THE EVOLUTION OF OVIPARITY WITH EGG GUARDING AND VIVIPARITY IN LIZARDS AND SNAKES: A PHYLOGENETIC ANALYSIS

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Abstract.—This paper investigates the evolution of viviparity and of egg guarding in lizards and snakes in which three modes of reproduction can be described: oviparity without egg guarding, oviparity with egg guarding, and viviparity. All possible transitions of reproductive modes were detected in each taxon using Maddison's method. We then tested two specific hypotheses. First, egg guarding can be regarded as an alternative to viviparity. A relatively frequent association of egg guarding and viviparous species in the same taxon may be due to similar environmental conditions or species characteristics leading to two different solutions. Second, egg guarding may facilitate the evolution of viviparity. This hypothesis is supported by the high frequency of viviparous species in taxa containing egg guarding species and by a tendency for prolonged uterine retention of eggs in brooding squamates. Our analyses demonstrate that the first hypothesis is the best supported. Egg guarding and viviparity most often evolved independently. If a major benefit of egg guarding is the repulsion of potential predators, size is one of the most obvious morphological characters that should be correlated with the evolution of reproductive modes. The two reproductive traits were correlated to a reduction in body size for viviparous species and an increase in body size for egg guarding species. This could partly explain why the evolution of these reproductive modes seems almost antagonist.

Key words.—Egg guarding, lizard, parental care, snake, squamata, viviparity.

Most species of lizards and snakes bury their eggs and do not guard them (Brattstrom 1974; Shine 1988). Egg guarding by females occurs in about 0.8% of species (Greer 1971; Shine 1988). Viviparity occurs in about 20% of all species (Blackburn 1982), and about 71% of the viviparous species belong to either the lizard families Iguanidae or Scincidae, or the snake families Colubridae or Viperidae. Thus, viviparity is distributed discontinuously among the squamate taxa, and families vary greatly in their proportions of viviparous species. This observation supports the hypothesis that selective pressures, preadaptations, and constraints vary at high taxonomic levels (Blackburn 1985). However, both oviparity with egg guarding and viviparity sometimes cooccur in the same lineages, suggesting a possible relationship between the evolution of viviparity and egg guarding (Shine and Bull 1979; Gross and Shine 1981; Shine 1985, 1988). Although several papers have considered the evolution of viviparity in squamates (Tinkle and Gibbons 1977; Shine and Bull 1979; Guillette et al. 1980; Pilorge and Barbault 1981; Guillette 1981; Blackburn 1982; Shine 1985), only one has discussed the evolution of egg guarding (Shine 1988).

From these studies, two specific hypotheses have been suggested. First, egg guarding can be regarded as an alternative to viviparity (Fitch 1970; Packard et al. 1977). A relatively frequent association of viviparous species and oviparous species with egg guarding in the same taxon may be due to similar environmental conditions or species characteristics leading to two different solutions. Second, egg guarding may be an intermediate step in the evolution of viviparity (Shine and Bull 1979). This hypothesis is supported by the high frequency of viviparous species in taxa containing egg-guarding species, especially in snakes, and by an apparent tendency for prolonged uterine retention of eggs in brooding squamates (Shine 1985). Thus, Fitch (1970) proposed an evolutionary transition from oviparity without egg guarding to viviparity (O→V) or from oviparity without egg guarding to oviparity with egg guarding (O→G), whereas Shine and Bull (1979) proposed an alternative scenario implying the evolution sequence from oviparity without egg guarding to oviparity with egg guarding and then to viviparity (O→G→V). If Fitch (1970) is correct, we expect to see a statistical difference between O↔V, O↔G transitions and G↔V transitions taking into account the number of respective cases of oviparity, viviparity, and egg guarding, whereas if Shine and Bull's (1979) hypothesis is right, we expect a statistical difference between G→V and V→G transitions. Our goal in this paper is to study in a phylogenetic context the evolution of viviparity and egg guarding in lizards and snakes to test Fitch's and Shine and Bull's hypotheses. Both hypotheses make the implicit assumptions that character evolution is irreversible and that oviparity with egg guarding and viviparity are derived. In our analysis, the irreversibility was tested, and the three reproductive modes were allowed to reverse freely.

MATERIALS AND METHODS

We followed the majority of workers on reproductive modes and classified species as either "oviparous" (shelled eggs are laid) or "viviparous" (the young are fully formed at laying; Budker 1958; Hoar 1969; Blackburn 1982, 1985). As egg-guarding behavior takes diverse forms in Squamata (lizards and snakes), following Shine (1988), we defined "egg guarding" as any form of postovipositional parental behavior or any action of the parent after oviposition that increases the chances of survival of the offspring. All species were therefore classified as (1) oviparous without egg guard-

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TABLE 1.   A. Number of oviparous, egg-guarding, and viviparous genera known in the literature among lizard and snake families, in which the three types of reproductive mode are known. In parentheses are the number of genera employed in our analyses. B. Number of oviparous, viviparous, and egg-guarding species among genera in which the three types of reproductive mode are known in the literature. In parentheses is the number of species employed in our analyses.

A.	O	V	G	O/V	O/G	O/V/G	References
Boidae	3 (3)	11 (15)	9 (8)	0 (0)	2 (1)	0 (0)	8, **13, 22,** 27, **46,** 55, 60, 66, 72, 73, 78, **87, 88, 89.**
Colubridae	117 (4)	24 (0)	1 (0)	3 (0)	10 (0)	2 (1)	8, **12, 13, 22,** 27, 72, 73, 78, 86, 89.
Elapidae	10 (3)	14 (15)	5 (0)	0 (0)	3 (2)	0 (0)	1, 8, **13, 22,** 27, 52, 56, **57,** 70, 72, 73, **89, 91.**
Typhlopidae	0 (0)	0 (0)	1 (1)	1 (1)	1 (0)	0 (0)	1, 8, **27,** 72, 73.
Viperidae	3 (3)	7 (7)	1 (1)	2 (0)	1 (0)	2 (0)	3, 6, 8, 10, **13,** 20, **22,** 27, 47, 51, 68, 72, 73, **89.**
Anguidae	3 (1)	7 (3)	0 (0)	1 (1)	3 (3)	2 (0)	5, 7, 17, 19, 27, **31, 33, 34, 45,** 49, 53, 62, **67,** 69, 72, 73, **75, 80,** 82, **84, 90.**
Iguanidae	24 (23)	3 (1)	4 (4)	5 (6)	1 (1)	0 (0)	2, 7, 14, 15, 16, 21, 23, 24, **25,** 27, **28,** 32, 40, 41, 44, **45,** 50, 54, 59, 64, 71, 72, 73, 74, 77, 79, 83, 85, 93.
Scincidae	25 (10)	20 (0)	0 (0)	11 (7)	2 (1)	1 (0)	4, 6, 7, 9, 11, 18, 24, 26, 27, 30, 35, 36, 37, 38, **39,** 42, 43, **45,** 63, 72, 73, 92.

B.	O	V	G	References
Colubridae				
Elaphe	12 (4)	1 (1)	4 (2)	8, **27,** 29, 58, 72, 73.
Natrix	3 (1)	6 (1)	1 (1)	8, 27, 48, 72, 73, **76.**
Viperidae				
Agkistrodon	2 (2)	6 (1)	2 (1)	6, 8, 10, **72,** 73.
Trimeresurus	4 (2)	11 (3)	1 (1)	6, 8, 20, 27, **47,** 61, 65, 72, 73.
Anguidae				
Diploglossus	1 (2)	9 (9)	2 (1)	5, 7, 27, **34,** 69, 72, 73, 82.
Elgaria	5 (5)	2 (1)	1 (1)	7, 27, **33,** 72, 73.
Scincidae				
Eumeces	13 (13)	7 (7)	20 (20)	7, 18, 26, 27, 35, 36, 37, 38, 42, 72, 73, **81,** 92.

References: 1. Alvarez del Toro (1960), 2. Amaral (1977), 3. Andren and Nilson (1979), 4. Arnold and Leviton (1977), 5. Barbour and Ramsden (1919), 6. Baverstock and Donnellan (1990), 7. Blackburn (1982), 8. Blackburn (1985), 9. Brain (1959), 10. Brattstrom (1964), 11. Broadley (1968), **12.** Cadle (1987), **13.** Cadle (1988), 14. Carey (1975), 15. Carpenter (1966), 16. Cole (1978), 17. Conant and Downs (1940), 18. Cooper et al. (1983), 19. Daniel (1983), 20. Deoras (1978), 21. Donoso-Barros (1966), **22.** Duellman (1978), 23. Duellman (1979), 24. Estes and Pregill (1988), **25.** Etheridge and De Queiroz (1988), 26. Fitch (1954), **27.** Fitch (1970), **28.** Frost and Etheridge (1989), 29. Fukada (1978), 30. Garland et al. (1991), **31.** Gauthier (1982), 32. Goldberg (1971), **33.** Good (1988), **34.** Greer (1967), 35. Greer (1970), 36. Greer (1974), 37. Greer (1977), 38. Greer (1979), **39.** Greer (1989), 40. Guillette et al. (1980), 41. Guillette (1981), 42. Hikida (1981), 43. Hutchinson et al. (1990), 44. Iverson (1979), **45.** Jansen and Paukstis (1991), **46.** Kluge (1991), **47.** Koba et al. (1970), 48. Kuntz (1963), 49. Langerwerf (1981), 50. Lowe and Howard (1975), 51. Marx and Rabb (1965), 52. McCarthy (1985), 53. McConkey (1954), 54. McCoy (1968), 55. McDowell (1979), 56. Mengden (1985a), **57.** Mengden (1985b), 58. Mishima et al. (1977), 59. Montanucci (1979), 60. Murphy et al. (1978), 61. Nickerson (1974), 62. Noble and Masson (1933), 63. Piennar and FitzSimons (1966), 64. Presch (1969), 65. Reitinger (1978), 66. Rieppel (1979), **67.** Rieppel (1988), 68. Saint Girons and Nauleau (1981), 69. Schmidt and Inger (1957), 70. Schwaner et al. (1985), 71. Shaw (1954), **72.** Shine (1985), 73. Shine (1988), 74. Smith (1939), **75.** Smith (1942), **76.** Smith (1943), 77. Smith and Hall (1974), 78. Smith et al. (1977), 79. Stebbins (1954), **80.** Stebbins (1958), **81.** Taylor (1935), 82. Taylor (1956), 83. Thomas and Dixon (1976), **84.** Tihen (1949), 85. Trillmich (1979), 86. Underwood (1967), **87.** Underwood (1976), **88.** Underwood and Stimson (1990), **89.** Vitt (1987), **90.** Waddick and Smith (1974), **91.** Wallach (1985), 92. Wang (1966), 93. Werner (1982). Numbers in bold character are references used for analysis.

ing (O), (2) oviparous with egg guarding (G), or (3) viviparous (V).

Phylogenetic and reproductive data were gathered from the literature (see references in Table 1). We analyzed only taxa showing all three reproductive modes. Consequently, the number of times they appeared in our sample is different than that recorded in the literature. When estimates of phylogenetic relationships were available, all taxonomic levels at which transitions were detected were employed for the analysis. For example, in Anguidae, we analyzed transitions occurring (1) among species within two genera (*Diploglossus* and *Elgaria*), (2) among genera or species within two sub-

families (Diploglossinae and Gerrhonotinae; Anguininae was excluded because all species are viviparous) and, (3) among all subfamilies, genera, or species within the family. We analyzed phylogenetic relationships (1) of the lizard and snake families; (2) within eight families (Boidae, Colubridae, Elapidae, Typhlopidae, Viperidae, Anguidae, Iguanidae, and Scincidae); (3) within ten subfamilies (Alsophiinae, Colubrinae, Natricinae, and Psammophiinae for Colubridae; Viperinae and Crotalinae for Viperidae; Diploglossinae and Gerrhonotinae for Anguidae; and Lygosominae and Scincinae for Scincidae); and (4) within seven genera (*Elaphe* and *Natrix* for Colubridae; *Agkistrodon* and *Trimeresurus* for Viperidae; *Di-*

oviparity
viviparity
polymorphic
equivocal

GOOD (1988)
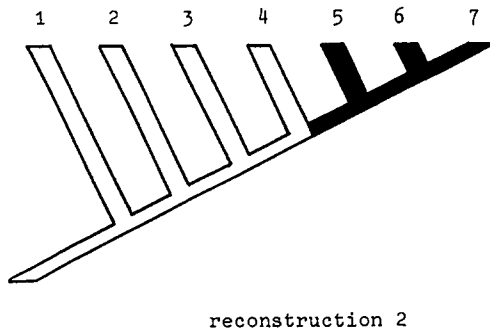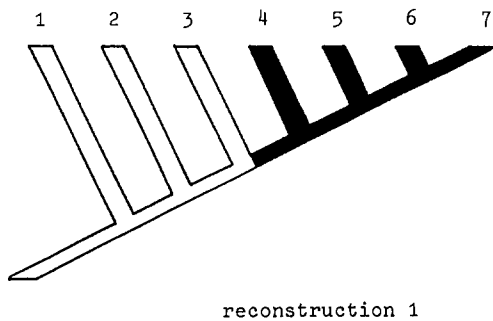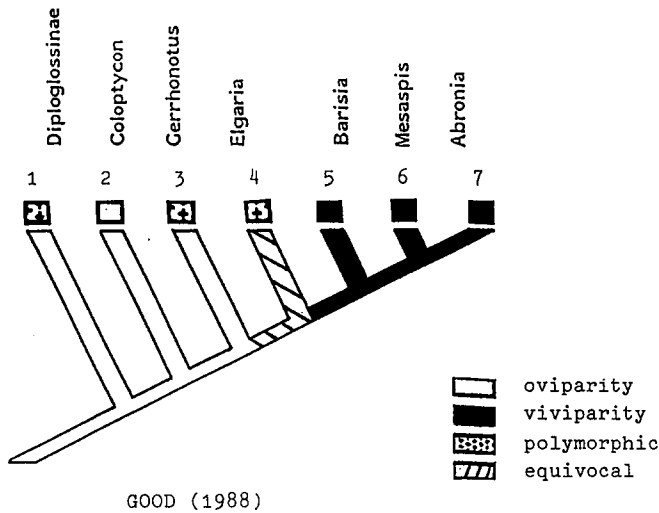
reconstruction 1

reconstruction 2

FIG. 1. Phylogenetic trees among the genera of Gerrhonotine as suggested by Good (1988) and all possible reconstructions by the cycling option of McClade's program (Maddison and Maddison 1990).

reproductive characters, we used outgroup comparisons (Farris 1982; Maddison et al. 1984; Wiley et al. 1991). To use this method, it is necessary that the studied group (ingroup) be monophyletic because members of a monophyletic group are bound together by common ancestry relationships that they do not share with any other taxa (Brooks and McLennan 1991). The outgroup (any group used in an analysis not included in the taxon under study) is used for comparative purposes, usually in arguments concerning the relative polarity of characters (Wiley et al. 1991). To determine polarity, simple parsimony arguments are used in conjunction with an optimization routine developed by Maddison et al. (1984). These authors showed that hypotheses about the relationship among ingroup and outgroup(s) can have a profound influence on measures of character polarity.

RESULTS

Phylogenetic Analyses of the Familial Level

For lizards, we used phylogenetic data from Camp (1923), Underwood (1957, 1971), Northcutt (1978), Schwenk (1988), Estes and Pregill (1988), Estes et al. (1988), Presch (1988), Rieppel (1988), Greene (1988), and Greer (1989). For snakes, we used data from Rage (1987), McDowell (1987), Rieppel (1988), Greene (1988), and Cadle (1987, 1988).

Among all phylogenetic trees of lizard relationships at the family level, a maximum of 21 transitions were identified depending on the tree and the reconstructions used. Among phylogenetic trees of snake relationships at the family level, a maximum of 16 transitions were identified. We found a maximum of 15 transitions from oviparity without egg guarding (O) to viviparity (V), 10 transitions from oviparity without egg guarding (O) to oviparity with egg guarding (G), 8 transitions from viviparity to oviparity (V→O), and 5 transitions from viviparity to oviparity with egg guarding (V→G, Table 2A). Within all cladograms of lizard relationships, oviparity without egg guarding represents the plesiomorphic condition, and egg guarding and viviparity the apomorphic conditions. For snakes, depending on the reconstructions, oviparity or viviparity represent the plesiomorphic conditions and egg guarding always the apomorphic condition. At this taxonomic level, no transitions from egg guarding to viviparity were found. Moreover, the results clearly show that viviparity appears earlier than egg guarding (Table 3).

Phylogenetic Analyses of the Generic Level

The data of lizards and snakes used for generic relationships are shown in Table 1B. Among all phylogenetic trees of generic relationships at the familial or interfamilial levels, a maximum of 26 transitions were identified for lizards and a maximum of 29 transitions were identified for snakes depending on the tree used. We found 15 transitions from O→V, 16 transitions from O→G, 8 transitions from G→O, 8 transitions from V→O, 6 transitions from V→G, and 2 transitions from G→V.

The two G→V transitions were detected in Cadle's (1988), and Rieppel's (1988; Fig. 2) cladograms. The first case (Cadle 1988) is found in a tree based on albumin immunological distances, which is under debate (Savitsky 1980; McCarthy

ploglossus and *Elgeria* for Anguidae; and *Eumeces* for Scincidae). Finally, when several cladograms were available for a taxon, we used all of them to analyze the sensitivity of our results with respect to possible misclassifications. As the irreversibility was tested, the character in the transformation series was considered as unordered (Fitch Parsimony). We used McClade (Maddison and Maddison 1990) for analyzing all phylogenies and studying character evolution. We used the cycling option to look for all possible reconstructions of the life-history character (Fig. 1). To infer polarity among

TABLE 2. A. Maximum of transitions occurred among lizard and snake families. B. Maximum of transitions occurred among lizard and snake genera. C. Maximum of transitions occurred among lizard and snake species.

A.	O→V	O→G	V→O	G→O	V→G	G→V
Lizard families	10	6	3	0	2	0
Snake families	5	4	5	0	3	0
Total	15	10	8	0	5	0
Percent	40	26	21	0	13	0

B.	O→V	O→G	V→O	G→O	V→G	G→V
Boidae	0	2	2	2	1	0
Colubridae	1	2	0	0	1	0
Elapidae	3	2	0	0	0	0
Typhlopidae	1	2	0	0	0	0
Viperidae	2	2	2	3	1	1
Anguidae	2	2	3	2	2	1
Iguanidae	5	3	1	1	0	0
Scincidae	1	1	0	0	1	0
Total	15	16	8	8	6	2
Percent	27	29	14.5	14.5	11	4

C.	O→V	O→G	V→O	G→O	V→G	G→V
Colubridae						
Elaphe	1	0	0	0	0	0
Natrix	0	0	0	0	0	0
Viperidae						
Agkistrodon	0	0	0	0	0	0
Trimeresurus	0	0	0	0	0	0
Anguidae						
Diploglossus	1	1	1	0	1	0
Elgaria	2	3	0	0	2	0
Scincidae						
Eumeces	1	2	0	3	0	2
Trees with mixed species	11	6	10	0	1	0
Total	16	12	11	3	4	2
Percent	33	25	24	6	8	4
Total	46	38	27	11	15	4
Percent	33	27	19	8	11	2

TABLE 3. Number of reconstructions and ancestral character states for each phylogenetic tree of lizard and snake relationships at the family level.

Phylogenetic tree	Number of reconstructions	Ancestral character		
		Ovi-parous	Vivi-parous	Egg guarding
Lizards				
Camp (1923)	3	3	0	0
Underwood (1957)	2	2	0	0
Underwood (1971)	2	2	0	
Northcutt (1978)	2	2	0	0
Schwenk (1988)				
Dibamidae excluded	1	1	0	0
Lepidosaurs	1	1	0	0
Estes, de Queiroz and Gauthier (1988)				
A Wagner.S cladogram PHYSYS	2	2	0	0
B Wagner.S cladogram PHYSYS	1	1	0	0
C PAUP cladogram	1	1	0	0
conservative cladogram	1	1	0	0
Presch (1988)				
cladogram with characters A	4	4	0	0
cladogram with characters B	4	4	0	0
cladogram with characters C	4	4	0	0
Rieppel (1988)	2	2	0	0
Greene (1988)	1	1	0	0
Greer (1989)	1	1	0	0
Snakes				
Rage (1987)	3	1	2	0
McDowell (1987)	1	1	0	0
Rieppel (1988)	2	1	1	0
Greene (1988)	1	1	0	0
Cadle (1987)	1	0	1	0
Cadle (1988)	3	3	0	0
Total	39	4	0	
Percent	91	9	0	

1985). Indeed, this tree assumes monophyly between 18 genera of colubrids, elapids, and viperids when it turns out to be not the case (Bogert 1943; Underwood 1967; McDowell 1969; Voris 1977; Cadle and Gorman 1981; Schwaner et al. 1985). In the second case, one G→V transition was found in one reconstruction of Gerrhonotinae phylogeny constructed by Rieppel (1988; Fig. 2), but in all other phylogenetic trees proposed by Smith (1942), Tihen (1949), Stebbins (1958), Waddick and Smith (1974), Gauthier (1982; Fig. 3), or Good (1988, Fig. 1) no V→G transition nor vice-versa are found.

To summarize, cases of G→V transitions are rare, and these transitions occur only in trees that are still under debate. As at the family level, oviparity and viviparity represent in all cases except one the plesiomorphic characters and egg guarding the derived character (in 70.5% of all reconstructions, oviparity is the ancestral character; in 29.49%, it is viviparity; and in only 0.01%, it is egg guarding).

Phylogenetic Analyses of the Species Level

The data of lizards and snakes used for species relationships are shown in Table 1B. Among all phylogenetic trees of species relationships at the generic, familial, or interfamilial levels, a maximum of 19 transitions were identified for lizards and a maximum of 29 transitions were identified for snakes, depending on the tree used and the different possible reconstructions (Table 2C). We found 16 transitions from O→V, 12 transitions from O→G, 11 transitions from V→O, 3 transitions from G→O, and 2 transitions from G→V.

The two G→V transitions were detected in a long phylogenetic tree of 56 species of *Eumeces* (Scincidae) based on morphological characteristics constructed by Taylor (1935). Several authors (Greer 1970; Hikida 1978) questioned Taylor's (1935) hypothesis and concluded that *Eumeces* is not monophyletic. In the phylogenetic tree proposed by Murphy et al. (1983), the relationships among 11 populations of five species from the North American *fasciatus* group of *Eumeces* do not show V↔G transitions. In this study, the authors chose as the outgroups two species of *Eumeces* to determine the evolutionary polarity of the reproductive modes of the *fasciatus* group of the *Eumeces*.

Thus, the results show at all taxonomic levels very few of G→V transitions (only 2% G→V versus 11% V→G transitions, Table 2). As in the cases of families and genera, oviparity and viviparity represent in all cases the plesiomorphic character states and egg guarding the derived character state
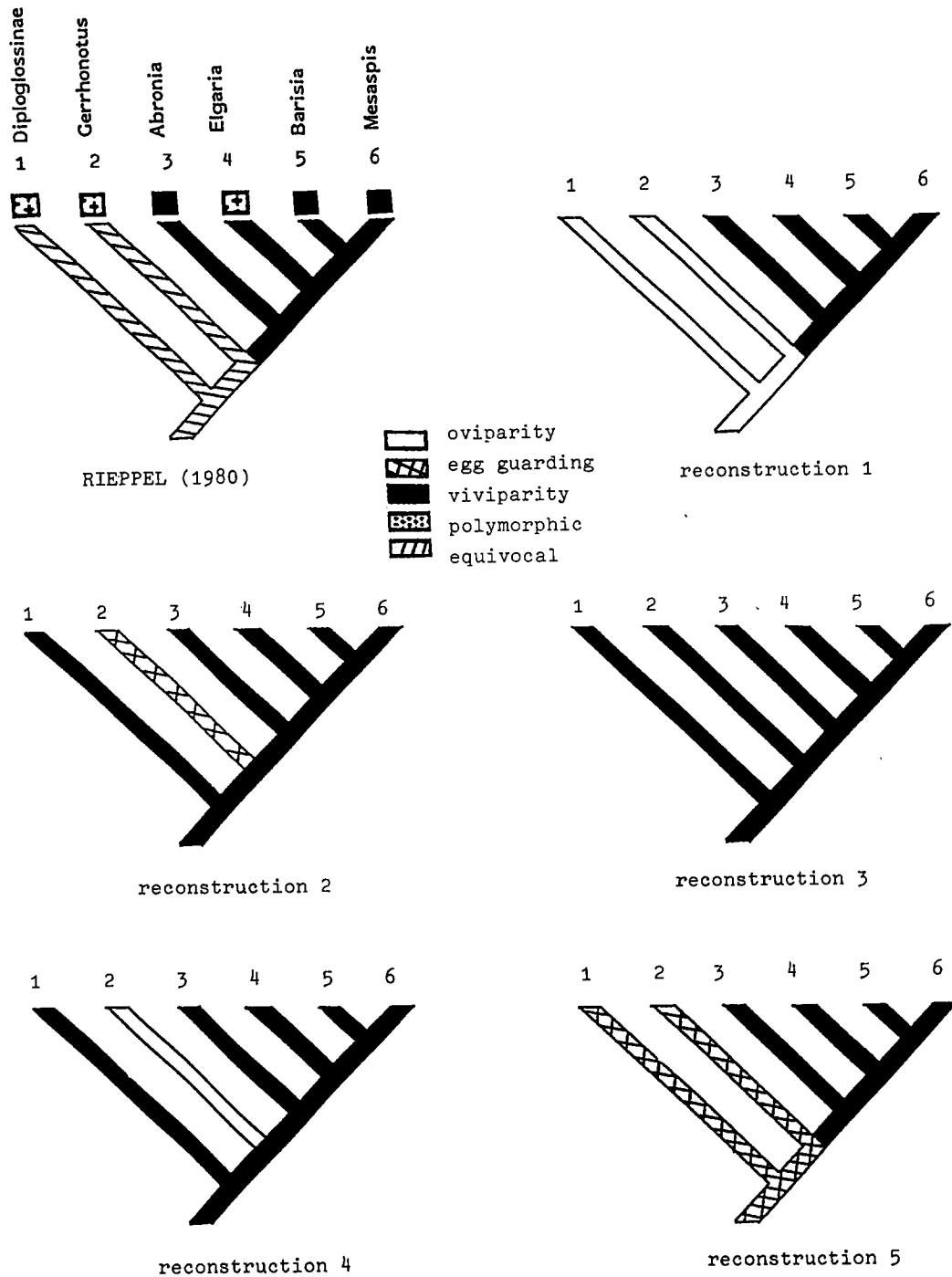
FIG. 2. Phylogenetic trees among the genera of Gerrhonotine as suggested by Rieppel (1979) and all possible reconstructions by the cycling option of MacClade's program (Maddison and Maddison 1990). In reconstruction 5, a transition G→V is found.

(in 60% of all reconstructions, oviparity is the ancestral character; and in 40%, it is viviparity).

DISCUSSION

In total, a maximum of 141 independent transitions (73 O↔V, 49 O↔G, and 19 V↔G) were detected. As we consider only phylogenetic trees with taxa showing all three reproductive modes, the percentage of oviparous, viviparous, or egg-guarding families, genera, and species used in our analyses are different than those generally cited in the literature (for our analyses, the percentage of families, genera, and species being oviparous: 135 cases or 46%, viviparous: 100 cases or 33%, and egg guarding: 63 cases or 21%). Based on these numbers, we can calculate the probability of occurrence of each type of transitions under the hypothesis of independence among transition types ($\chi^2_5 = 54.95$; $P <$
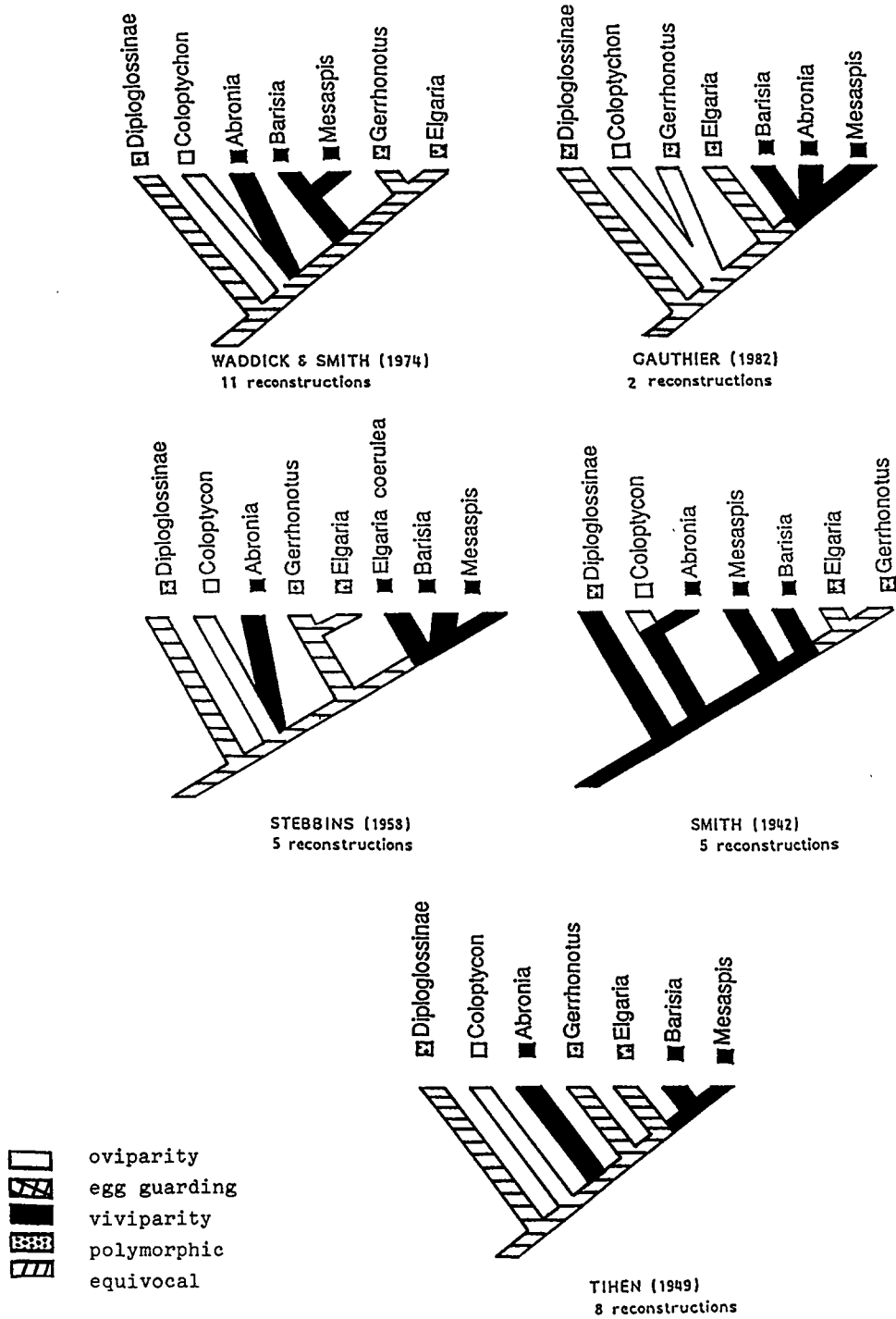
FIG. 3. Phylogenetic trees among the genera of Gerrhonotine as suggested by several authors. In 38 reconstructions among seven different phylogenetic trees, only one shows a G→V transition.

0.001). In particular, there is a strong deficit in the transition between egg guarding to viviparity compared with viviparity to oviparity with egg guarding ($\chi_2^2 = 13.01$; $P < 0.001$). The hypothesis that egg guarding preadapted lizards to viviparity (Shine and Bull 1979) seems to have little support (only four "G→V" transitions).

All reconstructions with MacClade of the life-history char-acter show that oviparity is the ancestral character in 73.6%, viviparity in 26.397%, and egg guarding in 0.003%. Viviparity and egg guarding arose independently several times in the evolution of lizards and snakes, and within cladograms of family relationships, viviparity usually appeared before egg guarding. Egg guarding is widespread only within a restricted number of phylogenetic lineages of squamates (Fitch

1970; Shine 1988). By parsimony, this suggests that egg guarding has evolved only once in each group, early in its history, and has been retained during subsequent speciations (Ridley 1983). However, the transition from oviparity to viviparity does not seem to be as irreversible as we first thought. A hybridization experiment between oviparous and viviparous populations of *Lacerta vivipara* was conducted by Heulin et al. (1989). Numerous fertile F_2 hybrids were obtained, implying that there is no reproductive isolation between the two forms. Moreover, if egg guarding facilitates the evolution of viviparity, we might expect that species with mixed reproductive modes, such as *L. vivipara*, would have some oviparous populations with egg guarding and some viviparous ones. Among the 11 species within the families studied here showing more than one reproductive mode, all are either oviparous without egg guarding or viviparous.

Without underestimating the fact that viviparity is relatively easier to detect than is egg guarding, which depends on detailed field studies, all results suggest that egg guarding probably appeared more recently in the history of each taxon than did viviparity. Thus, our results are more consistent with Fitch's (1970) prediction that egg guarding probably did not evolve as an evolution history to viviparity than with Shine and Bull's hypothesis of guarding as an intermediate condition. That some transitions were observed between egg guarding and viviparity seems to be open to another interpretation. Although a complete analysis of the factors influencing the evolution of viviparity and egg guarding was not the goal of our study, we will consider a few hypotheses particularly relevant to lizards and snakes.

Environmental conditions that favor high maternal investment (viviparity, egg guarding, and even uterine retention of eggs) might influence the evolution of any of these strategies. Hence, the cooccurences in eight families (Boidae, Colubridae, Elapidae, Typhlopidae, Viperidae, Anguidae, Iguanidae, and Scincidae) of egg guarding and viviparous species may relate to common causation rather than to one factor (egg guarding) preadapting a species for another (viviparity).

Cold climates seem to have been the most important single selective agent favoring viviparity (Shine 1988), but it is equally obvious that this single force cannot explain all cases. For example, viviparity in *Lygosoma* or *Sphenomorphus* is not explainable by the cold-climate hypothesis (Shine 1988; Shine and Guillette 1988). Other hypotheses for the effects of environmental influences (e.g., hot climates, unpredictability of environment, and soil moisture) or species characteristics (e.g., nest predation and physiological constraints) either have not been tested (lack of data) or are unlikely to have general importance (Shine 1988).

In contrast to their effect on the evolution of viviparity, cold climates are not an important factor favoring egg guarding (Shine 1988). One factor that may promote the evolution of egg guarding is limited availability of nest sites (Shine 1988). If nest sites are scarce relative to the number of nesting females, older nests are likely to be excavated and destroyed by other females. Active defense of nest sites by females occurs in iguanines and is correlated with nest site availability (Wiewandt 1982). Although the limited availability of nest sites is consistent with egg guarding in Iguanidae, it is un-

TABLE 4. Body-size means (snout-vent length) between oviparous and viviparous species or between oviparous and egg-guarding species within a genus. In parentheses is the number of species for which size and reproductive data are available in the literature. O, oviparity without egg guarding; G, oviparity with egg guarding; and V, viviparity.

	Oviparous (cm)	Viviparous (cm)	Egg guarding (cm)	Ratio V/O	Ratio G/O
Anguidae					
Elgeria	354 (2)	232 (1)	369 (1)	0.65	1.04
Ophisaurus	505 (1)		930 (4)		1.84
Chamaeleonidae					
Chamaeleo	187 (7)	85 (4)		0.45	
Iguanidae					
Liolaemus	68 (1)	89 (9)		1.32	
Phrynosoma	110 (8)	106 (2)		0.96	
Sceloporus	168 (2)	202 (6)		1.20	
Cyclura	225 (1)		471 (2)		2.09
Scincidae					
Eumeces	62 (5)	62 (6)	75 (2)	1.00	1.20
Scelotes	180 (2)	138 (1)		0.77	
Harrisoniascincus	56 (1)	45 (1)		0.80	
Typhlosaurus	285 (2)	153 (2)		0.54	
Leiolopisma	66 (6)	57 (1)		0.86	
Anamolopus	127 (3)	102 (1)		0.80	
Glaphyromorphus	61 (7)	72 (1)		1.17	
Lerista	62 (2)	59 (3)		0.95	
Mabuya	132 (1)	135 (1)		1.02	
Varanidae					
Varanus	313 (2)		544 (3)		1.74
Boidae					
Python	180 (1)		595 (4)		3.30
Colubridae					
Elaphe	158 (3)		220 (3)		1.39
Heterodon	75 (2)		116 (1)		1.55
Lampropeltis	133 (5)		199 (1)		1.50
Elapidae					
Naja	210 (3)		270 (2)		1.28
Viperidae					
Causus	44 (1)		100 (1)		2.27
Vipera	145 (2)	73 (7)		0.50	

likely to be of general importance, because scarcity of suitable nesting sites may be a rare phenomenon (Shine 1988).

Although the same ecological factors may explain the appearance of both egg guarding and viviparity, the evolution of correlated traits that favor or are linked to their appearance could be quite different. In particular, a major benefit of egg guarding is the repulsion of potential egg predators, then egg guarding should evolve most often in species in which the parent is capable of deterring predators (Shine 1988). This is most likely in large species. To test the hypothesis that large size cooccurs with egg guarding, we have taken the mean snout-vent length for each mode, and using within-genera, pairwise comparisons, we can calculate size differences between O and V, and O and G (Felsenstein 1985; Burt 1989; Harvey and Pagel 1991; Table 2). Our results show that egg guarding is associated with an increase in size (t_{11} = −5.96; $P < 0.001$, one-tailed test). Although viviparity is associated with a reduction in size (t_{15} = 2.00; $P < 0.035$,

one-tailed test). The small size of viviparous species may be explained by the benefits of viviparity in terms of an increase in the number of surviving offspring (Neil 1964). In this case, size might relate to the decrease of a viviparous female's fecundity. On the contrary, reduction in fecundity in viviparous species could have been linked in a reduction in size (Dunham et al. 1988). The increase in size of egg guarding species is consistent with the prediction that this behavior should be found most often in groups in which parents are able to defend their eggs. Although this latter result may explain why egg guarding and viviparity seem to be independent, almost antagonistic, evolutionary events, a similar analysis on a larger sample size and using more life-history traits would be necessary to fully support this prediction.

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