert and Del Campo, 1956; Fitch, 1958; Gans, 1960; Simms, 1970, as cited in Cooper, 1989a; Kubie and Halpern, 1979; Auffenberg, 1981, 1984; Vitt and Cooper, 1986; Chiszar et al., 1988; Meyer-Rochow, 1989].

19. Chemosensory identification of conspecifics absent (0); present (1). [Duvall, 1979; Duvall et al., 1980; Burghardt, 1983; Simon and Moakley, 1985; Cooper and Vitt, 1986; Werner et al., 1987; Brillet, 1990; Dussault and Krekorian, 1991; Graves and Halpern, 1991].

20. Tongue-flicking absent during courtship (0); present (1). [Parshad, 1916, as cited in Noble and Bradley, 1933; Noble, 1937; Kitzler, 1941, as cited in Bauwens et al., 1987; Greenberg, 1943; Berry, 1974; Kubie et al., 1978; Werner, 1978; Perrill, 1980; Auffenberg, 1981; Tollustrup, 1981; Andren, 1982; Montanucci and Bauer, 1982; Halpern and Kubie, 1983; Gans et al., 1984; Bauwens et al., 1987; Brillet, 1990; Mason and Gutzke, 1990].

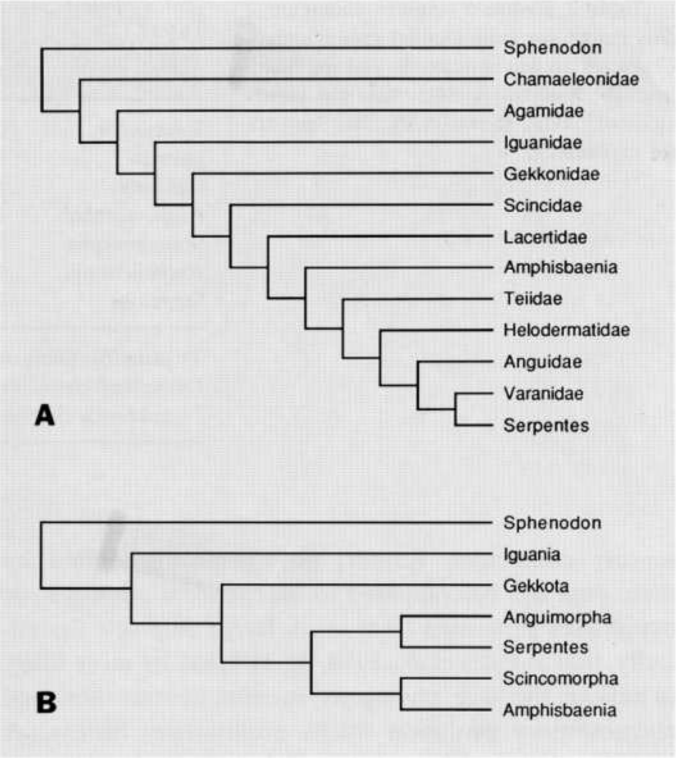


Fig. 2. Computer-generated cladograms based on chemosensory characters only. **A** One of 12 equally parsimonious trees generated by PAUP from data in table 1. All trees shared the same basic topology, differing only in details of resolution among Amphisbaenia, Teiidae and the anguimorph taxa. In all cases the anguimorph taxa cluster together, Teiidae are allied with those (amphisbaenians also in a few trees), the scincomorph families are outside those, the Gekkonidae is next outside, and the iguanian families are outside all others. Note that Iguania and Scincomorpha are not identified as monophyletic groups on the basis of chemosensory characters, but the Anguimorpha is. There is no evidence of a dichotomy in chemosensory evolution. Although all suprafamilial groups are not identified, the general pattern of relationships is remarkably similar to the hypothesis of Estes et al. [1988] (fig. 1B). Consistency index = 0.867 (0.833 excluding uninformative characters). **B** Single, perfectly parsimonious tree for suprafamilial taxa generated by PAUP based on table 2. The pattern of relationships is identical to that of Estes et al. [1988; fig. 1B], with the exception that snakes and amphisbaenians are included. Consistency index = 1.0.

21. Chemosensory detection of predators absent (0); present (1). [Bogert, 1941; Weldon and Burghardt, 1979; Thoen et al., 1986; Dial et al., 1989; Cooper, 1990a; van Damme et al., 1990].

Phylogeny as Determined by Chemosensory Characters

It is not the purpose of this analysis to generate definitive hypotheses of squamate relationships based on chemo-

Table 2. Reduced taxon-by-character data matrix for suprafamilial groups only. Character 16 was unscorable and excluded from the analysis. A single tree was generated by PAUP, shown in fig. 2B. See text for explanation

Taxon	Character																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Sphenodon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	0	0	0	0	0
Iguania	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	–	?	0	1	1	?
Gekkota	1	1	1	0	1	1	1	0	0	0	1	1	1	0	1	–	1	?	1	1	1
Anguimorpha	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	–	1	1	?	?	?
Scincomorpha	1	1	1	0	1	1	1	1	0	1	1	1	1	1	1	–	1	1	1	1	1
Amphisbaenia	1	1	1	0	1	1	1	1	0	1	?	1	1	1	1	–	1	1	?	?	?
Serpentes	1	1	1	1	1	1	1	1	1	?	1	1	1	1	1	–	1	1	1	1	1

0 = primitive character state.
1 = derived character state.
? = unknown character state.

sensory characters. Rather, phylogenies generated by these data can be compared to independent phylogenetic hypotheses generated from much larger data sets (specifically, that of Estes et al., 1988, fig. 1B) that are more likely to indicate the 'true' phylogeny, in order to assess how well chemosensory evolution tracks evolutionary history. A high correlation of hypotheses might indicate that chemosensory characters are constrained by phylogeny and are not subject to rapid, adaptive evolution in unrelated organisms with similar ecologies. Poor correlation would indicate the opposite. Thus, such a comparison helps to dissect out the relative roles of phylogeny and ecology in determining chemosensory form and function (see Discussion). Chemosensory-generated phylogenies can also be used to help affirm or reject evolutionary generalizations such as the 'visual Ascalabota vs. chemosensory Autarchoglossa'.

As noted above, preliminary analysis indicated that data for several families are too incomplete to analyze at this time (indicated by an asterisk in table 1). Those families remaining, however, represent all suprafamilial groups of Camp [1923] and Estes et al. [1988], as well as Serpentes and Amphisbaenia.

The taxon by character matrix shown in table 1 (excluding taxa with an asterisk) was analyzed on a Macintosh IIx computer using PAUP (Phylogenetic Analysis Using Parsimony), version 3.0k [Swofford, 1990]. The program identifies the most parsimonious (shortest) trees, minimizing homoplasy (parallelism and convergence) and reversals. *Sphenodon* was designated as the outgroup, and the 'branch-and-bound' algorithm was employed. Runs were initiated with multistate characters unordered in order to eliminate assumptions about the direction of character transformation, other than designation of the primitive state. The analysis resulted in 12 equally parsimonious trees. All trees shared the same basic topology, varying only slightly in the degree of resolution of terminal nodes. For the purposes of this analysis, the differences are trivial. One completely resolved tree was chosen arbitrarily for illustration (fig. 2A).

In a second stage of this analysis, I collapsed the number of taxa further, considering only the four suprafamilial groupings of Estes et al. [1988], Iguania, Gekkota, Anguimorpha, and Scincomorpha, as well as Serpentes and Amphisbaenia (table 2). This involved generalization of the data in table 1 to fewer, more inclusive taxa. I did this by eliminating multistate characters, so that derived states 1 and 2 were simply considered 'derived' and scored 1. This required the assumption that multistate characters are ordered, i.e. evolved in the sequence 0, 1, 2. I did not make this assumption in the first analysis because there is no direct evidence to support it, however, it is not unreasonable here, because in all cases such an ordering reflects the most parsimonious interpretation of a morphocline. Finally, I considered any families for which I had data to be representative of the larger group. Character 16 (olfactory epithelium development) is present in both primitive and deived states *within* the Anguimorpha and was, therefore, considered unscorable and excluded from the analysis. A single tree was obtained (fig. 2B).

The Evolution of Chemoreception as Determined by Phylogeny

In this analysis, I examined the historical origin and transformation of chemosensory characters by 'mapping' them onto an already existing, independent phylogenetic hypothesis [Estes et al., 1988]; (fig. 1B, 3). For consistency, the taxa represented in the phylogeny are restricted to those used in the first analysis, above, for which there are

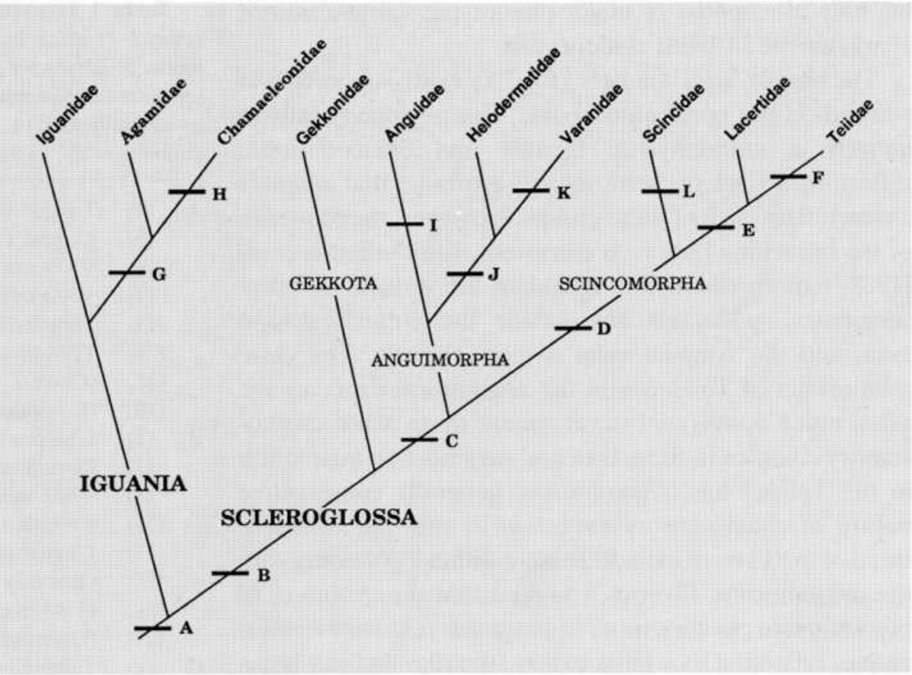


Fig. 3. Cladogram based on Estes et al. [1988; fig. 1B] showing only those taxa considered in initial computer analysis (fig. 2A). Lettered bars represent points of evolutionary origin for derived chemosensory character states indicated in table 3.

the most data. In Estes et al. [1988] snakes and amphisbaenians are placed within Squamata *incertae sedis*, hence these are not included either. The characters that evolve at each of the labelled points in figure 3 are indicated in table 3.

Discussion and Conclusions

Missing Data

The first and most obvious result of this study is its graphic revelation of a profound dearth of chemosensory data for squamate reptiles, despite the remarkable strides of recent years. Our ignorance is taxonomically biased, i.e., there are certain taxa which remain little-studied (e.g. Dibamidae, Xantusiidae, Cordylidae, Lanthanotidae, Anguidae, and Agamidae), whereas others are heavily so (Scincidae, Serpentes) (table 1). Even in well-studied groups, generic and specific coverage is spotty. For example, we know a great deal about one or two species of *Eumeces,* family Scincidae, but little about the rest of this extremely speciose and diverse family. Likewise, the pioneering work of Burghardt, Halpern and their colleagues has provided us with a wealth of detailed data for the highly derived natricine snakes, particularly the genus *Thamnophis*. It would be valuable to have comparable data for less derived snake lineages, such as the boids and typhlopids.

There is an obvious need for the reporting of negative results. Investigators are often loathe to publish negative results because they believe them to be uninteresting. It is clear in attempting to evaluate evolutionary transformations, particularly for behavioral characters, that the *failure* of a species to exhibit a behavior (for example chemical prey discrimination) is equally as significant as the presence of a behavior. Similarly, there is a need for replication of both positive and negative results, with special attention to experimental design, a weak point in many studies.

General Phylogenetic Patterns

Results of the first analysis indicate that chemosensory characters are a surprisingly good predictor of squamate phylogeny, but with notable exceptions (compare fig. 2 with fig. 1B). The suprafamilial tree (fig. 2B) agrees exactly with the Estes et al. [1988] hypothesis of relationships among these groups. Furthermore, the placement of snakes as the sister group of Anguimorpha and of amphisbaenians with Scincomorpha is consistent with several other analyses, including those of Camp [1923] and Schwenk [1988]. These results imply that, overall, the chemosensory biology of squamates is primarily a reflection of group membership and not ecological radiation (i.e. local adaptation). This further suggests that chemosensory aspects of squamate structure and function might be constrained in their evolution and ancient in their origin, evolv-