

Comparative biology and the importance of cladistic classification: a case study from the sensory biology of squamate reptiles

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Evolutionary taxonomy has all but succumbed to cladistic methodology, but it continues to exert considerable influence in the realm of higher classification. Some systematists accept cladistic methods in phylogeny inference, but allow paraphyly in formal classifications. Most important, however, many traditional classifications based on paraphyletic groups (e.g. 'Reptilia') remain in force, deeply entrenched in the literature. Cladists have argued that such paraphyletic classifications can mislead comparative biologists into false evolutionary generalizations, but this assertion has rarely, if ever, been supported by example. This paper provides a case study, illustrating in detail the influence of a traditional paraphyletic classification of squamate reptiles on the historical development of ideas regarding the evolution of sensory modes (chemoreception vs. vision) in the group. The paraphyletic classification is shown to have led to false generalizations and incorrect conclusions stemming directly from the fact that the classification did not reflect accurately the phylogeny of Squamata, particularly the cladistic relationships of Gekkota. This study provides direct evidence that evolutionary generalization must be rooted in the branching pattern of phylogeny and not the potentially arbitrary categorical ranks of traditional taxonomies. It further supports recent calls for a truly phylogenetic taxonomy that has as its philosophical core the concept of descent.

ADDITIONAL KEY WORDS:—Reptilia – Squamata – Evolution – Systematics – Taxonomy – Cladistics – Paraphyly – Chemoreception.

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... a good classification, like a theory, permits one to make 'predictions'. [Mayr and Ashlock, 1991: 125]

Camp's major division of the Sauria has thus passed one of the tests of classification—it has proven to have predictive value. [Underwood, 1971: ix]

It is obvious that groups held to be equal or dichotomous on the basis of classification may not have had an equal extent of geologic history, and when it is intended to illustrate this history simultaneously with the classification some difficulties present themselves. [Camp, 1923: 336].

INTRODUCTION

Systematic biology, in its narrow sense, has three overlapping charges: the naming of species, their classification, and the reconstruction of their phylogenies. The first of these pursuits is little changed since Linnaeus, but the manner in which the latter two are undertaken depends on the school of thought to which an investigator adheres: phenetics, evolutionary taxonomy or cladistics (e.g. Wiley, 1981; Ridley, 1986; Mayr & Ashlock, 1991). These have been admirably reviewed by these authors and others, and it is not the purpose of this paper to discuss their various merits and deficiencies. Rather, I focus on, perhaps, the most contentious aspect of the controversy, namely criteria on which we base organismal classifications in light of recovered phylogenies.

Purely phenetic classification has fallen into ill favour among most systematists owing largely to its failure to differentiate among similarity stemming from convergence, similarity stemming from retention of ancestral attributes, and similarity stemming from shared evolutionary novelty uniquely evolved in a common ancestor (homoplasy, symplesiomorphy and synapomorphy, respectively, in cladistic parlance). Arguably, the greatest contribution of cladistics is its recognition that phylogeny can only be inferred from synapomorphy (e.g. Wiley *et al.*, 1991). Early evolutionary taxonomists used a more informal method of phylogeny reconstruction that did not explicitly exclude symplesiomorphy (e.g. Simpson, 1945); however, recent workers have accepted the central role of synapomorphy in phylogenetic inference (e.g. Mayr, 1981). Therefore, in their current incarnations, the schools of evolutionary taxonomy and cladistics (*sensu* Hennig, 1966) differ little or not at all in the way in which species are named and phylogenies reconstructed. However, when constructing a classification based on a phylogeny so-inferred, they may be at odds in their choice of criteria on which to base supraspecific taxa.

Cladists argue that classifications and named taxa should reflect evolutionary entities and therefore rely only on the branching pattern of the phylogeny. Every named taxon will, therefore, be monophyletic. All other aspects of phenotypic evolution, such as rate and degree of divergence from a common ancestor, while interesting, are of secondary importance (Ridley, 1986). This convention allows any investigator to extract accurate information about a phylogeny from the classification. In contrast, evolutionary taxonomists such as Mayr (1974, 1981) and Mayr & Ashlock (1991) believe that a classification should contain information in addition to the branching pattern of phylogeny. They might emphasize some aspect of phenotypic evolution, usually the relative degree of morphological divergence among lineages, by formally recognizing a paraphyletic taxon (a lineage containing an ancestor and some, but not all of its descendants). The classic example of this practice and its difference from cladistic classification is the treatment of birds and reptiles (Fig. 1). The evolutionary taxonomist's notion of a reptile excludes birds because birds, have, in their view, diverged so radically from conventional reptiles (e.g. they have

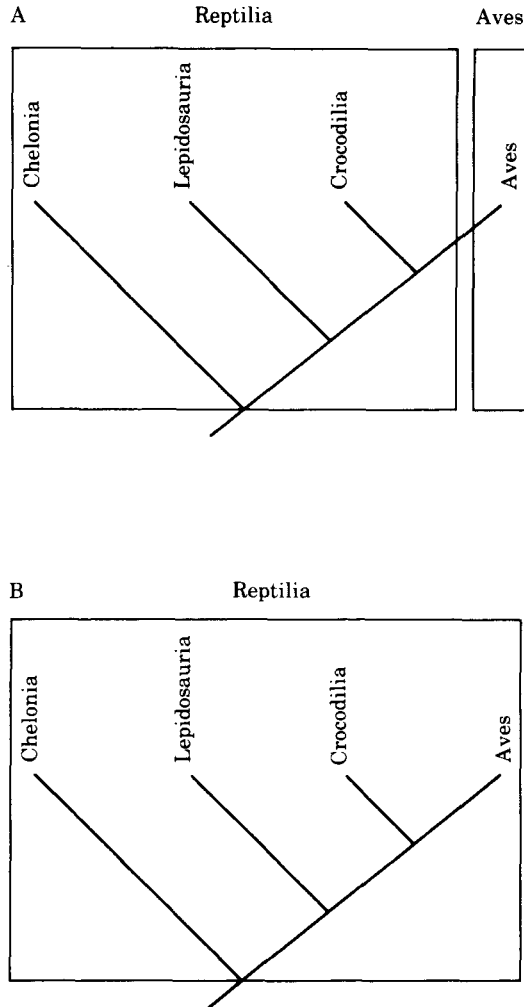


Figure 1. The phylogeny of living reptiles and a classic example of evolutionary versus cladistic classification. (A) an evolutionary-taxonomic classification; (B) a cladistic classification. Note that the evolutionary classification assumes that the ancestors of birds were reptiles, but the precise point along the clade where this transformation occurred is unspecified. The situation is actually more confusing than shown, because if the next outgroup, Synapsida/Mammalia, were illustrated, the polygon enclosing the paraphyletic 'Reptilia' would become more complex, including the base of the mammal stem (Synapsida, considered to be reptiles) but not its terminal end (Mammalia).

feathers, they fly, they are endothermic, etc.) with which they share a common ancestor. The formal taxon Reptilia in such a scheme is paraphyletic because it excludes one descendant lineage, the birds. Birds are accorded their own taxon (*Aves*) of equal rank as Reptilia. The cladistic taxon Reptilia must include birds because they share a common ancestor with all the other, traditionally named reptilian taxa. Hence birds are regarded as a specialized subset of reptiles and are named as such (e.g. Rowe, 1986). The potential problem explored in this paper is that, to a naive investigator, lizards and crocodylians must appear more closely related than either is to birds. Can this false notion mislead his or her evolutionary conclusions?

Classifications, like language, not only reflect our thought, but direct and constrain it (Harvey and Pagel, 1991; Woese, Kandler & Wheelis, 1991). The reason for this is simply that *many comparative biologists rely on classifications and not phylogenies* to shape their evolutionary and functional generalizations. Can a non-cladistic classification, in fact, misdirect biological generalization? In this paper I document one such case taken from the literature on the sensory biology of squamate reptiles (lizards, snakes and their allies). I show that a traditional, evolutionary-taxonomic (paraphyletic) classification of squamate reptiles has resulted in false generalizations regarding the sensory biology of the group; in particular it has contributed to the mischaracterization of one speciose lineage, the Gekkota, despite the existence of contradictory evidence.

This case study serves two purposes: first, it provides systematists with a concrete example illustrating the pitfalls of non-cladistic classification, pitfalls feared and alluded to by proponents of cladism (e.g. Harvey & Pagel, 1991; 52), but rarely, if ever, documented. Second, it provides a cautionary tale to all comparative biologists, pointing to the need to use phylogenies and not classifications in evolutionary analyses, and to reconsider resistance to cladistic revisions of traditional taxonomies.

SQUAMATE CLASSIFICATION AND PHYLOGENY: BACKGROUND

In 1923 Camp published his classic monograph on the relationships of the lizards. This study has remained the basis for our understanding of squamate relationships until very recently. Camp was a product of his time, so it is not surprising that his classification is in conflict with the cladistic relationships expressed in his own published phylogeny (Fig. 2A). He divided squamates into two 'Divisions,' the Ascalabota and the Autarchoglossa. His Ascalabota contained the clades Iguania and Gekkota (the latter containing, at the time, only the single family Gekkonidae). In so doing, Camp (1923) was fully aware that gekkotans were more closely related to Autarchoglossans than to Iguanians and that Ascalabota represented, in modern terminology, a paraphyletic group. He chose to emphasize in his classification the retention by both iguanians and gekkotans of certain primitive morphological states.

Using a larger data set and cladistic methodology, Estes, de Queiroz & Gauthier, (1988) re-examined squamate relationships. Remarkably, their phylogeny does not differ substantively from that of Camp (1923) (Fig. 2). In their cladistic classification, Estes *et al.* (1988) abolished Ascalabota as a formal taxon, recognizing the sister relationship between Gekkota and Camp's Autarchoglossa, and referred to this inclusive clade as 'Scleroglossa' (Fig. 2b). Their classification reflects the basal dichotomy between the clade Iguania and the remaining squamates, the Scleroglossa.

Kluge (1989) reanalysed Estes *et al.*'s (1988) data and found that there is more ambiguity in relationships among some scleroglossan taxa than originally suggested, but he confirmed the Iguania-Scleroglossa dichotomy. This dichotomy was also independently corroborated by Schwenk (1988). There is some evidence that two of the three nominal 'families' of Iguania are themselves paraphyletic (Frost & Etheridge, 1989), but the evidence is equivocal and is not relevant to the ensuing discussion. For clarity these taxa (Iguanidae and Agamidae) are treated here as if monophyletic.

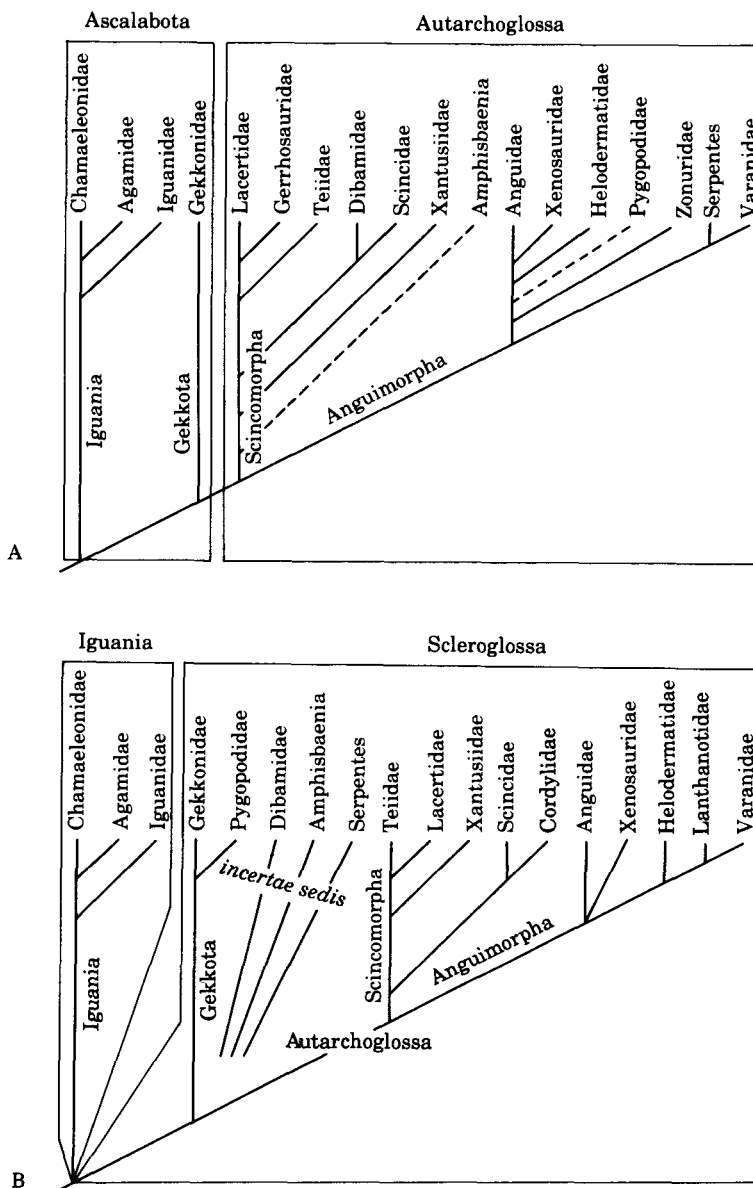


Figure 2. (A) Camp's (1923) phylogeny of squamate reptiles and his evolutionary classification of same. Note that Ascalabota is paraphyletic, containing the Gekkonidae, sister group of the Autarchoglossa. Zonuridae = Cordylidae; (B) Estes, de Queiroz & Gauthier's (1988) cladistic phylogeny and classification. The taxon Scleroglossa is monophyletic, including Gekkota plus Autarchoglossa. Note that the taxa are defined on the basis of *lineages*, a common ancestor and its descendants, thus obviating the confusion caused by an anagenic transition from one form to another (e.g. 'reptile' to bird, or 'reptile' to mammal).

Finally, I note, because it becomes significant in the discussion below, that Camp (1923) made two undoubted errors in his taxonomic assignments: inclusion of the Pygopodidae and Zonuridae (Cordylidae) in the Anguimorpha (Fig. 2A). These taxa are now established unequivocally as the sister taxa of

Gekkonidae and Scincidae, respectively (e.g. Estes *et al.*, 1988 and references therein). Indeed, pygopodids may be derived from *within* Gekkonidae (Kluge, 1987). Salient here is the recognition that change in the placement of the Pygopodidae resulted in its transfer from Camp's (1923) Autarchoglossa to his Ascalabota.

Until publication of the Estes *et al.* (1988) phylogeny and classification, and for a year or two after, nearly all workers in squamate sensory biology turned to Camp (1923) for evolutionary interpretations of their work. Unfortunately, virtually all such workers (cited below) referred not to Camp's (1923) phylogeny, but to his classification, specifically to his dichotomous division of the group into Ascalabota and Autarchoglossa. These investigators failed to make the distinction between classification and phylogeny and either did not realize the paraphyletic nature of Ascalabota or did not recognize its significance to the interpretation of their results. Below I discuss examples of this work, emphasizing development of ideas regarding the evolution of sensory modalities among squamates, in particular chemoreception and the biology of gekkotans.

SQUAMATE CHEMORECEPTION: BACKGROUND

The chemical senses of squamate reptiles have been ably reviewed elsewhere (e.g. Burghardt, 1980; Simon, 1983; Halpern, 1992). It is sufficient to note here that most squamates have recourse to at least three different chemosensory systems: gustation, olfaction and vomerolfaction. Gustation is the sense of taste, a plesiomorphic attribute of vertebrates and one for which little information is available for squamates (Schwenk, 1985, 1993b). A growing body of circumstantial evidence suggests, however, that its primary role is in determining palatability of food once it is held within the mouth. As such, gustation might mediate learned behaviour related to food preference (e.g. Burghardt, Wilcoxon & Czaplicki, 1973; Schwenk, 1985, 1986, 1993b). Olfaction and vomerolfaction represent the chemical senses of the nasal capsule, and refer to stimulation of the sensory epithelia of the nasal chamber *sensu stricto* and the vomeronasal (Jacobson's) organs, respectively. Olfaction, like gustation, has received little attention in squamate biology (Schwenk, 1993a) and is, therefore, difficult to evaluate functionally and phylogenetically. Vomerolfaction, however, has been the subject of extensive experimental and behavioural investigation (see Halpern, 1992). It is highly developed in many squamates, as in many mammals, and is associated, in squamates, with a unique form of chemical sampling, tongue-flicking. During chemosensory exploration, the tongue is protruded from the mouth and in some species, oscillated (e.g. Gove, 1979). It usually contacts another individual, an object, or the substrate, but it might not. The mechanism by which molecules so-retrieved are delivered to the vomeronasal organs is not yet fully understood (e.g. Halpern, 1992; Young, 1993).

Vomeronal and nasal olfactory sensory cells project, respectively, to the accessory and main olfactory bulbs of the telencephalon. Their pathways remain almost entirely distinct throughout the brain (Lohman & Smeets, 1993). This anatomical segregation is reflected in functional partitioning of the two systems: (1) nasal olfaction is a more general sense sensitive to volatile chemicals and operating over large distances. It is implicated in food and predator detection in

some species (Schwenk, 1993a), but it may be most important as a general exploratory sense that, along with vision, triggers tongue-flicking and vomerolfaction (e.g. Cowles & Phelan, 1958; Duvall, 1981; Halpern, 1992; Graves, 1993); (2) vomerolfaction seems most important in sensing more proximate and circumscribed chemical sources of lower volatility. It is clearly important in species and sex discrimination, sexual behaviour, and investigation of novel stimuli, in general. Vomerolfaction may have additional functions, particularly in snakes (e.g. Burghardt, 1970, 1980; Simon, 1983; Halpern, 1992).

CLASSIFICATION AND CHEMORECEPTION

A conflation and its consequences

The cladistic classification of Squamata reflects a nested hierarchy of taxa in contrast to Camp's (1923) fundamental dichotomy. As currently conceived, the sensory biology of squamates is more accurately represented by the former than the latter. As such, there is no obvious dichotomy in sensory modes, only lineage-specific combinations of traits expressing a continuum, of sorts (Schwenk, 1993b). It is now clear that the gekkotans (Gekkonidae and Pygopodidae) are highly chemosensory and in most details are more similar to their fellow scleroglossans than they are to iguanians (Schwenk, 1993a, b). It is particularly this relationship, cladistic and biological, that is misrepresented by Camp's (1923) association of gekkotans with iguanians in an inclusive, paraphyletic taxon, Ascalabota. And it is this misrepresentation, I argue below, that has particularly misled comparative biologists who have followed Camp's classification.

Although the basis for Camp's (1923) division of squamates into Ascalabota and Autarchoglossa was anatomical, he recognized some correlates. The principal dichotomy noted by Camp was the presence among autarchoglossans of many limbless forms and the absence of such forms among ascalabotans. He believed that limblessness in the Autarchoglossa was 'permitted' by the presence of a particular abdominal muscle and that the absence of this muscle in the Ascalabota precluded limblessness as a viable evolutionary strategy. According to Camp, the ascalabotan condition arose as a result of arboreal and climbing specialization with concomitant reduction of axial locomotory musculature. Thus we see in Camp (1923: 385) the first expression of a biological dichotomy based on his own paraphyletic classification: ascalabotans as largely arboreal, or at least, climbing lizards and autarchoglossans as terrestrial lizards tending toward "worm-like burrowing, or a limbless, snake-like, grass-living habitus."

Camp (1923) made no reference to chemoreception, although he has been incorrectly attributed with this connection (e.g. Simon, 1983). He believed, like most others at the time, that tongue-flicking was a tactile, not a chemosensory, behaviour (see Camp, 1923: 374).

Twenty-five years later, Pratt (1948) published a comparative study of the lizard nasal capsule and the relative development of the olfactory and vomeronasal organs. He made no reference to Camp's (1923) classification, focusing instead on the relationship between nasal capsule form (i.e. chemosensory development) and *habitat*. Pratt (1948: 183) suggested that there is a trade-off between 'eye specialization' and development of the olfactory

chamber owing to space limitation in the head, erroneously believing that an increase in visual ability must be linked to an increase in eye size. He then went on to discuss the relationship between habitat and vomeronasal development (p. 184):

Jacobson's organ is a specialized part of the olfactory apparatus associated with a ground living-existence. . . . The degree of specialization varies within the lizards and can be classified according to the functioning mechanisms. . . . In arboreal forms the organ loses its importance in the life of the lizards, and as a consequence becomes very reduced—as in some agamids, non-sensory—as in *Anolis*, or completely absent—as in chameleons. . . . Scansorial lizards have a Jacobson's organ whose development is intermediate between the conditions in terrestrial and arboreal lizards.

Thus we see in Pratt (1948) the establishment of two generalizations: (1) there is a trade-off between vision and chemoreceptions; and (2) arboreality is associated with an increase in vision and therefore, a decrease in chemoreception, whereas terrestriality is associated with a reliance of chemoreception.

Given first Camp's (1923) dichotomous classification (*Ascalabota* vs. *Autarchoglossa*), second, his generalization of this to include arboreality vs. terrestriality (arboreal *Ascalabota* vs. terrestrial/fossorial *Autarchoglossa*), and third, Pratt's (1948) association of habitat with sensory modality (visual arboreal species vs. chemosensory terrestrial/fossorial species), it was perhaps inevitable that classification and sensory modality would ultimately be linked (*visual Ascalabota* vs. chemosensory *Autarchoglossa*). I find this syllogism first expressed in Underwood (1951: 184):

Camp divides the lizards into two groups: the *Ascalabota* and *Autarchoglossa*. He points out that the *Ascalabota* show a strong tendency towards an arboreal habit and no tendency towards reduction of the limbs. On the other hand, the *Autarchoglossa* show relatively slight arboreal tendencies, but a pronounced tendency towards reduction of the limbs. . . . It may be pointed out that the *Ascalabota* are sight feeders and as such seem to be relatively little dependent on Jacobson's organ in the finding of food. . . . On the other hand, the *Autarchoglossa* show a strong tendency for smell to supersede sight as the important sense in food-finding, with corresponding elaboration of Jacobson's organ. Speaking generally, autarchoglossids which tend towards secretive habits rely more than ever on the sense of smell, with consequent further reduction in the relative importance of the eye. . . . The pygopodids and the snakes are perhaps exceptions to this generalization.

Once the initial syllogism was made, linking Camp's (1923) classification and sensory modality, subsequent reviews and general statements reiterated and reinforced this generalization. However, a natural consequence of such serial citation is a certain amount of information decay and a tendency to over-generalize. For example, most of the earlier formulators of the biological generalizations were aware of exceptions. Camp (1923: 335) himself only meant his arboreal vs. terrestrial dichotomy as an expression of evolutionary 'tendencies' within groups, noting, for example, that "many permanently arboreal lizards are developed among both of the divisions." Likewise, Pratt (1948) admitted that scansorial (rock-climbing) lizards formed an intermediate class between his visual arboreal forms and chemosensory terrestrial forms (see quote above). Underwood (1951) pointed out that pygopodids and snakes were exceptions to his generalization (quote above), and Evans (1961, 1967) singled

out gekkonids as exceptions, noting that, though ascalabotans, they are nevertheless highly chemosensory. Despite these cautionary statements, most subsequent studies fail to mention them, relying primarily on previous reviews. For example, Bogert & Martin del Campo (1956: 103) reiterated Underwood's (1951) statement (but without noting exceptions). Madison (1977: 150) relied heavily on Evans' (1961, 1967) generalizations: "An excellent review by Evans (1961), and a subsequent update (Evans, 1965 [sic]), form a good starting point for a consideration of chemical communication in the lizards." Underwood (1971: viii-ix) made one of the most all-inclusive statements linking Camp's (1923) divisions to sensory mode and many other aspects of squamate biology, including tongue form, direction of evolutionary transformation, terrestrial vs. aquatic habitats, sexual dimorphism and dichromatism, and pituitary development. He concluded with the assertion quoted at the beginning of this paper, that Camp's (1923) divisions has passed the test of classification; they have predictive power. Underwood's (1971) paper was published as an introduction to a reprint of Camp's (1923) monograph and this juxtaposition with Camp's classification makes it a particularly powerful statement. More recently, Simon (1983: 129-130) stated the dichotomy clearly:

The importance of the vomeronasal system varies somewhat with taxonomic affinities of lizards. Camp (1923) divided lizards into two major groups, the ascalabotans (Chamaeleonidae, Agamidae, Iguanidae, Gekkonidae and Xantusiidae) and the autarchoglossans (Lacertidae, Scincidae, Teiidae, Cordylidae, Helodermatidae, Varanidae and all other lizard families)... The ascalabotans seem to rely most heavily upon vision, whereas most autarchoglossans use both vision and chemoreception (Camp, 1923; Evans, 1961, 1967; Underwood, 1970; Bissinger & Simon, 1979; Duvall, 1980; Duvall, Herskowitz & Trupiano-Duvall, 1980).

In a recent and thorough review, Halpern (1992: 426) reiterated Simon's (1983) phylogenetic conclusions.

Although I have focused on influential reviews above, the same problem is repeated in the primary literature. Once established in the literature, the dichotomy of a visual Ascalabota and a chemosensory Autarchoglossa quickly became the organizing evolutionary framework within which authors interpreted their studies (e.g. Underwood, 1970; Stamps, 1977; Bissinger & Simon, 1979; Duvall *et al.*, 1980; Duvall, 1981; Cooper, 1981, 1989a, 1989b, 1990a; Nicoletto, 1985; Simon & Moakley, 1985; Mason & Gutzke, 1990).

While information decay is certainly not an outcome peculiar to paraphyletic classifications, there is likely to be a certain sensitivity to starting conditions. A cladistic classification might have mitigated the effects of this decay by providing a more accurate starting point and by eliminating at the outset some of the taxonomic exceptions required by early workers. In any case, the salient result of this process was a poorly supported dogma and eventually, confusion.

Confusion

Several factors have conspired to create confusion regarding the evolution of sensory systems in Squamata. First, as noted above, the original formulators of the generalizations under discussion here, as well as many subsequent workers, have noted exceptions and qualifications, but these have been only sporadically

noted in the literature. Second, the constituent families of the Ascalabota and Autarchoglossa have changed over the years as additional systematic work has been completed (e.g. Pygopodidae is included in Gekkota in studies since Camp, as is Xantusiidae in some). Third, the primary literature on squamate sensory biology has focused on different behaviours, e.g. predatory behaviour, courtship behaviour, kin recognition, conspecific recognition, heterospecific identification, predator detection, aggregation, etc. (see Halpern, 1992). Thus the data available for different taxa vary both qualitatively and quantitatively, further confounding attempts at generalization (Schwenk, 1993b). The chemosensory literature has been varyingly successful at incorporating these changes; however, there has been a general failure to reject the basic dichotomy. Rather, some workers have attempted to retain the dichotomy while simultaneously incorporating the rapidly accumulating modifications and exceptions. For example, Nicoletto (1985: 411) attempted to assimilate the growing body of chemosensory data into the flawed dichotomy:

The importance of chemosensation is associated with the major subdivision of lizards, the Ascalobota [sic] and the Autarchoglossa (Stamps, 1977). Ascalobotans (e.g., Agamidae, Chamaeleonidae, Gekkonidae, Iguanidae and Xantusiidae) have blunt tongues, low rates of tongue flicking (RTF) and generally use visual cues to mediate social behavior and predation (Bissinger & Simon, 1979; Burghardt, 1970; Reznick *et al.*, 1981). However, some iguanids use chemical cues to detect conspecifics (Duvall, 1979, 1981) and geckos may use chemical cues to detect prey (Dial, 1978), thus demonstrating that chemosensation may be used by ascalobotans. Autarchoglossan lizards (e.g. Anguidae, Lacertidae, Teiidae, Scincidae and Varanidae) have slender modified tongues (forked to varying degrees), high RTF, and use both visual and chemical cues to mediate social and predatory behavior (Burghardt, 1970, 1980; Duvall *et al.*, 1980; Perrill, 1980). Although autarchoglossan lizards use both visual and chemical cues during predation, the manner in which these cues interact to initiate predatory behavior is unknown.

Cooper, (1989a: 472) similarly attempted to reconcile the existing dichotomy with new behavioural data and also alluded to a growing dissatisfaction with the traditional classification. Apparent in both papers, and elsewhere, is the recognition, first, that the sensory biology of squamates does not break down neatly into a dichotomy, and second, that the dichotomous classification is, itself, suspect. One wonders why these observations, combined with the often noted exceptional nature of gekkotans as highly chemosensory ascalobotans, did not trigger sooner a rejection of the original hypothesis of a visual Ascalabota and a chemosensory Autarchoglossa. Rather, there is repeated retention of this original association. Such is the power of a classification.

Resolution

Estes *et al.* (1988) made available a cladistic reanalysis of relationships among the squamate families (Fig. 2B). Perhaps of most importance to the non-systematic community was its explicit formulation of a cladistic classification (see above) reflecting the sister relationship between the Gekkota (Gekkonidae + Pygopodidae) and the Autarchoglossa (retaining, essentially, Camp's (1923) constituent taxa), by including these together in the monophyletic taxon, Scleroglossa. A phylogenetic dichotomy is therefore evident

between the *Iguania* and the *Scleroglossa*. This phylogenetic information has forced a new interpretation of the available data (e.g. Schwenk, 1993b). In many cases, original conclusions are corroborated, in others they are suspect. The principal difference communicated by the monophyletic taxon 'Scleroglossa' versus the paraphyletic taxon 'Ascalabota' is the clarification of gekkotan affinities. Recognition that gekkonids are allied with autarchoglossans and not iguanians immediately obviates the need to view them as aberrant ascalabotans whose chemosensory prowess requires some sort of special evolutionary explanation (usually nocturnality). Rather, they are typical scleroglossans that utilize both visual and chemosensory information in directing their behaviour. Indeed, such a cladistic view unifies and organizes the growing number of observations that indicate the importance of chemosensory-directed behaviour in gecko biology (see Schwenk, 1993a for a summary and references). Thus in a recent paper Cooper (1990b: 535), could write that studies of prey discrimination in geckos contradict the notion of 'Ascalabota', but are consistent with the cladistic taxon *Scleroglossa*.

In a cladistic context, false generalizations are recognized as such and their apparent contradictions and exceptions dissolve. First, inclusion of the *Pygopodidae* within *Gekkota* (and therefore *Ascalabota*) eliminates the principal basis of Camp's (1923) classification as well as his functional dichotomy: pygopodids and some geckos retain the abdominal muscle thought by Camp (1923) to be lost in ascalabotans (Hoffstetter, 1962; Kluge, 1976) and the pygopodids have become virtually limbless. Second, Pratt's (1948) habitat/sensory mode dichotomy is seen to be based on examination of too few taxa. He generalized from several highly arboreal taxa, all of which have secondarily reduced their chemosensory abilities (Schwenk, 1993b). Consideration of highly arboreal forms such as *Iguana* and the *Gekkonidae* in general falsifies his association between habitat and chemoreception (Alberts, 1993; Schwenk, 1993a, b). Third, since the work of Duvall (1979, 1981) it has become increasingly apparent that chemoreception is commonplace in iguanid behaviour (see also Kjekorian, 1989; Cooper & Alberts 1991, among others). Conversely, since Burghardt's (1970) review, evidence has been readily available on the importance of visual cues in directing autarchoglossan behaviour. These factors analysed in light of phylogeny reveal not a dichotomy between sensory modalities, as suggested by Underwood (1951), but a continuum among squamate families, with specialization evident within certain lineages (Schwenk, 1993a, b). In a cladistic context, each of the initial generalizations is falsified, and the original syllogism negated.

Conclusions

It is the goal of any nomothetic discipline, such as evolutionary biology, to seek generalizations and a good classification can be the starting point for such generalizations. However, if a classification is built upon a circumscribed phenotypic category, then associations based on criteria other than those on which the classification is based will nearly always err. I agree with Mayr & Ashlock (1991), quoted at the outset of this paper, in suggesting that a *good* classification will have predictive power, but I vehemently disagree with them in suggesting that a classification with paraphyletic taxa is good in this sense.

Certainly, Underwood (1971) was wrong in suggesting that Camp's (1923) classification of squamates has passed the critical test of predictive power. Rather, I submit that Camp's (1923) paraphyletic classification has hindered and falsely constrained our elucidation of squamate evolution, not enhanced and accelerated it. I further suggest that the availability of a cladistic classification and its incorporation into the non-systematic literature would have obviated many of the flawed associations and generalizations posited at the outset of sensory studies and then promulgated through time. In particular, a cladistic classification would have suggested the natural association between gekkotans and autarchoglossans and, on the basis of their shared ancestry, is more likely to have led to correct predictions regarding their biology.

As a final testament to the power of a classification to influence our interpretations, even in the face of contradictory evidence, I offer the following passage from Malan (1946: 124). Malan (1946) studied the comparative anatomy of the squamate nasal capsule and hence provided an early study of significance to chemosensory biology. She was, unfortunately, so influenced by Camp's (1923) classification that she contradicted herself and her own findings, unwittingly helping to hatch the nascent visual-chemosensory dichotomy. I have quoted this passage elsewhere (Schwenk, 1993b), but it is particularly significant in the present context:

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 the remaining 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].

Is it insufficient to suppose that comparative biologists who have not consulted an explicit phylogeny are guilty of poor science. Phylogenetic awareness outside of systematic biology is a recent phenomenon (e.g. Harvey & Pagel, 1991). Therefore, it is incumbent on systematists to provide classifications that contain information most likely to lead to correct interpretations of comparative data. The information that will most often lead to such interpretations is an exact knowledge of the branching pattern of phylogeny, and only a cladistic classification can communicate this to the majority of workers in evolutionary biology. Conversely, comparative biologists must seek out phylogenies and not classifications to shape their evolutionary generalizations. Finally, it is worth noting that many of the difficulties discussed in this paper arise from an innate conflict between the nested nature of phylogenetic hierarchies and the Linnean system of equal, categorical ranks. Recently, a formal system of phylogenetic taxonomy has been proposed (de Queiroz & Gauthier, 1990; 1992; de Queiroz, 1992) that would obviate this conflict and move us towards a taxonomy that is rooted in evolution. Such a system should be embraced by all comparative biologists.

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