

## REPTILIAN VIVIPARITY AND DOLLO'S LAW

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**Abstract.**—It has been suggested repeatedly that the evolutionary transition from oviparity (egg-laying) to viviparity (live-bearing) in reptiles is irreversible. However, these adaptive arguments have yet to be tested by detailed examination of the phylogenetic distribution of oviparity and viviparity across a broad range of taxa. Using available data on reproductive modes and phylogenetic relationships within reptiles, we here quantify the numbers and directions of evolutionary transitions between oviparity and viviparity. Phylogenetic relationships among three diverse squamate groups (scincid lizards, colubrid snakes, elapid snakes) are currently inadequately known for inclusion in this study. Among the remaining reptiles, oviparity has given rise to viviparity at least 35 times. Five possible instances of “reversals” (from viviparity to oviparity) are identified, but closer examination indicates that all have weak empirical support (i.e., they could be “unreversed” with little loss in parsimony, and/or are based on poorly substantiated phylogenetic hypotheses). Viviparity is clearly more frequently (and presumably easily) gained than lost in several disparate groups so far examined (reptiles, fishes, polychaete worms); this evolutionary bias should be considered when reproductive mode is optimized on a phylogeny or employed in phylogenetic reconstruction.

**Key words.**—Character evolution, oviparity, phylogeny, reproductive mode, reptiles, squamates, viviparity.

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Models of the evolutionary process have often been used to argue that changes are more likely to proceed in one direction rather than the reverse (e.g., Bull and Charnov 1985). However, empirical studies have challenged many of these assertions regarding absolute or partial irreversibility. Two of the most well-known, but relatively poorly tested, principles in biology involve evolutionary irreversibility (Kurtén 1953): Cope's rule and Dollo's law.

Cope's rule (Cope 1887, 1896) states that lineages generally evolve from small toward large body size rather than the reverse. Cope's vitalist notion that an internal drive caused lineages to evolve greater size has now been replaced by selectionist explanations, such as the presumed physiological efficiency and ecological superiority of large body size (e.g., Newell 1949; Kurtén 1953). An alternative explanation is that new, higher taxa usually originate from small, generalized ancestors with developmental and ecological flexibility, with large specialized forms congealing into evolutionary “dead ends” (e.g., Stanley 1973; Hayami 1978). However, both these assumptions are questionable (e.g., LaBarbera 1986; Dial and Marzluff 1988; McKinney 1990), and recent empirical studies suggest size decrease is just as prevalent as size increase (see Jablonski 1997; Gould 1997).

Dollo's law (Dollo 1893, 1922) states that complex organs, once lost, can never be regained in exactly the same form. This assumes that complex organs have complex genetic and developmental bases (Gould 1970) and, furthermore, that once morphological structures are lost, the appropriate genetic and developmental machinery also soon decays. Thus, complex traits, once lost, must evolve *de novo*, and it is highly improbable that the complex sequence of independent events (mutation and selection) required to build them will again arise (e.g., Muller 1939). However, atavisms demonstrate that even after morphological structures are lost, the genetic and

developmental information for constructing them can be retained for long periods (Berg 1969; Lande 1978). Furthermore, many complex structures have relatively simple genetic and developmental bases (e.g., Raff 1996). If this is true, it might be comparatively easy to reevolve such structures.

It is commonly assumed that, in reptiles, viviparity can evolve readily from oviparity, but not the reverse (Neill 1964; Fitch 1970; Guillette et al. 1980; Blackburn 1992). However, the arguments behind this assumption have rarely, if ever, been clearly detailed. For instance, Guillette et al. (1980, p. 207) stated that “once the trait of viviparity is evolved, it is irreversible” and cited three studies in support of this claim: Neill (1964), Packard et al. (1977), and Tinkle and Gibbons (1977). However, Neill's (1964) arguments consisted simply of two assertions, with no further discussion: “reversion from viviparity to oviparity is improbable” (p. 51) and “reversion from viviparity to oviparity is deemed unlikely” (p. 53). Packard et al. (1977) presented a model for the evolution of viviparity from oviparity, but never claimed that the reverse transition is impossible or mentioned any reasons why this should be the case. Tinkle and Gibbons (1977, p. 37) made the less extreme claim that the “transition from viviparity to oviparity is less likely than the reverse.” The evolution of viviparity from oviparity mainly entails loss of organs and enzymes involved in eggshell production, and is thus “easy,” whereas the reverse transition would entail the reevolution of these complex structures and is thus “difficult.” Fitch (1970), Shine and Bull (1979), and Shine (1985) made similar suggestions.

The argument for irreversibility of viviparity appeals to Dollo's law and the improbability of losing and later reevolving, complex structures. However, the transition to viviparity involves not just the loss of complex structures associated with egg production, but the evolution of (perhaps equally) complex structural and physiological adaptations for fetal respiration and in some cases nutrition (e.g., Packard et al. 1977; Guillette 1982; Blackburn 1992). Thus, it is not obvious that the evolution of viviparity involves mainly

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losses of complex structures, whereas the re-evolution of oviparity involved mostly gains of such structures. Furthermore, both oviparity and viviparity entail numerous ecological advantages and disadvantages (e.g., Packard et al. 1977; Tinkle and Gibbons 1977; Shine and Bull 1979; Guillette et al. 1980; Shine 1985). Because neither strategy is universally "superior," no compelling reason exists to expect that selection will always act only in one direction (i.e., from oviparity to viviparity). Thus, there is only weak theoretical support for the widespread assumption that viviparous reptiles cannot give rise to oviparous forms.

Clearly, therefore, the evolutionary arguments for irreversibility need to be tested empirically. One rigorous test involves mapping (or optimizing) the feature in question onto well-corroborated phylogenies and examining whether the implied transitions occur in only one direction or in both directions (e.g., Proctor 1991; Rouse and Fitzhugh 1994; Dulvy and Reynolds 1997). Here, we use this method to investigate the evolution of viviparity in reptiles (sensu Gauthier et al. 1988: including birds). This is a potentially illuminating example because it has often been argued that the oviparity-viviparity transition is irreversible; reproductive modes in reptiles—especially squamates—are highly labile, with many groups (even some "bimodal" species) exhibiting both viviparity and oviparity (e.g., Heulin et al. 1991; Smith and Shine 1997); and robust phylogenetic hypotheses exist for most reptile groups, making it possible to assemble a highly resolved and mostly well-supported cladogram for the entire Reptilia. We here examine whether the selectionist arguments for irreversibility are supported empirically by phylogenetic patterns; in particular, whether the most parsimonious interpretation of reproductive evolution on a phylogeny of all reptiles entails only forward transitions (oviparity to viviparity), as predicted by many, or both forward and reverse (viviparity to oviparity) transitions. We then examine the degree of support for any heterodox (reverse) transitions identified.

Changes in reproductive modes in polychaete worms (Rouse and Fitzhugh 1994) and elasmobranch fishes (Dulvy and Reynolds 1997) have recently been examined in a similar fashion, and these results are later compared with ours (see Discussion). In addition, Fraipont et al. (1996) attempted to quantify changes in reproductive mode in a particular group of reptiles (squamates). However, the approach used in that study contained some shortcomings, and the results were consequently questionable. A detailed discussion of that study can be found elsewhere (Shine and Lee 1998; see also Dulvy and Reynolds 1997). Briefly, Fraipont et al. (1996) did not use only the most highly corroborated phylogeny for each group, but instead used several alternative (and often, weakly supported) phylogenies and, when applicable, multiple equally parsimonious optimizations on each phylogeny. It seems more reasonable to accept as well-supported only the changes that occur on the best-corroborated phylogeny and are common to all possible optimizations on that phylogeny. Additionally, Fraipont et al. (1996) did not combine these phylogenies into a single global phylogeny. This is potentially problematic because the primitive reproductive mode (and thus, the optimization of reproductive mode) in particular

clades might change depending on the positions of these clades within the global phylogeny.

#### MATERIALS AND METHODS

A phylogeny for the entire Reptilia (Figs. 1, 2) was assembled by synthesizing information from published phylogenetic studies. Morphological, molecular, and combined studies were included. For convenience, the composite phylogeny (Figs. 1, 2) represents diverse clades exhibiting only one reproductive mode (e.g., archosaurs, turtles) as single terminal taxa. Similarly, taxa for which reproductive mode was unknown (e.g. most fossil taxa) were not included in the trees. These simplifications have no effect on the subsequent optimization of reproductive mode (see below), but substantially reduce the size of the figures.

Reproductive mode was determined for each living taxon from published reviews (Blackburn 1982, 1985; Shine 1985) and the primary sources cited therein. Since those reviews were published, however, reproductive modes within some *Sceloporus* have been reinterpreted: The *S. megalepidurus* group appears to be entirely viviparous and *S. subniger* oviparous (Mendez de la Cruz et al. 1998; *contra* Wiens and Reeder 1997). For fossil taxa, sauropterygians are known to be oviparous because eggs with embryos have been found (e.g., Sander 1988), and ichthyosaurs have been fossilized in the process of giving birth to live young (e.g. Carroll 1988; McGowan 1991). Mosasauroids are viviparous, as demonstrated by fossils with embryos (Bell et al. 1996) and by pelvic morphology (Dobie et al. 1986).

In this analysis, all egg-laying forms are classified as "oviparous" and all live-bearing forms as "viviparous" regardless of the degree of maternal provisioning of embryos. These definitions are unambiguous and allow almost all taxa to be assigned readily into one or the other category. We follow most recent workers in using this terminology (for a review see Blackburn 1993). The only ambiguous cases involve a few species in which fully developed embryos are deposited enclosed in soft membranes and emerge almost immediately afterward (e.g., Shine 1985; Smith and Shine 1997); these belong to groups not analyzed here (scincids, colubrids). Because the amount of maternal provisioning of embryos represents a continuum, attempting to further divide viviparous forms into "ovoviviparous" and truly "viviparous" forms is somewhat subjective, and in many cases impossible because of lack of information on reproductive biology (Blackburn 1993).

Reproductive mode was optimized onto the entire cladogram using the maximum-parsimony criterion by MacClade 3.01 (Maddison and Maddison 1992). On certain regions of the phylogeny, reproductive mode can optimize in more than one pathway equally parsimoniously (Fig. 3). In such cases, only transitions common to both optimizations should be accepted as compelling (Shine and Lee 1998; *contra* Fraipont et al. 1996). Thus, the arrangement in Figure 3 provides compelling evidence for only a single forward transition. Similar assessment of the equivocal region in tropidurine iguanids and viperine snakes reveals evidence for a single forward transition, and the equivocal regions in carphodactylid geckos and basal higher snakes each imply a single reversal. The

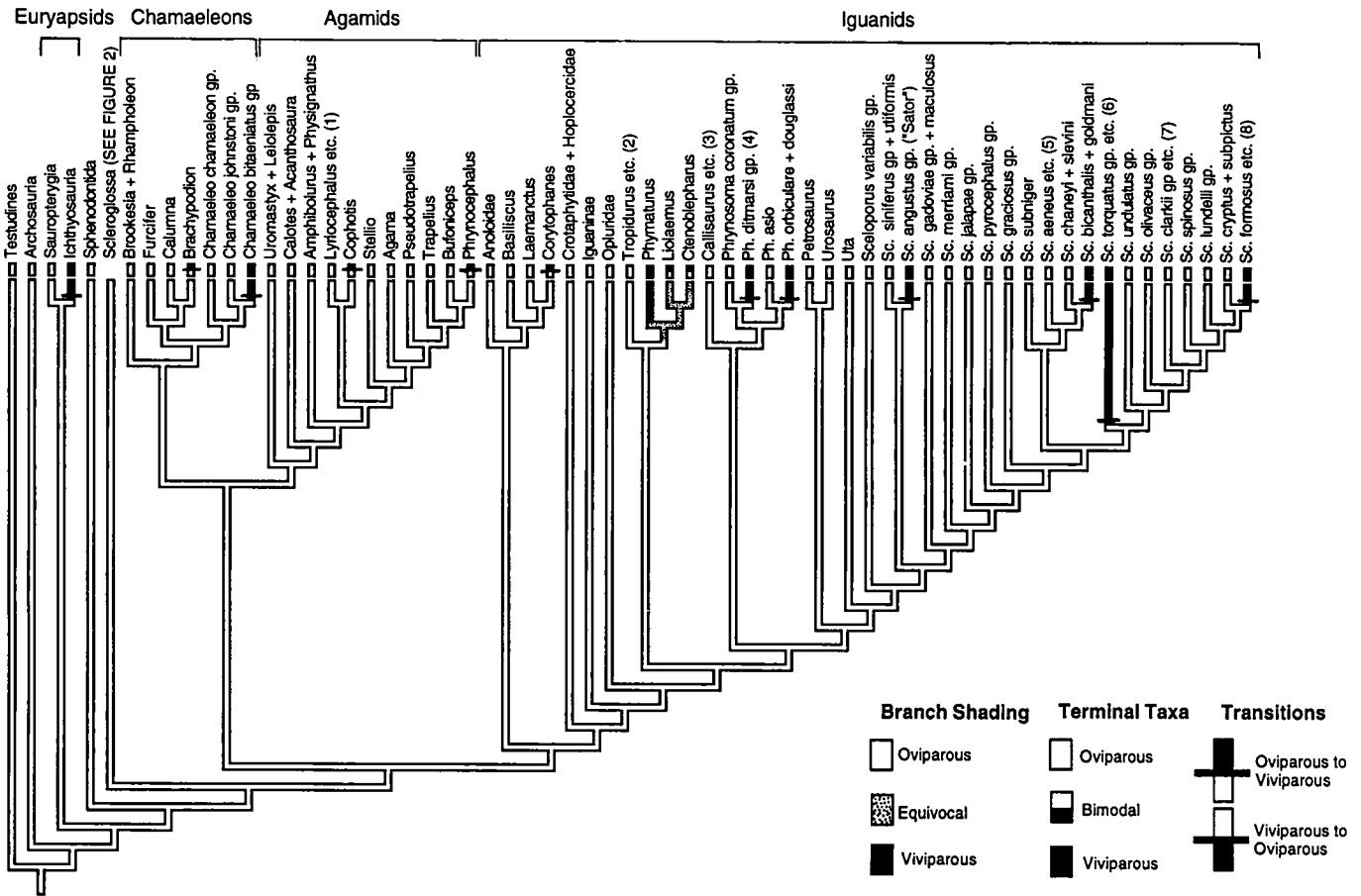


FIG. 1. A phylogeny of reptiles, with details of reproductive mode in terminal taxa indicated and transitions in reproductive mode marked along branches. Changes in equivocal regions are not indicated (see text). Note that this cladogram is continued in Figure 2, where relationships within one diverse clade (scleroglossan lizards) are depicted. Further details of terminal taxa: (1) *Lyriocephalus*, *Ceratophora*, *Gonocephalus chamaeleontinus*, *G. interruptus*; (2) *Tropidurus*, *Uranoscodon*, *Stenocercus*, *Leiocephalus*; (3) *Callisaurus*, *Uma*, *Cophosaurus*, *Holbrookia*; (4) *Phrynosoma ditmarsii*, *P. taurus*, *P. braconnieri*; (5) *Sceloporus aeneus*, *S. scalaris unicanthalis*, *S. scalaris samcolemani*, *S. scalaris scalaris*; (6) *Sceloporus torquatus* group, *S. grammicus* group, *S. megalepidurus* group; (7) *Sceloporus clarkii* group, *S. edwardtaylori* group, *S. magister* group; (8) *Sceloporus formosus* group excluding *S. cryptus* and *S. subpictus*.

extensive equivocal region in viperines can be interpreted as four forward transitions, or a single forward transition and three reversals, or any intermediate combination.

Finally, it should be acknowledged that, given the frequency of character change, maximum-likelihood optimization might yield different ancestors (and thus transitions) to those inferred by parsimony-based methods. An analysis using this method should also be attempted when the relevant programs are available, and the results compared to the current, parsimony-based analysis (see Schluter et al. 1997).

RESULTS

Reproductive mode has changed a minimum of 49 times within reptiles, even when omitting the three diverse groups (scincids, colubrids, elapids) for which we were unable to compile reliable phylogenies. Many transitions in reproductive mode have occurred within these three groups (e.g., Blackburn 1982, 1985; Shine 1985). Nevertheless, transitions in other taxa are sufficiently numerous for strong patterns to emerge. Apart from the evolution of viviparity in ichthyo-

saur, all changes in reproductive mode have occurred in squamates ("lizards" and snakes). When the changes implied in the equivocal regions are treated conservatively, as discussed above, there is evidence for 35 forward transitions and five reversals. The remaining nine implied transitions might be either forward or reverse transitions depending on the optimization adopted. If the optimization chosen maximally favors forward transitions, the ratio of forward:reverse transitions is 44:5. Conversely, if the optimization maximally favors reverse transitions, the ratio is 35:14.

The greater proportion of forward transitions is statistically significant in even in the last, most equitable case (chi-square = 9.0, 1 df, *P* < 0.01). Nevertheless, the implied existence of at least a few reversals appears inconsistent with the common assumption that viviparity, once evolved, is irreversible. Hence, we have critically evaluated the evidence for each reversal. We consider a reversal to be strongly supported if the following two criteria are satisfied: (1) an oviparous taxon has many successive viviparous outgroups; and (2) the phylogenetic arrangement is strongly supported. The more vi-

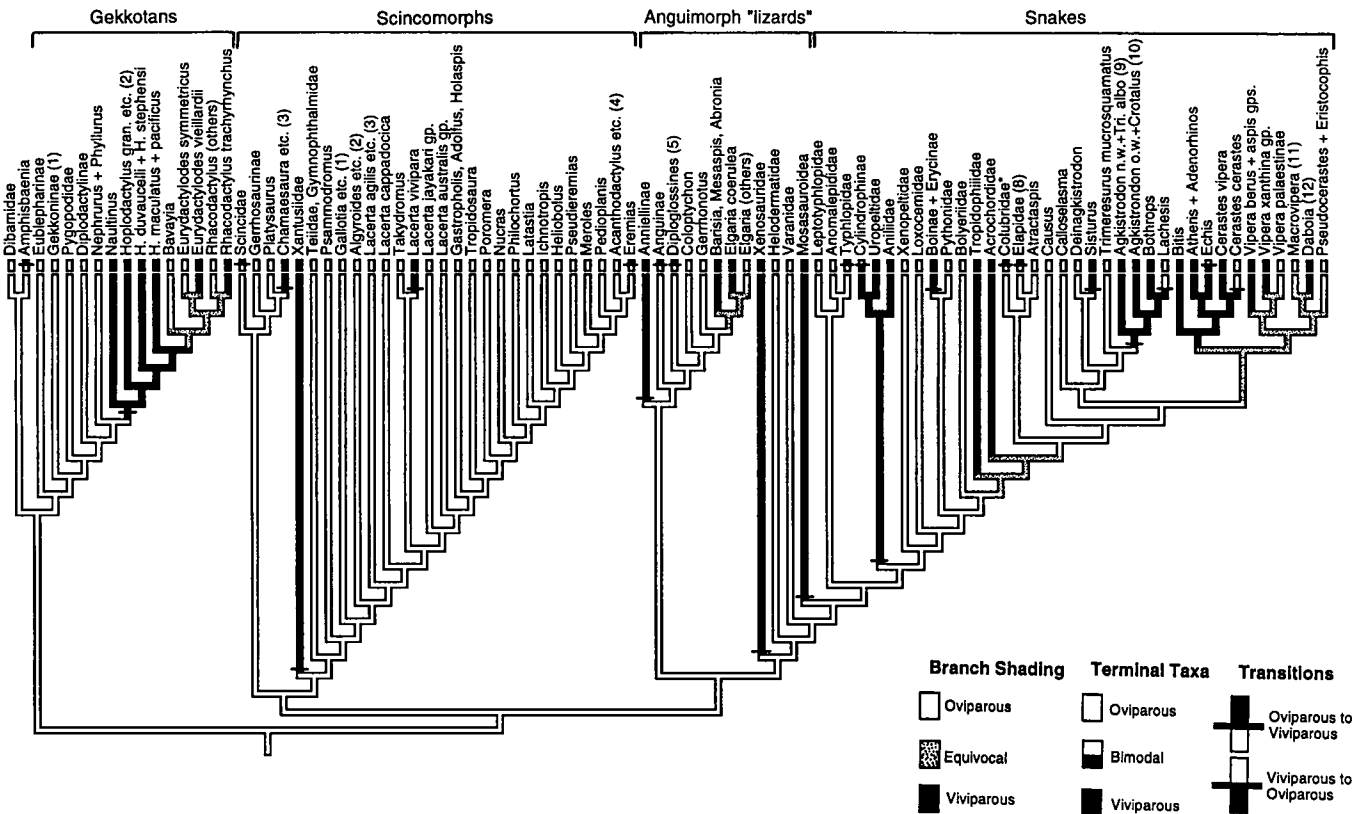


FIG. 2. A phylogeny of scleroglossan lizards, with details of reproductive mode in terminal taxa and changes in reproductive mode indicated along branches. Changes in equivocal regions are not indicated (see text). Further details of terminal taxa: (1) including Sphaerodactylinae; (2) *Hoplodactylus granulatus*, *H. kahutarae*, *H. rakiurae*; (3) *Chamaesaura*, *Cordylus*, *Pseudocordylus*; (4) *Gallotia*, *Lacerta frassi*, *L. parva* group, *L. brandtii*; (5) *Algyroides*, *Archaeolacerta*, *Podarcis*, *Lacerta danfordi*, *L. laevis*, *L. andreanszkii*, *L. perspicillata*, *L. dugesii*; (6) *Lacerta agilis*, *L. lepida*, *L. princeps*; (7) *Acanthodactylus*, *Ophiops*, *Cabrita*, *Mesalina*; (8) includes Hydrophiidae and Laticaudidae; (9) New World *Agkistrodon* plus *Trimeresurus albolabris*; (10) Old World *Agkistrodon* plus *Crotalus*, (11) "*Vipera*" *lebetina* group, (12) "*Vipera*" *russelli*.

viviparous outgroups there are, the more unparsimonious it becomes to assume that the oviparous taxon is primitively oviparous and that each viviparous outgroup has evolved viviparity independently. To calculate how many extra evolutionary steps are required to eliminate each reversal, reproductive mode was optimized via MacClade on the relevant portion of the phylogeny assuming that forward and reverse transitions are equally possible, and then optimized again assuming that only forward changes are possible (using the "irreversible" option). The extra number of steps entailed in the second optimization corresponds to the loss of parsimony required to eliminate an implied reversal (Table 1).

A related way to measure the strength of the evidence for heterodox transitions—in this case reversals—is derived from a recent study (Omland 1997). The probabilities of forward and reverse transitions, originally assumed to be equal, were manipulated using the stepmatrices function in MacClade so that reversals are made increasingly more costly (and thus increasingly less probable) compared to forward transitions. If a proposed reversal can be eliminated by assuming that reversals are only slightly more costly (and thus slightly less probable) than forward transitions, the proposed reversal has little empirical support. This would occur if the oviparous forms are not deeply nested within a viviparous

clade. However, if a proposed reversal can only be eliminated by assuming that reversals are much more costly (and thus much less probable) than forward transitions, the proposed reversal would be considered to have strong empirical support. This would happen if the oviparous forms are deeply nested within a viviparous clade. The degree of differential weighting required in the overall phylogeny before each implied reversal is eliminated is also shown in Table 1; if reversals are made only twice as costly as forward transitions, all reversals except one are eliminated.

If the phylogenetic arrangement is strongly supported, there is little possibility that new systematic data will shift the oviparous taxon to a more basal position within the viviparous clade, or outside it all together, in which case the evidence for a reversal disappears. We now examine the support for each reversal based on these criteria.

*Carphodactylinae Geckos*.—Oviparity in *Bavayia*, *Eurydactyloides symmetricus*, and most *Rhacodactylus* appears to be a reversal because these taxa have four successive viviparous outgroups: (*Hoplodactylus maculatus* + *pacificus*), (*H. duvauceli* + *stephensi*), (*Hoplodactylus granulatus* group), (*Naultinus*). The most-parsimonious scenario entails a single acquisition at the *Naultinus* level followed by a subsequent loss. However, an optimization without reversals can be ob-

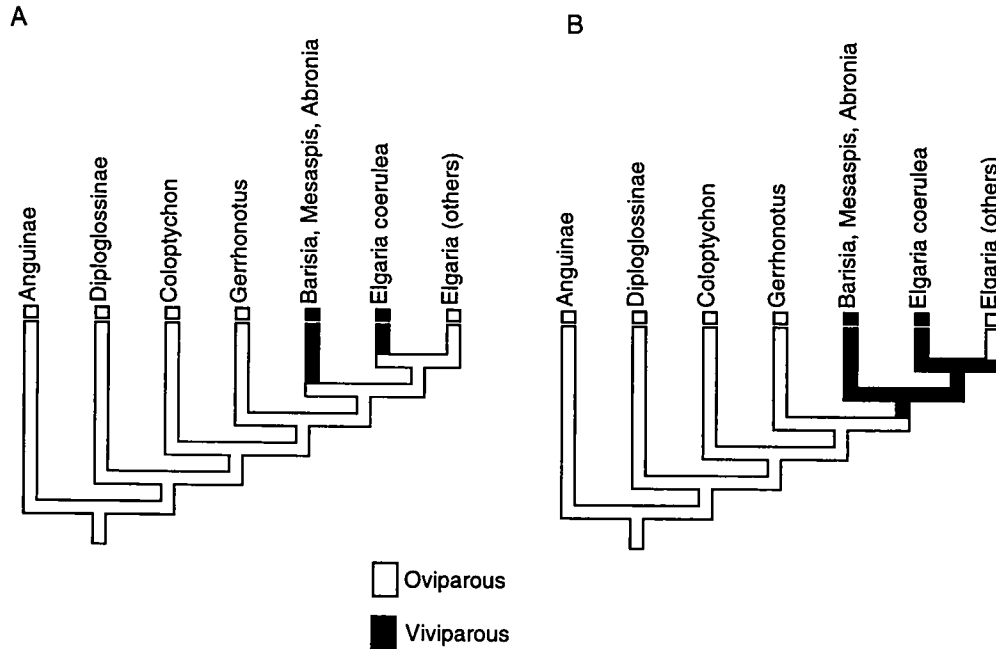


FIG. 3. Details of relationships among advanced anguids in Figure 2, where optimization of reproductive modes is ambiguous. The distribution of modes in the terminal taxa can be explained either via (a) two origins of viviparity or (b) a single origin followed by a reversal.

tained if one assumes that viviparity has evolved convergently four times. Thus, the implied reversal can be eliminated by assuming either a slight loss in parsimony (two steps) or a slight difference in transition probabilities (3:1; see Table 1). Furthermore, the arrangement of the four outgroups is not very robust. In particular, all species of *Hoplodactylus* are rather similar and thus only a few characters support the paraphyly of the genus (Bauer 1990; Bauer, pers. comm. 1997). There is a distinct possibility that new analyses will support the monophyly of *Hoplodactylus*, in which case the oviparous taxa *Bavayia*, *E. symmetricus*, and most *Rhacodactylus* will have only two viviparous outgroups (*Hoplodactylus* and *Naultinus*). With this eventuality, it will be equally parsimonious to assume either convergent evolution of viviparity in *Hoplodactylus* and *Naultinus*, or a single acquisition at the base of the clade containing both genera followed by a reversal. Thus, this instance is not a compelling case of reversal because neither criterion (1) or (2), is satisfied.

*Cylindrophine Snakes*.—The implied reversal in some cylindrophines is also poorly supported. Instead of assuming a

single acquisition at the base of the aniliid-uropeltid-cylindrophid clade followed by a reversal in some cylindrophines, one can eliminate the reversal by assuming convergent evolution of viviparity in aniliids, uropeltids, and some cylindrophines. Thus, one can avoid the implied reversal by assuming a single extra step or slightly different transition probabilities (Table 1). Furthermore, the arrangement of the three taxa is not very robust and alternative interpretations exist (e.g., Cundall et al. 1993). Thus, neither criterion (1) or (2) is satisfied.

*Lachesis*, *Echis*, *Cerastes*.—These oviparous viperids are not deeply nested within viviparous taxa, and it takes only an extra step, or a slight change in transition probabilities, to eliminate these three implied reversals (Table 1). Thus, the evidence for these reversals is not compelling, even though the phylogenetic relationships in this case appear to be well supported based on recent analyses of diverse types of data.

Thus, none of the implied reversals is strongly supported. In contrast, not only are forward (oviparity to viviparity) transitions more numerous, but the evidence for at least some of them is very strong. Again, evidence for an oviparity-viviparity transition is considered strong if the viviparous lineage is deeply embedded within oviparous groups, and the phylogenetic arrangement is strongly supported. Many of the "forward" transitions are very strongly supported, because the viviparous lineages are deeply embedded within oviparous groups, and the phylogenetic relationships of most of these groups are well established. Such cases include *Phrynocephalus*, *Corytophanes*, the *Sceloporus formosus* group, the *Sceloporus angustus* group, amphisbaenians, the gekko clade including *Naultinus* and *Hoplodactylus*, *Lacerta vivipara*, and *Eremias*. Eliminating the forward transitions at the base of each of these groups would involve assuming more

TABLE 1. Support for each implied reversal on the composite phylogeny, expressed in terms of number of extra steps and degree of differential weighting required to eliminate each reversal (see text for detailed explanation).

	Extra steps	Differential weighting
Carphodactylinae geckos	2	3:1
Cylindrophine snakes	1	2:1
<i>Lachesis</i> (Viperidae)	1	2:1
<i>Cerastes</i> group (Viperidae)	1	2:1
<i>Echis</i> (Viperidae)	1	2:1

than five extra steps, or a differential weighting of more than 6:1. There are, however, also cases where implied convergent forward transitions could instead optimize as a forward transition followed by one or more reversals with only slight loss in parsimony, or only moderate differential weighting of transition probabilities. Such cases include *Phrynosoma*, basal anguils, scincoids, and basal varanoids.

#### DISCUSSION

This analysis clearly demonstrates that transitions from oviparity to viviparity are much more frequent, and generally more strongly supported, than the reverse. This is in broad agreement with conventional assumptions (e.g., Fitch 1970; Tinkle and Gibbons 1977; Guillette et al. 1980; Shine 1985; Blackburn 1992). Fraipont et al.'s (1996) heterodox suggestion that forward and reverse transitions are equally prevalent is not supported. Thus, a mild version of Dollo's law is upheld: Viviparity appears relatively easy to acquire but difficult to lose. However, absolute irreversibility is not supported: Some reversals are implied on the most-parsimonious tree. Although all of these reversals are weakly supported, they nonetheless warrant detailed study. If these oviparous forms are indeed descended from viviparous ancestors, one might expect them to exhibit differences from "normal" (primitively oviparous) forms in traits such as eggshell morphology or reproductive cycles. Such "reinventions" of previously lost traits can provide important insights into evolutionary processes—as in the classic example of the panda's thumb (Gould 1980). The phylogenetic pattern that implies these reversals should also be critically examined.

The results confirm that the origins of viviparity are non-random, as noted by previous authors (e.g., Shine 1985). In particular, reproductive mode has never changed in two very diverse clades (archosaurs and turtles), whereas it has changed at least 49 times in squamates. The real disparity is even greater, because the 49 changes here identified within squamates do not include numerous transitions in scincids, colubrids, and elapids. For example, analyses by Shine (1985) and Blackburn (1982, 1985) suggest that approximately half of all transitions in reproductive mode within squamate reptiles have occurred within these three groups (estimated at 51 of 95 and 39 of 90 by these authors, respectively). These lineages were omitted from our analysis because robust phylogenies are not yet available.

The observation that archosaurs and turtles have all remained oviparous, in contrast to the lability of reproductive mode in squamates, has strong empirical support and deserves further investigation. Williams (1992) identified the absence of origins of viviparity among birds and especially turtles as a major challenge for evolutionary theory. However, a plausible explanation had already been suggested. Embryonic diapause appears to be widespread in archosaurs (including birds) and turtles, but not in squamates (Shine 1983). With embryonic diapause, eggs suspend development if retained in the uterus and only resume development after they are laid. Thus, prolonged retention of eggs will not lead to shorter-and-shorter incubation periods and final hatching in utero (viviparity). This physiological constraint may have precluded the evolution of viviparity in archosaurs and turtles

(Shine 1983). Significantly, the tuatara *Sphenodon* also has embryonic diapause: This is consistent with the observation that it has remained oviparous, despite living in an extremely cold region, where viviparity is advantageous and is found in most squamates (e.g., Whitaker 1968). In contrast to *Sphenodon*, archosaurs, and turtles, squamates (except some chameleons) lack embryonic diapause; retained eggs undergo normal development and prolonged retention can lead to viviparity. Experimental (manipulative) tests of this proposition are needed, however; at present, this hypothesis is merely plausible. Furthermore, this constraint is not absolute. Some archosaurs such as cuckoos can commence embryonic development in utero, presumably because of the fitness advantages accruing to earlier hatching in these brood parasites. Also, some (but not all) chameleons possess embryonic diapause (de Vosjoli and Ferguson 1995), yet viviparity has evolved within this group.

The conclusion that transitions from oviparity to viviparity within reptiles are much more common than the reverse, but that a few reversals might have occurred, is consistent with similar studies involving elasmobranch fishes (Dulvy and Reynolds 1997) and polychaete worms (Rouse and Fitzhugh 1994). The elasmobranch study identified nine or 10 origins of viviparity and only two or three reversals. In polychaetes, six transitions from broadcast spawning ("oviparity") to brooding ("viviparity") were identified, with only one change in the opposite direction. Thus, although the existence of reversals remains contentious, the pattern that gains of viviparity are several times more likely than losses appears to be strong and general across very disparate groups. It has been argued recently that optimization of such traits will be inaccurate if forward and reverse transitions are naïvely assumed to be equally likely (Omeland 1997): Rather, the transitions should be weighted differentially so that the more "difficult" transitions are more costly. One might go further and propose that differential weighting of such transitions might also be employed if these traits are to be used in phylogenetic reconstruction (e.g., Goloboff 1997). If phylogenetic and selectionist evidence all suggest that viviparity is more easily gained than lost, a tree implying two gains of viviparity must be viewed as more likely than one implying two losses. However, such differential weighting of transition probabilities makes the dangerous assumption that these constraints are universal, whereas they might be restricted to just the clade under study or portions of the clade. Panchen (1992) emphasises that most biological "laws" are only "taxonomic statements" that apply to particular portions of phylogeny. To justify such a priori weighting, therefore, the causal factors responsible for the assumed trend should be identified (e.g., via developmental, genetic, or experimental microevolutionary studies) and confirmed to be present in all taxa under investigation (Lee, unpubl.). Alternatively, the transition probabilities might be evaluated to see if they are uniform throughout the tree; if not, it might be possible to measure them for each part of the tree and apply different weighting schemes to each part (Philippe et al. 1996).

Finally, it must be emphasized that the above inferences are contingent on the accuracy of available phylogenies. Further phylogenetic analyses might strengthen or refute these conclusions. In particular, this study could not incorporate

information from the three major clades of squamates for which comprehensive phylogenies are not yet available. Examination of the evolution of reproductive modes in a phylogenetic context in these diverse and reproductively labile taxa should provide extensive new data to test the conclusions of our study.

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#### APPENDIX

##### *Phylogenetic Sources*

Sources used to compile the composite phylogeny are listed below; where there are other proposed arrangements we have given reasons for our preferred topology.

The higher-level reptilian phylogeny of Gauthier et al. (1988) and Laurin and Reisz (1995) has been adopted. These studies supported the traditional view that turtles lie outside a monophyletic Diapsida. Recent arguments that turtles belong within diapsids, as a sister group to lepidosaurs (deBraga and Rieppel 1997), appear to be poorly supported (Lee 1997a). The relationships of ichthyosaurs have until recently been contentious (e.g. Carroll 1988). However, the most recent analyses have shown that they are the sister group to sauropterygians (plesiosaurs and relatives), together forming the Euryapsida (Caldwell 1996; Lee and Spencer, unpubl.). Euryapsids appear to be related to lepidosaurs (Rieppel 1994; de Braga and Rieppel 1997), although archosauriform affinities have been suggested (Caldwell 1996).

For lepidosaurs, *Sphenodon* is the sister group to a monophyletic Squamata (e.g., Benton 1985; Estes et al. 1988; Evans 1988). Squamate phylogeny is based on Estes et al. (1988). Within squamates (lizards and snakes), detailed and well-corroborated phylogenetic hypotheses were available for all major groups with oviparous and viviparous forms, except for three diverse and problematic assemblages: scincids, colubrids, and elapids. The higher-level relationships within each of these three groups have yet to be resolved rigorously, for example, via numerical cladistic analysis of large numbers of morphological characters or molecular sequences. Preliminary analyses have considered only relatively few taxa or traits, and have produced weakly resolved and often conflicting arrangements (e.g., for colubrids: Lawson and Dessauer 1981; Dessauer et al. 1987; Keogh 1996). As a result, lower-level analyses have suffered because it has been difficult or impossible to delineate discrete monophyletic subgroups to analyze in detail. There are more exhaustive molecular sequence studies in progress for each of these groups, and their results might fill these gaps in the composite phylogeny.

Relationships between major groups of iguanians are based on Frost and Etheridge (1989) and Macey et al. (1997). The latter study demonstrates iguanid monophyly and resolves the relationships between the subfamilies identified in the former. Relationships within phrynosomatids are based on Reeder and Wiens (1996) and within *Sceloporus* on Wiens and Reeder (1997). Reeder and Wiens (1996) only included four species of *Phrynosoma* in their analysis, but their results were consistent with the much more detailed phylogeny of this group by Montanucci (1987). Frost and Etheridge (1989) presented two alternative arrangements of acrodont iguanians: Agamids are either monophyletic, or paraphyletic with respect to chameleons. The former arrangement is supported by genetic data (Joger 1991) and adopted here. Relationships within agamids are based largely on an analysis of selected genera by Joger (1991). *Cophotis* and *Lyriocephalus* have been inserted into this phylogeny in the positions suggested by Moody (1980) and *Pseudotrapelius*, *Trapelius*, and *Bufoiceps* in the positions suggested by Arnold (1990); these taxa have been added because they are either viviparous or closely related to viviparous forms. Relationships within chameleons are based on the morphological analysis of Klaver and Böhme (1987); genetic data are “more or less concordant” (Hofman et al. 1991, p. 260) with this morphological analysis.

Among scleroglossans, the major clades in Estes et al. (1988) are provisionally accepted. However, the affinities of three limbless taxa left *incertae sedis* in that analysis were resolved in a reanalysis of Estes et al.'s data that included fossil taxa and new characters: Snakes are related to mosasauroids and varanids (Schwenk 1988; Lee 1997b, unpubl.), whereas amphisbaenians and dibamids are sister taxa, together having gekkotan affinities (Caldwell 1998; Reynolds 1998; Lee, unpubl.). Also, the anguid-xenosauroid-varanoid polytomy in Estes et al. (1988) was resolved in favour of a xenosauroid-varanoid clade (Lee 1998b).

Higher-level gekkotan phylogeny is based on Kluge (1987), and relationships within carphodactylines on Bauer (1990). Within cordylids, the sister-group relationship between cordylines and gerrhosaurines proposed by Lang (1991) is accepted. However, within cordylines, recent molecular analysis has shown that *Platysaurus* is basal to the other three genera (Mouton 1997; *contra* Lang 1991). This arrangement is further supported by dermal gland morphology (E. Arnold, pers. comm. 1996). Relationships within lacertids are based on the morphological analysis of Arnold (1989); molecular data are highly congruent with this arrangement (Harris et al., unpubl.). Within anguids, *Anniella* is basal to all other taxa (Good 1987), and anguines lie outside the diploglossine-gerrhonotine clade (Gauthier 1982). Relationships within gerrhonotines have been analyzed in detail by Good (1988). Varanoid relationships are well resolved (Rieppel 1980; Pregill et al. 1986; Estes et al. 1988), and recent work confirms the old hypothesis that snakes are embedded within this taxon (Schwenk 1988, 1993; Cooper 1997; Young 1997) and, in particular, are related to mosasauroids (Lee 1997b, unpubl.; Caldwell 1998).

Higher-level snake phylogeny has been investigated by Kluge (1991), Cundall et al. (1993), Heise et al. (1995), and Scanlon (1996). The basal position of scolecophidians is supported in the first three studies and accepted here. Among other taxa, aniliids, uropeltids, and cylindrophids formed a paraphyletic assemblage with respect to higher snakes in Cundall et al. (1993) but a clade with respect to higher snakes in Kluge (1991) and Scanlon (1996). The latter arrangement is more parsimonious when certain fossil taxa such as *Pachyrhachis* (Caldwell and Lee 1997) are included (Lee, Scanlon, and Caldwell, unpubl. data) and is accepted here. The affinities between boines, erycines, pythonines, and higher snakes were unresolved or very weakly resolved in Kluge (1991), Cundall et al. (1993), and Heise et al. (1995); a reanalysis by Scanlon (1996) provides moderate support for the group (((boines+erycines) pythonines) higher snakes).

Among higher snakes, the position of *Atractaspis* near elapids is supported by molecular sequences (Heise et al. 1995), although morphology suggests a more basal position, possibly outside most colubroids (Underwood and Kochva 1993). Because the molecular evidence appears strong (99% bootstrap frequency) whereas the morphological evidence has yet to be analysed cladistically, elapid affinities are provisionally assumed here.

## APPENDIX. Continued.

Viperids consist of two major clades, viperines and crotalines (e.g., Liem et al. 1971). *Causus* lies outside the viperine-crotaline dichotomy (Cadle 1992; *contra* Ashe and Marx 1988). Among crotalines, evidence for close relationships between *Bothrops* and *Lachesis*, to the exclusion of all other major genera, is presented in Werman (1992). The nearest relatives to this clade are *Crotalus* and New World *Agkistrodon* followed by Old World *Agkistrodon* (Cullings et al. 1997). *Trimeresurus* appears to be paraphyletic: viviparous forms are closely related to Old World *Agkistrodon*, but the oviparous *T. mucrosquamatus* lies outside a clade containing all crotaline genera just mentioned (Knight et al. 1992; Heise et al. 1995). A recent analysis by Malhotra and Thorpe (1997) is consistent with this: The oviparous *T. mucrosquamatus* is only distantly

related to other *Trimeresurus*, although the monophyly of *Trimeresurus* was assumed rather than tested in the analysis. The most basal crotalines are *Deinagkistrodon*, *Sistrurus*, and *Calloselasma* (Knight et al. 1992).

Viperine relationships are based on a detailed cladistic analysis of morphology (Groombridge, unpubl.); immunological data are broadly concordant with this arrangement (Herrmann and Joger 1997). Further detail of relationships within Eurasian vipers (clade D in Herrmann and Joger 1997) has been provided by Nilson and Andr en (1997). The position of *Macrovipera* and *Daboia*, left *incertae sedis* in these studies, is tentatively resolved here based on immunological distances, which suggest that they are sister groups (Herrmann and Joger 1997, fig. 3) and together related to *Pseudocerastes* and *Eristocophis* (Herrmann and Joger 1997, fig. 7).