

POINTS OF VIEW:

EDITOR'S NOTE.—The following three papers are a discussion of the evolution of viviparity and egg-guarding in squamate reptiles.

A REANALYSIS OF THE EVOLUTION OF VIVIPARITY
AND EGG-GUARDING IN SQUAMATE REPTILES

RICHARD SHINE AND MICHAEL S. Y. LEE¹

¹*School of Biological Sciences, Zoology Building A08, The University of Sydney, NSW 2006, Australia*

ABSTRACT: A recent publication (de Fraipont, Clobert, and Barbault—*Evolution* 50:391–400, 1996) reached two heterodox conclusions concerning the evolution of reproductive modes in squamate reptiles. Firstly, “reversals” from viviparity back to oviparity have been almost as frequent as “forward transitions” of oviparity to viviparity. Secondly, maternal egg-guarding has not facilitated the evolution of viviparity. However, methodological problems in the analysis make these conclusions tenuous. In particular, the analysis (1) relied upon poorly supported (as well as strongly supported) transitions, (2) counted particular transitions more than once, (3) placed too much emphasis on differences between very distantly related higher taxa, and (4) contained consistent biases in the raw data, so that many egg-guarding taxa must have been incorrectly scored as lacking egg-guarding. A reanalysis of the (family-level) data reveals little support for reversals from viviparity back to oviparity while the relationship (if any) between egg-guarding and viviparity cannot be ascertained without additional data.

Key words: Squamates; Viviparity; Oviparity; Phylogeny; Egg-guarding; Reproduction

EVOLUTIONARY transitions in reproductive mode (e.g., from egg-laying to live-bearing) have occurred far more frequently in snakes and lizards than in any other vertebrates (e.g., Blackburn, 1982, 1985; Shine, 1985). Thus, the selective forces responsible for these life-history transitions have attracted considerable scientific attention (e.g., Packard et al., 1977; Shine and Bull, 1979; Tinkle and Gibbons, 1977). Recently, a detailed study by de Fraipont et al. (1996) assessed the frequencies of evolutionary transitions between the three reproductive modes in squamates: oviparity, oviparity with maternal egg-guarding, and viviparity (“viviparity” in this context includes all live-bearing species, regardless of the degree of placentotrophy). They assembled published phylogenies for reproductively trimodal squamate lineages, scored taxa for reproductive mode, optimized reproductive mode onto these phylogenies using parsimony, and calculated the frequencies of each type of transition. The analysis yielded two main results, both of

them in strong disagreement with conclusions reached by previous studies on this topic. (1) “Reversals” from viviparity back to oviparity are almost as frequent as “forward transitions” of oviparity to viviparity (42 versus 50 cases, respectively), suggesting that the widely held view of irreversibility of the oviparity–viviparity transition is in serious error. This conclusion from de Fraipont et al.’s work has been cited in more recent studies (e.g., Creer et al., 1997; Gans, 1996) as intriguing evidence for the reversibility of the evolution of viviparity. (2) Egg-guarding oviparous taxa give rise to viviparous forms in only a very small number of lineages ($n = 4$ transitions), casting doubt on the hypothesis that maternal nest-attendance facilitates the evolution of viviparity (Shine and Bull, 1979).

We show below that the analysis of de Fraipont et al. (1996) contains methodological problems and that, when the data are analyzed correctly, neither conclusion is strongly supported. More generally, our study reveals that application of phylogenetically based methods can yield spurious conclusions if the inferred transitions have

¹ PRESENT ADDRESS: *Department of Zoology, University of Queensland, Brisbane, QLD 4072, Australia.*

little empirical support and the data base contains consistent biases. In our paper, as in that of de Fraipont et al. (1996) and most other phylogenetic analyses of morphological and ecological data, parsimony-based models of evolution are adopted. The reconstruction of character state changes will differ if less widespread models, such as maximum-likelihood (common in molecular analyses), are used.

THE EVOLUTION OF OVIPARITY FROM VIVIPARITY

A few authors have argued that reptilian phylogeny includes occasional cases of "reversals" from oviparity to viviparity, either very early in the history of the squamates (e.g., Aoki, 1995; Webb and Cooper-Preston, 1989) or within family-level groups (e.g., van Wyk and Mouton, 1996). However, most workers have either assumed that oviparity is the ancestral state, with little possibility of reversal after viviparity arises, or have concluded that phylogenetic evidence gives no clear evidence of any such reversal (e.g., Blackburn, 1982, 1985; Packard et al., 1977; Shine, 1985; Tinkle and Gibbons, 1977). Why does the analysis by de Fraipont et al. yield such a different result? The apparently high frequency of "reversals" (from viviparity to oviparity) is due to two problems: (1) failure to distinguish strongly supported changes from transitions with little empirical support and (2) inadequacies in the data set.

(1) Poorly Supported Transitions

The frequencies of transitions reported by de Fraipont et al. contain many poorly supported instances because of four methodological problems.

(a) First, the maximum number of transitions possible in each optimization was counted, rather than the number unequivocally supported. For example, the MacClade program (Maddison and Maddison, 1990) used by de Fraipont et al. optimizes reproductive mode on the branches of the cladogram of Underwood (1971) in four equally parsimonious ways (differences restricted to changes within terminal taxa are not considered "different" optimizations by MacClade). One of the four

optimizations is shown in Fig. 1: oviparity to viviparity transitions occur on the branches leading to feyliniids and the annielline-xenosaurid clade. However, even on this single optimization, the maximum and minimum numbers of transitions inferred to have occurred depend on how one interprets transitions within trimodal terminal taxa. Up to nine oviparity without egg-guarding (hereafter simply referred to as "oviparity") to viviparity transitions *might* have occurred: in feyliniids, in the annielline-xenosaurid clade, and within gekkonids, agamids, chamaeleonids, scincids, cordylids, lacertids, and anguids. However, only six of these *must* have occurred (assuming this particular optimization is correct—see next point): the transitions in feyliniids, in the annielline-xenosaurid clade, and within agamids, chamaeleonids, lacertids, and cordylids. The postulated direct transitions from oviparity to viviparity within reproductively trimodal terminal taxa (scincids, gekkonids, and anguids) might not have occurred if one assumes that in each taxon reproductive mode changed from oviparity to egg-guarding, and then from egg-guarding to viviparity. Similarly, up to six transitions from oviparity to egg-guarding *might* have occurred under this particular optimization: within iguanids, gekkonids, teiids, scincids, and anguids. However, only two of these *must* have occurred: the transitions within iguanids and teiids. The other transitions do not occur unless particular patterns of changes within trimodal taxa are assumed. If we are to make robust inferences about changes in reproductive mode, we should count only the transitions that are unequivocally supported, as opposed to merely allowed, by the data. However, de Fraipont et al. use the latter approach, and thus accept many poorly supported transitions as well as robustly supported ones.

To clarify the magnitude of this effect, we repeated the family-level analyses of de Fraipont et al. Using the same trees that they used (their Table 3), with the following exceptions: (1) McDowell (1987) did not publish a cladogram, and we were unable to extract a well resolved phylogeny

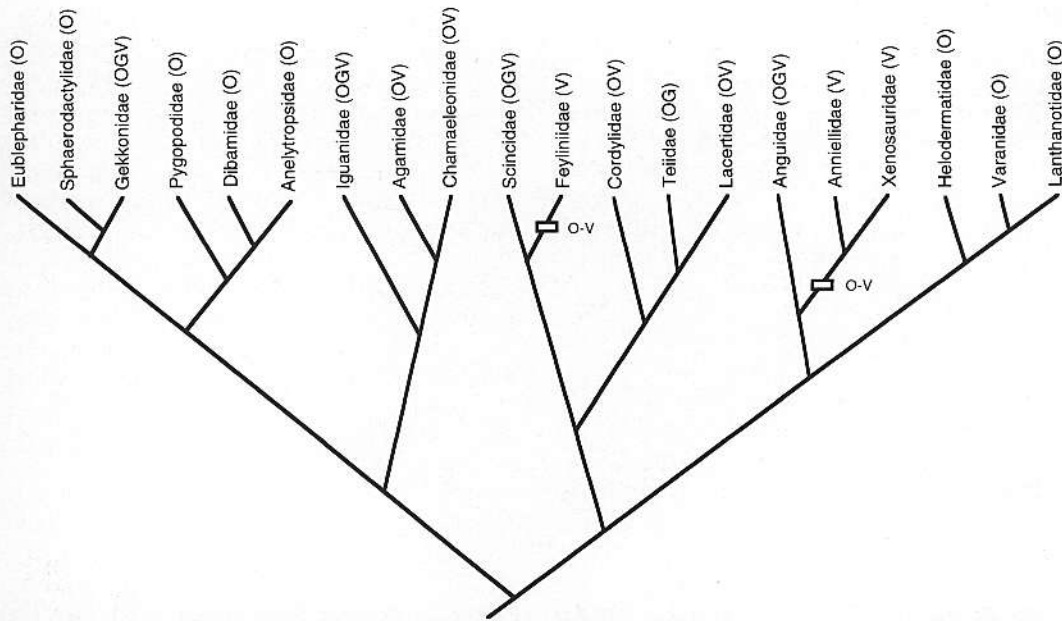


FIG. 1.—Reproductive mode optimized onto the cladogram of Underwood, (1971; as drawn by Schwenk, 1988). This is one of the four equally-parsimonious optimizations identified by the “equivocal cycling” option in MacClade. Note, however, that even in this particular “optimization” the number of each type of transition (e.g., oviparity to viviparity) depends heavily on how we interpret changes within bimodal and trimodal terminal taxa (Table 1): see text for further discussion. Abbreviations: O = oviparous without egg-guarding, G = oviparous with egg-guarding, V = viviparous.

from either his text or his proposed Linnean classification; (2) de Fraipont et al. used two squamate trees in Schwenk (1988): the “Dibamidae excluded” phylogeny (Schwenk’s Fig. 12) and the “lepidosaur” phylogeny (Schwenk’s Fig. 14). However, these phylogenies are identical (the only difference is that one more outgroup is shown in the latter). Accordingly, we use only a single phylogeny from Schwenk (1988); and (3) “Cladogram C” in Presch (1988) represents the scincomorph portion of “Cladogram B” and is thus totally included in that cladogram. We therefore use “Cladogram B” but not “Cladogram C”. Presch (1988) converted the phylogenetic discussions in Camp (1923), Northcutt (1978), and Underwood (1957, 1971) into explicit dichotomous cladograms, and we have used these cladograms (as did, presumably, de Fraipont et al.). Although Cadle (1988) provided several trees, the only one relevant to this analysis (and presumably the one used by de Fraipont et al.) is the shortest family-level tree that

does not involve a negative immunological branch (his Fig. 2A). We similarly used the most resolved tree in Cadle (1987), his Fig. 3-1A.

Our Table 1 compares the maximum number of each type of transition allowed by each optimization on a particular phylogeny (the number recognised by de Fraipont et al.) along with the number unequivocally supported (the number that we believe should be accepted); these numbers are usually very different. In particular, in most phylogenies many heterodox transitions (from viviparity to egg-guarding, or from viviparity to oviparity) are allowed but none are unequivocally supported. This trend is very consistent; the averages for each type of transition over all possible cladograms are shown for lizards and snakes in our Table 1. For instance, the various “lizard” cladograms and optimizations imply an average of 8.8 possible transitions from oviparity to viviparity, of which 5.4 are well supported (61%). Conversely, they imply an average of three

TABLE 1.—Types and frequencies of changes in reproductive mode implied on the cladograms examined by de Fraipont et al. (1996). In some cladograms, reproductive mode could optimize in multiple equally-parsimonious ways. The changes implied on each of these optimizations ("opts") are indicated. The first number represents the number unequivocally supported under each optimization, the second (in parentheses) represents the maximum number that may have occurred given the most "favorable" interpretation (see text) of changes within terminal taxa. Abbreviations: O = oviparous without egg-guarding, G = oviparous with egg-guarding, V = viviparous.

	No. of opts	O->V	O->G	G->O	V->O	V->C	G->V
"Lizards"							
Camp, 1923	1	5 (12)	1 (7)	0 (1)	0 (1)	0 (6)	0 (5)
Underwood, 1957	2	6 (10)	1 (6)	0 (1)	0 (1)	0 (5)	0 (4)
Underwood, 1971	4	6 (9)	1 (6)	0 (2)	0 (2)	0 (5)	0 (3)
		6 (10)	1 (5)	0 (0)	0 (0)	0 (4)	0 (4)
		6 (9)	1 (5)	0 (1)	0 (1)	0 (4)	0 (3)
		6 (9)	1 (5)	0 (1)	0 (1)	0 (4)	0 (3)
Northcutt, 1978	2	6 (8)	1 (5)	0 (2)	0 (2)	0 (4)	0 (2)
		6 (11)	1 (6)	0 (0)	0 (0)	0 (5)	0 (5)
		6 (10)	1 (6)	0 (1)	0 (1)	0 (5)	0 (4)
Schwenk, 1988	2	7 (13)	1 (7)	0 (0)	0 (0)	0 (6)	0 (6)
		6 (11)	1 (7)	0 (1)	1 (2)	0 (6)	0 (5)
Estes et al., 1988							
PHYSYS A	2	5 (12)	1 (7)	0 (0)	0 (0)	0 (6)	0 (6)
		5 (11)	1 (7)	0 (1)	0 (1)	0 (6)	0 (5)
PHYSYS B	1	5 (10)	1 (5)	0 (0)	0 (0)	3 (4)	3 (4)
PAUP	1	5 (10)	1 (5)	0 (0)	0 (0)	0 (4)	0 (4)
"Conservative"	1	6 (12)	1 (7)	0 (0)	0 (0)	0 (6)	0 (6)
Presch, 1988							
Cladogram A	4	6 (11)	1 (6)	0 (0)	0 (0)	0 (5)	0 (5)
		6 (10)	1 (6)	0 (1)	0 (1)	0 (5)	0 (4)
		5 (9)	1 (6)	0 (1)	1 (2)	0 (5)	0 (4)
		4 (9)	1 (6)	0 (1)	2 (3)	0 (5)	0 (4)
Cladogram B	4	6 (10)	1 (5)	0 (0)	0 (0)	0 (4)	0 (4)
		6 (9)	1 (5)	0 (1)	0 (1)	0 (4)	0 (3)
		5 (8)	1 (5)	0 (1)	1 (2)	0 (4)	0 (3)
		4 (7)	1 (5)	0 (1)	2 (3)	0 (4)	0 (3)
Rieppel, 1988	1	6 (9)	1 (5)	0 (0)	0 (0)	0 (4)	0 (4)
Greene, 1988	1	6 (12)	1 (7)	0 (0)	0 (0)	0 (6)	0 (6)
Greer, 1989	1	2 (5)	0 (3)	0 (0)	0 (0)	0 (3)	0 (3)
<i>Average (lizards)</i>		5.4 (9.9)	1 (5.7)	0 (0.63)	0.26 (0.89)	0.11 (4)	0.11 (4.1)
"Snakes"							
Rage, 1987	2	0 (0)	0 (5)	0 (5)	1 (6)	0 (5)	0 (0)
		0 (1)	0 (5)	0 (4)	1 (5)	0 (5)	0 (1)
Rieppel, 1988	1	0 (0)	0 (3)	0 (3)	1 (4)	0 (3)	0 (0)
Greene, 1988	1	0 (5)	0 (5)	0 (0)	0 (0)	0 (5)	0 (5)
Cadle, 1987	1	0 (0)	0 (3)	0 (3)	1 (4)	0 (3)	0 (0)
Cadle, 1988	1	0 (4)	0 (4)	0 (0)	0 (0)	0 (4)	0 (4)
<i>Average (snakes)</i>		0 (1.7)	0 (4.2)	0 (2.5)	0.66 (3.2)	0 (4.2)	0 (1.7)

possible "reversals" from viviparity to egg-guarding, of which only 0.11 are well supported (<4%). No clear patterns are observable in the snake data, for reasons discussed below.

Many of the genus- and species-level phylogenetic studies used by de Fraipont et al. (their Table 1) contain several cladograms. Information on which cladograms were used from each reference was not provided (unlike the case for family-level

references: their Table 3). For this reason, we did not attempt reanalyses of the genus- and species-level data at this stage.

(b) Second, for a particular phylogenetic hypothesis, it is often possible to optimize changes along the cladogram branches (as opposed to within terminal taxa—see above) in several equally parsimonious ways. For example, in Schwenk's (1988) cladogram, the distribution of oviparity, egg-guarding, and viviparity in terminal

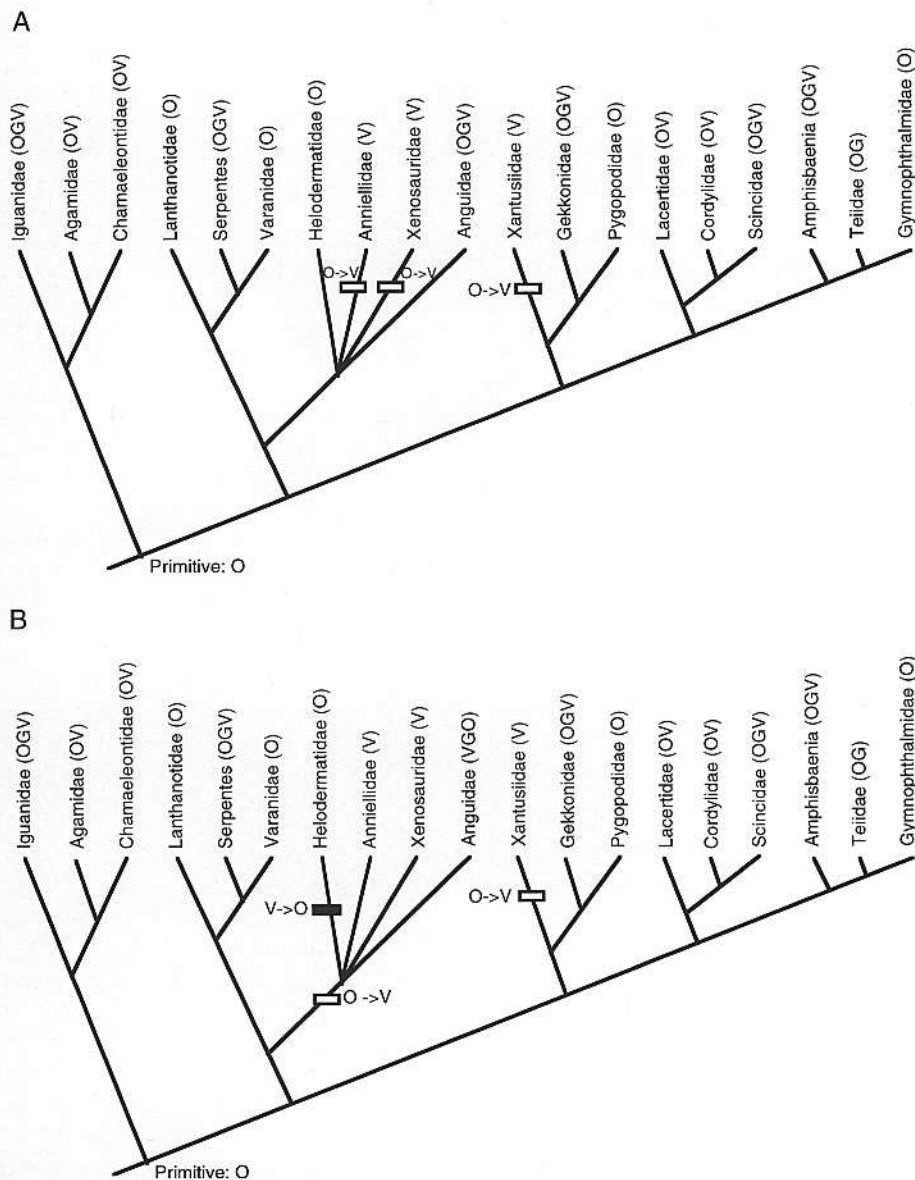


FIG. 2.—Two equally-parsimonious ways that reproductive mode can be optimized on the cladogram of Schwenk (1988). Each involves three changes: (A) entails three "forward" (oviparity to viviparity) transitions, not counting changes within terminal taxa; (B) entails two "forward" transitions and one reversal (viviparity to oviparity). Abbreviations as in Fig. 1.

taxa can be explained by assuming either three transitions from oviparity to viviparity along the cladogram branches (our Fig. 2A), or by assuming two such transitions and a reversal (our Fig. 2B). The first optimization implies a minimum of six oviparity to viviparity transitions and two oviparity to egg-guarding transitions (count-

ing changes within terminal taxa), while the second implies a minimum of five transitions from oviparity to viviparity, two from oviparity to egg-guarding and one from viviparity to oviparity (Table 1). Clearly, only one of these scenarios can have happened, and one should ask "regardless of which scenario is correct, what

transitions *must* have occurred?" In this case, the data provide compelling evidence for only five transitions from oviparity to viviparity and two from oviparity to egg-guarding. Whether a sixth transition from oviparity to viviparity, or a "reversal" from viviparity to oviparity, occurred depends on which optimization we accept (Fig. 2). However, instead of only considering robustly supported transitions (i.e., those common to all most-parsimonious optimizations), de Fraipont et al. counted the maximum number of each type of transition across all optimizations. Thus, they would have counted the number of transitions from oviparity to viviparity that occurred under the first optimization (which maximises the number of such transitions), and counted the number of "reversals" from viviparity to oviparity under the second optimization (which maximises the number of such transitions). Furthermore, as discussed under (a) above, they counted not just the number unequivocally supported by the most "favorable" optimization, but the maximum number possible. They would thus have interpreted these data as providing evidence for 11 transitions from oviparity to viviparity, seven transitions from oviparity to egg-guarding, one transition from egg-guarding to oviparity, one transition from viviparity to oviparity, five transitions from viviparity to egg-guarding, and five transitions from egg-guarding to viviparity (Table 1). In reality, this particular tree, with its two optimizations, provides compelling evidence for only five transitions from oviparity to viviparity and two from oviparity to egg-guarding.

(c) The third problem is related to the previous one, and involves their use of multiple phylogenetic hypotheses for the same (or very similar) sets of taxa. These different phylogenetic hypotheses can obviously result in different inferred patterns of character changes. Thus, de Fraipont et al. optimized characters on alternative trees for the same taxa. Again, only one tree can be correct, and one should ask "regardless of what phylogeny is correct, what transitions *must* have occurred?" However, instead of counting only well

supported transitions (common to all or most tree topologies), they again counted the maximum number of each transition type across all phylogenies. They thus further inflate the number of possible transitions by including poorly supported transitions which occur on only one or a few (perhaps dubious) trees, as well as better-supported transitions.

These three problems considerably inflate the numbers of transitions identified by de Fraipont et al. For example, for the "lizard" (squamate) data, the maximum number of each type of transition, assuming the most favorable interpretation of a particular optimization, the most favorable optimization, and the most favorable phylogeny, is as follows (Table 1): 11 transitions from oviparity to viviparity, seven transitions from oviparity to egg-guarding, two transitions from egg-guarding to oviparity, three transitions from viviparity to oviparity, five transitions from viviparity to egg-guarding, and five transitions from egg-guarding to viviparity. These are the numbers of "implied transitions" that one obtains using de Fraipont et al.'s method. However, when one counts only the transitions that must have occurred (i.e., common to all interpretations of all optimizations of all possible trees), one gets a much more conservative result. These data imply only four transitions from oviparity to viviparity and two transitions from oviparity to egg-guarding. Greer's (1989) phylogeny entails fewer transitions, because it incorporates fewer taxa (mainly those that occur in Australia, and that happen to be either uniformly, or partially, oviparous). However, the absence of interfamilial transitions in Greer's tree is an artifact of the limited selection of squamate taxa, and the conservative numbers implied by this tree can be disregarded. When all the other trees are considered, only four transitions from oviparity to viviparity and two transitions from oviparity to egg-guarding are definitely implied.

Analyses of the snake phylogenies generate an even more conservative result. No type of transition, not even the universally accepted oviparity-viviparity transition, is common to all trees and all optimizations

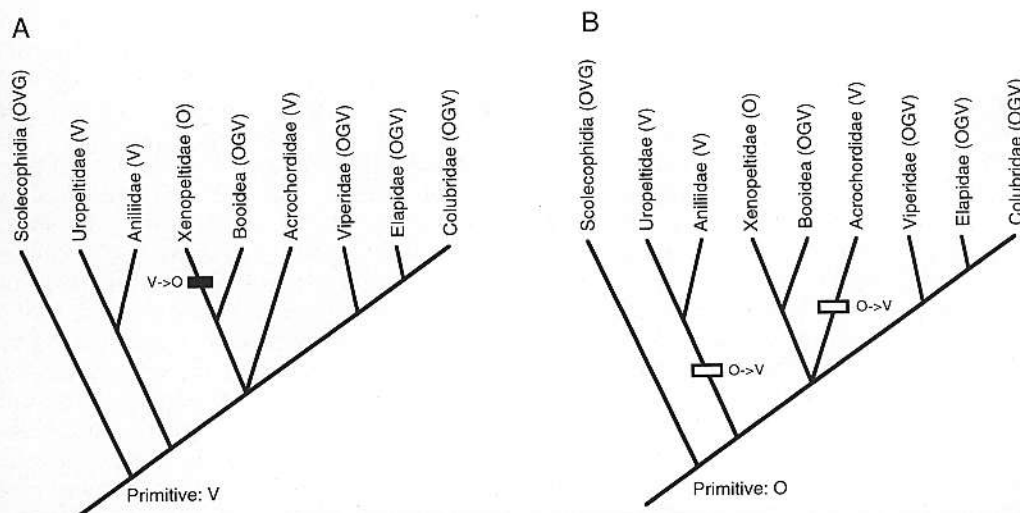


FIG. 3.—(A) One of the two most equally-parsimonious ways that reproductive mode can be optimized on the cladogram of Rage (1987). Viviparity is primitive for snakes, and a single reversal (to oviparity) is required (not counting transitions within terminal taxa). Again, transitions within polymorphic terminal taxa are not counted. (B) Alternative interpretation that does not involve reversals. Oviparity is primitive for snakes, and two "forward" transitions (to viviparity) are required (not counting transitions within terminal taxa). Abbreviations as in Fig. 1.

(Table 1). This is because most of the terminal taxa ("families") in these phylogenies are bimodal or trimodal, permitting very different optimizations on each phylogeny. Thus, the snake phylogenies at this level do not provide compelling evidence for the existence of any particular type of transition.

Thus, our reanalysis of the family-level data reveals strong evidence for only six transitions in reproductive mode, all in "lizards": four transitions from oviparity to viviparity and two from oviparity to egg-guarding. There is no compelling evidence for any other transitions. This conclusion stands in stark contrast to de Fraipont et al.'s report that these same data provide evidence for 38 transitions (15 transitions from oviparity without egg-guarding to viviparity, 10 from oviparity without egg-guarding to egg-guarding, eight reversals from viviparity to oviparity without egg-guarding, and five reversals from viviparity to oviparity with egg-guarding).

Why, then, did de Fraipont et al.'s analysis identify so many "reverse" transitions? As discussed above, they counted dubious "reversals" which only occurred on certain

interpretations of certain optimizations on certain phylogenies: many of these will not occur under other interpretations of the same optimization, or on other (equally-parsimonious) optimizations, or on other proposed phylogenies of the same taxa (Fig. 1). Furthermore, the polarity of many of the apparent "reverse" transitions could be unreversed by allowing a single additional step (i.e., one more change in a character state at some point in the tree). For example, not counting changes within terminal taxa, the phylogenetic hypothesis of Rage (1987) implies a single viviparity-oviparity "reversal" under either of the two most-parsimonious optimizations (Fig. 3A, Table 1). However, it takes only one extra step (two oviparity-viviparity changes) to make the tree consistent with the common view that reversals are unlikely (Fig. 3B). We do not consider this compelling evidence for the occurrence of such reversals (Lee and Doughty, 1997; Lee and Shine, 1998).

Our reanalysis of the family level data showed that the majority of reversals accepted by de Fraipont et al. are poorly supported: only transitions from oviparity

to viviparity and from oviparity to egg-guarding are common to all optimizations and phylogenies. Even on the few phylogenies that unequivocally imply (as opposed to merely allow) a reversal under all most parsimonious optimizations (Table 1: Cadle, 1987; Rage, 1987; Rieppel, 1988; "snakes"), these reversals can be eliminated by assuming a single extra step. If the reversals reported in the genus and species level analyses are similarly weakly supported, the high frequencies of reversals reported in de Fraipont et al. include so many poorly supported cases that they are unlikely to be meaningful.

(d) Finally, the totals reported in de Fraipont et al. are inflated by pseudoreplication. Changes counted in higher level analyses are counted again during lower level analyses. For example, reproductive mode transitions with gerrhonotine anguid lizards were included in the study as (1) polymorphism within a terminal taxon (anguids) in the family-level analyses, (2) changes between individual gerrhonotine genera in the genus-level analyses, and (3) changes between species in *Elgaria* (a gerrhonotine) in the species level analysis. The same shifts are, therefore, counted three times and contribute to the totals reported in the family, genus, and species level analyses.

(2) Inadequacies in Parts of the Data Set

Family-level phylogenies are unlikely to provide an accurate picture of shifts in reproductive mode, because reproductive traits are very labile. There have been over 100 separate transitions of reproductive mode within squamates alone, and in several lineages independent convergent transitions have occurred within closely related taxa (e.g., Blackburn, 1982, 1985; Qualls et al., 1995; Lee and Shine, 1998; Shine, 1985; Smith, 1996; Smith and Shine, 1997). Thus, most of the families used in de Fraipont et al.'s analysis (Figs. 1, 2) contain representatives with two or three reproductive modes, making it very difficult to optimize reproductive modes on family-level trees with any degree of confidence. Furthermore, where an entire family shows one mode, and its most close-

ly related family another, the divergence is likely to be relatively ancient, and numerous intermediate forms extinct. Between families, therefore, there is likely to have been a long and complex history of changes in reproductive mode which we cannot discern. This is why there are often so many alternative optimizations of reproductive mode for family-level phylogenies (Table 1). Shifts in reproductive mode at the generic and specific levels offer a much stronger opportunity to discern the direction and phylogenetic distribution of evolutionary transitions. Table 2 lists all of the squamate lineages in which reproductive bimodality has been reported at the intrageneric or intraspecific level, in which we can confidently discern the direction of the transition in reproductive mode (i.e., we have reliable data on phylogenetic affinities and reproductive modes of all the relevant taxa). In each of these 19 cases, oviparity has given rise to viviparity. This bias is not an artefact of ease of detection of one direction of transition versus another. For example, a single egg-laying species nested deeply within a large viviparous lineage [e.g., American garter snakes (*Thamnophis*) or rattlesnakes (*Crotalus* plus *Sistrurus*)] would provide an unequivocal demonstration of a reversal. The absence of any documented example of this phenomenon suggests that such "reverse" transitions are indeed rare. If the frequency of "forward" and "reverse" transitions was approximately equal (as suggested by de Fraipont et al.'s analysis), the probability of all 19 of these transitions occurring in the "forward" direction (Table 2) would be very low ($\chi^2 = 12.1$, 1 df, $P < 0.0005$).

MATERNAL EGG-GUARDING AS A TRANSITIONAL STAGE TO VIVIPARITY

Shine and Bull (1979) suggested that egg-guarding may facilitate the evolution of viviparity, because egg-guarding females experience many of the "costs" of viviparity without experiencing some of the "benefits". The analyses of de Fraipont et al. set out to test this hypothesis. They concluded that the frequency of evolutionary transitions from egg-guarding to viviparity was lower than the transition in the re-

TABLE 2.—Squamate lineages in which reproductive mode has changed, and in which it is possible to infer confidently the direction of that change. Criteria for inclusion of cases were: (i) reproductive bimodality occurs at either the species or generic level, and (ii) information is available on the identity of outgroups, and on reproductive mode of most species within both the ingroup and outgroup. Thus, the Table omits lineages where the putative outgroups are unclear, or contain both oviparous and viviparous species (so that the direction of the transition in reproductive mode is unclear). For references to these cases, see Shine (1985) and Blackburn (1982, 1985); superscripts provide references to information that has been published subsequent to these reviews.

Family	Outgroup for comparison	Taxon with "different" mode	Direction of reproductive transition
<i>Lizards</i>			
Agamidae	Other Asian agamids	<i>Cophotis ceylanica</i>	Oviparous to viviparous
	Other Asian agamids	<i>Phrynocephalus theobaldi</i>	Oviparous to viviparous
Chamaeleonidae	Other chamaeleonids and agamids	Viviparous chamaeleons	Oviparous to viviparous
Corytophanidae	Other basiliscines	<i>Corytophanes percarinatus</i>	Oviparous to viviparous
Lacertidae	European lacertids	Viviparous <i>Lacerta vivipara</i>	Oviparous to viviparous
Scincidae	Other ablepharines	Viviparous <i>Ablepharus alaicus</i>	Oviparous to viviparous
	<i>Lerista</i> plus <i>Ctenotus</i> and <i>Notoscincus</i>	<i>L. microtis</i>	Oviparous to viviparous
	<i>Lerista bougainvillii</i>	Viviparous <i>L. bougainvillii</i> ¹	Oviparous to viviparous
	<i>Saiphos equalis</i> plus <i>Anomalopus</i>	Viviparous <i>S. equalis</i> ²	Oviparous to viviparous
<i>Snakes</i>			
Colubridae	Old World natricines	Viviparous <i>Amphiesma pryeri</i> ³	Oviparous to viviparous
	Aparallactines	<i>Aparallactus jacksoni</i>	Oviparous to viviparous
	Other colubrines	<i>Coronella austriaca</i>	Oviparous to viviparous
	Other colubrines	<i>Elaphe rufodorsata</i>	Oviparous to viviparous
	<i>Ophedryx</i> and relatives	<i>Ophedryx vernalis</i>	Oviparous to viviparous
	<i>Psammophylax</i>	Viviparous <i>P. variabilis</i>	Oviparous to viviparous
	Old World natricines	<i>Simonatrix annularis</i>	Oviparous to viviparous
Elapidae	Afro-Asian Elapidae	<i>Pseumachatus haemachatus</i>	Oviparous to viviparous
	<i>Pseudechis</i> , <i>Pseudonaja</i> and <i>Oxyuramus</i>	<i>Pseudechis porphyriacus</i>	Oviparous to viviparous
Typhlopidae	Other scolecophidians	<i>Typhlops bibronii</i>	Oviparous to viviparous

¹ Fairbairn, 1993; Qualls et al., 1995;

² Smith and Shine, 1997;

³ Ota et al., 1991.

verse direction. Although this comparison is not directly relevant to the hypothesis of Shine and Bull (1979), the conclusion that the transition from egg-guarding to viviparity is very rare (in absolute terms) does cast doubt on the idea. Unfortunately, the estimates by de Fraipont et al. may be in serious error, for several reasons. Some of these are discussed above; their counts include many poorly supported transitions, are inflated by pseudoreplication, and the lability of reproductive mode will often make polarities difficult to infer (particularly on family-level phylogenies). These will simply introduce much random error into the analysis. In addition, however,

their study incorporates a consistent bias, because one of the character states (oviparity without egg-guarding) is defined by the absence of positive records of maternal attendance, rather than by any information to suggest that egg-guarding does *not* occur. Observations of maternal post-ovipositional behavior are much more difficult to make than identifying simply whether eggs or live young are deposited. For a high proportion of squamate taxa, published records of reproductive mode have been based on dissection of preserved specimens in museums, or egg-laying by recently-captured females in situations (e.g., in collecting bags) where egg-guard-

ing behavior could not possibly be exhibited. Additionally, captivity stress often induces nest desertion even in taxa that normally guard their eggs (e.g., Ross and Marzec, 1990). In some egg-guarders, maternal attendance is facultative, in response to environmental conditions (e.g., Shine et al., 1997). All of these features mean that a high proportion of egg-guarding taxa will be scored as being "oviparous without egg-guarding".

It is difficult to estimate the magnitude of this underestimation, but it is likely to be very large. For example, as part of a research program on Australian snakes, the senior author has published empirical reports of reproductive mode in 46 oviparous species (see references in Shine, 1991). He has recorded egg-laying in captivity, or found natural nests in the field, for only eight of those taxa. Thus, even if all of the species recorded as oviparous were actually egg-guarders, he has had the opportunity to discover this fact for <20% of the taxa for which he has established reproductive mode. Inspection of published references shows that a similar proportion (<20%) of the reports of reproductive mode for "oviparous, non-guarding" species were accompanied by information suggesting that the author had the opportunity to record egg-guarding behavior even if it occurred.

This consistent error in scoring will have a substantial impact on conclusions about transitional polarities. Even if viviparity invariably evolved from egg-guarding, a high proportion of these transitions would be misinterpreted as arising from taxa that are "oviparous without guarding" because the maternal brooding behavior has not been reported. The exact bias in estimating transition frequencies will depend upon the topology of the tree, and the phylogenetic position of the species that have been incorrectly categorized. With a simple tree topology, failure to record egg-guarding in 80% of the species in which it occurs (as is likely, if Shine's own experience is typical: see above) will mean that 80% of the evolutionary transitions from egg-guarding to viviparity will be misclassified as transitions from oviparity (without

egg-guarding) to viviparity. Hence, most attempts to quantify transition frequencies, including de Fraipont et al.'s are strongly biased against detecting transitions involving egg-guarding species.

This bias also affects the allocation of ancestral versus derived character states. Even a single report of egg-guarding within a lineage will reveal a transition, but almost always in the direction of the egg-guarding being a derived rather than ancestral trait. This is because the other reproductive modes will simply be more widely distributed on the tree, and thus will be interpreted as primitive. However, as more and more instances of "oviparity without egg-guarding" become rescored correctly as instances of egg-guarding, the situation will change. Egg-guarding will change from optimizing as a single specialization, to multiple convergent specializations, to finally (if widespread enough) being primitive for the entire lineage (and thus ancestral to the other modes). This factor further biases such analyses from detecting transitions from egg-guarding to viviparity. Hence, phylogenetic analyses will always be strongly biased against detection of changes away from egg-guarding (e.g., to viviparity). In order to correct for this, one needs to accumulate detailed ecological information on each poorly known oviparous taxon (to determine correctly the presence or absence of egg-guarding), or to reduce the data set to include only taxa where such observations are available.

Although de Fraipont et al. disputed the direction of transitions, they accepted earlier conclusions (e.g., Shine, 1985; Shine and Bull, 1979) that egg-guarding behavior is disproportionately common in squamate lineages in which viviparity has arisen. They attribute this pattern to the possibility that both egg-guarding and viviparity represent adaptations to particular kinds of environmental conditions: i.e., those that favor high levels of maternal investment. This hypothesis has also been proposed by Shine (1985), as an alternative to the preadaptation hypothesis (Shine and Bull, 1979).

CONCLUSIONS

We agree with de Fraipont et al. (1996) that analyses of reproductive changes within squamates should be investigated in a rigorous phylogenetic framework, in order to test selectionist arguments that transitions can only occur in particular directions. However, as a result of the problems discussed above, we dispute two major conclusions of their study. Available evidence suggests that the transition from oviparity to viviparity occurs far more frequently than the reverse transition, and data on the distribution of egg-guarding are too fragmentary to allow any firm conclusions to be reached regarding the relationship between egg-guarding and viviparity. More generally, we suggest that attempts to apply the comparative method to identify evolutionary transitions should avoid the problems encountered in the study by de Fraipont et al. We agree that all most-parsimonious optimizations on all proposed phylogenies should be investigated when interpreting evolutionary transitions. However, we think that the only transitions that should be accepted are those that are common to all (or at least most) well supported phylogenetic arrangements for a given clade, and all (or at least most) possible optimizations for each of these phylogenies. Furthermore, workers should report measures of the confidence with which they can assign polarities in such transitions. If the direction of a particular evolutionary transition can be changed by assuming very few extra steps (a single step in the case of the reported viviparity-oviparity "reversals"), it is difficult to have much confidence in these transitions. Consistent biases in scoring characters (e.g., reliance on negative evidence to assert the absence of egg-guarding) can also confound such analyses. We thus strongly concur with de Fraipont et al. that more work is required to elucidate the complex interrelationships among life-history variables in squamate reptiles.

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