CHAPTER

8

# The Evolution of Viviparity in Reptiles: An Ecological Analysis

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## I. INTRODUCTION

Of the four orders of living reptiles, three are entirely oviparous (turtles and crocodilians), but approximately one-fifth of all species of lizards, snakes and amphisbaenians are viviparous. Most egg-laying squamates studied to date retain eggs *in utero* for almost one-half of the total period of embryonic development and, thus, have evolved part of the way toward viviparity (Shine, 1983a). Clearly, viviparity has arisen many times (e.g., Tinkle and Gibbons, 1977; Shine and Bull, 1979), and the dichotomy between oviparity and viviparity is a puzzling aspect of reptilian reproduction. Consequently, it has attracted considerable attention. (For recent reviews see Packard et al., 1977; Tinkle and Gibbons, 1977; Shine and Berry, 1978; Shine and Bull, 1979; Pilorge and Barbault, 1981; Blackburn, 1982.)

Several hypotheses have been proposed to explain why live-bearing has evolved; most of these invoke factors that kill eggs in the nest, but not *in utero*, and hence favor the evolution of prolonged uterine retention of eggs. Theory also suggests that certain types of species should be most likely to evolve viviparity; specifically, groups in which the survivorship or food intake of the reproducing female would not be markedly affected if she retained eggs *in utero*. The present review examines the validity of these ideas in terms of the arguments and inherent assumptions in each hypothesis, summarizes the empirical support for each hypothesis (based on published literature), and tests predictions from these hypotheses by identifying the squamate lineages in which viviparity has evolved and by looking for the ecological correlates predicted by theory. For this purpose, available phylogenetic and reproductive data on taxa containing both oviparous and viviparous forms are reviewed.

## II. TERMINOLOGY

Most reptiles reproduce by laying shelled eggs that contain relatively undeveloped embryos; they are termed *oviparous* or *egg-laying*. However, many squamate species retain eggs *in utero* until embryonic development is complete. In these cases the young are fully formed at birth and are capable of independent movement and feeding; this reproductive mode is referred to as *live-bearing* or *viviparity*.

Some authors have restricted the term viviparity to species with an intimate physiological connection between the reproducing female and her uterine young; this may involve complex placentation, absence of calcified egg-membranes, or maternal-fetal transfer of nutrients (Weekes, 1935; Bauchot, 1965; Spellerberg, 1976). Although the distinction between *ovoviviparity* (no maternal–fetal nutrient transfer) and *euviviparity* may be attractive conceptually, it is difficult to apply to reptiles. The available data suggest that most, but not all, live-bearing reptiles are ovoviviparous (Thompson, 1981; Yaron, Chapter 7, this volume). Exceptions to this statement include the New World skinks of the genus *Mabuya*, which show reduced ovum size and extensive maternal–fetal nutrient transfer (Vitt and Blackburn, 1983). Throughout this chapter, I use the term *oviparity* in those cases where shelled eggs are laid, and *viviparity* where young are either born alive or are deposited in thin-walled membranous sacs from which they emerge within a few days of parturition. This terminology follows the recommendations of Smith et al. (1973), Guillette (1982a), and Yaron (Chapter 7, this volume) and corresponds to that used by most authors (e.g., Weekes, 1933; Rahn, 1939; Dumas, 1964; Neill, 1964; Greer, 1966; Jenkins and Simkiss, 1968; Greene, 1970; Yaron, 1972; Huey, 1977; Sexton and Claypool, 1978; Thompson, 1981, 1982).

## III. HYPOTHESES ON REPTILIAN VIVIPARITY

### A. Types of Hypotheses

The selective forces underlying the transition from oviparity to viviparity have been a subject of speculation for many years. The resulting hypotheses may be framed in terms of the relative "benefits" and "costs" of the two reproductive modes to a female reptile, that is, the probable lifetime production of offspring (= fitness) of an oviparous female is compared to that of a viviparous female under a variety of parallel ecological conditions. Most authors have emphasized the benefits of viviparity in terms of an increase in the number of surviving offspring (e.g., Weekes, 1933; Neill, 1964). Eggs retained *in utero* may be protected from many sources of mortality, which they would normally experience in the nest: for example, extremes of temperature or humidity, fungal attack, and predation. The benefit from viviparity could equally well be the loss of a cost associated with oviparity: for example, the need for reproductive females to make long and possibly hazardous journeys to suitable nesting areas (e.g., Neill, 1964; Fitch, 1970).

However, it is misleading to look only at the benefits of viviparity and to ignore the associated costs. A more balanced view considers that viviparity may increase the fitness of a female only under a limited set of conditions (e.g., Fitch, 1970; Tinkle and Gibbons, 1977; Shine and Bull, 1979). Although viviparity may benefit survivorship of the offspring, it also may confer a cost to the food intake of the reproducing female, to the probability of her survival, and to subsequent fecundity. The nature of these costs can be used to frame predictions about the types of species or habitats in which viviparity would be most likely to evolve (Fitch, 1970; Shine and Bull, 1979).

In summary, both viviparity and oviparity confer costs and benefits. The advantages of viviparity may lie primarily with increasing survivorship of the offspring, whereas its disadvantages may lie with the effects of physically burdening the female with eggs for a prolonged period. The relative importance of these advantages and disadvantages will depend upon both environmental conditions and species characteristics. Published hypotheses regarding possible selective forces are reviewed below.

## B. Hypotheses Based on Environmental Factors

### 1. COLD CLIMATES

The earliest and the most widely accepted hypothesis of reptilian viviparity is that it evolved as an adaptation to cold climates. Tinkle and Gibbons (1977) traced this idea to Mell (1929) and cite several examples that indicate its currently widespread acceptance. The argument usually runs as follows. In cold climates, behavioral thermoregulation allows the body temperature of females to be much higher than that of the soil. Thus, eggs retained *in utero* will develop at higher temperatures (and hence more rapidly) than will eggs deposited in the soil. Early hatching, due to accelerated development, may be adaptive in at least the three following ways: (1) Eggs may hatch prior to the onset of lethal autumn frosts. (2) Eggs spend less time in the soil in which they may be vulnerable to factors such as predation and desiccation. (3) Early hatching enables the offspring to feed and accumulate energy reserves before hibernation, thus increasing their chances of survival over winter and subsequent growth rates.

An alternative and simpler version of the "cold-climate" hypothesis is that soil temperatures at the time of ovulation will be so low as to be lethal to developing eggs. Thus, unless body temperatures of gravid females fall to soil temperatures, uterine retention will protect eggs from these lethal extremes (Shine and Bull, 1979). (The same argument can be applied to very hot climates in which uterine retention might protect eggs from lethally high temperatures; Shine and Bull, 1979). Also, high elevations may play a role in stimulating the evolution of placentation, because low ambient oxygen concentrations might favor more efficient oxygen delivery systems to the embryo (Guillette et al., 1980).

### 2. ENVIRONMENTAL UNPREDICTABILITY

It has been suggested that prolonged uterine retention of eggs would be most likely to evolve in highly variable environments (Tinkle and Gibbons, 1977). In such areas, a reproducing female would "experience difficulty in predicting, at the time of egg deposition, whether the site chosen would remain favorable throughout the period of incubation and early life of the hatchlings. In such environments selection might favor females which held their eggs through some part of this period of developmental uncertainty. Cold environments may exacerbate this problem of predictability by increasing the length of the incubation period and making it less likely that the egg deposition site chosen by the parent will remain favorable until after hatching. The more unpredictable the environment (whether for reasons of climate, predation, or resource availability) of the eggs and hatchlings the more likely that the complete transition to viviparity will be favored" (Tinkle and Gibbons, 1977).

#### 3. OTHER ENVIRONMENTAL FACTORS

Any factor that kills eggs in the nest, but not *in utero*, might establish a possible selective pressure for the evolution of prolonged oviducal retention of eggs and might favor viviparity. Several authors have referred to factors, such as extremes of soil moisture, that may kill eggs and, hence, favor the evolution of viviparity (e.g., Sowerby, 1930; Neill, 1964). Laboratory studies show that substrate moisture levels are important determinants of hatching success and also may affect hatchling size (e.g., Muth, 1980; Packard et al., 1982). On the other hand, extreme aridity may prevent the evolution of viviparity, because thinning of the eggshell (assumed to be a necessary precondition for viviparity) is impossible in these environments (Weekes, 1933; Packard, 1966). Another factor is egg predation, the impact of which may be reduced by uterine retention of eggs (Neill, 1964), but this factor has to be balanced against increased predation upon females during pregnancy.

### C. Hypotheses Based on Species Characteristics

#### 1. DEFENSIVE ABILITY

It has been suggested that viviparity should evolve most often in large or venomous species, because gravid females of these forms are less vulnerable to predation; eggs inside of such females would have a greater chance of survival than eggs in the nest (Neill, 1964; Pilorge and Barbault, 1981). Also, such reptiles would have reduced "costs" for egg retention in terms of female survivorship (Shine and Bull, 1979). In less formidable species, the physical burden on the female during gestation might lower female survivorship to the point that natural selection could not favor prolonged uterine retention of eggs.

#### 2. NONDEPENDENCE ON SPEED OF MOVEMENT

Viviparity may be more likely to evolve in species that do not depend on rapid movement for feeding or for escape from predators (Fitch, 1970). In these species, the additional physical burden on the gravid female should have less impact on survivorship or food intake. Ambush predators or sluggish herbivorous species may fit such criteria. However, the common cessation of feeding by gravid reptiles may reduce the importance of this factor (and the previous one) by tending to equate the costs of egg retention among different species (Shine and Bull, 1979).

### 3. ARBOREAL OR AQUATIC HABITS

Females of some species migrate to egg-laying sites. This migration may be hazardous or energetically expensive, and viviparity may confer an advantage, for instance, in aquatic or arboreal reptiles or in habitats where suitable nest sites are rare. Hence, viviparity might be likely to evolve under these conditions (Neill, 1964; Fitch, 1970). This argument has been attacked strongly (Packard et al., 1977; Shine and Bull, 1979), because it offers no selective advantage for the intermediate stages of prolonged egg retention leading up to the evolution of viviparity. There are many conditions in which viviparity will be favored over oviparity, but in which viviparity will not evolve because no advantage accrues to the necessary intermediate stages. Additionally, viviparity seems less likely to evolve in certain arboreal species that rely upon agility in climbing and may be greatly disadvantaged by the weight and volume of the clutch (Shine and Bull, 1979).

### 4. FOSSORIAL OR SECRETIVE HABITS

Females of fossorial or secretive species may be rarely exposed to predation; hence, the prolonged physical burden of viviparity might not decrease their survivorship (Fitch, 1970). This might facilitate the evolution of live-bearing. However, this prediction may be challenged on the following three grounds: (1) The assumption of low predation intensity on fossorial species may be false, because it is based on the inability of herpetologists, not natural predators, to find these animals. (2) Fossorial species may depend upon slender bodily form for burrowing, and hence the volume of developing young would impede the female or would affect the size of the tunnels needed. (3) The thermal advantages of egg retention may be less evident in fossorial species, because maternal body temperatures may be similar to soil temperatures, at least in some species (e.g., Brattstrom, 1965; Shine, 1983b; but see Huey, 1982).

### 5. MATERNAL CARE OF EGGS

Egg-guarding ("brooding") behavior by females has usually been seen as an alternative to viviparity (e.g., Fitch, 1970; Packard et al., 1977). However, prolonged uterine retention of eggs may be more likely to evolve in egg-guarding species; certainly, females of these species face little additional "cost" in retaining eggs *in utero* (Shine and Bull, 1979). Because egg-guarding females generally cease feeding, prolonged retention of eggs increases the period of time during which the female can continue to feed. However, the common cessation of feeding in gravid females (Shine, 1980a) reduces the force of this argument.

### 6. THERMOREGULATORY STRATEGY

The "cold-climate" hypothesis relies upon behavioral selection of high body temperatures by the ovigerous female. Heliothermic squamates may maintain body temperatures much higher than the substrate especially in cold climates, but some thigmothermic forms may not (Brattstrom, 1965; Shine, 1983b). In some nocturnal species, female body temperatures actually may average lower than soil temperatures (Huey, 1982); hence, females could accelerate embryonic developmental rates by being oviparous rather than viviparous! Viviparity should be more likely to evolve in heliotherms.

### 7. REPRODUCTIVE FREQUENCY

A major "cost" of egg retention may be the reduced time available to produce a second clutch within the same season (Sergeev, 1940; Tinkle and Gibbons, 1977). Hence, viviparity should evolve more readily in single-clutching species.

### 8. PHYSIOLOGICAL CONSTRAINTS

The lack of viviparity in turtles and crocodilians may be due to their inability to effect adaptive reductions in the thickness of the eggshell (Packard et al., 1977). This hypothesis is supported by differences in calcium metabolism of developing embryos between squamate and nonsquamate reptiles. However, the hypothesis has been criticized as intrinsically implausible on the grounds that some alternate mechanism of calcium supply to the embryo could have evolved if natural selection had favored retention of developing embryos *in utero* (Tinkle and Gibbons, 1977). Highly calcified shells also may reduce gas exchange *in utero* and, thus, may prevent the evolution of viviparity (Blackburn, 1982).

Other physiological constraints on the evolution of viviparity are possible. For example, turtle embryos are killed if the eggs are rolled over early in development (e.g., Limpus et al., 1979; Ewert, 1984); squamate eggs are more resilient (Marcellini and Davis, 1982). It is difficult to see how natural selection could favor intra-uterine retention of developing embryos in turtles; as soon as the eggs were laid the resulting movement would kill the embryos. Indeed, turtles appear to have some mechanism to prevent embryogenesis *in utero;* if gravid females are prevented from ovipositing for several weeks, embryogenesis does not proceed (Packard et al., 1977; J. M. Legler, personal communication; Ewert, 1979, Vol. 14). It is difficult to distinguish cause and effect in such evidence; if, for some other reason, selection does not favor embryogenesis *in utero,* then there is no selective advantage in resistance of developing embryos to overturning of the eggs (because this situation almost never occurs).

Other types of physiological constraints might determine which groups among squamates could evolve viviparity. For example, uterine retention of eggs might be most likely to be favored in taxonomic groups with relatively "delicate" eggs (e.g., those capable of developing successfully only under a restricted range of temperature or humidity). It also is plausible that some squamates may be barred from evolving egg retention because the preferred body temperature of the female is much higher than the soil temperatures at which the eggs normally develop. For example, in the montane lizard, *Sceloporus graciosus*, the preferred temperatures of individuals average over 35°C (Brattstrom, 1965), but eggs incubated in the laboratory fail to develop at temperatures above 29°C (Ferguson and Brockman, 1980; Shine, unpublished data). A similar situation occurs in several oviparous Australian skinks; however, the mean temperature of females (i.e., allowing for a nighttime decrease) is within the range of embryonic tolerance, and successful oviducal retention of eggs is observed (Shine, 1983b).

Certain sex-determining systems may also constrain the evolution of viviparity. For example, prolonged uterine retention of eggs at maternal body temperatures may not evolve if incubation temperature determines the sex of the hatchling (Bull, 1980). Temperature sex determination has been recorded in a variety of crocodilians, testudines, and squamates (Bull, 1980). Similarly, female heterogamety might constrain viviparity because maternal hormones would tend to influence embryonic sexual differentiation (Mittwoch, 1975).

## IV. ASSUMPTIONS AND LOGIC OF HYPOTHESES

### A. General

Hypotheses concerning the selective pressures responsible for the evolution of a trait are difficult to test because they concern past events which cannot be directly observed. However, such hypotheses can be evaluated by examining their assumptions and logic, and deriving and testing their predictions. The following section first considers some underlying assumptions and the logic of current hypotheses on the evolution of viviparity. It then considers assumptions and theory relevant to specific hypotheses. Basic to such considerations is that the same condition may have been produced by different selective pressures and that presently observed effects may have been produced in response to pressures no longer operative.

### B. Oviparity as the Primitive Condition

There is general agreement that viviparity is derived from the primitive condition of oviparity, rather than vice versa. This is based on the following evidence: (1) The vertebrate progenitors of reptiles (amphibians, fishes) are primarily oviparous. (2) Neonates of many viviparous squamates possess small "egg teeth"; these occur in all oviparous squamates and are lost shortly after hatching. They enable the hatchlings to cut or chip the eggshell, but lack functional significance in live-bearers (although one could argue that they are needed to tear the embryonic membranes). If they *are* nonfunctional, they offer some evidence that the present-day live-bearers had an oviparous ancestry. (3) It has been argued on logical grounds that it is simpler to lose a structure (the eggshell) than it is to evolve a new one (Gans, 1974). Hence, an evolutionary transition from oviparity to viviparity may be more likely than the reverse.

Phylogenetic trees of squamate groups in which viviparity has evolved may be examined to determine the direction of the suggested transition. If oviparity is the primitive condition, it should be found in species with "primitive" morphological characteristics within each group, whereas viviparity should be restricted to "derived" forms. Among the squamate taxa reviewed later in this chapter, there are 16 cases in which this is clearly true (viviparity derived from oviparity). There are only four cases (in *Lerista, Gerrhonotus-Barisia, Platysaurus,* and *Vipera*) in which the reverse might be true. However, in these cases the data are dubious because comparisons of relatively distantly related species are involved. Overall, the evidence supports the assumption that oviparity evolves to viviparity rather than vice versa.

### C. The Cost of Viviparity

A critical assumption underlying virtually all life-history theory, including the hypotheses considered here, is that reproduction imposes a "cost" to the reproducing animal. This cost is anything that decreases Residual Reproductive Value (Fisher, 1958; Williams, 1966); for example, the cost may be increased vulnerability to predation or a decrease in feeding ability (and hence in the energy gathered, which could be used for subsequent clutches).

Some theoretical predictions on the evolution of viviparity are based directly on consideration of these costs (e.g., most of the "species characteristics" hypotheses discussed above), whereas others (e.g., the cold-climate hypothesis) do not involve such reproductive costs in any obvious way. However, all of these ideas assume that reproduction has some cost: Specifically, that viviparity is assumed to be more costly to the female than is oviparity. If this is false, all of these ideas on the supposed benefits of viviparity to egg survival would yield the same inaccurate prediction: Viviparity should evolve in all reptiles, because it confers a benefit at no cost.

The possible costs of viviparity have been couched in terms of female survivorship and subsequent fecundity (Tinkle and Gibbons, 1977). Cost–

benefit models have been used to provide an algebraic formulation of the problem (Shine and Bull, 1979). Recently, the reasonableness of the concept of "reproductive costs" in reptiles has been assessed by studies on scincid lizards and by a review of published literature (Shine, 1980a). Gravid female skinks are physically slowed down by the weight of the clutch. Females with full-term clutches lose about 25% of their nongravid running speed. Probably because of this effect, gravid females have been shown to be particularly vulnerable to predation by small elapid snakes in laboratory trials. Gravid females also bask more often than nongravid ones; this behavior may increase vulnerability to avian predators (Shine, 1980a). The mobility of gravid *Lacerta vivipara* is similarly reduced, but they rely more on crypsis than on flight to escape predation (Bauwens and Thoen, 1981). Although the gravid skinks did not reduce their food intake during reproduction, a review of published literature suggested that this is a common phenomenon (Shine, 1980a). Also, metabolic rates may be much higher in gravid than in nongravid females (Guillette, 1982b). Hence, reptilian reproduction probably often involves costs, although their nature may vary (Shine, 1980a).

### D. The Importance of Intermediate Stages

The evolution of viviparity must almost certainly have been a gradual process (e.g., Packard et al., 1977; Shine and Bull, 1979). In the early stages, females carry the eggs long enough to permit some embryonic development *in utero* but lay the eggs prior to the completion of embryogenesis. Continued selection for progressively longer egg retention might eventually result in complete intrauterine incubation (live-bearing).

The need for intermediate stages is supported by the argument that many physiological and anatomical changes in parent and offspring must accompany the transition from oviparity to viviparity. These requirements probably prevent any rapid evolutionary "jump" from oviparity (without *in utero* embryogenesis) to viviparity. For example, retention of the embryo requires vascular structures in the oviduct for gaseous exchange, as well as for thinning of the eggshell. Changes likely to have accompanied the evolution of viviparity are reviewed by Weekes (1935), Bauchot (1965), Yaron (1972, this volume), Packard et al. (1977), and Guillette (1982a).

There is relatively little information concerning the extent of embryogenesis *in utero* in oviparous reptiles. Many authors merely comment that eggs contain "very small" embryos when laid (e.g., Ditmars, 1942). However, available evidence suggests that prolonged uterine retention of eggs is the rule, rather than the exception, in egg-laying squamates (Shine, 1983a). Generally, eggs are retained *in utero* for almost one-half of the total period of embryonic development, to the equivalent of stage 30 for *Lacerta vivipara* in the table of Dufaure and Hubert (1961). In contrast, turtles appear to retain eggs only briefly between ovulation and oviposition. At the time of laying, embryos are no further advanced than the gastrula stage (Shine, 1983a; Ewert, Vol. 14). Further studies on this topic would be of great value.

In order for viviparity to arise from oviparity, some advantage must accrue to an intermediate reproductive strategy in which females retain eggs *in utero* for progressively longer periods of time. Hence, theory predicts that the conditions under which viviparity evolves should be those favoring a progressive increase in the duration of intra-uterine retention of eggs. Such conditions may differ from those under which viviparity, as such, is favored. In particular, several situations might confer an advantage to viviparity, but not to intermediate stages of egg retention (Weekes, 1935; Tinkle, 1967; Packard, 1966; Packard et al., 1977; Tinkle and Gibbons, 1977; Shine and Bull, 1979). For example, viviparity might be advantageous to females under conditions in which suitable nesting sites or calcium supply are limited. However, these circumstances do not confer an advantage to the intermediate strategy of prolonged intra-uterine retention of eggs. The same argument applies to the avoidance of nesting costs, for instance those imposed on ovipositing females that make long migrations to nesting areas (energetic costs) or are vulnerable to predators (survivorship cost). Hence, it is important to distinguish between the evolutionary origin of viviparity (i.e., circumstances under which selection favors intra-uterine retention of eggs in oviparous forms) and the subsequent radiation of viviparous species into new habitats (i.e., those under which selection favors viviparity over oviparity).

Some authors have failed to make this distinction. Consequently, their hypotheses relate to reasons for the present-day distribution of viviparity, rather than to reasons for its origin (e.g., the hypothesis that viviparity is favored in aquatic or arboreal species). Hypotheses that are equally applicable to both phenomena include the cold-climate hypothesis, unpredictability, defensive ability, nondependence on speed of movement, and fossorial or secretive habits. Intermediate stages of egg retention may not be favored merely because of high rates of egg predation. In this case, the time course of mortality is critical. If predation is concentrated in the period just after oviposition, and is relatively independent of the duration of time eggs spend in the nest, brief oviducal retention of eggs would reduce incubation period but would not reduce mortality due to predation (Shine and Bull, 1979). Unfortunately, few data are available on egg survivorship in natural nests, so that the importance of this objection is difficult to judge.

### E. Causes of Egg Mortality in the Wild

There is remarkably little information on rates or determinants of egg survivorship in natural nests of squamate reptiles; more data are available for turtles (e.g., Moll and Legler, 1971; Burger, 1977) and for crocodilians (e.g., Webb et al., 1977).

Incomplete development and death by frost is suggested, but not required, by the cold-climate hypothesis for eggs deposited in marginal habitats. Such reduced survivorship has been documented in three European reptiles, *Podarcis muralis, Lacerta viridis* (Cooper, 1965), and *Natrix natrix* (Smith, 1973). When eggs of an oviparous lizard *(Phrynosoma)* were transferred to the cold-climate habitat of a viviparous congener, the embryos died due to low temperatures before completing development (Dumas, 1964). Eggs of several cold-climate species of Australian lizards only hatch shortly before the onset of lethally low temperatures in autumn (Shine, 1983b).

Squamate eggs are vulnerable to many other sources of mortality, including predation; several groups of fossorial snakes are obligate egg eaters (Broadley, 1979; Shine, 1984). A single species of snake, *Salvadora grahami lineata,* is the most important cause of egg mortality in the lizard *Sceloporus olivaceus* (Blair, 1960). Other causes include desiccation, which has been shown to be important in an unusually dry year (Blair, 1960). Eggs of the desert iguana, *Dipsosaurus dorsalis,* develop successfully under a restricted range of conditions of temperature and humidity; suitable conditions are found only in a limited geographic area and in specific microhabitats (Muth, 1980; Porter and Tracy, 1983). Thermal sensitivity of embryos also may constrain nesting sites and seasons of other iguanids (Rand, 1972). Predation by ants may kill many eggs of anoline lizards (Andrews, 1982).

Although hatching success in natural nests may often be high (Van Devender and Howard, 1973; Sexton and Claypool, 1978), there is little doubt that there are many different causes of mortality. Information on the relative importance of each cause, and the time-course of mortality would allow assessment of the probable effect of a slightly shorter incubation period on egg survivorship. All other things being equal, selection would favor oviducal retention of eggs if a reduced incubation period increased egg survivorship.

### F. Thermal Relations of Eggs

The cold-climate hypothesis requires that eggs retained within the body of the female are kept warmer than eggs laid in the nest and that this temperature difference has a significant effect on the rate of embryonic development and, hence, on total incubation period. The former assumption is likely to be valid for most heliothermic species in cold climates, but it is unlikely to be true for many thigmotherms (e.g., Brattstrom, 1965). Even in heliotherms, female body temperatures are likely to be the same as soil temperatures at night (or lower, if the female remains above ground). The second assumption is supported by many laboratory studies, which show that incubation period is highly dependent on temperature (see Tinkle and Gibbons, 1977). However, at high temperatures, incubation periods may be relatively insensitive to temperature (Ewert, 1979, for turtles; Muth, 1980; Shine, 1983b, for squamates). There seems little doubt that the increased temperature of the body of a female will speed embryogenesis in cold climates; the problem is whether or not this effect will be great enough to be significant.

An intensive study of several montane skinks (Shine, 1983b) suggests that these assumptions are valid. The temperature difference between eggs in the nest and eggs retained *in utero* averages about 7°C in heliothermic species, but is negligible in a thigmothermic form. Egg retention for about half of embryonic development reduces the total incubation period from 160 to 110 days in the heliotherms, because embryonic development at female body temperature (average of 24°C) is about twice as rapid as at nest temperatures (average of 17°C).

The acceleration of embryonic development depends on the temperature difference between the body of the female and the nest. It has been suggested that oviparous females in cold areas could select the warmest possible microhabitat for their nest (Sexton and Claypool, 1978); such nest-site selection would reduce the effect of uterine retention on the duration of embryonic development. However, this hypothesis has the problem that there are a limited number of microhabitats that are warmer than the surrounding soil as well as being moist enough to allow egg survival. Natural selection does seem to favor the choice of warm microhabitats as nest sites, as witnessed by oviposition of *Natrix natrix* in decomposing haystacks (Spellerberg, 1975). However, it seems unlikely that most severely cold regions will contain microhabitats, otherwise suitable for egg deposition, that are both moist and have temperatures as high as the body temperatures of females.

One further assumption of the cold-climate hypothesis is that the relationship between temperature and incubation period for any given species cannot be modified greatly by natural selection. Otherwise, selection in cold environments could simply favor accelerated development at low temperatures; incubation periods then could be reduced without uterine retention of eggs. Such adaptations of embryonic development rates are common in invertebrates, teleost fishes, and amphibians; the rapid development of anuran tadpoles in temporary pools is perhaps the most striking example (Zweifel, 1960). No such cases of accelerated development have been documented in reptiles.

### G. The Role of Unpredictability

The unpredictability hypothesis suggests that viviparity should evolve in cold climates, because cold climates are variable, exposing the eggs to many unpredictable sources of mortality; cold climates also lengthen the period of incubation, so that the eggs are vulnerable for a longer period of time (Tinkle and Gibbons, 1977). Although the unpredictability hypothesis is highly original, I have doubts about its validity. The level of predictability should not affect selection for egg retention unless the female has the option of adopting alternative egg-laying strategies. For example, if it is going to rain, the female must deposit the eggs in higher locations where they will not be inundated; during drought she should deposit them on low ground where they may stay moist. A female must then be programmed to predict the probability of rain or retain eggs until she "knows" whether or not it will rain; in this case, environmental unpredictability may favor egg retention. However, if some important event occurs both infrequently and unpredictably, selection is unlikely to favor retention. Increased predictability of the event is likely to increase the advantage of facultative retention of eggs. This means that unpredictability may sometimes select against retention instead of favoring it.

In any case, long durations of retention are unlikely to evolve in response to this kind of unpredictability (Guillette et al., 1980). The longer the mother retains the eggs, the higher the cost that she must pay for the advantage of knowing what to do. Unless the occurrence of the event makes a vast difference in the suitability of a given nest site, the mother would benefit from a compromise strategy and lay the eggs soon after ovulation. There is no compelling reason why unpredictability as such should be important in the evolution of live-bearing, although unpredictability may favor short intervals of egg retention.

## V. EMPIRICAL SUPPORT FOR THE HYPOTHESES

### A. General

All the listed hypotheses have some degree of empirical support, but in many cases authors merely point to a particular viviparous species and suggest that their hypothesis explains why viviparity confers a selective advantage to that species. This approach has been criticized as providing only weak support for the hypothesis; an array of oviparous species can be assembled that show ecological characteristics similar to those of members of a viviparous array (Tinkle and Gibbons, 1977) so that the criticism is valid. Another common problem stems from failure to consider the origin of viviparity separately from the subsequent maintenance of the trait.

### B. The Cold-Climate Hypothesis

The correlation between climate and the incidence of viviparity is well documented. In most cases, some variable related to temperature (either latitude or elevation) has been shown to correlate with the proportion of the squamate fauna which is viviparous. Viviparity is proportionately more common at higher latitudes in Eurasia, China (Sergeev, 1940), North America, and Australia (Tinkle and Gibbons, 1977). Also, the proportion of viviparous squamate species increases with increasing elevation in Australia, Europe (Weekes, 1933; Sergeev, 1940), East Africa (Greer, 1968) and Mexico (Duellman, 1965; Greene, 1970). Within the lizard genus *Sceloporus*, viviparous forms tend to be found at higher elevations (and perhaps higher latitudes) than oviparous ones (Guillette et al., 1980). This type of analysis has been extended by comparison of the incidence of viviparity with a climatic measure (average summer temperature) rather than simply with latitude. As expected, viviparous species comprise a higher proportion of the squamate fauna in colder areas (Tinkle and Gibbons, 1977). The incidence of viviparity also has been correlated with a variety of climatic estimates (Shine and Berry, 1978). In both Australia and North America, there is little relationship between temperature and percentage of viviparity over a wide range of relatively warm climates, but the proportion of viviparous species rises rapidly in extremely cold areas, in which mean midsummer minimum air temperatures average lower than 15°C (Shine and Berry, 1978).

Great emphasis has been placed on the fact that, although the *proportion* of viviparous species is highest in cold areas, the *absolute number* of viviparous species is higher in the species-rich warm climates (Tinkle and Gibbons, 1977). It is suggested that "Proportions can be misleading because far northern or southern and high altitude faunas are exceedingly impoverished . . . an explanation for the evolution of viviparity should also consider those situations in which the majority of viviparous species occur" (Tinkle and Gibbons, 1977). This does not seem to be an important criticism. Theory attempts to explain reasons for the success of viviparity relative to oviparity. The tendency for species richness to increase toward the tropics is a common phenomenon in many groups, and I doubt that it has much to do with the evolution of viviparity.

Several authors have pointed out that the overall present-day distribution of viviparity may tell us very little about factors favoring the *origin* of viviparity (references above). An alternative approach has restricted attention to (1) oviparous species showing prolonged oviducal retention of eggs and to (2) live-bearing species within genera with both oviparous and viviparous forms (Shine and Bull, 1979). This procedure was designed to find "recent" origins of viviparity. The approach assumes that the ecologies of these live-bearers (or oviparous egg-retaining species) may still represent the environments that favored the evolution of viviparity. One problem with this criterion for "recent" evolution lies in the assumption that speciation rates are similar in different taxonomic groups. Unless this is true, viviparity may be of very ancient origin within some genera; the group may have remained relatively unchanged over a long period. On the other hand, divergences between wholly viviparous and wholly oviparous genera may be of recent origin in a rapidly speciating group.

The proportion of species inhabiting "cold" climates (using a subjective judgment of "cold") among squamates in general (44%) is lower than among "recently evolved" live-bearers (28 of 13 cases, or 85%) or among oviparous species with prolonged egg retention *in utero* (72%) (Shine and Bull, 1979). A similar analysis on 75 taxa (Blackburn, 1981, 1982) reached the same conclusions. These data support the hypothesis that viviparity evolves in cold regions. However, the subjective evaluations of "cold" climates, and "prolonged" oviducal retention of eggs represent major weaknesses of the analyses. A stronger test of the prediction that viviparity evolves in cold climates is to compare climatic conditions in the habitats of closely related oviparous and viviparous forms. This procedure was applied to sceloporine lizards (Guillette et al., 1980) and to taxa involved in 71 evolutionary origins of viviparity (Shine, 1981), and the "cold climate" hypothesis was supported in both cases. The present review provides the detailed results and analysis of my earlier abstract (Shine, 1981).

### C. The Environmental Unpredictability Hypothesis

The unpredictability hypothesis is a very general one and is of little use in deriving predictions unless one is willing to specify the particular variables for which predictability is to be important. The variability of many significant factors, for example, rainfall, is likely to be no greater in cold climates than in hot ones. For this reason, the hypothesis predicts that viviparity should evolve under a wide range of different climatic conditions, perhaps with a slight bias toward cold climates because of the lengthening of incubation periods in these areas. Any strong bias toward cold climates in the evolution of viviparity (as found by Shine and Bull, 1979) is difficult to reconcile with this hypothesis in its general form, although these data would be consistent with a specific form of the hypothesis (e.g., the important unpredictability is that of the date of onset of lethally low soil temperatures). However, such a simplified version of the unpredictability hypothesis is little different to the conventional "cold climate" hypothesis.

### D. Other Environmental Factors

Several hypotheses deal with causes of egg mortality and predict that viviparity should evolve wherever the survival of eggs is at risk. Hence, viviparity should evolve in regions in which nests are subject to desiccation, flooding, temperature extremes, fungal attack, or high rates of predation. If desiccation of eggs is important, viviparity should evolve in arid regions; if flooding is important, viviparity should evolve in frequently inundated areas; if fungal or microbial attack is significant, viviparity should evolve in areas with moist soil; if high temperatures are critical, very hot regions should be implicated. It is difficult to derive any testable prediction from the "nest predation" hypothesis.

An analysis of "recently evolved" viviparous species (Shine and Bull, 1979) provides little support for these hypotheses; the species examined do not show any consistent tendency to occupy areas with the predicted characteristics insofar as they could be tested. The "hot climate" prediction is easily falsified; most viviparous species inhabit cold climates. A detailed analysis of the iguanid lizard genus, *Sceloporus*, indicates that its viviparous species most often occur at higher elevations and in more mesic habitats than its oviparous ones (Guillette et al., 1980). However, climatic variables such as temperature and rainfall tend to be correlated (Shine and Berry, 1978; Guillette et al., 1980). Hence, high-elevation habitats tend to be moist as well as cool. The separate influences of these correlated factors are best investigated in areas in which temperature and soil moisture are not associated. For example, if moist soils are important, viviparity should evolve in warm moist areas (e.g., tropical lowland rainforests) as well as cool moist areas. In contrast, if temperature is the important variable, viviparity should evolve in dry as well as moist cold-climate habitats. The consistent trend for viviparity to evolve in cold areas, apparently independent of moisture (Shine and Bull, 1979), suggests that temperature is more important. In summary, there are few empirical data to support the hypotheses that environmental unpredictability, soil moisture levels or high temperatures favor the evolution of viviparity. This suggests that these hypotheses lack general importance, but it does not imply that these factors may not be important in specific cases. The roles of unpredictability and of high predation rates on eggs remain speculative.

### E. Defensive Ability

Viviparity should evolve in large and venomous species, because the prolonged retention of offspring would not lower female survivorship, and eggs *in utero* would be very safe (Neill, 1964; Shine and Bull, 1979). There are many examples of species that combine viviparity with toxic venom or large body size (Neill, 1964; Fitch, 1970). However, it is possible to counterpose an array of oviparous species with the same characteristics (Tinkle and Gibbons, 1977); examination of selected examples does not provide any useful test of such an idea.

The "defensive ability" hypothesis applies to the maintenance as well as to the origin of viviparity. The hypothesis predicts an association between viviparity and venomosity in snakes. Seventy-two percent of the 212 nonvenomous snakes for which reproduction data have been presented (Fitch, 1970) are oviparous, whereas only slightly more than half (54%) of the 139 venomous species are oviparous. This difference is significant (with the assumption that each species represents an independent data point: $n = 351$, $X^2 = 10.8$, 1 d.f., $p < .01$). These data support the hypothesis that viviparity is likely to be favored in species in which the gravid females are relatively invulnerable to predation.

## F. Other Species Characteristics

"Recently-evolved" viviparous species do not exhibit a higher frequency of arboreal or aquatic habits than do squamates in general (Shine and Bull, 1979). However, a greater fraction of the viviparous species of *Sceloporus* is arboreal or saxicolous than is true for the oviparous species, but such arboreality may have evolved as adaptation to viviparity (for thermoregulation), rather than the reverse (Guillette et al., 1980).

The hypothesis that maternal brooding facilitates the evolution of viviparity is supported by a high frequency of origins of viviparity in genera that also contain brooding species and by an apparent tendency for prolonged uterine retention of eggs in brooding squamates (Shine and Bull, 1979). However, it is difficult to define "prolonged" retention of eggs and this association may not be valid (Shine, 1983a). Also, the link between brooding and the evolution of viviparity is open to another interpretation. Uterine retention of eggs, viviparity, and maternal care of eggs all involve increased parental investment. The environmental conditions or species characteristics favoring such investment might favor any of these strategies. Hence, the correlations between brooding and viviparity may relate to common causation rather than to a single factor (brooding) that protoadapts for another (viviparity).

The hypothesis that viviparity evolves primarily in species that produce a single clutch per year is consistent with the tendency for "recently-evolved" live-bearers to inhabit cold climates, because single-clutching is usual in these areas (Fitch, 1970). However, single-clutching also is common over most regions except the tropics (Fitch, 1970; Tinkle and Gibbons, 1977). If single-clutching were an important constraint, viviparity should evolve over a wide variety of climatic conditions and not be restricted to severely cold areas. The other hypotheses on species characteristics (non-dependence on speed, fossoriality, secretive habits, heliothermy) are more difficult to quantify and have not been tested.

It is difficult to derive specific predictions from the hypothesis that physiological constraints may prevent the evolution of viviparity in certain taxa. One approach has been to look for a taxonomic correlation between the incidence of viviparity and the incidence of prolonged retention of eggs *in utero* on the grounds that a physiological inability to retain eggs should be evident in both sets of data. Hence, one might expect that viviparity would be most frequent in taxonomic groups in which egg retention has often appeared (Blackburn, 1982). This prediction was confirmed by an analysis of lizard families (Blackburn, 1982). However, Blackburn's conclusion may be falsified as it relies upon subjective evaluations of "prolonged" egg retention. Objective data on embryonic developmental stages invalidate the differences upon which the analysis relies (Shine 1983a). The mode of sex determination is another physiological constraint that also may play some role in the evolution of viviparity; however, data are inadequate to reach any conclusions at present (Bull, 1980; Blackburn, 1982).

### G. Overview

The selective pressures responsible for the evolution of reptilian viviparity have been a subject of vigorous debate for over half a century (e.g., Mell, 1929; Weekes, 1933; Sergeev, 1940). Some of the ideas proposed lack generality, or require a quantum phenotypic change before they are advantageous, with the intermediate stages neutral at best. The hypothesis that reptilian viviparity has evolved as an adaptation to cold climates is the only one that has achieved general acceptance (Tinkle and Gibbons, 1977). There are at least three reasons why it may be more powerful than alternative ideas.

1. Uterine retention of eggs speeds embryonic development in cold climates because the body of the female can be warmer than the soil. A relatively short retention period can greatly decrease the total period required for incubation. This would reduce the mortality from those factors that would kill eggs in the nest.
2. Geographic clines of temperature are common and usually reflect latitude or elevation. If a species invaded colder areas, there would be an advantage to individuals that tended to retain their eggs longer, facilitating the evolution of viviparity. Clines in other variables, such as intensity of egg predation, may be less common.
3. Any uterine retention of eggs would be advantageous in cold climates; hence, the intermediate stages as well as full viviparity would be adaptive.

The "cold-climate" hypothesis also is supported on empirical grounds. Data on montane Australian skinks suggest that the major assumptions of the hypothesis are realistic (Shine, 1983b). Present-day distributions of viviparous species are highly correlated with environmental temperatures (e.g., Tinkle and Gibbons, 1977; Shine and Berry, 1978). Prolonged retention of eggs may be more common in colder areas (Huey, 1977; Shine and Bull, 1979; Guillette et al., 1980; but see Shine, 1983a). Recently-evolved viviparous species also tend to be found in cold areas (Shine and Bull, 1979; Blackburn, 1982), although this conclusion is weakened by its reliance on subjective evaluations of "cold" and on broad comparisons among squamate groups that are only distantly related.

Speculations on species characteristics likely to favor the evolution of viviparity have rarely been tested. Available data suggest that maternal egg brooding may protoadapt for the evolution of viviparity (Shine and Bull, 1979) and that there is an association between venomous capacity and viviparity among present-day snakes (see above).

# VI. EVOLUTIONARY ORIGINS OF VIVIPARITY IN SQUAMATE REPTILES

## A. General

The preceding section shows that there are many alternative hypotheses and predictions on the selective forces favoring the evolution of viviparity, but few satisfactory attempts to test these ideas. This chapter reanalyzes the data, first identifying the reptilian taxa in which viviparity has evolved and next comparing these groups with the remaining squamates to see if they show the characteristics predicted by theory. This approach has been applied previously to origins of viviparity occurring within squamate genera (Shine and Bull, 1979) and to all identifiable origins of squamate viviparity (Shine, 1981; Blackburn, 1981, 1982. The present analysis was performed independently of the latter two studies; discrepancies are discussed below).

The analysis starts with a review of all squamate taxa in which viviparity has evolved. Lineages for which few data are available, or within which considerable speciation has occurred subsequent to the evolution of viviparity, are noted without discussion. The approach is conservative: it is designed to assess the minimum number of independent evolutionary origins of viviparity.

Geographic distributions have been determined for most taxa, as have climatic conditions over the range of each species. Judgments as to whether a species occupies a colder or hotter climate than another are based on mean midsummer temperatures over the geographic range of each species (data from Arakawa, 1970; Gentilli, 1971; Wallen, 1971; Griffiths, 1972; Bryson and Hare, 1974; Schwerdtferger, 1976; Landsberg and Wallen, 1977; Lydolph, 1977; Takahashi and Arakawa, 1981). Judgments of "wet" or "dry" soil were based on habitat preferences of the species, in combination with broad climatic averages. These procedures offer only a rough approximation to conditions of temperature or moisture under which eggs develop, but they may be useful to compare geographic distributions of related species (rather than as any absolute estimate of soil temperatures or humidity).

## B. Amphisbaenia

Reproductive modes are known for only a few species (Gans, 1978). Viviparity has been recorded in *Trogonophis wiegmanni* (Trogonophidae: Bons and Saint Girons, 1963), whereas both oviparity and viviparity occur in the Amphisbaenidae. Oviparity characterizes *Rhineura floridana* (Gans, 1967), *Dalophia ellenbergeri* (Broadley et al., 1976), *D. pistillum,* and *Chirindia ewerbecki* (Loveridge, 1941), whereas *Monopeltis capensis* is viviparous (Visser, 1967). Prolonged uterine retention of eggs may occur in *Rhineura*

(Gans, 1967). At least two origins of viviparity are suggested, one in the *Trogonophis* lineage and another in the *Dalophia–Monopeltis* group. Data are insufficient for further analysis.

## C. Sauria

### 1. AGAMIDAE

Only two agamid genera contain viviparous species. *Cophotis* includes the oviparous *C. sumatrana* and the slow-moving arboreal viviparous *C. ceylanica* of the Sri Lankan mountains (Willey, 1906; Smith, 1935; Tryon, 1979). The latter may be phylogenetically closer to the other earless dragons of Sri Lanka *(Lyriocephalus* and *Ceratophora)* than to "C." *sumatrana* (S. Moody, personal communication). In Sri Lanka, the oviparous genera inhabit lower elevations than the viviparous form (up to 2100 m; Smith, 1935).

The small "toad-headed" agamids of the genus *Phrynocephalus* inhabit steppes and deserts of central Asia (for ecology see Rustamov and Shammakov, 1967; Shammakov et al., 1973). Most are oviparous (i.e., *P. euptilopus, P. guttatus, P. helioscopus, P. interscapularis, P. luteoguttatus, P. maculatus, P. mystaceus, P. ornatus, P. reticulatus, P. scutellatus*—Pope, 1935; Smith, 1943; Terentev and Chernov, 1965; Minton, 1966). However, *Phrynocephalus theobaldi* is found at higher elevations than any other reptile (above 5000 m, Daan, 1968) and appears to be oviparous at low elevations but viviparous at high ones (Sergeev, 1940). Other high-mountain species of *Phrynocephalus* may be viviparous also (Daan, 1968), suggesting at least two origins of viviparity in the genus. However, the present review treats this as a single origin, because detailed data are not available.

### 2. ANGUIDAE

The subfamily Anguinae consists of two genera that are limbless, primarily terrestrial, and often associated with grassy habitats. The European genus *Anguis* has only a single and viviparous species, whereas the ten species of the Eurasian and North American genus *Ophisaurus* are oviparous. Maternal brooding behavior is common in *Ophisaurus* (Noble and Mason, 1933); this may have protoadapted the anguines for the evolution of viviparity (Shine and Bull, 1979). The viviparous *Anguis* occupies cooler climates than its oviparous relatives (Fig. 1); it is often found at high elevations (up to 2400 m, Petzold, 1968a).

The elongate galliwasps *(Diploglossus)* of Central America have both oviparous, egg-guarding species *(D. bilobatus, D. delasagra)* and at least one viviparous form (*D. pleei*, Greer, 1967a). Other viviparous diploglossines recently have been transferred to the genus *Celestes (C. costatus, C. crusculus, C. curtissi;* Greer, 1967a; Strahm and Schwartz, 1977). We lack data on the reproductive modes of most species. Phylogenetic reconstructions suggest that the viviparous genera *Celestes* and *Ophiodes* arose indepen-

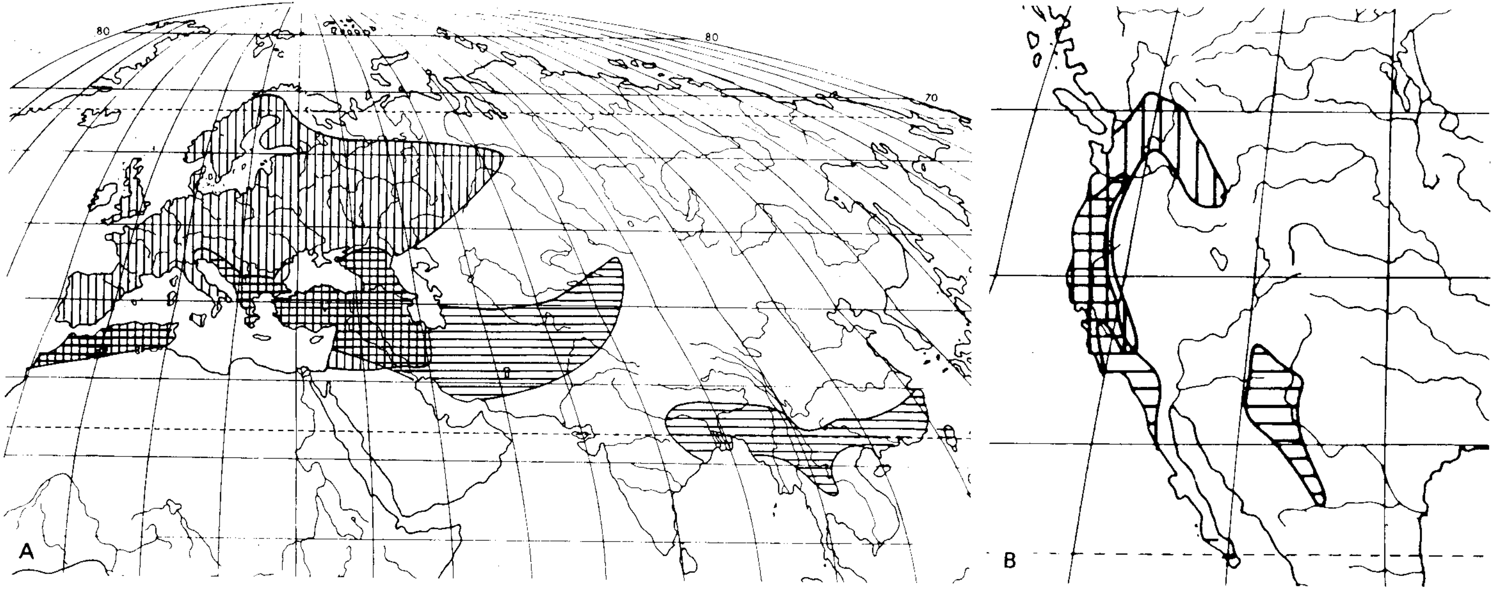

**Fig. 1.** Geographic distributions of oviparous (horizontal lines) and viviparous (vertical lines) (A) anguinine lizards of the Old World; (B) anguid lizards of the genus *Gerrhonotus* (oviparous species plus *G. coeruleus*).

dently from a pro-*Diploglossus* stock (Strahm and Schwartz, 1977), suggesting two further origins of viviparity within the diploglossine radiation.

The gerrhonotine anguids contain both oviparous and viviparous forms within *Gerrhonotus,* and the viviparous *Abronia* (Stebbins, 1958; Fitch, 1970). Mode of reproduction has been used to separate the oviparous subgenus *Gerrhonotus (G. cedrosensis, G. kingi, G. multicarinatus, G. panamintinus, G. paucicarinatus)* from the viviparous *Barisia* (*G. coeruleus, G. gadovi, G. imbricatus, G. monticolos, G. moreleti*—Fitch, 1970). Taxonomic studies suggest that *G. coeruleus* is the viviparous form most closely related to the oviparous ones (e.g., Criley, 1968; Waddick and Smith, 1974). This viviparous species inhabits cooler and moister areas than do its oviparous congeners (Fig. 1).

It may be that viviparity arose at least twice within the gerrhonotiform lizards. *Barisia* is thought to be the most primitive subgenus, from which *Gerrhonotus* has been derived (Waddick and Smith, 1974). All present-day *Barisia* are viviparous, leading to the following possible postulates: (1) oviparous *Gerrhonotus* are derived from viviparous ancestors (a position considered unlikely), (2) ancestral *Barisia* were oviparous (viviparity evolved within the genus after which the oviparous species disappeared), or (3) the phylogenetic hypothesis of Waddick and Smith (1974) is false. An alternative phylogeny based on electrophoretic and morphological studies of the gerrhonotines also suggests two independent origins of viviparity (D. A. Good and J. W. Wright, personal communication).

### 3. ANNIELLIDAE, XENOSAURIDAE

Both of the small families, Anniellidae and Xenosauridae, consist entirely of viviparous species (Fitch, 1970). Probably, both are derived from primitive anguids (McDowell and Bogert, 1954; Scherpner, 1968; Bezy et al., 1977). Because viviparity is found in several anguid lineages, it may have been inherited rather than evolving separately in the Anniellidae and Xenosauridae. Hence, the conservative approach is to omit these taxa from further analyses.

### 4. CHAMAELEONIDAE

The genus *Chamaeleo* contains approximately 70 species distributed through Africa, Madagascar, and western Europe. Several authors have attempted to reconstruct the phylogeny of the group, mainly on lung anatomy, cytology, and cranial morphology (e.g., Hillenius, 1959; Rand, 1963; Visser, 1972; Klaver, 1973, 1977; Raw, 1976, 1978). Reproduction is described by Bons and Bons (1960) and Blanc (1974), but detailed data are lacking for most species. Most chameleons are oviparous, but the eastern African *C. bitaeniatus* group and the southern African *C. pumilis* group (*Bradypodion* of Raw, 1976, 1978) are viviparous. These two groups are only distantly related to each other (Klaver, 1977, 1981), so it seems that viviparity arose twice.

The viviparous *C. bitaeniatus* group (*C. bitaeniatus, C. jacksonii, C. rudis, C. fuelleborni, C. tempeli, C. werneri, C. hoehnelii*) may derive from the *C. johnstoni* group (*C. monachus, C. namaquensis, C. melleri, C. cristatus, C. montium, C. wiedersheimi, C. oweni,* and *C. johnstoni*), all of which probably are oviparous (Klaver, 1977). The viviparous forms occupy high elevations (*C. bitaeniatus* is found at over 3000 m), whereas most of the *C. johnstoni* group live below 1700 m (Klaver, 1977; Fig. 2). A more rigidly cladistic analysis (Klaver, 1981) suggests that a subset of the *C. bitaeniatus* group above (the *C. werneri* group) is closest to the lineage in which viviparity evolved (Klaver's, 1981, "group E").

The second group of interest contains eight apparently oviparous species (*C. nasutus, C. fallax, C. gallus, C. boettgeri, C. guibei, C. linotus* from Madagascar, and *C. tenuis* and *C. spinosus* from eastern Africa), plus the viviparous "*C.*" *pumilis* group from southern Africa. The *pumilis* group has recently been divided into 11 species and elevated to generic level (*Bradypodion:* Raw, 1976, 1978), but appears related to the *C. nasutus* group on the basis of lung structure and karyology (Klaver, 1973). However, the *C. nasutus* group may itself be polyphyletic (Klaver, 1981). The viviparous forms range further south than their oviparous relatives (Fig. 2; Schmidt and Inger, 1957). It has also been suggested that "the perils of a descent to the ground (for egg-laying) are escaped by the few chamaeleons that are viviparous and are therefore able to carry out all reproductive functions in the relative safety of bushes and trees" (Schmidt and Inger, 1957). Although viviparity could be advantageous in arboreal species, it remains unlikely that it evolved because of arboreal habits (Shine and Bull, 1979).

## 5. CORDYLIDAE

The two subfamilies (Gerrhosaurinae and Cordylinae) of cordylids are small- to medium-sized heavily armored African and Madagascan lizards. The gerrhosaurines are all oviparous, whereas the cordylines include both oviparous (*Platysaurus*) and viviparous (*Cordylus, Pseudocordylus, Chamaesaura*) genera (Broadley, 1974). *Chamaesaura* is elongate and almost limbless. The geographic range of the viviparous species encompasses that of the oviparous forms (Fig. 2).

## 6. GEKKONIDAE

The gekkonid subfamily Diplodactylinae is distributed in Australia, New Caledonia and the Loyalty Islands, and New Zealand (Kluge, 1967). Viviparity has evolved at least twice in this subfamily; once in the ancestors of the three endemic and viviparous New Zealand genera *Heteropholis, Hoplodactylus,* and *Naultinus* (see Fitch, 1970, for references), and once in the large endemic geckoes of New Caledonia. The climate of New Zealand is much colder than the climates inhabited by the oviparous diplodactylines. In keeping with the "cold-climate" hypothesis, these viviparous geckoes

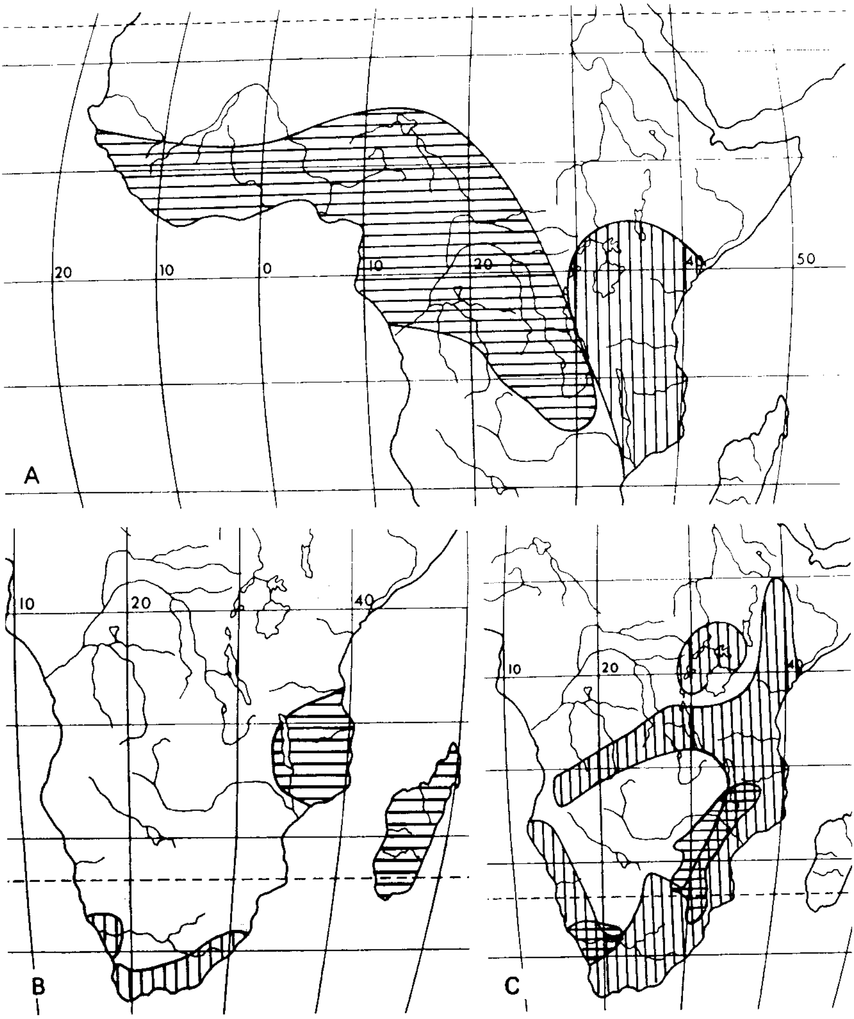

Fig. 2. Geographic distributions of oviparous (horizontal lines) and viviparous (vertical lines) species, within (A) the *Chamaeleo bitaeniatus* group, Chamaeleonidae; (B) the *Chamaeleo pumilis* group; (C) the lizard subfamily Cordylinae.

are unusual in being diurnal and heliothermic (Werner and Whitaker, 1978; Thomas, 1980).

The New Caledonian *Rhacodactylus* includes both viviparous (*R. trachyrhynchus*, Bartmann and Minuth, 1979) and oviparous species (*R. leachianus*, Roux, 1913; H. Cogger, personal communication; Mertens, 1964, suggested without specific data that some populations might be viviparous; *R. auriculatus*, personal observation). Distributions and habitats of New Caledonian *Rhacodactylus* are too poorly known to analyze correlates of viviparity. Interestingly, gekkonid viviparity occurs only within the diplodactylines, rather than in the more widespread gekkonines or eublepharines that produce calcareous-shelled rather than parchment-shelled eggs.

## 7. IGUANIDAE

The helmeted iguanids of central America consist of two oviparous species *(Corytophanes cristatus, C. hernandesii)* and one viviparous one (*C. percarinatus;* McCoy, 1968). The oviparous *C. cristatus* is restricted to humid lowlands (Stuart, 1948), whereas *C. percarinatus* occupies cold high-elevation regions (McCoy, 1968; Fig. 3).

The medium-sized, heavy-bodied iguanids of the genus *Ctenoblepharis* are fossorial and live in sandy soils on the western slopes of the Andes (Cei, 1974). The species *C. adspersus, C. stolzmanni, C. reichei* and *C. nigriceps* form a closely related group (Cei, 1979). The oviparous *C. reichei* inhabits the Tarapaca and Antofagosto deserts of northern Chile (Donoso-Barros, 1966; Peters and Donoso-Barros, 1970; Cei, 1979), whereas the viviparous *C. nigriceps* occurs in the Atacama desert of Chile, reaching latitude 33°S (Cei, 1974). The modes of reproduction of the other species are unknown (J. Cei, personal communication).

The smooth-throated lizards (genus *Liolaemus*) of South America resemble the Central American *Sceloporus,* both in morphology and in the great diversity of species. The Chilean species include two species groups with oviparous and viviparous forms (Donoso-Barros, 1966). In Group A, viviparity is known in the species *L. darwinii, L. cyanogaster, L. schroederi, L. gravenhorstii, L. alticolor,* and *L. bibronii,* whereas *L. lemniscatus* and *L. fuscus* are egg-layers. In Group B, viviparous forms include *L. dorbignyi, L. fitzingeri, L. kingii, L. nigroviridis, L. ornatus,* and *L. pictus,* whereas *L. monticola, L. platei,* and *L. tenuis* are oviparous. In both groups, the range of the viviparous forms is more extensive than, and encompasses, the range of the egg-laying species. However, the species in the coldest climates tend to be viviparous (Fig. 3); this applies to all of the far southern and high montane *Liolaemus* (Fitch, 1970; Donoso-Barros and Cei, 1971).

Most species of "horned toads" (genus *Phrynosoma*) of North and Central America are oviparous *(P. asio, P. cornutum, P. modestum, P. platyrhinos, P. solare, P. mcalli),* but those from the Mexican highlands are viviparous (*P. braconnieri, P. ditmarsi, P. douglassi, P. orbiculare,* Fitch, 1970; Montanucci, 1979; Pianka and Parker, 1975). The early phylogeny of Reeve (1952) has been replaced by that of Presch (1969), which is based primarily on osteology. The oviparous *coronatum* and the viviparous *orbiculare* are very similar to each other and apparently to the ancestral *Phrynosoma* stock. Hence, one may infer that viviparity evolved in an animal similar to these two recent forms. The live-bearer *(P. orbiculare)* inhabits elevated country in Mexico (the Sierra Madre Occidental), whereas the oviparous *P. coronatum* is found in warmer lowland regions of California (Fig.3).

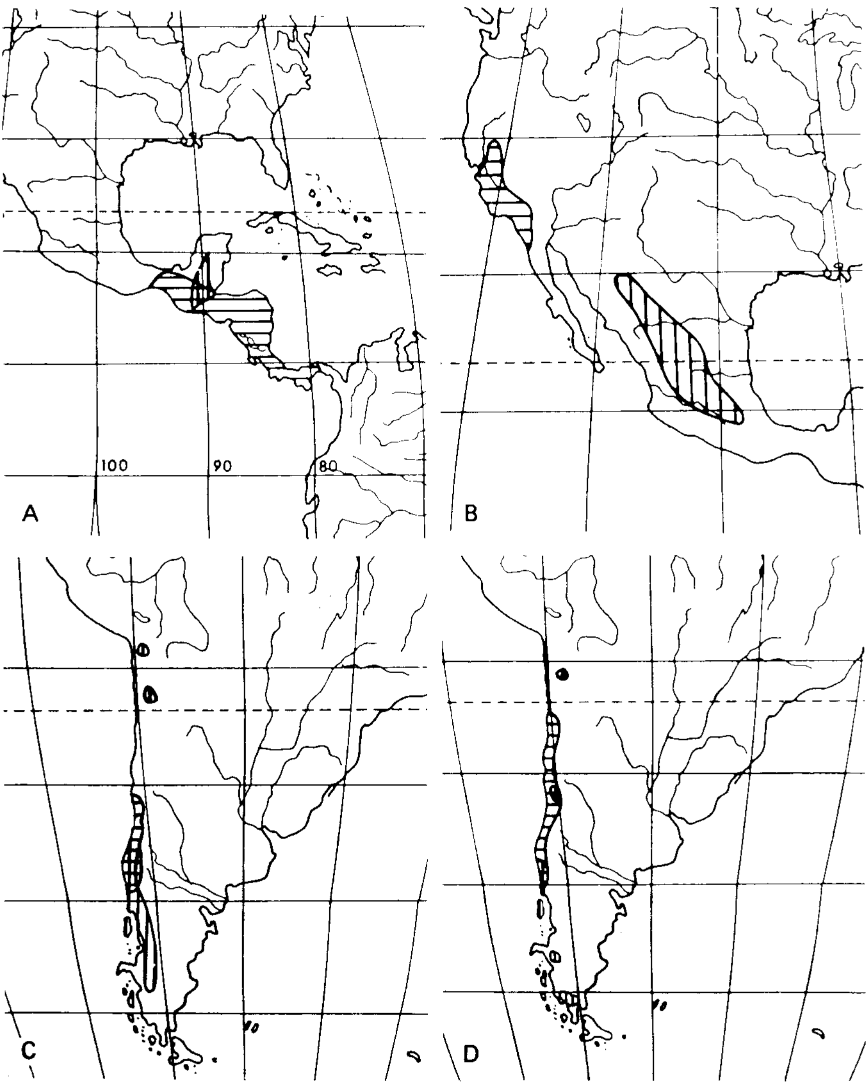

Fig. 3. Geographic distributions of oviparous (horizontal lines) and viviparous (vertical lines) iguanid lizard species of (A) the genus *Corytophanes*; (B) the species *Phrynosoma coronatum* and *P. orbiculare*; (C, D) the genus *Liolaemus*, Group A (C), the genus *Liolaemus*, Group B (D).

The viviparous iguanids of the genus *Phymaturus* live in the Andes of Chile and Argentina at elevations of 2800 to 4200 m (Cei, 1980). Osteological data suggest that *Phymaturus* is most closely related to the oviparous *Leiocephalus* of South America and the West Indies (Paull et al., 1976; Etheridge, 1966; Fitch, 1970). Hence, *Phymaturus* occupies colder regions than do its oviparous relatives.

*Sceloporus* is a large Central and North American genus of active diurnal lizards in which the modes of reproduction, and their correlates have been extensively reviewed (Guillette et al., 1980). The live-bearing species occur at higher elevations than the egg-laying ones (Smith, 1939).

Phylogenetic reconstructions for *Sceloporus* generally agree with each other. One of the species groups defined by Smith (1939), the *scalaris* group, contains both egg-laying and live-bearing species. There are two other cases of closely related oviparous and viviparous species. These are *S. grammicus* (viviparous) with *S. megalepidurus* (oviparous), and the large *S. spinosus* group (oviparous) with the viviparous *S. formosus* and *S. poinsetti* groups. The viviparous *S. acanthinus,* which was initially placed with the oviparous *spinosus* group (Smith, 1939), was later transferred to the viviparous *formosus* group (Smith and Taylor, 1950). The *S. torquatus* assemblage probably has evolved viviparity independently of the above, but it is not closely related to any present-day oviparous species. Subsequent taxonomic work has supported the analysis of Smith; thus, viviparity arose at least four and probably six times within *Sceloporus.*

The evolution of viviparity within the *Sceloporus scalaris* group is the most clear-cut case of independent origins. The close relatedness of the three species within this group *(S. aeneus, S. goldmani, S. scalaris)* is indicated both by conventional morphological measurements (Smith, 1939) and by karyotypes (Cole, 1978). *S. scalaris* is oviparous and *S. goldmani* is viviparous (Smith and Hall, 1974). However, the mode of reproduction of *S. aeneus* has been the subject of debate. There is no doubt that the high-elevation (3000–4500 m) subspecies *S. a. bicanthalis* is viviparous (Smith, 1939; Guillette, 1981). The subspecies *S. a. aeneus* occurs at lower (2500–3500 m) elevations, and it has been reported to be both oviparous (Davis and Smith, 1953; Thomas and Dixon, 1976) and viviparous (Smith and Hall, 1974). Reproductive bimodality in this species has been confirmed by Guillette (1981, 1982a); two separate origins of viviparity in different populations may be involved (L. J. Guillette, Jr., personal communication). In addition to the evolution of viviparity in *S. aeneus,* the closely related *S. goldmani* may have evolved viviparity separately (see phylogeny of Larsen and Tanner, 1975). Hence, viviparity arose two or three times within the *scalaris* group.

Viviparity also arose within the *Sceloporus grammicus* and *S. megalepidurus* groups. The viviparous *S. grammicus* is thought to be closest phylogenetically to the oviparous *S. megalepidurus* (Smith, 1939; Larsen and Tanner, 1975). Both species inhabit high elevations in Mexico or Central America, with the viviparous form occurring at higher elevations but lower latitudes (Guillette et al., 1980; Fig. 4). The viviparous *S. grammicus* also inhabits more mesic areas, and it is more arboreal than its oviparous relative (Guillette et al, 1980).

A further origin of viviparity has occurred within Group III of Larsen and Tanner (1975, their Fig. 5). The phylogenies of these authors and of

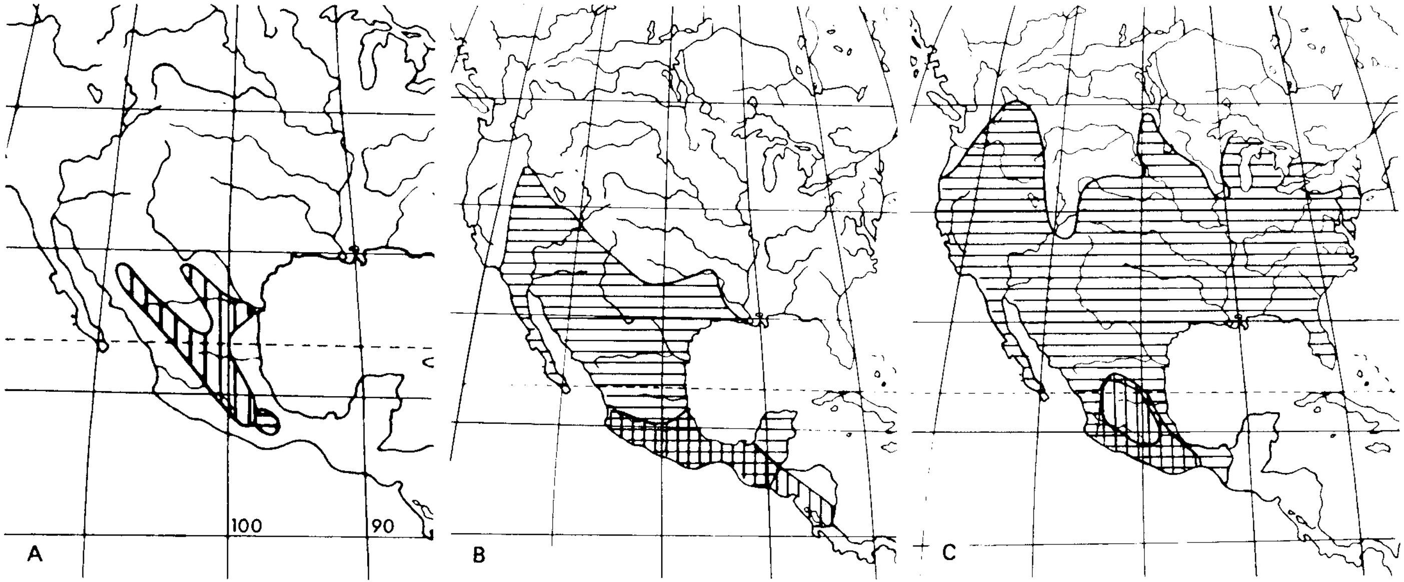

**Fig. 4.** Geographic distributions of oviparous (horizontal lines) and viviparous (vertical lines) lizards within (A) the *grammicus* and *megalepidurus* species groups of the iguanid genus *Sceloporus;* (B) the *spinosus* and *formosus* species-groups of *Sceloporus* as well as (C) the scincid genus *Eumeces* in the New World.

Smith (1939; his Fig. 3) suggest that the *Sceloporus spinosus* and *S. formosus* species groups are closely related. The oviparous *spinosus* group is restricted to elevations below 2000 m, whereas the viviparous *formosus* group inhabits elevations up to 3000 m (Smith, 1939; Fig. 4). The live-bearers generally occupy more mesic areas (Guillette et al., 1980).

Apart from these five or six independent origins of viviparity in *Sceloporus,* two further cases are suggested by reports of intraspecific reproductive bimodality. The evidence for *S. "microlepidotus"* (= *S. grammicus*) is weak (Smith, 1939; L. J. Guillette, Jr., personal communication). The other case is that of *S. variabilis,* which although oviparous over most of its geographic range (Guatemala, Mexico, Nicaragua, Costa Rica; Fitch, 1970) has been reported to be viviparous at high elevations (2500 m) in Veracruz, Mexico (Werler, 1951). This record of viviparity is based upon a dissection of a single female, and has been rejected as unreliable (Tinkle and Gibbons, 1977) on the grounds of possible misidentification of the specimen.

Viviparity in the Patagonian *Vilcunia* may represent an independent origin of the trait especially if this group has arisen from a primitive iguanid lineage rather than from some *Liolaemus*-type line (Cei and Scolaro, 1982). (I thank D. G. Blackburn for drawing my attention to this example.) Lizards of this group inhabit high elevation (1000–1400 m) areas of the Cordilleras. However, the group is omitted from further analysis because no related oviparous form can be identified.

## 8. LACERTIDAE

The genus *Eremias* comprises about 34 species of desert lizards. Most are oviparous (*E. argus, E. arguta, E. grammica, E. namaquensis, E. intermedia, E. lineoocellata, E. lugubris, E. neumanni, E. nigrocellata, E. nikolskii, E. persica, E. pleskei, E. regeli, E. scripta, E. strauchi,* and *E. velox,* Fitch, 1970; Terentev and Chernov, 1965; FitzSimons, 1943; Minton, 1966; R. Huey, personal communication). However, three species from Mongolia are viviparous (*E. kessleri, E. multiocellata, E. przewalskii,* Sergeev, 1940; Terentev and Chernov, 1965; Klemmer, 1968).

A reconstruction of the phylogeny of *Eremias* suggests that viviparity may have arisen twice within the genus (Shcherbak, 1971). One of Shcherbak's species groups includes both the oviparous *E. argus,* the viviparous *E. multiocellata,* and *E. brenchleyi* (most closely related to *E. argus,* Sowerby, 1930) for which the mode of reproduction is unknown. Another species group contains the viviparous *E. przewalskii,* plus *E. buechneri, E. quadrifons,* and *E. vermiculata* of unknown reproductive mode. Shcherbak (1971, p. 54) made the following suggestion:

> The poverty of the herpetofauna of Central Asia can undoubtedly be explained by the very difficult environment. The rapid worsening of the climate evidently occurred relatively recently, and perhaps was related to the fact

> that because of powerful orogenic forces there appeared a mountain barrier, which isolated this area from warmer and moister neighbouring country. The ecological conditions of Central Asia forced a number of *Eremias* species (*E. multiocellata, E. przewalskii,* and possibly several others) to change to ovoviviparity, otherwise unknown in Central Asian *Eremias*. (Translation of N. Apouchting.)

The large Old World genus *Lacerta* contains only one viviparous species, *L. vivipara;* early reports of egg-laying in some of its populations seem to be erroneous (Packard et al., 1977; Tinkle and Gibbons, 1977). All other species within the genus apparently are oviparous (Fitch, 1970). In his review of its taxonomic relationships, Arnold (1973) concludes that the affinities of *L. vivipara* lie with the northern members of his "subgroup 2," the presumably oviparous species *L. armeniaca, L. caucasica, L. chlorogaster, L. dahli, L. derjugini, L. horvathi, L. monticola, L. praticola, L. rostombekovi, L. rudis, L. saxicola,* and *L. unisexualis;* Arnold disagrees with earlier hypotheses that *L. vivipara* is particularly close to either *L. derjugini* or *L. praticola*. *L. vivipara* is unusual in its enormous geographic range, extending to severely cold areas (Fig. 5).

## 9. SCINCIDAE

The scincid lizards may be divided into four subfamilies (Greer, 1970) of which two, the Scincinae and the Lygosominae, contain both oviparous and viviparous species, whereas the Feylininae and Acontinae are small and entirely viviparous. The latter two groups are specialized burrowers thought to have evolved independently from the scincines of sub-Saharan Africa (Greer, 1970). Although viviparity may have evolved in both these subfamilies, the conservative view is adopted that they may be descended from viviparous scincines.

The Scincinae contain about equal numbers of oviparous and viviparous species (Greer, 1970), but available phylogenetic data are insufficient to determine the number of evolutionary origins of viviparity. Apart from *Eumeces* and perhaps *Scincus* (see below), all scincine genera are exclusively oviparous or viviparous (Greer, 1970). Viviparity is known in *Brachymeles* (Philippines; Brown and Alcala, 1980), *Ophiomorus* (Pakistan; Minton, 1966), *Chalcides* (Africa, Europe and Asia; Fuhn, 1968; Fitch, 1970), and *Proscelotes, Scelotes, Sepsina, Typhlacontias* and *Melanoseps* (Africa; Fitch, 1970; Greer, 1970). The five latter genera are closely related to each other (FitzSimons, 1943; Greer, 1970) and to the "*Scelotes*" of Madagascar (Greer, 1970). At least one Malagassy species, *Scelotes igneocaudatas*, is oviparous (Blanc and Blanc, 1967). It seems clear that viviparity has evolved in this lineage. Thus, the most closely related oviparous and viviparous forms may be the Madagascan "*Scelotes*" and the African *Proscelotes* (Greer, 1970). However, data are too few for a quantitative analysis.

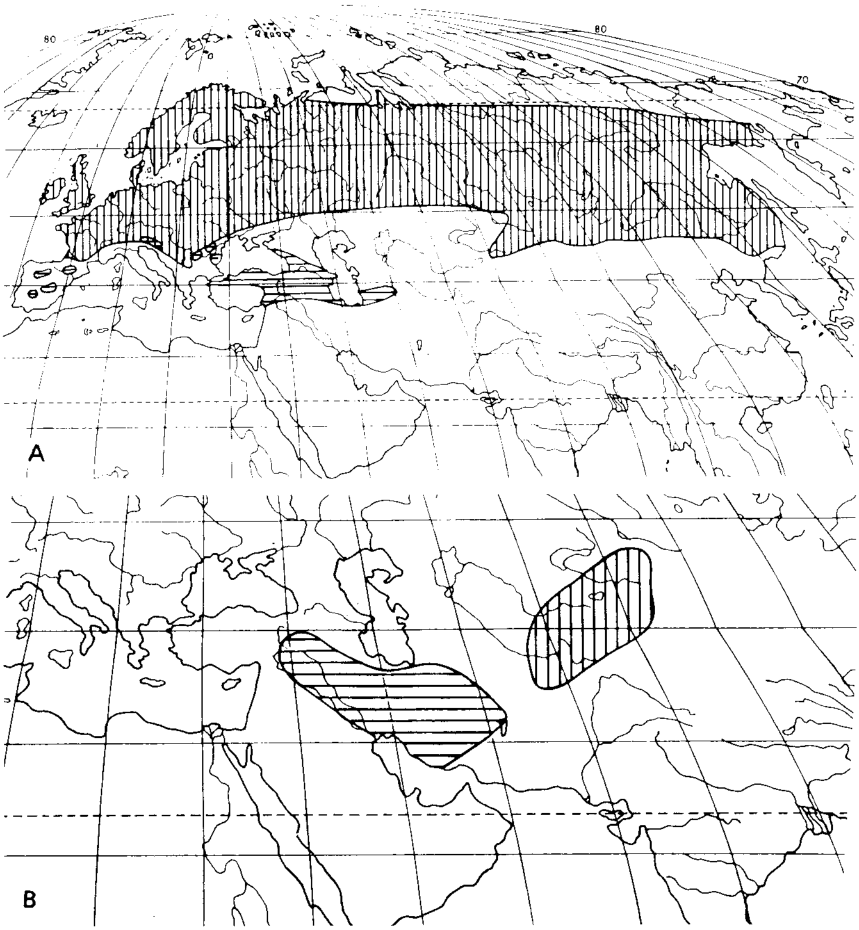

**Fig. 5.** Geographic distributions of oviparous (horizontal lines) and viviparous (vertical lines) lizards within (A) "Subgroup 2" of the genus *Lacerta*, Lacertidae; (B) the scincid species *Ablepharus bivittatus*.

The other viviparous scincine genera may well have evolved viviparity independently. For example, except for the oviparous *Eumeces*, *Brachymeles* is the only scincine in eastern Asia. However, the present distribution of scincines may be a relict one (Greer, 1970) and hence *Brachymeles* may have inherited viviparity from an extinct or geographically distant ancestor. The viviparity of *Brachymeles*, *Ophiomorus* and *Chalcides* is likely to represent one or more origins of viviparity.

Viviparity also has evolved within the large scincine genus *Eumeces*, which occurs throughout all of the North Temperate Zone except Europe. Most *Eumeces* are oviparous. Many show maternal brooding behavior; prolonged retention of eggs *in utero* is known in *E. brevilineatus*, *E. callicephalus*, and *E. fasciatus* (Campbell and Simmons, 1961; Werler, 1951; Fitch, 1954). Viviparity has been recorded in the montane Mexican species *E. brevirostris, E. colimensis, E. copei, E. dugesi, E. lynxe* and *E. ochoterenai* (Axtell, 1960; Taylor, 1936; Webb, 1968; Van Devender and Van Devender, 1975; Guillette, 1983). A phylogenetic reconstruction for *Eumeces* (Taylor, 1936) suggests that viviparity evolved three separate times: once in *ochoterenai–brevirostris–colimensis–dugesi,* once in *lynxe* (including *"furcirostris"*) and once in *copei.* However, *E. copei* may belong with the *brevirostris* group (Dixon, 1969) leaving two origins of viviparity within *Eumeces,* both occurring in the high Mexican plateau (Taylor, 1936). Most oviparous *Eumeces* live at lower elevations, and hence in warmer climates, than do the viviparous ones (Fig. 4).

The sand-swimming skinks of northern Africa and Arabia *(Scincus)* apparently include both oviparous and viviparous forms (Fuhn, 1968; Mertens, 1972; Arnold and Leviton, 1977). However, reproductive data are lacking for most species, and this case is included only tentatively.

The Lygosominae includes more than 40 genera and over 600 species and is the most numerous and diverse scincid lineage (Greer, 1970). Approximately one-third of species are viviparous (Greer, 1970), and many separate origins of viviparity are involved. Viviparity and oviparity cooccur in thirteen genera. Phylogenetic reconstructions also point to independent origins of viviparity in the ancestry of several wholly viviparous genera. For example, the large viviparous lizards of the Australasian genera *Corucia, Egernia,* and *Tiliqua* are thought to have evolved from an oviparous *Mabuya* of southeast Asia (Greer, 1970). Similarly, *Isopachys* of Thailand (fossorial and viviparous, Taylor, 1963) probably is derived from the *Sphenomorphus "laturense* group," at least one member of which is oviparous (Greer, 1977, and personal communication). The fossorial viviparous *Hemiergis* of Australia may share a common ancestry with *Lerista* and *Sphenomorphus "solomonis* group"; the taxa of both are primarily oviparous (Greer, 1967c; Greer and Parker, 1974). Although all of these cases indicate independent origins of viviparity, the transition of reproductive modes has occurred too early in phylogeny to permit useful ecological comparison of present-day oviparous and viviparous forms.

Not all of the wholly viviparous lygosomine genera are likely to represent independent origins of viviparity; some may have inherited viviparity from a live-bearing ancestor. An example is the African *Eumecia,* which probably has evolved from *Mabuya* (Greer, 1967b), most species of which are viviparous. Hence, there is no need to postulate an independent evolution of viviparity in *Eumecia.* A lack of phylogenetic information makes it difficult to determine whether viviparity in the semiaquatic southeast Asian *Tropidophorus* (Brown and Alcala, 1980) and *Ophioscincus* of Thailand (Taylor, 1963) should be regarded also as independent origins of live-bearing.

Some subgroups of the Lygosominae (Greer, 1974, 1979b) consist entirely of oviparous species (e.g., *Dasia–Lamprolepis; Lampropholis* subgroup of the *Eugongylus* group; Greer, 1974), whereas others include viviparous ones (especially the *Sphenomorphus* group, which contains taxa showing at least 17 independent origins of viviparity). The 13 lygosomine genera containing both oviparous and viviparous species (*Ablepharus, Anomalopus, Leiolopisma, Lerista, Lipinia, Lobulia, Lygosoma, Mabuya, Prasinohaema, Scincella, Saiphos, Sphenomorphus,* and *Tribolonotus*) are now considered in more detail.

*Ablepharus* contains five species of small skinks from central Asia (Fuhn, 1969). Oviparity has been reported in *A. deserti* (Terentev and Chernov, 1965), *A. kitaibeli* (Arnold and Burton, 1978), and tentatively in *A. pannonicus* (Smith, 1935). The mode of reproduction of *A. grayanus* appears unknown. Most interest centers on the remaining form, *A. bivittatus*. The subspecies *A. b. bivittatus* is oviparous, whereas the subspecies *A. b. alaicus* (given full specific status by some authors) is viviparous (Terentev and Chernov, 1965). The oviparous subspecies is found below 2000 m in the USSR, whereas the live-bearing subspecies occurs up to 3800 m (Terentev and Chernov, 1965; Fig. 5).

*Anomalopus* contains burrowers with elongate bodies and greatly reduced or no limbs. Two species of Australia's central eastern coast (*A. lentiginosus, A. verreauxii*) are oviparous, whereas the more southern *A. swansoni* ("species 3": Cogger, 1975) is viviparous. The live-bearer occupies cooler climates than its egg-laying relatives (Fig. 6).

Both oviparity and viviparity have been reported in the Australian "sand swimming" skinks of the genus *Eremiascincus*, but the data are unreliable (Greer, 1979a).

*Leiolopisma* contains small, active, diurnal Australasian skinks with well-developed limbs. Live-bearing has evolved at least three times. The first case is in the group containing the viviparous *L. coventryi* of the Australian southern highlands and the oviparous *L. zia* of mideastern coastal Australia (Greer, 1982 and personal communication; Ingram and Ehmann, 1981). The second case is in the "*baudini*" species group (Greer, 1982); thus, *L. duperreyi, L. platynotum* and *L. trilineatum* are oviparous, but *L. entrecasteauxi* and *L. metallicum* are live-bearers. In both of these groups, the viviparous forms occupy cooler climates than the egg layers (Fig. 6). A third origin of viviparity is probably represented by four other Australian species of *Leiolopisma*, belonging to the *spenceri* species-group; these are viviparous also (Greer, 1982).

Viviparity may have evolved also in the species of *Leiolopisma* inhabiting two island groups: New Zealand and New Caledonia. However, both cases are doubtful because of insufficient phylogenetic information. Within New Zealand, the northern (= warm climate) *L. suteri* is oviparous (Towns, 1975), whereas all other species are live-bearers. It seems likely that *L. suteri* represents an independent invasion of New Zealand, and is not closely related to the other endemic scincid lizards (Hardy, 1977). How-

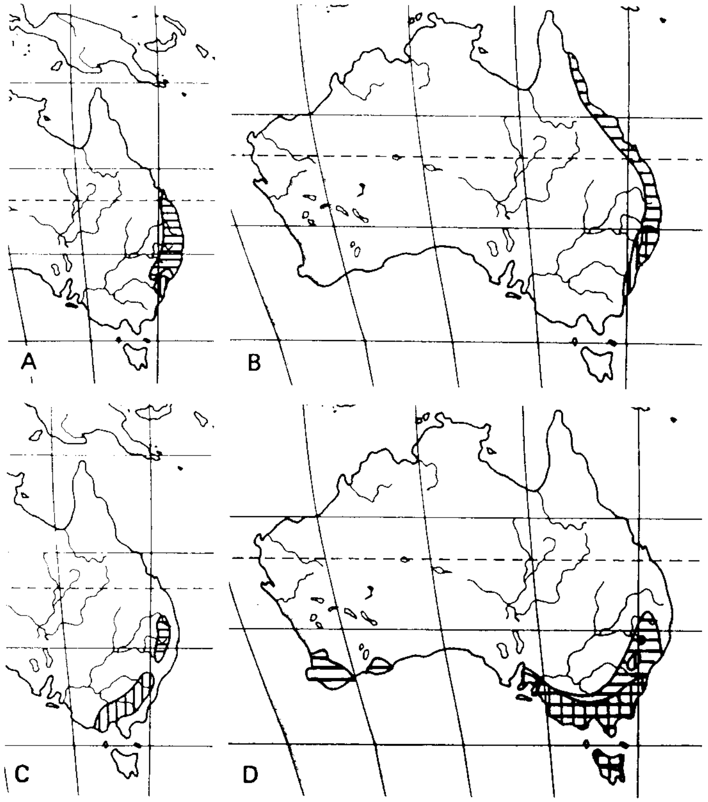

Fig. 6. Geographic distributions of oviparous (horizontal lines) and viviparous (vertical lines) scincid lizards within (A) the genus *Anomalopus;* (B) *Saiphos* and related oviparous forms; (C) the *coventryi* species-group within *Leiolopisma;* (D) the *baudini* species-group within *Leiolopisma.*

ever, the viviparous New Zealand skinks, together with some viviparous Australian forms (*L. spenceri* group), may be derived from an oviparous lineage (Hardy, 1977, 1979; Greer, 1982).

The other leiolopismid assemblage containing both egg-layers and live-bearers occupies New Caledonia. *Leiolopisma tricolor* is viviparous (Roux, 1913), and several other species are oviparous (R. Sadlier, personal communication). This suggests that live-bearing has evolved within the group, but this conclusion may be in error if, as in the New Zealand example, the group is polyphyletic. The taxonomy of these lizards is too poorly known to permit any definite conclusions.

*Lerista* includes many burrowing skinks, some with reduced limbs, of the arid regions of Australia. The southerly *L. bougainvillei* contains both oviparous and viviparous forms (A. Greer and P. Robertson, personal communication; Shine, personal observation); as viviparity occurs in two allopatric populations it may have evolved independently in each case.

However, this is listed here as a single origin. Eight other species of *Lerista* are known to be oviparous, but the southwestern *L. microtis* is live-bearing (Greer, 1967c and personal communication). Morphological characters render it unlikely that *L. microtis* is descended from *L. bougainvillei* (A. Greer, personal communication), so it seems probable that viviparity has evolved independently in this form. Both in the comparison of the viviparous *L. microtis* to oviparous species and of the viviparous *L. bougainvillei* to its oviparous conspecifics, the viviparous forms occur in cooler regions (Fig. 7).

*Lipinia* includes small slender arboreal skinks that are distributed widely through the island archipelagos of the southwest Pacific (Greer, 1974). Modes of reproduction are known for ten of its 20 species (A. Greer, personal communication). The species *L. infralineata, L. pulchella, L. quadrivittata,* and *L. vittigera* are oviparous. The species *L. auriculata, L. noctua, L. rabori, L. relicta, L. semperi,* and *L. venemai* are viviparous. In the Philippines, the viviparous *L. auriculata* occurs at higher elevations than the oviparous *L. pulchella* or *L. quadrivittata* (Brown and Alcala, 1980), but data are insufficient for a thorough comparison.

*Lobulia* contains five small robust-bodied skinks from New Guinea. Reproductive modes are known for two of them. The oviparous *L. stanleyana* is terrestrial and lives between 1200 and 2000 m, rarely to 2500 m, whereas the viviparous *L. elegantoides* is arboreal and lives at 1500 to 3500 m (F. Parker, personal communication). Both species are diurnal heliotherms, and *L. stanleyana* nests communally (F. Parker, personal communication).

A review of reproductive modes and probable phylogenetic relationships within the scincid genus *Lygosoma* suggests two independent origins of viviparity (Greer, 1977). The oviparous *afer* group (*L. afer, L. fernandi, L. guineense, L. sundevalli,* and *L. pembanum*) are closely related to the viviparous *L. laeviceps* and *L. vinciguerra*. The oviparous *L. bowringi* and *L. punctatum* form a group with the viviparous *L. tanae* (Greer, 1977). The viviparous *Lygosoma* do not inhabit cool climates: All three live-bearers are endemic to arid regions of Somalia and eastern Kenya (Greer, 1977). Within the *afer* group, the egg-layers are widely distributed over the African continent. For example, *L. fernandi* and *L. guineense* extend into West Africa, and *L. sundevalli* is distributed through southern and eastern parts of the continent. Within the *bowringi–punctatum–tanae* group, the two oviparous species occur in Asia.

The cosmopolitan tropical *Mabuya* contains a great variety of ground-dwelling skinks. Oviparous as well as viviparous species occur both in Asia and Africa; however, all South American forms are viviparous (at least some with elaborate placentation, Vitt and Blackburn, 1983). One African species (*M. quinquetaeniata*) was reported to show different modes of reproduction in different parts of its range (Fitch, 1970); subsequent investigation disproved this (Visser, 1975; Spellerberg, 1976). Authorities disagree on the reproductive mode of *M. carinata* (Smith, 1935; Badhuri, 1943). Both

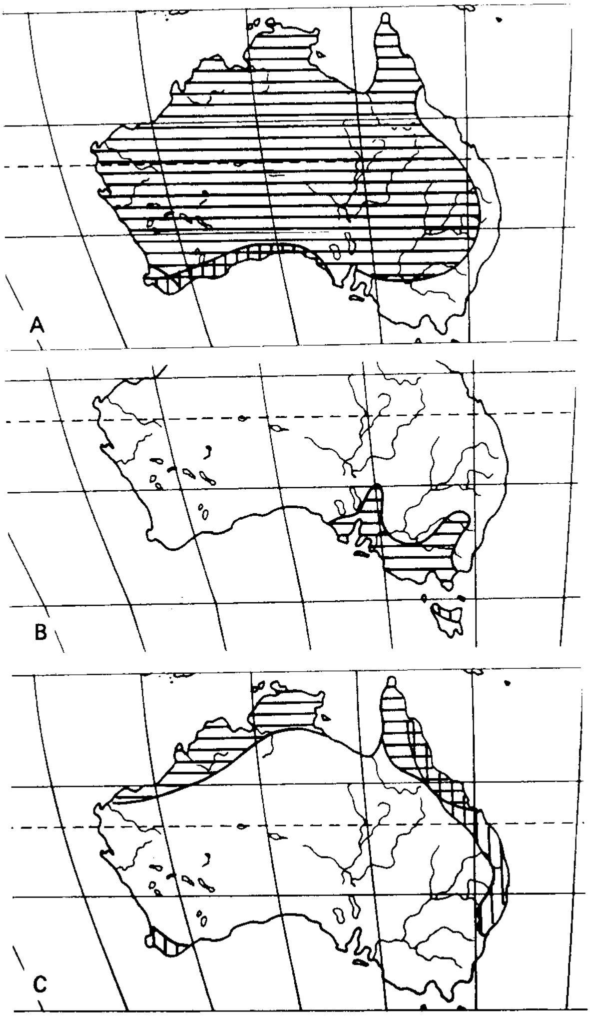

Fig. 7. Geographic distributions of oviparous (horizontal lines) and viviparous (vertical lines) scincid lizards within (A) the genus *Lerista*, excluding *L. bougainvillei*, (B) the species *L. bougainvillei*; (C) the *Sphenomorphus* "*fasciatus* group".

oviparity and viviparity occur in *M. capensis* (W. Haacke, personal communication) and *M. sulcata* (D. Horton, personal communication).

The genus *Mabuya* may be divided into three species groups (Horton, 1973), one of which consists entirely of viviparous South American forms apparently derived from a lineage including the oviparous *M. perroteti* and the viviparous *M. brevicollis* (Horton, 1973); hence, it represents at least one origin of viviparity. Each of the other two species groups (one African, one Asian) contain both oviparous and viviparous forms. Viviparity has evolved in a group containing the oviparous *M. aureopunctata*, *M. bensoni*, *M. lacertiformis, M. maculilabris,* and *M. quinquetaeniata,* and the viviparous *M. bayoni, M. irregularis, M. striata, M. sulcata, M. varia,* and *M. vittata.* All of these species are African except the Iranian *M. vittata.* The live-bearers occur in more southerly, and hence cooler, climates in both of these viviparous origins.

A phylogeny for Asian *Mabuya* (Horton, 1973) derives the viviparous *M. aurata* from a lineage including the oviparous *M. macularia;* the viviparous *M. multifasciata* is tentatively thought to be related to the oviparous *M. longicaudata.* Overall, a total of six evolutionary origins of viviparity may have occurred with *Mabuya.*

*Prasinohaema* includes arboreal skinks of small to medium body size, with prehensile tails. Its species are remarkable in having the blood plasma and other tissues colored green (Greer and Raizes, 1969). All five species in the genus occur on New Guinea, but one species extends its range into the Solomons (Greer, 1974). The small *P. virens* is oviparous (Greer, 1974) and occurs from sea level up to 820 m elevation. Three other species are known to be viviparous and are found at higher elevations (*flavipes,* 1070 to 2500 m; *prehensicauda,* 1200 to 2300 m; *semoni,* sea level to 1800 m).

*Scincella* is distributed widely in the Old World and to a lesser extent in the New World (Greer, 1974). Modes of reproduction are known only for seven of 32 recognized species. *S. barbouri, S. bilineata, S. formosa, S. ladacensis, S. modesta,* and *S. sikkimensis* are oviparous (Smith, 1935; A. Greer, personal communication), whereas *S. himalayana* is viviparous (Smith, 1935). Analysis is precluded by the lack of reproductive data. However, *S. himalayana* occurs between 1300 and 4000 m (Smith, 1935), suggesting that cold climates may have played a role in the evolution of viviparity. Most other members of the genus live at lower elevations than does *S. himalayana,* but at least one oviparous species *(S. ladacensis)* ranges even higher (Smith, 1935; Greer, 1974).

The monotypic fossorial *Saiphos equalis* is unusual in displaying oviparity and viviparity in different geographic areas. In the relatively mild climate of the Australian east coast, it is oviparous and its poorly calcified eggs hatch within a week or two of being laid (Bustard, 1964; Cogger, 1975). In the cold highlands of the New England Plateau, young are born alive (Shine and Thompson, unpublished; Greer, 1983). It is of interest that those *Sphenomorphus* that are the closest relatives of *Saiphos* (Greer, 1983) and inhabit warmer climates (Fig. 6) are oviparous and lay normally calcified eggs with a much longer incubation period than the oviparous populations of *Saiphos* (Shine, personal observation).

*Sphenomorphus* includes a large but probably monophyletic group of Australasian skinks. Analysis reveals that viviparity originated at least five times within the genus. The *Sphenomorphus* "*crassicaudus* group" contains several elongate fossorial species including the oviparous *S. crassicaudus* from northern Australia and Papua New Guinea. This species is morphologically similar to *S. fragilis* of southeastern New Guinea, which produces fully developed young, although with a thicker and more opaque "shell" than the thin transparent membranes seen in most viviparous species (Greer and Parker, 1979). *Sphenomorphus fragilis* is found from sea level to 670 m, probably at a climate similar to that experienced by the related oviparous *S. crassicaudus.*

The 40 species of the fossorial *Sphenomorphus "fasciatus* group" are distributed in New Guinea, the Solomon Islands, the Philippines, northern Australia, and the Lesser Sunda Islands (Greer and Parker, 1967). In many cases modes of reproduction are unknown, but both oviparous and viviparous forms occur within Australia (oviparous: *S. brongersmai, S. douglasi, S. isolepis, S. pardalis, S. punctulatus, S. fuscicaudus;* viviparous: *S. gracilipes, S. murrayi, S. tenuis*) and within New Guinea (oviparous: *S. nigrilineatus, S. brunneus, S. cranei, S. derooyae, S. nigriventris, S. oligolepis, S. undulatus, S. schultzei;* viviparous: *S. longicaudatus, S. cinereus, S. leptofasciatus*). Analysis of the Australian species suggests that the viviparous species occur in slightly cooler climates than the oviparous ones (Fig. 7).

Viviparity also originated in the elongate fossorial *Sphenomorphus nigricaudus,* which is closely related to both of the *Sphenomorphus* groups discussed above. New Guinea specimens of *S. nigricaudus* are oviparous, but Australian specimens from Cape York, Queensland, are viviparous (A. Greer, personal communication). Within New Guinea, this species is restricted to the south coast savannah belt, reaching 600 m elevation on the Sogeri plateau near Port Moresby (F. Parker, personal communication). Australian specimens occur from sea level to over 1000 m (Cogger, 1975).

The body form of the *Sphenomorphus "variegatus* group" is more robust than that of the "*fasciatus* group," discussed above. Modes of reproduction are known for 29 species, and at least two separate origins of viviparity are indicated (A. Greer, personal communication). One origin lies within a group containing the oviparous *S. boulengeri* (from China and Taiwan) and the viviparous *S. formosensis* and *S. indicus* (China, Taiwan, eastern Asia). Another group containing both oviparous and viviparous species occurs in New Guinea (*S. stickeli,* oviparous), Borneo (*S. multisquamatus,* oviparous) and the Solomon Islands (*S. concinnatus,* viviparous). There are no data on ecology or elevational distribution of *S. multisquamatus.* However, behavior and habitat of the other two species are similar to each other (F. Parker, personal communication). The oviparous *S. stickeli* occurs from sea level up to 700 m (F. Parker, personal communication), whereas the viviparous *S. concinnatus* occurs from sea level up to 1500 m (on Guadalcanal, M. McCoy, personal communication).

*Tribolonotus* has been described as "undoubtedly one of the most bizarre taxa of lizards" because of its abdominal glands, volar pores, and aberrant squamation (Greer and Parker, 1968). It occurs through New Guinea and the Solomon Islands. *T. annectens, T. blanchardi, T. gracilis, T. novaguineae,* and *T. pseudoponceleti* are oviparous, but *Tribolonotus schmidti* from the Solomon Islands is viviparous (Greer and Parker, 1968). Recent studies provide valuable information on the Solomon Islands *Tribolonotus* (McCoy, 1980, and personal communication). Only the viviparous *T. schmidti* occurs on Guadalcanal, where it is usually found under rotting fallen timber in forests and from sea level to over 1000 m. The superficially similar oviparous *T. blanchardi* replaces it on other islands of the Solomon group. On Nggela (= Florida Island), *T. blanchardi* is usually found in moist creek beds, often in drifts of dead leaves, and in other forest debris. It has been collected from sea level to 500 m (the tops of the highest hills on Nggela), but may occur at higher elevations on more mountainous islands.

### 10. XANTUSIIDAE

The small viviparous lizards of the Xantusiidae are distributed discontinuously in the West Indies, Central America, and the southwestern United States and apparently are derived from geckoes (McDowell and Bogert, 1954; Underwood, 1971; Northcutt, 1978). The only viviparous geckoes are in the southern hemisphere (New Caledonia and New Zealand) and, hence, are unlikely ancestors for the xantusiids. It can be inferred that viviparity evolved in the ancestors of the xantusiids.

## D. Serpentes

### 1. ANILIIDAE AND UROPELTIDAE

These so-called "primitive snakes" of South America and Asia are viviparous; they may be relatively closely related to each other (Fitch, 1970; McDowell, 1975; Rieppel, 1979). Because the superfamily Anilioidea contains the oviparous Xenopeltidae and Loxocemidae as well as these viviparous forms (McDowell, 1975; Rage, 1982), at least one origin of viviparity is indicated.

### 2. ACROCHORDIDAE

All three species of Australian and Asian file-snakes are aquatic and viviparous, and only distantly related to other living snakes. Their phylogenetic position (McDowell, 1975, 1979; Rieppel, 1979; Rage, 1982) renders it likely that viviparity has evolved independently in this group.

### 3. TYPHLOPIDAE

Most blindsnakes are oviparous, and one observation suggests that maternal care may be shown (Fitch, 1970). However, a female *Typhlops diardi* from Vietnam contained "14 embryos all perfectly developed" (Smith, 1943; p. 44). An earlier study concluded that this species was oviparous, but with considerable embryonic development prior to oviposition (Wall, 1918). The South African *Typhlops bibronii* deposits thin-walled eggs, which hatch in five days (Erasmus and Branch, 1983); hence I consider that this species, like northern populations of the colubrid snake *Opheodrys vernalis*, is effectively viviparous. Not all blindsnakes show such prolonged egg retention. Recorded incubation periods of other *Typhlops* include 30–42 days for *T. schlegelii* (FitzSimons, 1962) and 38 days for *Ramphotyphlops braminus* (Fitch, 1970). The number of independent origins of viviparity in typhlopids is difficult to estimate, because of the lack of phylogenetic information.

## 4. BOIDAE

The large Boidae are widely distributed throughout the tropics and subtropics; a few species invade temperate areas. Subfamilial classifications are a source of disagreement (e.g., McDowell, 1975), but only the two largest subfamilies are relevant for this discussion. One subfamily, the Boinae or "true boas," are viviparous. They are confined to the New World tropics with the exception of the Malagasian *Acrantophis* and *Sanzinia* and the South Pacific *Candoia*. The boines are similar in body form and habits to the Old World pythons (subfamily Pythoninae), except that the latter are oviparous. Maternal egg-guarding behavior is widespread, possibly universal, in the pythons (Shine and Bull, 1979). Morphological characters suggest that the pythonines gave rise to the boines rather than vice versa (Underwood, 1967). This is consistent with the assumption that viviparity evolved from oviparity. The origin of boid viviparity is so far back in evolutionary history that analysis of ecological correlates is impossible. A record of oviparity in the normally viviparous *Boa constrictor* is probably an error (Tinkle and Gibbons, 1977).

## 5. TROPIDOPHIIDAE

Several unique morphological features suggest that the tropidophiids are only distantly related to the boids with which they usually have been combined (McDowell, 1975). Apparently, all tropidophiids are viviparous (e.g., Dowling, 1974). The structure of the skull is similar to that in bolyerids (McDowell, 1975), one of which recently has been shown to be oviparous (Anonymous, 1982). Hence, viviparity has evolved within the tropidophiid lineage.

## 6. COLUBRIDAE

Viviparity has evolved several times within this large and diverse lineage, but interpretation is confused by differing phylogenetic schemes. In many cases, relationships are obscure. For example, the viviparous Asiatic treesnake *Ahaetulla* (Fitch, 1970) may be closely related to the oviparous African *Thelotornis* (Underwood, 1967, 1979). If the presumed relationship is valid, viviparity originated in the group. A similar problem occurs with xenodontine colubrids of the New World. Viviparity has been described in *Tomodon*, *Tachymenis, Ptychophis, Pseudotomodon,* and *Thamnodynastes* (Bailey, 1966, 1981; Gudynas, 1981; da Cunha and do Nascimento, 1981). On the basis of their phylogenetic relationship to these genera, Bailey (1981) suggests that *Calamodontophis* probably are viviparous also. All are small-to-medium-sized snakes with a generally southern distribution. *Tachymenis* may be related to the oviparous *Imantodes,* and perhaps *Leptodeira,* whereas *Tomodon* and *Thamnodynastes* may be related to the oviparous *Conophis* (Underwood, 1967). Yet another interpretation links *Tachymenis* with the oviparous *Philodryas* of subtropical South America (Duellman, 1979). In each case, the egg-layers occupy much warmer climates than do the live-bearers. Underwood's taxonomy suggests two independent origins of viviparity, whereas Bailey's requires only one; parsimony dictates the adoption of the latter view. Recent studies using microcomplement fixation are consistent with Bailey's conclusions, but do not reveal any close xenodontine relatives of the *Tomodon–Thamnodynastes* group (Cadle, 1984).

A problem arises with the viviparous *Psammodynastes pulverulentus,* which is widely distributed in southeastern Asia (Fitch, 1970). It has no clear taxonomic affinities with any other colubrids; it is placed in the boigine subfamily only provisionally (Underwood, 1967). Viviparity may have evolved independently in this case, as it seems unlikely that *Psammodynastes* is closely related to *Ahaetulla,* the only other viviparous Asiatic boigine. The situation is less clear in the case of the subfamily Homalopsinae, all members of which are viviparous (Gyi, 1970). Morphological data suggest that the homalopsines may be derived from the "boigines" (Underwood, 1979), so that it is conceivable, although unlikely, that homalopsines evolved from a viviparous ancestor (*Ahaetulla, Psammodynastes, Ptychophis, Tachymenis, Thamnodynastes, Tomodon, Pseudotomodon,* or their ancestors). However, biochemical data indicate that the homalopsines are related only distantly to other colubrids, including "boigines" (Schwaner and Dessauer, 1982), suggesting that viviparity may have evolved independently in this subfamily. Nonetheless, this case was not analyzed further.

Viviparity occurs also in the small Mexican *Conopsis* and *Toluca* (Greer, 1966). Duellman (1961) considered that these live-bearers are closely related to the oviparous genera *Ficimia* and *Gyalopion,* but Hardy (1975) argued against this view. It is difficult to identify the nearest relatives of *Conopsis* and *Toluca.* Underwood (1967) suggested that a group of oviparous genera (including *Sonora, Tantilla,* and *Stenorhina*) might be close to the live-bearers. Whichever of these taxonomies is accepted, the viviparous forms occur in much cooler climates and higher elevations (up to 3000 m) than do their oviparous relatives.

The small marsh-dwelling African *Amplorhinus multimaculatus* is viviparous (Broadley and Cock, 1975), but its taxonomic affinities are problematical (Branch, 1982). It may be included with the boigines (e.g., Broadley and Cock, 1975) or may be related to the natricines (Branch, 1982). In either case, it is likely to represent an independent origin of viviparity. The only other rear-fanged African snakes known to be viviparous are *Psammophylax v. variabilis* and *Aparallactus jacksoni;* neither is likely to be ancestral to *Amplorhinus.* Another boigine, the oviparous *Hemirhagerrhis notataenia,* was formerly included in the genus *Amplorhinus,* but it probably is not closely related (Bogert, 1940). *H. notataenia* is a lowland form, whereas *Amplorhinus multimaculatus* is montane (Vessey-Fitzgerald, 1958; Pienaar, 1978; Broadley and Cock, 1975). An alternative phylogenetic hypothesis is that *Amplorhinus* is related to the natricines of central and western Africa (Branch, 1982), which probably are oviparous (Fitch, 1970; Rossman and Eberle, 1977). In each of these putative phylogenies the live-bearer occupies a much cooler climatic region than its oviparous relatives. One cautionary note in accepting an independent origin of viviparity for *Amplorhinus* is its unexpected anatomical resemblance to the viviparous Neotropical *Thamnodynastes* and *Tomodon* (Underwood, 1967). Hence it is possible, although zoogeographically improbable, that the viviparity of *Amplorhinus* is inherited from a viviparous Neotropical ancestor.

Three species of the East African *Aparallactus (A. capensis, A. guentheri, A. lunulatus)* are oviparous, one *(A. jacksoni)* is viviparous (FitzSimons, 1962; Pitman, 1974; Spawls, 1973) and the mode of reproduction of the others remains unknown. All are small and fossorial; the range of *A. jacksoni* is included within those of its oviparous congeners (Fig. 8).

*Coronella* is a genus of moderate-sized colubrids from Europe and India. Oviparity has been recorded in the Indian *C. brachyura* (Deoras, 1971) and the European *C. girondica* (Street, 1973). The other European species, *C. austriaca,* is viviparous (Smith, 1973); its ecology is well known (Duguy, 1961; Andren and Nilson, 1976a; Spellerberg and Phelps, 1977). It is found at higher latitudes, in cooler climates, and over a wider latitudinal range than its nearest oviparous congener, *C. girondica* (Fig. 8).

The large colubrid genus *Elaphe* of North America, Europe, and Asia is almost certainly polyphyletic, but no satisfactory subdivision has been devised (see comments by Pope, 1935). Oviparity has been recorded in many species of *Elaphe,* including *E. bimaculata, E. carinata, E. climacophora, E. conspicillata, E. dione, E. flavolineata, E. guttata, E. helenae, E. hohenackeri, E. longissima, E. mandarina, E. moellendorffi, E. obsoleta, E. porphyracea, E. prasina, E. quadrivirgata, E. quatuorlineata, E. radiata, E. scalaris, E. schrencki, E. situla, E. subocularis, E. taeniura,* and *E. vulpina* (Chang and Fang, 1931; Deoras, 1971; Fukada, 1956; Kopstein, 1938; Pope, 1935; Smith, 1943; Steward, 1971; Fitch, 1970). Maternal care has been reported in three species (Fitch, 1970). The Chinese and Korean *E. rufodorsata* is viviparous (Sowerby, 1930; Sura, 1981) and also semiaquatic, unlike the other Chinese *Elaphe.* Biochemical data suggest that this species is only distantly related to any other *Elaphe* species (Lawson and Dessauer, 1980). It has been suggested that viviparity in *E. rufodorsata* evolved because "living, as these snakes do, in open swamps and marshes, their eggs would stand a poor

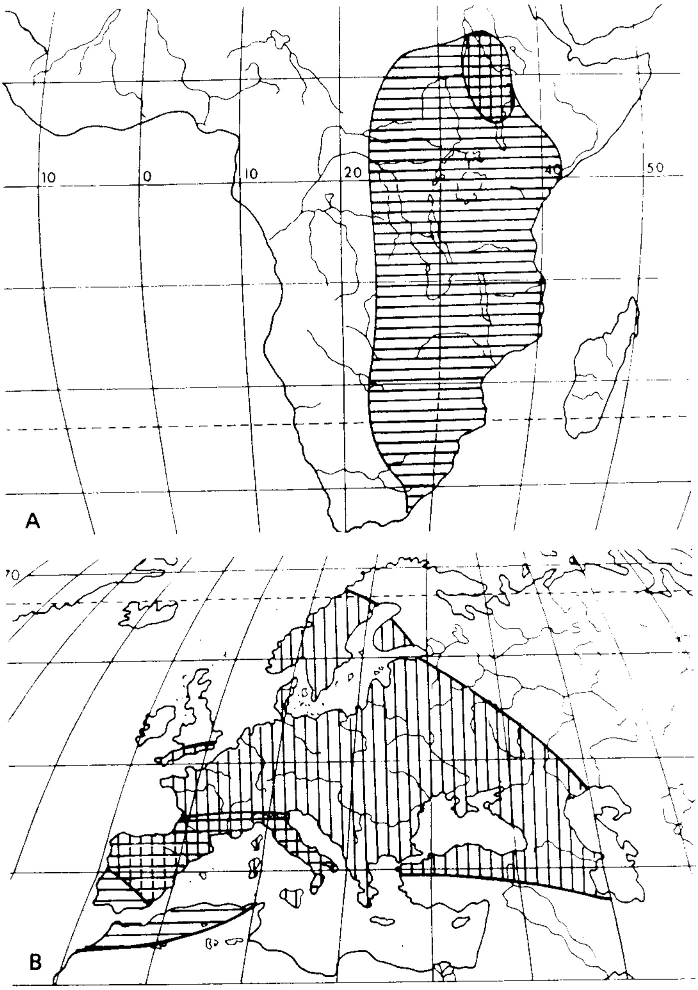

Fig. 8. Geographic distributions of oviparous (horizontal lines) and viviparous (vertical lines) colubrid snakes within (A) the genus *Aparallactus;* (B) the genus *Coronella.*

chance of hatching'' (Sowerby, 1930). However, many aquatic and semiaquatic Asian snakes are oviparous (Pope, 1935): nontheless, viviparity arose in the aquatic *Sinonatrix* (see below). The viviparity of *E. rufodorsata* could also be due to its inhabiting a cold climatic region (northeastern China and Korea). Although a few oviparous *Elaphe* occur even farther north (e.g., *E. dione, E. schrencki*), most European and Asian *Elaphe* occupy much warmer climates (Fig. 9).

The aquatic and semiaquatic colubrids of the genus *Grayia* inhabit tropical Africa. Four species, *caesar, ornata, smithii,* and *tholloni,* are generally recognized. *Grayia smithii* is oviparous (Angel et al., 1954; Pitman, 1974).

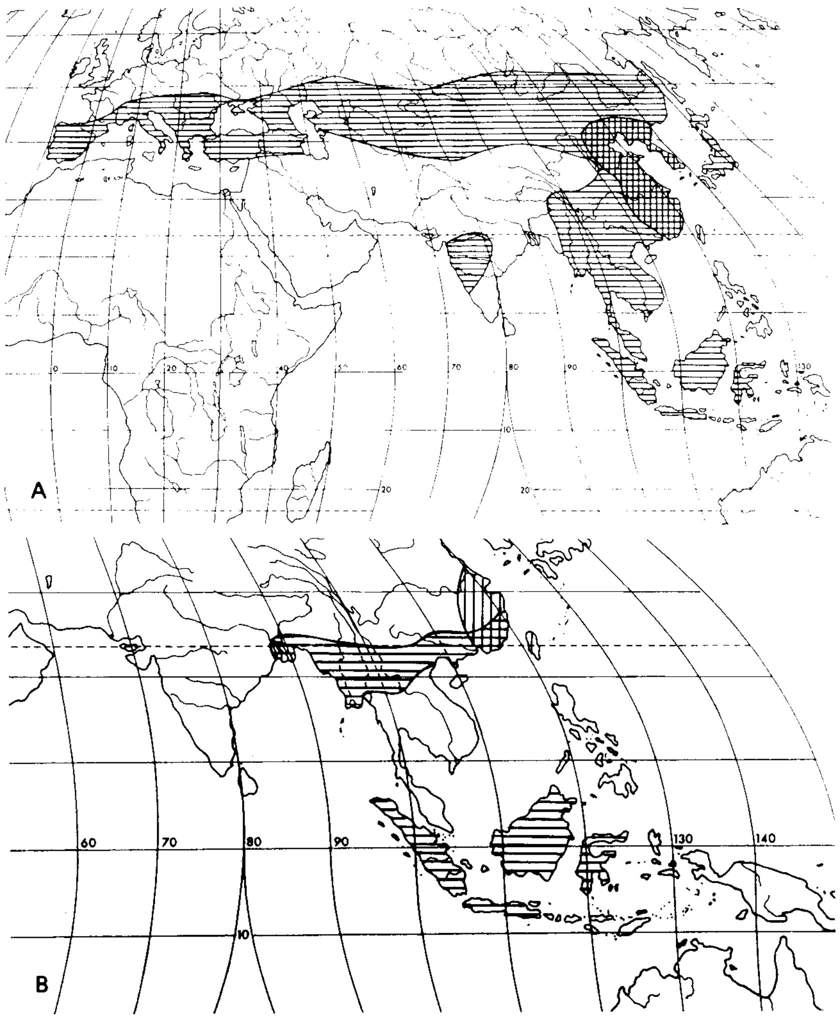

Fig. 9. Geographic distributions of oviparous (horizontal lines) and viviparous (vertical lines) colubrid snakes within (A) Old World species of the genus *Elaphe;* (B) the genus *Sinonatrix.*

Developing embryos *in utero* have been reported in *G. tholloni* (Loveridge, 1933), suggesting that this species may be viviparous. Both species have similar geographic distributions (Pitman, 1974). Modes of reproduction are unknown for the other species. The possibility of viviparity in *Grayia* is supported by the presumed relationship of this genus with the viviparous African colubrids *Duberria* and *Pseudaspis* (Bogert, 1940; Fitch, 1970). I infer that viviparity has evolved in this lineage, either within *Grayia* or in the ancestors of *Duberria* and *Pseudaspis.* Both of the latter two genera extend into cool regions; in Zimbabwe, *D. lutrix* is restricted to elevations higher than 1400 m, and *P. cana* occurs up to 1500 m (Broadley and Cock, 1975).

There are 15 species of South American watersnakes in *Helicops;* although Amaral (1977) suggested that all are viviparous, reproductive modes are known definitely for only a few of them. *Helicops carinicaudus* from central Brazil, Uruguay, and Argentina is viviparous (Mole, 1924; Shine, personal observation), and so are *H. polylepis* and *H. trivittatus* (da Cunha and do Nascimento, 1981) and probably *H. leopardinus* (Shine, personal observation from dissection of gravid female). Both oviparity and viviparity have been reported in the more northern *H. angulatus*: A female from Colombia laid eggs that hatched in only 16 days (Rossman, 1973), and a specimen from Trinidad was oviparous, whereas ones from Peru and the Amazon were viviparous (Rossman, 1984; da Cunha and do Nascimento, 1981). Data on this genus are insufficient for detailed analysis, but suggest two origins of viviparity.

The North American *Opheodrys vernalis* has a remarkably short incubation period in the northern (coldest) part of its range. Incubation averages 30 days in the Chicago region (Stille, 1954), but only four to 23 days in northern Michigan (Blanchard, 1933; MacGregor, 1975; Sexton and Claypool, 1978). Blanchard (1933) suggested that occasional viviparity was likely, but was not observed by him. Also, maternal care of the eggs may be shown (Blanchard, 1933). A four-day incubation period is only slightly longer than the time taken for the young of several viviparous species to emerge from the egg sac after parturition (e.g., *Saiphos equalis, Pseudechis porphyriacus,* Greer, 1983; Shine, personal observation; *Trimeresurus okinavensis,* Koba et al., 1970); hence this case is included as an example of viviparity.

The medium-sized African *Psammophylax* occur in grasslands. *P. tritaeniatus* and *P. rhombeatus* are oviparous, with the latter species showing maternal egg-guarding and prolonged oviducal retention of eggs (FitzSimons, 1962; Broadley, 1977). *P. variabilis* shows geographic variation in mode of reproduction: the lowland *P. v. multisquamis* is oviparous with egg-guarding, whereas the montane (> 1800 m) *P. v. variabilis* is viviparous (Broadley, 1977). *P. variabilis* is a slow-moving species that does not rely on speed to escape predation; in contrast, *P. rhombeatus* is an agile, fast-moving snake (FitzSimons, 1962). The viviparous *P. v. variabilis* is found in cooler, more southern areas than the oviparous *P. v. multisquamis* (distribution maps in Broadley, 1977).

On the basis of biochemical, karyological, scutellation, and cranial data, the large cosmopolitan snake genus *Natrix* has been divided into four genera (Rossman and Eberle, 1977). Five Asian species comprise *Sinonatrix;* Malnate (1960) had previously pointed out the close relationships between these forms. Oviparity has been reported in *S. trianguligera* (Kopstein, 1938) and the egg-guarding *S. percarinata* (Pope, 1935), whereas *S. annularis* is viviparous (Pope, 1935). There appear to be no records of mode of reproduction in *S. aequifasciata* or *S. bellula*. All the *Sinonatrix* are semi-aquatic, and are rarely found far from streams or flooded fields (Pope, 1935). Hatchlings of the oviparous *S. percarinata* show obvious egg teeth, whereas newborn *S. annularis* do not (Pope, 1935). This observation suggests that viviparity may not be too recent an acquisition in *S. annularis*. *S. annularis* is found farther north than any of the oviparous forms (Fig. 9; but see Tinkle and Gibbons, 1977).

All New World natricines (e.g., *Nerodia, Regina, Storeria, Thamnophis*) are viviparous. Many authors have suggested that viviparity evolved during the migration of oviparous Old World natricines across the Bering Strait (e.g., Neill, 1964). However, Malnate (1960) notes that the viviparous Old World *S. annularis* is close to the stock which gave rise to the New World natricines. Perhaps, viviparity arose only once in this group (in *S. annularis*).

Some records of the evolution of viviparity in colubrid snakes may be in error. Two reports of viviparity in the North American *Diadophis punctatus* (Ditmars, 1942; Peterson, 1956) are based on the sudden appearance of neonates in cages containing adult *D. punctatus;* the actual process of live birth was not observed. As extensive studies by other workers revealed no evidence of viviparity (review by Tinkle and Gibbons, 1977), this case is not considered further. Similarly, early reviews claimed that viviparity is shown by, and has evolved in, the colubrid genera *Boiga* (Mell, 1929), *Dendrelaphis, Hemirhagerrhis,* and *Meizodon* (Neill, 1964). Subsequent work indicates that all four genera are exclusively oviparous (Pope, 1935; Campden-Main, 1970; Broadley and Cock, 1975).

## 7. ELAPIDAE

The only viviparous African elapid is the spitting cobra *Hemachatus haemachatus* (Fitch, 1970); it is thought to be related to the true cobras of the genus *Naja,* based on similarity of overall morphology (FitzSimons, 1962) and venom fractions (Strydom, 1979). *Naja* are oviparous, and maternal egg-brooding has been reported (Kopstein, 1938; Fitch, 1970). *Hemachatus* is found in more southerly (and hence cooler) climates than are most of its oviparous relatives (Fig. 10), and it inhabits areas from sea level to over 2500 m elevation (Branch, 1979).

Viviparity characterizes all the hydrophiine sea snakes, but most or all laticaudine sea snakes are oviparous (Fitch, 1970). *Laticauda colubrina* has been reported to show both oviparity (Smedley, 1931; Dunson, 1975; Shine, personal observation) and viviparity (Smith, 1930; Taylor, 1965; Semper, cited in Smedley, 1931). Two of the latter cases (Taylor, Semper) were based on observations of females with newborn young: these may be due to prolonged egg-brooding rather than viviparity (Smedley, 1931). However, the record which is based on dissection of a gravid female (Smith, 1930) is difficult to dismiss, although it is surprising that subse-

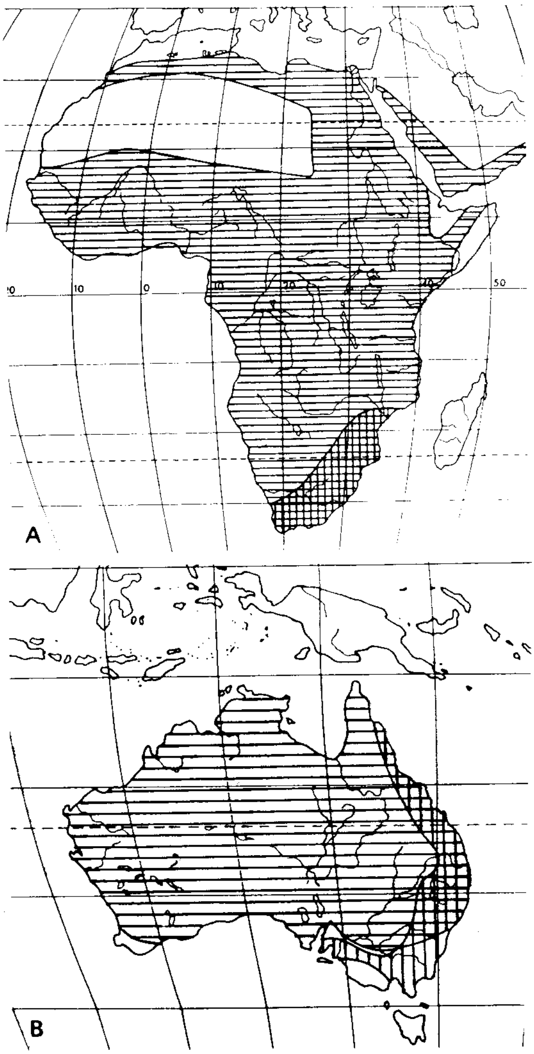

Fig. 10. Geographic distributions of oviparous (horizontal lines) and viviparous (vertical lines) elapid snakes within (A) the genera *Naja* and *Hemachatus;* (B) Australian species of the genus *Pseudechis*.

quent workers have not discovered viviparous populations of laticaudines (Solomon Islands native people suggest that *Laticauda crockeri* is viviparous: H. Heatwole, personal communication). This case is not considered further in the analysis.

Whether or not the viviparity of hydrophiine sea snakes is likely to represent an independent origin depends on whether they derive from the terrestrial Australian elapids (many of which are viviparous) or from the laticaudines, most of which are oviparous. Morphological and biochemical data (McDowell, 1969; Minton, 1979; Cadle and Gorman, 1981; Mao et al., 1977, 1983) are ambiguous on this point, so the case is not considered further.

Until recently, all the large venomous snakes of the genus *Pseudechis*, which are widely distributed in Australia and New Guinea, were thought to be viviparous (Worrell, 1963). However, oviparity is now known for *P. australis* (Fitzgerald and Pollitt, 1981; Shine, unpubl.), *P. guttatus* (Charles et al., 1979), *P. colletti* (Charles et al., 1983), and *P. papuanus* (E. Worrell, personal communication; Shine, unpubl.). The only viviparous species, *P. porphyriacus* (Shine, 1977), inhabits cooler and wetter areas than do its oviparous congeners (Fig. 10).

Viviparity occurs in at least 13 additional genera of Australian elapid snakes (*Acanthophis, Austrelaps, Cryptophis, Denisonia, Drysdalia, Echiopsis, Hemiaspis, Hoplocephalus, Notechis, Rhinoplocephalus, Suta, Tropidechis, Unechis;* Cogger, 1975, and Shine, unpublished), whereas ten genera are known to be oviparous (*Cacophis, Demansia, Furina, Glyphodon, Neelaps, Oxyuranus,* most *Pseudechis, Pseudonaja, Simoselaps, Vermicella*). These genera have been divided into four groups on the basis of venom gland musculature and the morphology of the hemipenes (McDowell, 1967). All four groups contain both oviparous and viviparous genera, suggesting at least four origins of viviparity. However, the classification is not consistent with karyotypic data (G. Mengden, personal communication). Data on scalation (Cogger, 1975) are significant in this respect: All of the viviparous genera except *Acanthophis* possess undivided subcaudals, whereas all of the oviparous genera display divided subcaudals (Shine, 1985). The correlation between subcaudal scalation and reproductive mode suggests that the oviparous and viviparous taxa represent distinct phylogenetic lineages. *Acanthophis* may represent an additional independent origin of viviparity, but only two other origins are likely in the Australian elapids; one in *Pseudechis* and one far back in the phylogeny of the group.

There are conflicting reports on reproductive mode in the elapid genus *Cacophis* (Tinkle and Gibbons, 1977), but a recent study demonstrates oviparity in all three species (Shine, 1980b). Viviparity in the Oriental genus *Calliophis* was suggested, but not documented, by Mell (1929) and Neill (1964). Oviparity has been reported in *C. japonicus* (Fukada, 1965), *C. maculiceps* (Phelps, 1981) and *C. melanurus* (Deoras, 1971). A gravid female *C. macclellandii* contained oviducal eggs with embryos up to 38 mm long (Pope, 1935), but this record also has been interpreted as indicating oviparity (Campden-Main, 1970; Whitaker, 1978). Further data are needed to clarify reproductive modes in this genus.

### B. VIPERIDAE

In the "Agkistrodon" group, large and deadly pit vipers of Asia and the Americas, two species are known to be oviparous (*Deinagkistrodon acutus,* *Calloselasma rhodostoma,* Pope, 1935), whereas seven others are viviparous (*Agkistrodon bilineatus, A. contortrix, A. halys, A. himalayanus, A. piscivorus, Hypnale hypnale, H. nepa,* Chang and Fang, 1931; Pope, 1935; Kopstein, 1938; Fukada, 1962; Telford, 1980). The mode of reproduction is unknown in *A. caliginosus; A. strauchi* is "apparently ovoviviparous," and the same is suggested for *A. monticola* (Pope, 1935). Taxonomists disagree on phylogenetic relationships within these pit vipers. Brattstrom's (1964) phylogeny suggests that viviparity has evolved independently at least twice, and possibly four times, within the genus. Burger (1971) removes both oviparous forms to the single genus *Calloselasma,* which suggests that viviparity has evolved only once. Recent revisions (Gloyd, 1977, 1979) incorporate an earlier suggestion (Chernov, 1957) and partition *"Agkistrodon"* into four genera. The two oviparous species occupy monotypic genera *(Calloselasma rhodostoma, Deinagkistrodon acutus).* Two small viviparous snakes of Sri Lanka and peninsular India *(A. hypnale* and *A. nepa)* are placed in the genus *Hypnale,* and the remaining seven viviparous species remain in *Agkistrodon.*

In the wider sense, whether one or two separate evolutionary origins of viviparity have occurred within *"Agkistrodon"* depends on the relationship between the two oviparous forms, *D. acutus* and *C. rhodostoma.* If they are closer to each other than to any of the viviparous forms (as suggested by Burger, 1971; and R. Conant, personal communication), then viviparity may have arisen only once. If they are related more closely to viviparous forms than to each other (as in Brattstrom's 1964 study, or the serological analysis of Kawamura, 1974), multiple origins of viviparity are suggested. The conservative position is that *"Agkistrodon"* provides only a single case of the evolution of viviparity.

The analysis is confused by geographic distribution: Both oviparity and viviparity occur in Asian *"Agkistrodon"*, but all three American species are viviparous. A review concluded "that no correlation between habitat preference or latitude of distribution and method of production of young can be found" (Pope, 1935). However, it seems clear that the viviparous Old World *"Agkistrodon"* tend to have a more northerly distribution than the oviparous ones. The viviparous *A. halys* occupies much colder climates than does any other *"Agkistrodon"* (Fig. 11). Female *Calloselasma rhodostoma* guard their eggs after laying (Smith, 1943); this behavior may facilitate the evolution of viviparity (Shine and Bull, 1979). Considerable embryonic development occurs prior to oviposition both in this species and in *Deinagkistrodon acutus* (Pope, 1935; Smith, 1943; Wall, 1921). The incubation period of the former is only 30 days (Phelps, 1981).

*Cerastes* (= *Aspis*) contains two small heavily built vipers occupying similar geographic ranges in sandy areas of North Africa and southwestern Asia. *Cerastes cerastes* is oviparous (Petzold, 1968b; Dmi'el, 1970; Saint Girons, 1962), and *C. vipera* is probably viviparous, despite conflicting statements in the literature (Werner, 1930; Vogel, 1963; Petzold, 1968b). *Cerastes*

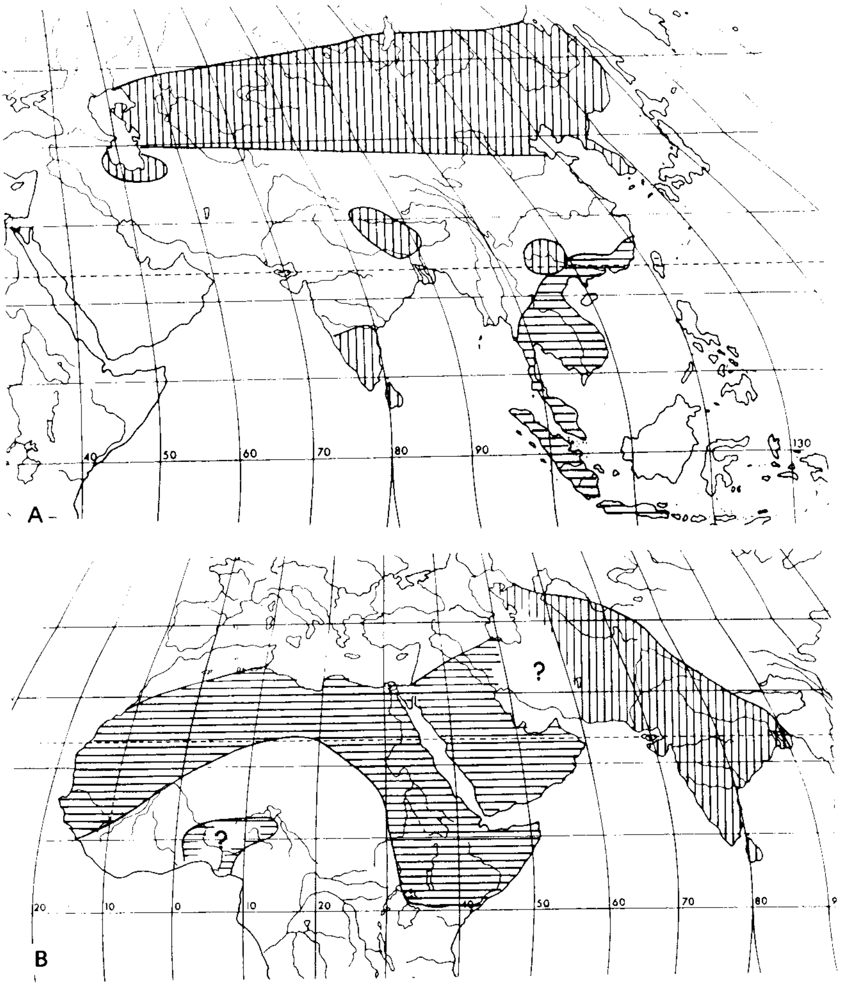

Fig. 11. Geographic distributions of oviparous (horizontal lines) and viviparous (vertical lines) viperid snakes within (A) the Old World species of the genus *Agkistrodon*; (B) the species *Echis carinatus*.

*vipera* is known to be viviparous in both the eastern (Mendelssohn, 1963) and central (Domergue, 1959) parts of its range, as well as in the "Biskra Oasis" (Schetty, 1951).

*Echis* is closely related to *Cerastes*, and the catch-all name "*E. carinatus*" has recently been shown to include multiple species (Hughes, 1976; Cherlin, 1981). *Echis coloratus* of southwestern Asia is oviparous (Mendelssohn, 1965; Dmi'el, 1970), but the *E. carinatus* group shows geographic variation in the mode of reproduction (Fig. 11). Specimens from Russia, India, and Pakistan are viviparous (Petzold, 1968b; Deoras, 1971; Mendelssohn, 1965; Stemmler, 1969, 1970; Stemmler-Gyger, 1965; Minton, 1966; Whitaker, 1978; Isemonger, 1962; Kramer and Schnurrenberger, 1963; Terentev and Chernov, 1965), whereas those from North Africa are oviparous (Mendelssohn, 1965; Isemonger, 1962; Stemmler, 1971; Kramer and Schnurrenberger, 1963; Duff-Mackay, 1965), as are those from Turkey and Asia Minor (Kramer and Schnurrenberger, 1963). Tinkle and Gibbons (1977) questioned Duff-Mackay's (1965) record of oviparity in African "*E. carinatus,*" but noted that oviparity had also been recorded by other authors. Unfortunately, the mode of reproduction is unknown for West African specimens, apart from an unsubstantiated comment in a popular book on the region (Cansdale, 1961) that "*E. carinatus*" (one of at least two local species) is viviparous. The boundary between oviparous and viviparous populations of "*E. carinatus*" occurs in the mountainous country of Iran and Afghanistan; "*E. carinatus*" occurs up to 1800-m elevation (Petzold, 1968b). A new species (*E. multisquamatus*: Cherlin, 1981) has recently been described from northern and eastern Iran and southern Afghanistan: Data on reproduction of this form would be of great interest. The transition from oviparity to viviparity apparently occurs in this region of severely cold climate. In other areas of its range, the species group occurs under much milder climatic conditions (Fig. 11). This is true of both oviparous and viviparous populations.

*Trimeresurus* is a large group of oriental pit vipers related to the American genus *Bothrops;* the latter group is not considered here, because all are apparently viviparous (Fitch, 1970), and it is likely to be a monophyletic group. *Trimeresurus* includes both terrestrial and arboreal forms, many of which are highly venomous. Modes of reproduction are known for a few species: *T. elegans, T. flavoviridis, T. monticola, T. mucrosquamatus,* and *T. tokarensis* are oviparous (Werler and Keegan, 1963; Koba, 1971; de Rooij, 1917; Pope, 1935; Nakamoto and Sawai, 1982), whereas *T. albolabris, T. gramineus, T. jerdoni, T. okinavensis, T. popeorum, T. puniceus, T. purpureomaculatus, T. stejnegeri, T. trigonocephalus,* and *T. wagleri* are viviparous (above references and Kopstein, 1938; Fitch, 1970; Stettler, 1971; Nickerson, 1974; Phelps, 1981; Reitinger, 1978). Extensive ecological and reproductive data are available for some species (Fukada, 1965).

A reconstruction of the phylogeny of *Trimeresurus* suggests that viviparity may have evolved independently many times within this group (Brattstrom, 1964). However, most inferred pathways are tenuous; the two strongest cases are small species groups, each containing oviparous and viviparous members. The first of these groups comprises the oviparous *T. flavoviridis* and *T. tokarensis* (both from Japan) and the viviparous *T. jerdoni* from eastern China and Indochina. The second group, placed within *Ovophis* by Burger (1971), contains the stout-bodied terrestrial forms *T. monticola,* an oviparous species from southeast China and Malaysia, and *T. okinavensis,* a live-bearer from the Ryukyu Islands near Japan. Hence, both cases involve a Japanese form (or forms) and a Chinese form; the difference is that in one case it is the Chinese species that is viviparous, whereas in the other case it is the Japanese (Fig. 12). Egg-guarding by the female is known in *T. monticola*, and eggs of this species are retained *in utero* for a long period prior to oviposition (Pope, 1935); this species has evolved part of the way toward viviparity.

Viviparity of the New World crotalines *Bothrops*, *Crotalus*, and *Sistrurus* (Fitch, 1970) is difficult to interpret. *Bothrops* may be derived from *Trimeresurus*, and *Crotalus* and *Sistrurus* from the "*Agkistrodon*" group (Brattstrom, 1964; Koba, 1973); in each case the ancestral group contains viviparous forms, so these taxa will not be treated as independent origins of viviparity.

The members of the genus *Vipera* are Old World in distribution, and almost all are terrestrial. *Vipera lebetina*, *V.* (formerly *Pseudocerastes*) *persica*, and *V. xanthina* are oviparous. All have fragmented head shields (Marx and Rabb, 1965) and are probably closely related to each other. *Vipera ammodytes*, *V. aspis*, *V. berus*, *V. latastei*, *V. russellii*, and *V. ursinii* are viviparous (Fitch, 1970). Both *V. lebetina* and *V. xanthina* have been claimed to be viviparous as well as oviparous (Terentev and Chernov, 1965; Mendelssohn, 1963). The following review suggests that *V. lebetina* is oviparous throughout its range but that the *V. xanthina* group does show both modes of reproduction.

The large *V. lebetina* occurs through northwestern Africa and southwestern Asia (Steward, 1971). A single report of viviparity for the entire species (Phelps, 1981) remains undocumented. Five subspecies are recognized. The African *Vipera l. mauritanica* (*V. mauritanica* of some authors) has been shown to be oviparous (Kratzer, 1968), despite earlier records to the contrary (Werner, 1930; Vogel, 1963). *Vipera l. obtusa* from the central part of the species range also is oviparous (Kratzer, 1968; Muskhelishvilli, 1971), contrary to an earlier speculation (Terentev and Chernov, 1965). *Vipera l. lebetina* is oviparous (Vogel, 1963; Kratzer, 1968; Arnold and Burton, 1978; contrary record by Petzold, 1968b), as are *V. l. schweizeri* (Schweizer, 1956; Kratzer, 1968) and *V. l. turanica* (Terentev and Chernov, 1965; Kratzer, 1968; Korneva, 1973). In summary, there are well-documented cases of oviparity in all subspecies of *V. lebetina*, and there are no authenticated cases of viviparity.

The situation is more complex in the case of the "*Vipera xanthina* group" of Asia Minor and Israel. *Vipera palaestinae* from Israel apparently is oviparous (Mendelssohn, 1963; but see Phelps, 1981), whereas *V. xanthina* from Turkey and surrounding areas is viviparous (Kratzer, 1968; Diesener, 1974; Andren and Nilson, 1976b). A closely related viper, *V. raddei* from Turkey, Iran, and central Asian parts of the USSR is viviparous (Kratzer, 1968; Darevsky, 1966; Terentev and Chernov, 1965). The oviparous *V. palaestinae* occupies a warmer and drier region than do its viviparous relatives (Fig. 12). Eggs of *Vipera palaestinae* contain advanced embryos when laid (Kochva, 1963). All three of the above species have been regarded as subspecies of *V. xanthina*, but a recent revision (Nilson and Sundberg, 1981)

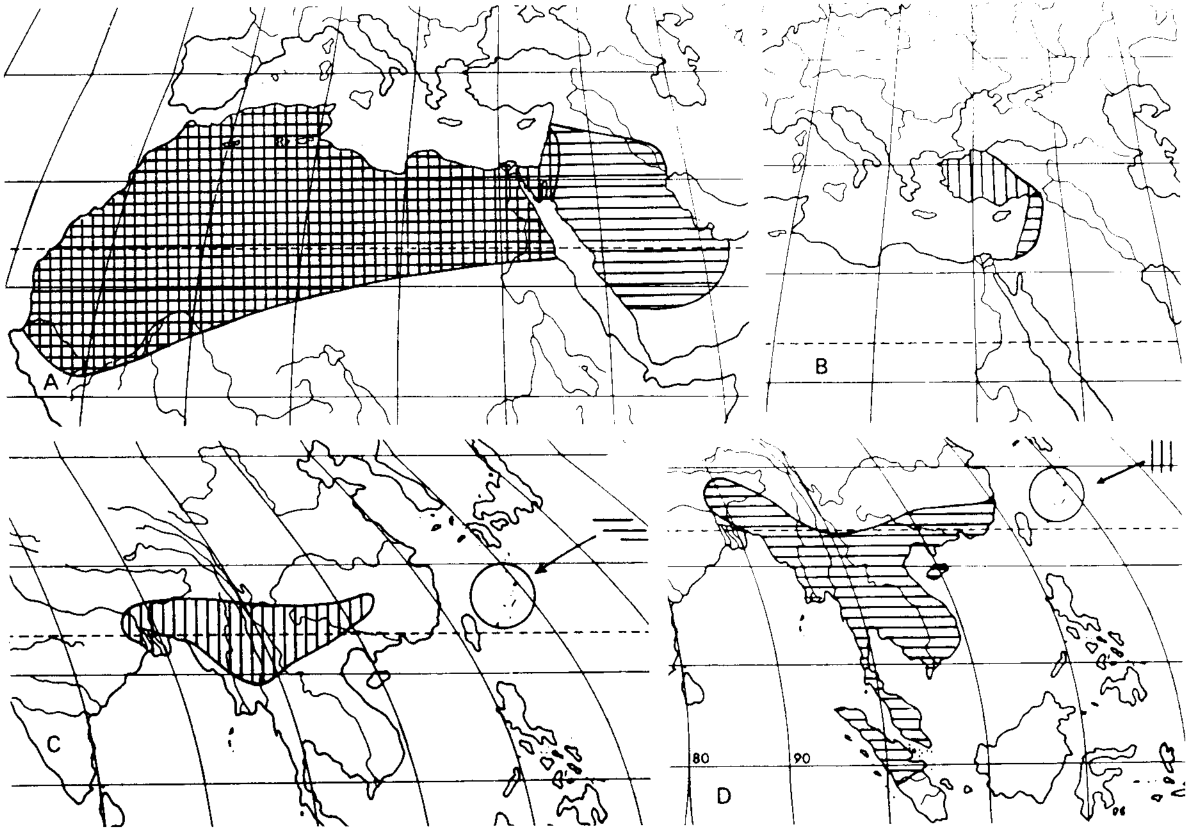

**Fig. 12.** Geographic distributions of oviparous (horizontal lines) and viviparous (vertical lines) viperid snakes within (A) the genus *Cerastes*; (B) the species *Vipera xanthina*; (C) the *Trimeresurus* "*jerdonii* group"; (D) the *Trimeresurus* "*okinavensis* group."

elevates all of them to full specific status. As might be expected from reproductive mode, *V. raddei* and *V. xanthina* are more closely related to each other than to *V. palaestinae*.

Viviparity may have evolved more than once within *Vipera*. All of the present-day oviparous forms show fragmented head shields, a "derived" character relative to the unfragmented head shields of many viviparous species (Marx and Rabb, 1965). Hence, the present-day oviparous vipers are unlikely to be ancestral to the viviparous forms. Either (1) oviparity has evolved from viviparity, or (2) viviparity in most present-day vipers evolved from the "*xanthina* group," but the viviparous forms retained the primitive feature of unfragmented head shields, whereas their oviparous progenitors evolved fragmented head shields, or (3) viviparity in most vipers has evolved from a now-extinct oviparous ancestor. The third hypothesis seems the most parsimonious and implies at least two evolutions of viviparity in *Vipera*.

Finally, at least one more origin of viviparity is suggested by a proposed phylogeny of viperid snakes (Marx and Rabb, 1965; their Fig. 46) in which the two viviparous African genera (*Atheris* and *Bitis*, Fitch, 1970) are thought to have evolved from oviparous forms.

## VII. EVALUATION OF CASE HISTORIES

### A. Frequency of Evolution of Viviparity

The preceding analysis reveals at least 95 independent origins of viviparity among the living squamate groups. Previous attempts to identify viviparous origins recognized 31 (Tinkle and Gibbons, 1977) and 38 (Shine and Bull, 1979) origins within genera, or 71 (Shine, 1981) and 75 (Blackburn, 1981) cases if all origins of viviparity, including those at the suprageneric level (i.e., where an entire genus, subfamily, or family is viviparous) are included. Reviews by Blackburn (1982, 1984, personal communication), entirely independent of the present study, have increased this total to 76 (47 in lizards, 28 in snakes, 1 in amphisbaenians), as compared to 95 (63 in lizards, 30 in snakes, 2 in amphisbaenians) in the present study. The two analyses generally agree on the lineages involved in the evolution of viviparity; many of the discrepancies are due (1) to unpublished records of reproductive bimodality and phylogeny obtained for the present study, although unavailable to Blackburn, and (2) to differences in interpretation of data on reproductive mode and phylogeny. For example, Blackburn (personal communication) argues that phylogenetic reconstructions of some taxa (e.g., *Liolaemus*, *Eremias*) are unreliable.

Although the number of independent evolutionary origins identified in the present study is much higher than revealed in previous reviews, it is likely to be well below the actual number. This reflects the conservative approach, which is coupled with inadequate information on the reproduction and phylogeny of most reptiles. However, two weaknesses of the current estimate should be noted. The number may be reduced if oviparity has often evolved from viviparity (rather than the reverse) or if available phylogenetic reconstructions are seriously in error. Nonetheless, additional information is more likely to increase than decrease the total.

Of the 95 identified origins, some are less well-documented than others. The data are least reliable in the 30 cases in which relatively distantly related species with different reproductive modes are compared. Examples are comparisons at the suprageneric level, for example, between genera (*Hemachatus* versus *Naja*) or subfamilies (Boinae versus Pythoninae). It may be that these groups are not as closely related to each other as we currently believe and that the viviparous group has inherited viviparity from an unrecognized viviparous lineage. Perhaps the best example here is the viviparous *Psammodynastes*; I have considered it an example of the evolution of viviparity because its phylogenetic affinities probably lie with oviparous colubrids rather than with any recent viviparous species.

The evidence is more reliable in the 65 instances in which congeneric species differ in reproductive mode. Most striking are the ten documented cases in which both viviparity and oviparity occur within a single species or small species-group (Table I). Only the single species *Sceloporus aeneus* was accepted as containing both oviparous and viviparous populations in a recent review (Tinkle and Gibbons, 1977), but this clearly is an underestimate. Reliable documentation of reproductive bimodality is available for at least ten such taxa, and data on a further eight species suggest that the same phenomenon occurs (Table I). It is interesting that all eight of the doubtful cases belong to genera in which viviparity is known to have evolved. This may reflect either multiple origins of viviparity in related species, or misidentification of similar species differing in reproductive mode. Further data on these taxa would be of great interest.

Many taxonomists would view mode of reproduction as a taxonomic character of sufficient importance to warrant elevation of related oviparous and viviparous forms to full specific status. Recent studies have suggested such divisions in the *Vipera xanthina* group (Nilson and Sundberg, 1981) and the *Echis carinatus* group (Cherlin, 1981). Future taxonomic studies may well divide many of the oviparous and viviparous "subspecies" listed in Table I. Nonetheless, these taxa provide exceptionally clear-cut examples of the evolution of viviparity within small groups of closely related animals. For six of the ten taxa, data are available to show that prolonged retention of eggs *in utero* is common in oviparous populations (*Helicops*, Rossman, 1973; *Lerista*, A. Greer, personal communication; *Opheodrys*, Blanchard, 1933; *Sceloporus aeneus*, Guillette, 1982a; *Saiphos*, Bustard, 1964; Greer, 1983; *Vipera*, Kochva, 1963).

Despite the many evolutionary transitions from egg-laying to live-bearing within the squamates, no single population of any species shows

## TABLE I
## Squamate Species Reported to Show Both Oviparity and Viviparity

| Species | Source |
|---|---|
| | *Records Considered Reliable* |
| *Ablepharus bivittatus*[a] | Terentev and Chernov, 1965 |
| *Echis carinatus*[a] | Kramer and Schnurrenberger, 1963 |
| *Helicops angulatus* | Rossman, 1973; da Cunha and dos Nascimento, 1981; D. A. Rossman, personal communication |
| *Lerista bougainvillei* | A. E. Greer, personal communication; Shine, personal observation |
| *Opheodrys vernalis*[b] | Blanchard, 1933 |
| *Psammophylax variabilis* | Broadley, 1977 |
| *Sceloporus aeneus* | Guillette, 1981, 1982a |
| *Saiphos equalis* | Shine and Thompson, unpublished; Greer, 1983 |
| *Sphenomorphus nigricaudus* | A. E. Greer, personal communication |
| *Vipera xanthina*[a] | Kratzer, 1968 |
| | *Records of Uncertain Validity* |
| *Amblyodipsas concolor* | Broadley, 1983 |
| *Mabuya capensis* | W. Haacke, personal communication |
| *M. carinata* | Smith, 1935; Badhuri, 1943 |
| *M. sulcata* | D. Horton, personal communication |
| *Phrynocephalus theobaldi* | Sergeev, 1940 |
| *Pseudechis guttatus* | Charles et al., 1979 |
| *Rhacodactylus leachianus* | Mertens, 1964 |
| *Sceloporus variabilis* | Werler, 1951; Fitch, 1970 |
| *Sphenomorphus pardalis* | Rankin, 1978 |
| *Typhlops diardi* | Wall, 1918; Smith, 1943 |
| | *Records That Are Probably Invalid* |
| *Aspidura drummondhayi* | Gans and Fetcho, 1982 |
| *Boa constrictor* | Hoover, 1936; Tinkle and Gibbons, 1977 |
| *Cacophis krefftii* | Cogger, 1975; Shine, 1980b |
| *Diadophis punctatus* | Ditmars, 1942; Tinkle and Gibbons, 1977 |
| *Lacerta vivipara* | Lantz, 1927; Tinkle and Gibbons, 1977 |
| *Lachesis muta* | Mole, 1924 |
| *Laticauda colubrina* | Smith, 1930; Smedley, 1931; Taylor, 1965; Fitch, 1970 |
| *Mabuya quinquetaeniata* | Fitch, 1970; Spellerberg, 1976 |
| *Python regius* | Pope, 1961 |
| *Sceloporus grammicus* | Smith, 1939 |
| *Trimeresurus okinavensis* | Fukada, 1965 |
| *Xenodermus javanicus* | Taylor, 1965 |

[a] Oviparous and viviparous subspecies elevated to full specific status by some authors.

[b] Viviparity not seen but incubation period variable and sometimes so brief (4 days) that it resembles other "viviparous" reptiles.

both oviparity and viviparity. Even when a species exhibits both modes of reproduction, the egg-layers and live-bearers inhabit different geographic areas. Facultative shifts of reproductive mode are unknown.

## B. Taxonomic Biases

The 95 identified origins of viviparity encompass all three squamate suborders, and are distributed among 20 families (Table II). A comparison of the squamate suborders shows that viviparity has arisen at least 63 times in lizards, 30 times in snakes, and two times in amphisbaenians. However, these apparent differences among suborders are due largely to different numbers of species in each group. If the data are calculated as the number of origins of viviparity per oviparous species in the suborder, lizards average one origin per 47 species, snakes one origin per 54 species, and amphisbaenians at least one origin per 40 species. [In this and subsequent calculations, species numbers are taken from the checklist of the U.S. National Fish and Wildlife Laboratory (1978); the proportion of oviparous forms in each taxa is taken from Fitch (1970), and other sources.] Chi-square analysis demonstrates that the relative frequency of evolution of viviparity does not differ significantly among the three suborders (expected = 95 origins in 4693 species = .020; d.f. = 2, $\chi^2 = 1.2$, $p > .5$). One corollary of this result is that the higher proportion of viviparous species in snakes, as compared to lizards (Tinkle and Gibbons, 1977), is not attributable to a higher frequency of the evolution of viviparity in snakes. Apparently, it reflects a greater speciation rate, or lower extinction rate, in viviparous as opposed to oviparous snakes, a phenomenon that is less pronounced in lizards.

The minimum number of separate origins of viviparity per squamate family ranges from zero to 34 (Table II). As is true in the comparison among suborders, the apparent differences among families in the frequency of evolution of viviparity are partly due to different species numbers in each family. However, even when this factor is taken into account, large differences among families remain (Table II). For example, the small family Anguidae (10 oviparous genera, 75 species) shows at least six origins of viviparity, whereas the larger Teiidae (38 genera, 230 species) is entirely oviparous. Among the lizards, the relative frequency of evolution of viviparity is highest among the anguids, skinks and cordylids, and lowest among teiids, agamids, and geckoes. Among the snakes, viviparity has arisen more frequently among vipers, boids, and elapids than among leptotyphlopids, typhlopids, or colubrids. Statistical analysis convincingly rejects the null hypothesis of equal probabilities of the evolution of viviparity (per oviparous species) in the different families of lizards and snakes ($n$ = 93 origins, 18 families, excluding cases where entire families are viviparous or have less than 20 oviparous species; $\chi^2 = 167.2$, 17 d.f., $p \ll .001$).

Similar taxonomic biases are evident at the generic level. The present

TABLE II

Minimum Estimates of the Number of Evolutionary Origins of Viviparity in Each Family of Squamate Reptiles[a]

| Suborder | Family | Number of Origins of Viviparity: Absolute Number | Number of Origins of Viviparity: Number per Oviparous Species in the Taxon |
|---|---|---|---|
| Amphisbaenia | Amphisbaenidae | 1 | 0.01 |
| | Trogonophidae | 1 | —[c] |
| Sauria | Agamidae | 2 | 0.01 |
| | Anguidae | 6 | 0.08 |
| | Chamaeleonidae | 2 | 0.03 |
| | Cordylidae | 1 | 0.03 |
| | Dibamidae | 0 | 0 |
| | Gekkonidae | 2 | 0.003 |
| | Helodermatidae | 0 | 0 |
| | Iguanidae | 12 | 0.02 |
| | Lacertidae | 3 | 0.01 |
| | Pygopodidae | 0 | 0 |
| | Scincidae | 34 | 0.05 |
| | Teiidae | 0 | 0 |
| | Varanidae | 0 | 0 |
| | Xantusiidae | 1 | —[b] |
| Serpentes | Aniliidae, Uropeltidae | 1 | —[b] |
| | Acrochordidae | 1 | —[b] |
| | Typhlopidae | 1 | 0.01 |
| | Boidae | 1 | 0.03 |
| | Tropidophiidae | 1 | —[b] |
| | Colubridae | 14 | 0.01 |
| | Elapidae | 3 | 0.02 |
| | Leptotyphlopidae | 0 | 0 |
| | Viperidae | 8 | 0.27 |

[a] Entirely viviparous families omitted, unless phylogenetic data suggest an independent origin of viviparity in ancestors of that group.

[b] Cannot calculate: all present day representatives are viviparous.

[c] Cannot calculate: reproductive data missing for most species.

review has identified 65 origins of viviparity *within* a genus among the 619 squamate genera containing oviparous species, so that the probability of viviparity evolving within any one genus is 65 in 619, or 0.10. The probability of two origins occurring by chance within a single genus is $0.10^2$, or 0.01. Hence, multiple origins of viviparity within a single genus should be extremely rare. In practice, the data reveal that more than half of the within-genus origins (36 of 65) occur in genera with multiple origins of viviparity. Thirteen genera account for these 36 origins. This figure probably underestimates multiple origins, because they are difficult to detect without strong phylogenetic data. Even allowing for the fact that many genera would be unlikely to evolve viviparity because they contain only one or two species, this concentration of the evolution of viviparity within a few genera is certainly nonrandom.

## C. Evaluation of Hypotheses

### 1. QUESTIONS AND CONCEPTS

The present-day distributions, morphologies, ecologies, and behaviors of the species reviewed above may provide some indication of the conditions under which viviparity evolved. Any selective pressure important in the evolution of viviparity could be revealed at any or all of the following three taxonomic levels:

1. Viviparity has evolved more often in some squamate *families* than in others. Do the former groups show the characteristics predicted by theory, whereas the other families do not?
2. Do the oviparous members of the *genera* in which viviparity has evolved, show the theoretically predicted characteristics to a greater degree than do other squamate genera?
3. Do the oviparous and viviparous forms *within a genus* (or species) differ from each other in the characteristics predicted by theory?

Any trends seen at the familial or generic level (categories 1 and 2) are likely to reflect factors that protoadapt a species to the evolution of viviparity. They will be characteristics shared by all or most members of a phylogenetic lineage. Of the hypotheses reviewed earlier, those concerning species characteristics (e.g., defensive ability, arboreal, aquatic, fossorial, or secretive habits; egg-guarding; physiological constraints) are likely to belong to this category, because closely related species are unlikely to differ markedly in these respects.

In contrast, consistent differences among oviparous and viviparous congeners (category 3) are likely to reflect factors that are directly involved in the transition from oviparity to viviparity. Hypothesized environmental influences (e.g., climate, habitat) may vary among related species and, hence, may be involved at this level. The comparison among closely related oviparous and viviparous species is a powerful one, because of the general similarity of the species being compared. This similarity controls for many variables unrelated to reproductive mode. However, it may be difficult to distinguish between intraspecific differences that have favored the evolution of viviparity and the differences that have arisen subsequent to the acquisition of viviparity. The change from oviparity to viviparity may in itself select for a suite of related adaptations, for example, changes in thermoregulatory strategy (Guillette et al., 1980), adoption of secretive habits by gravid females, invasion of colder areas, even an increase in the size of offspring (Shine, 1978). Year-to-year variance in egg survivorship is likely to be decreased, thus affecting selective pressures on optimal reproductive effort and age at sexual maturity (Murphy, 1968). Differences in size of offspring and reproductive seasonality among oviparous and viviparous subspecies of *Sceloporus aeneus* (Guillette, 1982a), confirm that the evolution of viviparity may be accompanied by other changes.

The following analysis examines whether the characteristics predicted by theory are exhibited by the taxa in which viviparity has arisen; either by all or most species within a family or genus or by the viviparous as opposed to the oviparous species.

## 2. ANALYSIS AT THE FAMILIAL LEVEL

Each squamate family containing more than 20 oviparous species was rated with respect to whether the majority thereof exhibits the characteristics predicted by theory (Table III). Hypotheses concerning environmental unpredictability, intensities of egg predation, frequency of reproduction (single versus multiple clutches), and thermoregulatory mode could not be tested, either because of difficulty in framing specific predictions from these ideas or because of lack of the necessary data. The number of characters scored as positive for each family ranged from zero to five. This score was not correlated with the relative frequency at which viviparity had evolved (combining data from Tables II and III, $n = 18$, $r^2 = 0.04$, n.s.). Indeed the combined score for the nine families with the highest frequency of viviparous origins (20) was almost the same as that for the nine families with fewest origins [$n = 18$, Table III].

Some trends are apparent from an analysis of individual factors. Most taxa tend to occupy hot rather than cold climates, as would be expected from latitudinal gradients in reptilian species diversity. Very few families include primarily aquatic, arboreal, or slow-moving species or forms that are largely restricted to very dry or very moist soils (Table III). Maternal care occurs in several of the families, especially among snakes, but is not clearly correlated with the evolution of viviparity at this level of analysis.

Within snakes, viviparity may have arisen most often in large and venomous species (Table III). The relative frequency of viviparous origins is highest in the Boidae, Viperidae, and Elapidae, is intermediate in the primarily nonvenomous Colubridae, and is lowest in the small fossorial Leptotyphlopidae and Typhlopidae (Table II). Although venomous species comprise fewer than one-fourth of the colubrid genera (Underwood, 1979), they represent six of the 14 identified origins of viviparity within the Colubridae. Overall, viviparity has arisen at least 25 times within the "advanced snakes"; eight of these origins occurred within the approximately 170 nonvenomous oviparous genera of the Colubridae (percentage of ori-

## TABLE III

## Degree to Which Characteristics Predicted by Theory Are Displayed by Different Squamate Families[a]

| | | Characteristics Shown by Majority of Oviparous Species in the Family | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Suborder | Family | Cold Climate | Hot Climate | Moist Soil | Dry Soil | Large or Venomous | Slow-Moving or "Ambush" | Fossorial or Secretive | Maternal Care[b] | Aquatic | Arboreal | Total Number |
| 1. Amphisbaenia | Amphisbaenidae | | X | | | | | X | | | | 2 |
| 1A. | Trosonophidae | | X | | | | | X | | | | |
| 2. Sauria | Agamidae | | X | | X | | | | | | | 2 |
| 3. | Anguidae | | | X | | | | X | X | | | 3 |
| 4. | Chamaeleonidae | | X | | | | X | | | | X | 3 |
| 5. | Cordylidae | | | | | | | | | | | 0 |
| 6. | Gekkonidae | | | | | | | | | | X | 1 |
| 7. | Iguanidae | | | | | | | | | | | 0 |
| 8. | Lacertidae | X | | | | | | | | | | 1 |
| 9. | Pygopodidae | | X | | X | | | X | | | | 3 |
| 10. | Scincidae | | X | | | | | | X | | | 2 |
| 11. | Teiidae | | X | | | | | | ? | | | 2 |
| 12. | Varanidae | | X | | | X | | | | | | 2 |
| 13. Serpentes | Boidae | | X | | | X | X | | X | | X | 5 |
| 14. | Colubridae | | | | | | | | X | | | 1 |
| 15. | Elapidae | | X | | | X | | | X | | | 3 |
| 16. | Leptotyphlopidae | | X | | | | | X | X | | | 3 |
| 17. | Typhlopidae | | X | | | | | X | ? | | | 3 |
| 18. | Viperidae | | | | | X | X | | X | | | 3 |
| | Total Number | 1 | 12 | 1 | 2 | 4 | 3 | 6 | 9 | 0 | 3 | 41 |
| | Number in 9 families with most origins of viviparity[c] | 0 | 4 | 1 | 0 | 3 | 3 | 1 | 6 | 0 | 2 | 20 |

[a] *Note:* Families with less than 20 oviparous species were excluded, although viviparity has evolved in at least four of the groups (trogonophids; xantusiids; acrochordids; aniliids, uropeltids).

[b] Maternal care scored as positive if known in any members of the Family. See Fitch (1970) and Shine and Bull (1979) for references.

[c] Number of characteristics shown by the 50% of families ($n = 9$) with the highest relative frequencies of the evolution of viviparity.

gins among genera is 4.7%), six origins occurred among the 70 venomous oviparous colubrid genera (8.6%), and the remaining eleven occurred among the 43 highly venomous oviparous elapids and vipers (25.6%). These data enable rejection of the null hypothesis that the relative frequency of evolution of viviparity is the same in all families of "advanced snakes" ($\chi^2 = 115.3$, 2 d.f., $p \ll .001$). Also, the frequency with which viviparity has evolved in venomous snakes (17 origins in 113 genera) is significantly higher than in nonvenomous snakes (13 origins in 170 genera; $\chi^2 = 4.3$, 1 d.f., $p < .05$). These data suggest that possession of potent venom acts as a major protoadaptation to facilitate the evolution of viviparity in snakes.

Data on lizards do not reveal such clear ecological or morphological differences among families with different frequencies of the evolution of viviparity. Viviparity has evolved most often in anguids and scincids, and least often in teiids, varanids, pygopodids, gekkonids, and agamids (Table II). Although no obvious trend emerges from Table III, it may be significant that many anguids and scincids are secretive animals adapted to moist, cool habitats. In contrast, the other taxa (especially agamids, varanids, teiids, and pygopodids) tend to predominate in hot dry areas. The lizard families with an intermediate frequency of viviparous origins (Iguanidae, Lacertidae, Cordylidae, Chamaeleonidae) appear to be intermediate on this habitat continuum.

## 3. ANALYSIS AT THE GENERIC LEVEL

Factors that protoadapt a species for the evolution of viviparity also may be looked for at the level of the genus (or group of genera) in which viviparity has arisen. Many of these groups show the characteristics predicted by theory (Table IV), but the problem is to determine whether the frequency of any factor among the groups is higher than would be expected by chance (i.e., from a random sample of squamate genera). Such "expected" frequencies from a sample of 1077 squamate species are given by Shine and Bull (1979; their Table 3). Analysis indicates that most characteristics tested are found about as frequently in the taxa with viviparous relatives as in Shine and Bull's (1979) "random" sample. The proportion of arboreal taxa is 0.14 in Table IV and 0.10 in the "random" sample; the difference is not significant ($\chi^2 = 0.06$, 1 d.f., n.s). Corresponding figures are 0.05 and 0.05 for aquatic taxa ($\chi^2 = 0.0$, 1 d.f., n.s.), 0.20 and 0.18 for taxa inhabiting dry areas ($\chi^2 = 0.3$, 1 d.f., n.s.), and 0.16 and 0.12 for taxa in areas of moist soil ($\chi^2 = 0.9$, 1 d.f., n.s.). In contrast to the theoretical prediction, the proportion of taxa inhabiting "cold" climates is *lower* among the groups in Table IV (.27) than among squamates in general (0.44), a difference that is statistically significant ($\chi^2 = 9.3$, 1 d.f., $p < 0.01$) but is probably due to the inclusion of viviparous species in the "random" sample of Shine and Bull (1979). Considerably more genera were found in hot (0.43) rather than cold

# TABLE IV

## Assessment of the Degree to Which Characteristics Predicted by Theory Are Displayed by the Closest Identifiable Oviparous Relatives of Squamate Species in Which Viviparity Has Evolved[a]

| Taxon in Which Viviparity Has Evolved | | | Characteristics Shown by Most of the Oviparous Species in the Taxon | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Suborder | Family | Group | Cold Climate | Hot Climate | Moist Soil | Dry Soil | Large or Venomous | Slow-Moving or "Ambush" | Fossorial or Secretive | Maternal Care[b] | Aquatic | Arboreal |
| 1. Amphisbaenia | Amphisbaenidae | *Monopeltis* group | | X | | | | | X | | | |
| 2. Sauria | Agamidae | *Cophotis* | X | | X | | | X | | | | X |
| 3. | | *Phrynocephalus* | | | | X | | | | | | |
| 4. | Anguidae | *Anguis* group | | | | | | | X | X | | |
| 5. | | *Diploglossus* | | X | X | | | | X | X | | |
| 6. | | *Gerrhonotus* | X | | | X | | | | | | |
| 7. | | *Barisia* group | X | | | X | | | | X | | |
| 8. | Chamaeleonidae | *C. bitaeniatus* group | | X | | | | X | | | | X |
| 9. | | "*C. pumilis*" group | | | | | | X | | | | X |
| 10. | Cordylidae | Cordylinae | | | | | | | | | | |
| 11. | Gekkonidae | New Zealand genera | | X | | | | | | | | |
| 12. | | *Rhacodactylus* | | X | | | | | | | | X |
| 13. | Iguanidae | *Corytophanes* | | X | X | | | X | | | | X |
| 14. | | *Ctenoblepharis* | | | | X | | | X | | | |
| 15. | | *Liolaemus*, group A | X | | | | | | | | | |
| 16. | | *Liolaemus*, group B | X | | | | | | | | | |
| 17. | | *Phrynosoma* | | X | | X | | X | | | | |
| 18. | | *Phymaturus* group | | X | X | | | | | | | |
| 19. | | *Sceloporus aeneus* | X | | X | | | | | | | |
| 20. | | *S. goldmani* | X | | | | | | | | | |
| 21. | | *S. grammicus* group | X | | | | | | | | | X |
| 22. | | *S. formosus* group | | X | | X | | | | | | |
| 23. | Lacertidae | *Eremias multiocellata* | X | | | X | | | | | | |
| 24. | | *E. przewalskii* | X | | | X | | | | | | |
| 25. | | *Lacerta* | X | | | | | | | | | |

(Continued)

## TABLE IV (*Continued*)

| Taxon in Which Viviparity Has Evolved | | | Characteristics Shown by Most of the Oviparous Species in the Taxon | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Suborder | Family | Group | Cold Climate | Hot Climate | Moist Soil | Dry Soil | Large or Venomous | Slow-Moving or "Ambush" | Fossorial or Secretive | Maternal Care[b] | Aquatic | Arboreal |
| 26. | Scincidae | *Scelotes* group | | X | | | | | X | | | |
| 27. | | *Eumeces ochoterenai* group | | | | | | | | X | | |
| 28. | | *E. lynxe* | | | | | | | | X | | |
| 29. | | *Scincus* | | X | | X | | | X | | | |
| 30. | | *Hemiergis* group | | | | | | | X | | | |
| 31. | | *Ablepharus bivittatus* | X | | | | | | | | | |
| 32. | | *Anomalopus* | | | | | | | X | | | |
| 33. | | *Leiolopisma entrecasteauxii* group | X | | | | | | X | | | |
| 34. | | *L. coventryi* group | X | | | | | | X | | | |
| 35. | | *L. palfreymani* group | | | | | | | | | | |
| 36. | | *Lerista bougainvillei* | X | | | X | | | X | | | |
| 37. | | *Lerista microtis* group | | X | | X | | | X | | | |
| 38. | | *Lipinia* | | X | | | | | | | | X |
| 39. | | *Lobulia* | X | | | | | | | | | |
| 40. | | *Lygosoma laeviceps* group | | | | | | | X | | | |
| 41. | | *L. tanae* group | | | | | | | X | | | |
| 42. | | *Mabuya capensis* | | | | | | | | | | |
| 43. | | *M. sulcata* | | | | | | | | | | |
| 44. | | *M. aurata* group | | | | | | | | | | |
| 45. | | *M. brevicollis* group | | X | | | | | | | | |
| 46. | | *M. bayoni* group | | X | | | | | | | | |
| 47. | | *M. multifasciata* group | | | | | | | | | | |
| 48. | | *Prasinohaema* | X | | | | | | | | | X |
| 49. | | *Scincella* | | | | | | | X | | | |
| 50. | | *Saiphos equalis* | | | X | | | | X | | | |
| 51. | | *Sphenomorphus fragilis* group | | X | | | | | X | | | |
| 52. | | *S. fasciatus* group | | X | | | | | X | | | |
| 53. | | *S. nigricaudus* | | X | | | | | X | | | |

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 54. |  |  | *S. formosensis* group |  |  |  |  |  |  |  |  |  |  |
| 55. |  |  | *S. concinnatus* group |  | X |  |  |  |  |  |  |  |  |
| 56. |  |  | *Tribolonotus* |  | X | X |  |  |  | X |  |  |  |
| 57. | Serpentes | Boidae |  |  | X |  |  | X | X |  | X |  |  |
| 58. |  | Colubridae | *Ahaetulla* group |  | X |  |  | X |  |  |  |  | X |
| 59. |  |  | *Tachymenis* group |  |  |  |  | X |  |  |  |  | X |
| 60. |  |  | *Conopsis* group |  | X |  | X |  |  | X |  |  |  |
| 61. |  |  | *Amplorhinus* group |  | X | X |  | X |  |  |  |  |  |
| 62. |  |  | *Aparallactus* | X |  |  |  | X |  | X |  |  |  |
| 63. |  |  | *Coronella* | X |  |  |  |  |  |  |  |  |  |
| 64. |  |  | *Elaphe* | X |  |  |  | X |  |  | X |  | X |
| 65. |  |  | *Grayia* |  | X | X |  |  |  |  |  | X |  |
| 66. |  |  | *Helicops angulatus* |  | X | X |  |  |  |  |  | X |  |
| 67. |  |  | *Helicops* spp. |  | X | X |  |  |  |  |  | X |  |
| 68. |  |  | *Opheodrys vernalis* | X |  |  |  |  |  |  | ? |  |  |
| 69. |  |  | *Psammophylax variabilis* | X |  |  |  | X | X |  | X |  |  |
| 70. |  |  | *Sinonatrix* |  | X | X |  | X |  |  | X | X |  |
| 71. |  | Elapidae | *Hemachatus* group |  |  |  |  | X |  |  | X |  |  |
| 72. |  |  | *Pseudechis* |  | X |  |  | X |  |  |  |  |  |
| 73. |  |  | Australian spp. |  |  |  | X | X |  |  |  |  |  |
| 74. |  | Typhlopidae | *Typhlops* |  | X |  |  |  |  | X | ? |  |  |
| 75. |  | Viperidae | "*Agkistrodon*" |  | X | X |  | X | X |  | X |  |  |
| 76. |  |  | *Cerastes* |  | X |  | X | X | X |  |  |  |  |
| 77. |  |  | *Echis* |  | X |  | X | X | X |  |  |  |  |
| 78. |  |  | *Trimeresurus jerdonii* group |  |  |  |  | X | X |  |  |  |  |
| 79. |  |  | *T. okinavenis* group |  | X |  |  | X | X |  | X |  |  |
| 80. |  |  | *Vipera xanthina* group |  |  |  | X | X | X |  |  |  |  |
| 81. |  |  | *Vipera* spp. |  |  |  |  | X | X |  |  |  |  |
|  |  |  | Totals (out of 82) | 22 | 36 | 23 | 16 | 17 | 14 | 23 | 14 | 4 | 11 |
|  |  |  | Proportions | 0.27 | 0.44 | 0.28 | 0.20 | 0.21 | 0.17 | 0.28 | 0.17 | 0.05 | 0.13 |

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[a] *Note:* Fourteen of the evolutionary origins of viviparity identified in this paper are omitted from the Table because there are no living oviparous species closely related to the present-day live-bearers. Hence, characteristics of these oviparous forms cannot be determined. The groups include one amphisbaenian lineage (ancestral trogonophids); two anguids (*Ophiodes* and *Celestes* ancestors); two iguanid lineages (*Sceloporus torquatus* and *Vilcunia* ancestors); three scincid lineages (*Brachymeles*, etc.; *Corucia–Egernia–Tiliqua; Isopachys*); the ancestral xantusiids; the ancestral tropidophiids; the ancestral aniliids and uropeltids; the ancestral acrochordids; the ancestral *Psammodynastes;* and the viperid lineage leading to *Atheris* and *Bitis*.

[b] Taxon counted as positive for maternal care if this behavior has been recorded in any of its component species. Characteristics predicted by theory but not tested are: high rates of nest predation; temperate climate; heliothermy.

(0.27) areas, probably reflecting the higher numbers of reptilian species in warm climates.

Maternal care is almost twice as common (0.7) among the oviparous relatives of live-bearers than among a sample of 231 oviparous squamate genera (Shine and Bull, 1979), although the difference falls short of statistical significance when calculated in this way ($\chi^2$ = 3.5, 1 d.f., $p \simeq 0.06$). However, closer analysis confirms the association between maternal care and the evolution of viviparity. The probability of viviparity evolving *within* a genus of squamates (i.e., a genus with both oviparous and viviparous members) is 65 in 619 or 10%. The probability of viviparity evolving in a genus in which brooding also has been recorded is 12 in 31 (39%). The difference is significant ($\chi^2$ = 25.7, 1 d.f., $p < .001$). Also, there are many brooding species in genera that are believed to be the closest oviparous relatives of viviparous genera (e.g., *Ophisaurus, Naja, Python*).

No published estimates of expected frequencies are available for the other characteristics listed in Table IV, but the observed frequencies of fossoriality (0.28), large body size and/or venomous capacity (0.21), and nondependence on speed (0.17) seem to be higher than one might expect among a random sample of squamates. However, it is difficult in these cases to distinguish an ecological bias from a taxonomic one. For example, 16 of 23 fossorial genera are scincid lizards, and seven of the 14 genera containing species that do not depend on speed for feeding or for escape from predation are vipers. The high proportion of venomous taxa in Table IV reflects the high frequency of viviparous origins in venomous snakes.

## 4. ANALYSIS AT THE SPECIES LEVEL

The preceding sections have searched for protoadaptations that result in viviparity evolving more often in certain taxa than in others. However, the selective forces actually driving the transition from oviparity to viviparity may best be investigated by looking for consistent differences between closely related oviparous and viviparous species. Such differences are here examined with respect to hot or cold climates, moist or dry soils, invulnerability to predation, nondependence on speed, and fossorial, secretive, aquatic, or arboreal habits. The prediction that maternal care favors the evolution of viviparity cannot be tested by a comparison of oviparous and viviparous forms, because maternal egg-guarding is impossible for a live-bearer. The prediction concerning rates of nest predation cannot be tested because of insufficient data.

An immediate problem is to decide on the criteria by which a prediction can be considered supported. With regard to the "cold-climate" hypothesis, for example, is the prediction confirmed only (1) if *all* live-bearers occupy cooler habitats than *all* egg-layers, (2) if live-bearers *tend* to be in cooler areas, or (3) if the species inhabiting the coldest climate is viviparous? The decision is difficult, because the only direct prediction from theory is that viviparity evolved in the coldest part of the geographic range occupied by the taxon *at that time.* The pattern may well have been obscured by subsequent speciation and shifts in distribution, and possibly even by reversals in reproductive mode.

Table V presents the results of an analysis of the viviparous origins with respect to the three criteria previously given for the "cold-climate" hypothesis. Of the 95 squamate taxa in which viviparity has evolved, 35 cases are accompanied by such poor data, or have apparently been followed by such extensive speciation, that they do not permit any comparison among the climates occupied by live-bearers and by egg-layers. In a further seven cases, the available data do not reveal any clear differences between oviparous and viviparous forms. Most of the remaining 53 cases show a strong bias toward viviparous species being found in colder climates. The most stringent criterion (all live-bearers in colder areas than all egg-layers) is met in 40 of the 53 taxa (74%), whereas the least stringent (the single coldest climate is occupied by a live-bearer) holds in 48 cases (91%). The similarity of these results using different criteria reflects the high proportion of groups in Table V that contain only a single viviparous species or subspecies and for which the different criteria yield identical results. Only in two cases do the data negate the prediction that viviparous species occur in colder climates; both cases involve the scincid genus *Lygosoma,* for which the live-bearers occupy hotter, drier climates than their congeners. Overall, the bias toward viviparity in cold climates is very strong. Using the most stringent criterion (all live-bearers occupy colder climates than all related egg-layers), and treating the seven cases lacking clear climatic differences as definite exceptions (i.e., live-bearers assumed to be in warmer areas), the observed bias toward viviparity in cold (39 of 60 cases) still differs significantly from the null hypothesis of 50% ($\chi^2 = 5.4$, 1 d.f., $p < .05$). An independent review of viviparous origins by Blackburn (1982, and personal communication) also concluded that most origins had occurred in "cold" climates.

Although quantitative analysis is difficult, the data in Table V offer little support for the generality of alternative hypotheses on environmental conditions that favor the evolution of viviparity. The strong association among viviparous taxa and unusually cold climates (Table V) in itself casts doubt on the generality of other hypotheses. This result is certainly inconsistent with the hypothesis that viviparity commonly evolves in hot climates or "unpredictable" environments with only a slight bias toward cold.

However, the result is consistent with the idea that single clutching is an important protoadaptation for viviparity; reproductive frequency is likely to be lower in cooler climates (Fitch, 1970). A problem with this hypothesis is the lack of data on reproductive frequencies for almost any of the taxa listed in Table V; available information would suggest that double clutching is likely to be rare, even in oviparous forms (e.g., Fitch, 1970). This simply may reflect inadequacies of the data (Tinkle and Gibbons, 1977).

# TABLE V

## Factors Predicted to Favor the Evolution of Viviparity: A Comparison of Closely Related Oviparous and Viviparous Reptiles

| Taxon in Which Viviparity Has Evolved | | | Characteristics of Viviparous (VP) Forms Compared to Oviparous (OP) Forms | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Colder Climates[a,b] | | | | | | | | | | |
| Suborder | Family | Group | All VP Colder Than All OP | Single Coldest Is VP | Most VP Colder Than Most OP | Hotter Climates | Moister Soil | Drier Soil | Larger or More Formidable | More Slow-Moving | More Fossorial | More Aquatic | More Arboreal |
| 1. Sauria | Agamidae | *Cophotis* | X | X | X | | | | | | | | |
| 2. | | *Phrynocephalus* | X | X | X | | | | | | | | |
| 3. | Anguidae | *Anguis* group | X | X | X | | | | | | | | |
| 4. | | *Gerrhonotus* | X | X | X | | X | | | | | | |
| 5. | Chamaeleonidae | *C. bitaeniatus* group | X | X | X | | | | | | | | |
| 6. | | "*C. pumilis*" group | X | X | X | | | | | | | | |
| 7. | Cordylidae | Cordylinae | NO | X | ? | | | | | | ? | | |
| 8. | Gekkonidae | New Zealand genera | X | X | X | | | | | | | | |
| 9. | Iguanidae | *Corytophanes* | X | X | X | | | | | | | | |
| 10. | | *Ctenoblepharis* | ? | X | ? | | | | | | | | |
| 11. | | *Liolaemus*, group A | NO | X | X | | | | | | | | |
| 12. | | *Liolaemus*, group B | NO | X | X | | | | | | | | |
| 13. | | *Phrynosoma* | X | X | X | | | | | | | | |
| 14. | | *Phymaturus* group | X | X | X | | | | | | | | |
| 15. | | *Sceloporus aeneus* | X | X | X | | | | | | | | |
| 16. | | *S. goldmani* | X | X | X | | | X | | | | | |
| 17. | | *S. grammicus* group | NO | X | ? | | X | | | | | | X |
| 18. | | *S. formosus* group | X | X | X | | X | | | | | | |
| 19. | Lacertidae | *Eremias multiocellata* group | ? | ? | X | | | X | | | | | |
| 20. | | *E. przewalskii* | ? | ? | X | | | X | | | | | |
| 21. | | *Lacerta* | X | X | X | | | | | | | | |
| 22. | Scincidae | *Eumeces ochoterenai* group | X | X | X | | | | | | | | |
| 23. | | *E. lynxe* | X | X | X | | | | | | | | |
| 24. | | *Ablepharus bivittatus* | X | X | X | | | | | | | | |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 25. | | | *Anomalopus* | X | X | X | | | | | | | | |
| 26. | | | *Leiolopisma entrecasteauxii* group | X | X | X | | | | | | NO | | |
| 27. | | | *L. coventryi* group | X | X | X | | | | | | | | |
| 28. | | | *L. palfreymani* group | X | X | X | | | | | | | | |
| 29. | | | *Lerista bougainvillei* | X | X | X | | | | | | | | |
| 30. | | | *L. microtis* group | X | X | X | | X | | | | | | |
| 31. | | | *Lobulia* | ? | X | ? | | | | | | | | X |
| 32. | | | *Lygosoma laeviceps* group | NO | NO | NO | X | | X | | | | | |
| 33. | | | *L. tanae* group | NO | NO | NO | X | | X | | | | | |
| 34. | | | *Mabuya brevicollis* group | X | X | X | | | | | | | | |
| 35. | | | *M. bayoni* group | NO | X | X | | | | | | | | |
| 36. | | | *Prasinohaema* | X | X | X | | | | | | | | |
| 37. | | | *Scincella* | NO | NO | X | | | | | | | | |
| 38. | | | *Saiphos equalis* | X | X | X | | | | | | | | |
| 39. | | | *Sphenomorphus fasciatus* group | X | X | X | | | | | | | | ? |
| 40. | | | *S. concinnatus* group | X | X | X | | | | | | | | |
| 41. | Serpentes | Colubridae | *Tachymenis* group | X | X | | X | | | | | | | |
| 42. | | | *Conopsis* group | X | X | X | | | | | | | | |
| 43. | | | *Amplorhinus* group | X | X | X | | ? | | ? | | | ? | |
| 44. | | | *Coronella* | X | X | X | | | | | | | | |
| 45. | | | *Elaphe* | NO | NO | X | | X | | | | | X | |
| 46. | | | *Opheodrys vernalis* | X | X | X | | | | | | | | |
| 47. | | | *Psammophylax variabilis* | X | X | X | | | | | ? | | | |
| 48. | | | *Sinonatrix* | X | X | X | | | | | | | | |
| 49. | | Elapidae | *Hemachatus* group | X | X | X | | | | | | | | |
| 50. | | | *Pseudechis* | X | X | X | | X | | | | | | |
| 51. | | Viperidae | *Agkistrodon* | X | X | X | | | | | | | | |
| 52. | | | *Echis carinatus* | ? | X | ? | | | | | | | | |
| 53. | | | *Vipera xanthina* | X | X | X | | X | | | | | | |
| | | | Total Number (out of 54) | 40 | 48 | 47 | 2 | 7 | 5 | 0 | 0 | 0 | 1 | 2 |
| | | | Proportion | 0.74 | 0.89 | 0.87 | 0.03 | 0.13 | 0.09 | 0 | 0 | 0 | 0.02 | 0.04 |

[a] Three alternative criteria for "cold climate" are explained in text.

[b] Taxa omitted from this analysis: (1) Insufficient data to judge climatic or other differences: All fourteen taxa omitted from Table IV, plus taxa represented by the following numbers in that Table: 1, 5, 7, 12, 26, 29, 30, 38, 43, 44, 47, 56, 57, 58, 65, 66, 67, 73, 74, 81. (2) Available data show no obvious climatic or other differences: Taxa represented by the following numbers in Table IV: 51, 53, 54, 62, 76, 78, 79.

Another objection to the clutch-frequency hypothesis is the observation that many of the viviparous forms in Table V occur in severely cold regions; the hypothesis would predict the evolution of viviparity in regions slightly too cool for double clutching, and these environments probably would be relatively mild and temperate rather than severely cold ones. Nonetheless, the data do not falsify the clutch-frequency hypothesis.

The number of taxa fitting the predictions that viviparous forms predominate in areas of wetter soil (7, or 13%) or drier soil (5, or 9%) are much lower than the number of taxa fitting the cold-climate trend. The cases in which live-bearers are found in more mesic areas all involve taxa for which the live-bearers are also in cooler areas and may reflect a correlation between temperature and moisture rather than an independent effect of moisture (as suggested by Guillette et al., 1980).

There are no substantial data in support of the predictions that viviparous species are likely to be more formidable (large or venomous), more slow-moving, or more fossorial or secretive (Table V). One of the viviparous cordyline genera *Chamaesaura* is elongate but not truly fossorial; the oviparous cordylines have normal-sized limbs. The opposite trend is seen in Australian *Leiolopisma*, in which the oviparous "*baudini* group" are more elongate and fossorial than their viviparous relatives. The prediction that viviparous species rely more on crypsis than on speed to escape predation may hold for the slow-moving viviparous *Psammophylax variabilis;* the oviparous *P. rhombeatus* is more active (FitzSimons, 1962). However, no data are available on motor patterns of the oviparous subspecies of *P. variabilis*.

The association of aquatic habits and viviparity is strongly confirmed for *Elaphe rufodorsata*, but the species inhabits small streams rather than large bodies of water; hence, females would not be faced with a long migration to land for egg-laying. Thus, *E. rufodorsata* is not aquatic in the manner envisaged in Neill's (1964) hypothesis; it is probably more in accord with the "moister soil" prediction (Sowerby, 1930). A greater tendency toward arboreality in viviparous forms is evident within *Lobulia*, the *Sceloporus* "*grammicus* group," and perhaps the *Sphenomorphus* "*fasciatus* group" (of 5 oviparous and 3 viviparous members, all are fossorial except the arboreal viviparous *S. tenuis* and perhaps *S. murrayi*).

The prediction that viviparous species will be more heliothermic than their oviparous relatives is not tested in Table V, because the necessary detailed data are lacking for most groups. However, data on six groups suggest that this prediction may often be verified: viviparous species are more diurnal and heliothermic than their oviparous relatives (*Coronella*, Steward, 1971; *Hemachatus*, FitzSimons, 1962; *Anguis*, Schmidt and Inger, 1957; *Naultinus*, Werner and Whitaker, 1978; *Pseudechis*, Cogger, 1975; Shine, 1979; *Leiolopisma entrecasteauxii*, Cogger, 1975; Shine, 1980a). In the last four taxa listed, the data indicate that the gravid viviparous females are most clearly heliothermic; presumably, basking is prolonged in order to accelerate embryonic development. Interpretation of this thermoregulatory difference among oviparous and viviparous relatives is difficult; three possibilities are that (1) heliothermy favored the evolution of viviparity, that (2) heliothermy evolved as an adaptation to viviparity, and that (3) heliothermy is an adaptation to the cooler climates occupied by the viviparous members of all these taxa. Similarly, a tendency for arboreality in viviparous sceloporine lizards may have evolved for thermoregulatory enhancement (Guillette et al., 1980). Undoubtedly, the oviparous and viviparous relatives listed in Table V exhibit many ecological differences not discerned in the present analysis; the documentation of such differences is an important task, but it is a task for biologists with first-hand knowledge of the relevant group.

## VIII. CONCLUSIONS

A summary of hypotheses, predictions, and tests of predictions on reptilian viviparity (Table VI) reveals a complex picture. The "cold-climate" hypothesis has strong empirical support, in that "recently evolved" viviparous species occur more consistently in cooler climates than do their oviparous relatives. Weaker evidence for the role of cold climates also comes from the present-day distribution of viviparous species (e.g., Weekes, 1935; Sergeev, 1940) and from a tendency for recently evolved viviparous species to inhabit climates that are subjectively judged as "cold" (Shine and Bull, 1979; Blackburn, 1982). Although the hypothesis that viviparity evolves in cold areas is supported, the exact nature of the selective force remains unclear. Several alternative versions of the "cold-climate" hypothesis have been proposed (Shine and Bull, 1979), and reproductive frequency also correlates with this factor.

Cold climates seem to have been the most important single selective agent favoring viviparity, but it is equally obvious that not all cases are explicable by this single force. For example, the origins of viviparity in *Lygosoma, Cerastes, Sphenomorphus fragilis,* and *S. nigricaudus* are difficult to reconcile with the "cold-climate" hypothesis. Other hypotheses on environmental influences either have not been tested (e.g., nest predation) or are unlikely to have general importance (hot climates, unpredictability, soil moisture).

Among factors that protoadapt a taxonomic group to evolve viviparity, the most important may be venom in snakes and maternal brooding behavior. Minor biases may be introduced by other factors. There is no evidence to support the hypotheses that arboreality or aquatic habits are major protoadaptations for viviparity (Table VI). The significance of physiological constraints remains untested.

The broad correlational analysis of the present study is designed to identify major and consistent biases in the evolution of viviparity. The

## TABLE VI
## Summary of Hypotheses, Predictions, and Empirical Tests on the Evolution of Reptilian Viviparity[a]

| Hypotheses | Predictions | Empirical Support | |
|---|---|---|---|
| | | Protoadaptation | Adaptation |
| *"Benefits" from uterine retention of eggs:* | *Viviparity evolves in regions with:* | *Factor is commonest in families or genera in which viviparity evolves* | *Factor is more common in "recently evolved" viviparous species than in their closest oviparous relatives* |
| 1. Eggs develop more rapidly, hatch earlier | Cold climates | No | Yes |
| 2. Eggs protected from lethally low temperatures | Cold climates | | |
| 3. Eggs protected from lethally high temperatures | Hot climates | No | Definitely not |
| 4. Eggs protected from flooding or fungal attack | Moist soils | Possibly, in lizards | No |
| 5. Eggs protected from desiccation | Dry soils | No | Inconsistent with observed strong bias with cold climates |
| 6. Eggs protected from predation | High rates of nest predation | Not tested | Not tested |
| 7. Female can predict optimal nest site | Environmental unpredictability | Not tested | Inconsistent with observed strong bias with cold climates |

|  |  |  |  |
|---|---|---|---|
| *Factors reducing female's "costs" of retaining eggs:* | *Viviparity evolves in species which are:* |  |  |
| 8. Invulnerable to predation | Large or venomous | Yes (venom in snakes) | No |
| 9. Nondependence on speed for feeding or escape from predation | Slow-moving, or "ambush" predators | ? | No |
| 10. Little exposure to predation | Fossorial or secretive | ? | No |
| 11. Egg-brooding female faces no extra "costs" | Egg-brooding | Yes | Not applicable |
| 12. Retention does not delay subsequent reproduction, because only a single clutch produced annually | Found in temperate rather than tropical climates | No? | Broadly consistent with data |
| *Other hypotheses:* |  |  |  |
| 13. Loss of "costs" associated with oviposition, such as migration or risk | Aquatic or arboreal | No | No |
| 14. Greater acceleration of embryonic development *in utero* with high body temperatures | Heliothermic | No | ? |
| 15. Physiological inability to retain eggs | In some taxa, but not others | Not tested | Not tested |

[a] Factors suggested to be of general importance in favoring the evolution of viviparity in squamate reptiles.

ability of the "cold-climate" hypothesis to explain most cases makes it unlikely that the alternative predictions have generality. However, correlational analyses are incapable of detecting factors that are important only in a few cases. Hence, none of the factors hypothesized to be important in the evolution of viviparity (Table VI) can be dismissed; any one of them may have been crucial in a particular case. Nonetheless, only the few hypotheses supported by data (Table VI) are likely to have general importance. They are capable of explaining strong biases in the taxa in which viviparity has evolved. For example, the probability of viviparity evolving within any given genus of snakes averages 6.1% for all snakes (18 within-genus origins in 294 genera with oviparous species), but this rises to 15% among genera with venomous species and to 35% among genera in which maternal care has been reported. Where both factors combine (venomous and brooding), the probability rises to 66% (six origins among nine genera). Within any genus in which viviparity has arisen, live-bearers usually occupy colder environments than egg-layers (Table V; 87% of cases if all uncertain cases are taken as exceptions; 96% of all cases for which sufficient data are available to make a clear judgment).

As these results are based on correlations, causation is inferred but cannot be demonstrated. Even those cases that accord with prediction may do so for a reason other than the one suggested. For example, a particular viviparous taxon may occupy a cold climate simply by chance or because of a rapid radiation into that environment after viviparity evolved. Also, reversals of reproductive mode (viviparity to oviparity) or errors in phylogenetic hypotheses may confound specific cases in the above analyses. Hence, it remains useful to continue tests by considering groups for which no breeding data are yet available. However, any evidence based on correlations is open to many alternative interpretations. Nonetheless, the data do strongly support the predictions of several hypotheses and falsify others; they provide the strongest evidence to date on the origin of viviparity.

The logical next step is to search for additional cases and to undertake detailed ecological and physiological studies on closely related oviparous and viviparous squamates. Such studies can overcome many of the problems associated with broad correlational analyses; for example, by directly measuring variables such as temperatures of nests and gravid reptiles, sources of egg mortality, and "costs" of egg retention (e.g., Guillette, 1981, 1982a, 1982b; Shine, 1980a, 1983b). This information should serve to illuminate the selective forces involved in the transition from oviparity to viviparity and to provide tests of many of the hypotheses and conclusions of the present study.

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## REFERENCES

Amaral, A. do (1977). *Serpentes do Brazil.* Editora da Universidade de São Paulo, Brazil.

Andren, C. and Nilson, G. (1976a). Hasselsnoken *(Coronella austriaca)* - en utrotningshotad ormart! *Fauna Flora* **2**, 61–76.

Andren, C. and Nilson, G. (1976b). Observations on the herpetofauna of Turkey in 1968–1975. *Brit. J. Herpet.* **5**, 575–584.

Andrews, R. M. (1982). Spatial variation in egg mortality of the lizard *Anolis limifrons. Herpetologica* **38**, 165–170.

Angel, F., Guibé, J., Lamotte, M., and Roy, R. (1954). La résérve naturelle integrale du Mont Nimba. *Mém. Inst. franç. d'Afrique noire* **40**, 381–402.

Anonymous. (1982). Boas breed *(Casarea dussumieri). Wildlife* (December), 460.

Arakawa, H. (1970). *Climates of Northern and Eastern Asia.* Vol. 8 in *World Survey of Climatology.* Elsevier, Amsterdam.

Arnold, E. N. (1973). Relationships of the Palaearctic lizards assigned to the genera *Lacerta, Algyroides* and *Psammodromus* (Reptilia, Lacertidae). *Bull. Brit. Mus. (nat. Hist.) Zool.* **25**, 291–366.

Arnold, E. N. and Burton, J. A. (1978). *A Field Guide to the Reptiles and Amphibians of Britain and Europe.* Collins, London.

Arnold, E. N. and Leviton, A. E. (1977). A revision of the lizard genus *Scincus* (Reptilia: Scincidae). *Bull. Brit. Mus. (nat. Hist.) Zool.* **31**, 187–248.

Axtell, R. W. (1960). A new subspecies of *Eumeces dicei* from the Sierra Madre of northeastern Mexico. *Copeia* **1960**, 19–26.

Badhuri, J. L. (1943). Notes on the viviparity of the common Indian skink *Mabuya carinata* (Schneider). *J. Bombay Nat. Hist. Soc.* **44**, 130–134.

Bailey, J. R. (1966). A redescription of the snake *Calamodontophis paucidens. Copeia* **1966**, 885–886.

Bailey, J. R. (1981). Notes on the genus *Thamnodynastes. Primeiro Symposio Internacional sôbre serpentes.* Instituto Butantan, São Paulo, Brazil, 16–18 Nov. 1981 (Abstract).

Bartmann, W. and Minuth, E. (1979). Ein lebendgebährender Gecko, *Rhacodactylus trachyrhynchus* Bocage 1873, aus Neukaledonien (Reptilia: Sauria: Gekkonidae). *Salamandra* **15**, 58–60.

Bauchot, R. (1965). La placentation chez les reptiles. *Ann. Biol.* **4**, 547–575.

Bauwens, D. and Thoen, C. (1981). Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara. J. anim. Ecol.* **50**, 733–743.

Bezy, R. L., Gorman, G. C., Kim, Y. J., and Wright, J. W. (1977). Chromosomal and genetic divergence in the fossorial lizards of the family Anniellidae. *Syst. Zool.* **26,** 57–71.

Blackburn, D. G. (1981). An evolutionary analysis of vertebrate viviparity. *Amer. Zool.* **21,** 936 (Abstract).

Blackburn, D. G. (1982). Evolutionary origins of viviparity in the Reptilia. I. Sauria. *Amphibia–Reptilia* **3,** 185–205.

Blackburn, D. G. (1984). Evolutionary origins of viviparity in the Reptilia. II. Serpentes, Amphisbaenia, and Ichthyosauria. *Amphibia–Reptilia,* in press.

Blanchard, F. N. (1933). Eggs and young of the smooth green snake, *Liopeltis vernalis* (Harlan). *Pap. Michigan Acad. Sci. Arts. Lett.* **17,** 493–508.

Blair, W. F. (1960). *The Rusty Lizard. A Population Study.* University of Texas Press, Austin.

Blanc, C. P. and Blanc, F. (1967). Observations biologiques (adultes, oeufs, jeunes) sur quelques sauriens du Mont Bity. *Annl. Univ. Madagascar, Ser. Sci.* **5,** 67–74.

Blanc, F. (1974). Table de developpement de *Chamaeleo lateralis* Gray, 1831. *Ann. Embryol. Morphol.* **7,** 99–115.

Bogert, C. M. (1940). Herpetological results of the Vernay Angola Expedition with notes on African reptiles in other collections. *Bull. Amer. Mus. Nat. Hist.* **109,** 1–238.

Bons, J. and Bons, N. (1960). Notes sur la réproduction et le dévéloppement de *Chamaeleo chamaeleon* L. *Bull. Soc. Sci. nat. phys. Maroc.* **40,** 323–335.

Bons, J. and Saint-Girons, H. (1963). Ecologie et cycle sexuel des amphisbaeniens du Maroc. *Bull. Soc. Sci. nat. phys. Maroc.* **43,** 117–158.

Branch, W. R. (1979). The venomous snakes of southern Africa. Part 2. Elapidae and Hydrophidae. *The Snake* **11,** 199–225.

Branch, W. R. (1982). Venomous snakes of southern Africa. 3. Concluding part: Colubridae. *The Snake* **14,** 1–17.

Brattstrom, B. H. (1964). Evolution of the pit vipers. *Trans. San Diego Soc. nat. Hist.* **13,** 185–268.

Brattstrom, B. H. (1965). Body temperatures of reptiles. *Am. Midl. Nat.* **73,** 376–422.

Broadley, D. G. (1974). Reproduction in the genus *Platysaurus* (Sauria: Cordylidae). *Herpetologica* **30,** 379–380.

Broadley, D. G. (1977). A revision of the African snakes of the genus *Psammophylax* Fitzinger (Colubridae). *Occ. Pap. Nat. Mus. Rhodesia* **B 6,** 1–43.

Broadley, D. G. (1979). Predation on reptile eggs by African snakes of the genus *Prosymna. Herpetologica* **35,** 338-341.

Broadley, D. G. (1983). *FitzSimons' Snakes of Southern Africa.* Delta, Johannesburg.

Broadley, D. G. and Cock, E. V. (1975). *Snakes of Rhodesia.* Longman, Salisbury.

Broadley, D. G., Gans, C., and Visser, J. (1976). Studies on amphisbaenians (Amphisbaenia, Reptilia). 6. The genera *Monopeltis* and *Dalophia* in southern Africa. *Bull. Amer. Mus. nat. Hist.* **157,** 313–485.

Brown, W. C. and Alcala, A. C. (1980). Philippine lizards of the family Scincidae. *Silliman Univ. Nat. Sci. Monogr. 2.*

Bryson, R. A. and Hare, F. (1974). *Climates of North America.* Vol. 11 in *World Survey of Climatology.* Elsevier, Amsterdam.

Bull, J. J. (1980). Sex determination in reptiles. *Q. Rev. Biol.* **55,** 3–21.

Burger, J. (1977). Determinants of hatching success in diamondback terrapin, *Malaclemys terrapin. Am. Midl. Nat.* **97,** 444–464.

Burger, W. L. (1971). "Genera of pitvipers (Serpentes: Crotalidae)." Ph.D. thesis, University of Kansas, Lawrence.

Bustard, H. R. (1964). Reproduction in the Australian rain forest skinks, *Saiphos equalis* and *Sphenomorphus tryoni*. *Copeia* **1964,** 715–716.

Cadle, J. E. (1984). Molecular systematics of neotropical xenodontine snakes. I. South American xenodontines. *Herpetologica* **40,** 8–20.

Cadle, J. E. and Gorman, G. C. (1981). Albumin immunological evidence and the relationships of sea snakes. *J. Herpetol.* **15,** 329–334.

Campbell, H. and Simmons, R. S. (1961). Notes on the eggs and young of *Eumeces callicephalus* Bocourt. *Herpetologica* **17,** 212–213.

Campden-Main, S. M. (1970). *A Field Guide to the Snakes of South Vietnam*. Smithsonian Inst., Washington, D.C.

Cansdale, G. S. (1961). *West African Snakes*. West African Nature Handbooks, Longmans, London.

Cei, J. M. (1974). Two new species of *Ctenoblepharis* (Reptilia, Iguanidae) from the arid environments of the central Argentina (Mendoza Province). *J. Herpetol.* **8,** 71–75.

Cei, J. M. (1979). A reassessment of the genus *Ctenoblepharis* (Reptilia, Sauria, Iguanidae) with a description of a new subspecies of *Liolaemus multimaculatus* from western Argentina. *J. Herpetol.* **13,** 297–302.

Cei, J. M. (1980). New endemic iguanid lizards from the Famatina Mountains of Western Argentina. *J. Herpetol.* **14,** 57–64.

Cei, J. M. and Scolaro, J. A. (1982). A new species of the Patagonian genus *Vilcunia*, with remarks on its morphology, ecology and distribution. *J. Herpetol.* **16,** 354–363.

Chang, T. H. and Fang, P. W. (1931). A study of the ophidians and chelonians of Nanking. *Contr. Biol. Lab. Soc. China* **7,** 249–288.

Charles, N., Watts, A. and Shine, R. (1983). Captive reproduction in an Australian elapid snake, *Pseudechis colletti*. *Herp. Rev.* **14,** 16–18.

Charles, N., Whitaker, P. and Shine, R. (1979). Oviparity and captive breeding in the spotted blacksnake, *Pseudechis guttatus* (Serpentes, Elapidae). *Aust. Zool.* **20,** 361–364.

Cherlin, V. A. (1981). The new saw-scaled viper, *Echis multisquamatus* sp. nov. from southwestern and middle Asia. *Proc. Zool. Institut.* **101,** 92–95 [In Russian].

Chernov, S. A. (1957). Systematic position of the poisonous snake *Ancistrodon rhodostoma* (Boie) (Serpentes, Crotalidae) in connection with its craniology. *Zool. Zhur.* **36,** 790–792.

Cogger, H. G. (1975). *Reptiles and Amphibians of Australia*. A. H. & A. W. Reed, Sydney.

Cole, C. J. (1978). Karyotypes and systematics of the lizards in the *variabilis, jalapae,* and *scalaris* species groups of the genus *Sceloporus*. *Amer. Mus. Novitates* (2653), 1–13.

Cooper, J. S. (1965). Notes on fertilization, the incubation period and hybridization in *Lacerta*. *Br. J. Herpet.* **3,** 218–220.

Criley, B. B. (1968). The cranial osteology of gerrhonotiform lizards. *Am. Midl. Nat.* **80,** 199–219.

da Cunha, O. R. and do Nascimento, F. P. (1981). Ophidia of Amazonia, 12. *Bol. Mus. Para. Emilio Goeldi Nova Ser. Zool.* **109,** 1–20.

Daan, S. (1968). Agamids. In *Grzimek's Animal Life Encyclopedia*. Vol. 6, *Reptiles* (B. Grzimek, ed.). Van Nostrand-Reinhold Co., New York, pp. 205–227.

Darevsky, I. S. (1966). Ecology of rock-viper (*Viper xanthina raddei* Boettger) in the natural surroundings of Armenia. *Memor. Inst. Butantan (Simp. Internac.)* **33,** 81–83.

Davis, W. B. and Smith, H. M. (1953). Lizards and turtles of the Mexican state of Morelos. *Herpetologica* **9,** 100–108.

Deoras, P. J. (1971). *Snakes of India*. National Book Trust, New Delhi.

de Rooij, N. (1917). *The Reptiles of the Indo-Australian Archipelago*. Vol. 2, *Ophidia*. E. J. Brill, Leiden.

Diesener, G. (1974). Beitrag zur Biologie der Bergotter. *Aqua. Terra-Z* **27,** 249–251.

Ditmars, R. L. (1942). *The Reptiles of North America.* Doubleday Doran, New York.

Dixon, J. R. (1969). Taxonomic review of the Mexican skinks of the *Eumeces brevirostris* group. *Los Angeles County Mus. Contrib. Sci.* **168,** 1–30.

Dmi'el, R. (1970). Growth and metabolism in snake embryos. *J. Embryol. exp. Morphol.* **23,** 761–772.

Domergue, C. A. (1959). Ovoviparité et oviparité chez deux Viperidae du gènre *Aspis* (L.). *Bull. Soc. Sci. nat. Tunis.* **9,** 73–74.

Donoso-Barros, R. (1966). *Reptiles de Chile.* Edicion de la Universidad de Chile, Santiago.

Donoso-Barros, R. and Cei, J. M. (1971). New lizards from the volcanic Patagonian plateau of Argentina. *J. Herpetol.* **5,** 89–95.

Dowling, H. G. (1974). The nearctic snake fauna. *Ybk. Herpetol.* **1,** 190–202.

Duellman, W. E. (1961). The amphibians and reptiles of Michoacan, Mexico. *Univ. Kansas Publ. Mus. Nat. Hist.* **15,** 1–148.

Duellman, W. E. (1965). A biogeographic account of the herpetofauna of Michoacan, Mexico. *Univ. Kansas Publ. Mus. Nat. Hist.* **15,** 627–709.

Duellman, W. E. (1979). The herpetofauna of the Andes: its origins, evolution, and dispersal. *Univ. Kansas Monogr.* **7,** 371–460.

Dufaure, J. P. and Hubert, J. (1961). Table de dévéloppement du lézard vivipare: *Lacerta (Zootoca) vivipara* Jacquin. *Arch. Anat. Microsc. Morphol. exp.* **50,** 309–328.

Duff-Mackay, A. (1965). Notes on the biology of the carpet viper, *Echis carinatus pyramidum* (Geoffroy), in the northern frontier province of Kenya. *J. east Afr. nat. Hist. Soc. natl. Mus.* **25,** 28–40.

Duguy, R. (1961). Le cycle annual d'activité de *Coronella austriaca* Laur. *Terre et Vie* **1961,** 401–436.

Dumas, P. C. (1964). Species-pair allopatry in the genera *Rana* and *Phrynosoma. Ecology* **45,** 178–181.

Dunson, W. A. (1975). Adaptations of sea snakes. In *The Biology of Sea Snakes* (W. A. Dunson, ed.). University Park Press, Baltimore, Maryland, pp. 3–19.

Erasmus, H. and Branch, W. R. (1983). Egg retention in the South African blind snake *Typhlops bibroni. J. Herpetol.* **17,** 97–99.

Etheridge, R. (1966). The systematic relationships of West Indian and South American lizards referred to the iguanid genus *Leiocephalus. Copeia* **1966,** 79–91.

Ewert, M. A. (1979). The embryo and its egg: development and natural history. In *Turtles, Perspectives and Research* (M. Harless and H. Morlock, eds.). John Wiley & Sons, New York, pp. 333–413.

Ewert, M. A. (1984). Reproduction and development in turtles. In *Biology of the Reptilia* (C. Gans, P. F. A. Maderson, and F. Billett, eds.). Vol. 14, John Wiley & Sons, Inc., New York.

Ferguson, G. W. and Brockman, T. (1980). Geographic differences of growth rate of *Sceloporus* lizards (Sauria: Iguanidae). *Copeia* **1980,** 259–264.

Ferguson, M. W. J. (1984). Development of crocodilians. In *Biology of the Reptilia* (C. Gans, P. F. A. Maderson, and F. Billett, eds.). Vol. 14, John Wiley & Sons, Inc., New York.

Fisher, R. A. (1958). *The Genetical Theory of Natural Selection.* 2nd Ed., revised. Dover Press Publ., Inc., New York.

Fitch, H. S. (1954). Life history and ecology of the five-lined skink, *Eumeces fasciatus. Publ. Mus. nat. Hist. Univ. Kansas* **8,** 1–156.

Fitch, H. S. (1970). Reproductive cycles in lizards and snakes. *Univ. Kansas Mus. nat. Hist., Misc. Publ.* **52,** 1–247.

Fitzgerald, M. and Pollitt, C. (1981). Oviparity and captive breeding in the mulga or king brown snake *Pseudechis australis* (Serpentes; Elapidae). *Aust. J. Herpetol.* **1,** 57–60.

FitzSimons, V. F. M. (1943). The lizards of South Africa. *Transvaal Mus. Mem.* **(1),** 1–528.

FitzSimons, V. F. M. (1962). *Snakes of Southern Africa.* Macdonald, London.

Fuhn, I. (1968). Scincidae. In *Grzimek's Animal Life Encyclopedia.* Vol. 6, *Reptiles* (B. Grzimek, ed.). Van Nostrand-Reinhold, New York, pp. 242–264.

Fuhn, I. (1969). Revision and redefinition of the genus *Ablepharus* Lichtenstein, 1823 (Reptilia, Scincidae). *Rev. Roum. Biol., Ser. Zool.* **14,** 23–41.

Fukada, H. (1956). Biological studies on the snakes. III. Observations on hatching of *Elaphe climacophora* (Boie), *E. conspicillata* (Boie), and *Natrix vibakari vibakari* (Boie). *Bull. Kyoto Gakugei Univ., Ser. B.* **9,** 21–29.

Fukada, H. (1962). Biological studies on the snakes. IX. Breeding habits of *Agkistrodon halys blomhoffii* (Boie). *Bull. Kyoto Gakugei Univ.* **B20,** 12–17.

Fukada, H. (1965). Breeding habits of some Japanese reptiles (critical review). *Bull. Kyoto Gakugei Univ.* **B27,** 65–82.

Gans, C. (1967). *Rhineura florida. Catalogue Amer. Amphib. Rept.* **43,** 1–4.

Gans, C. (1974). *Biomechanics: An Approach to Vertebrate Biology.* J. P. Lippincott, Philadelphia (1980, University of Michigan Press).

Gans, C. (1978). The characteristics and affinities of the Amphisbaenia. *Trans. zool. Soc. Lond.* **34,** 347–416.

Gans, C. and Fetcho, J. R. (1982). The Sri Lankan genus *Aspidura* (Serpentes, Reptilia, Colubridae). *Ann. Carnegie Mus.* **51,** 271–316.

Gentilli, J. (1971). *Climates of Australia and New Zealand.* Vol. 13 in *World Survey of Climatology.* Elsevier, Amsterdam.

Gloyd, H. K. (1977). Descriptions of new taxa of crotalid snakes from China and Ceylon (Sri Lanka). *Proc. biol. Soc. Wash.* **90,** 1002–1015.

Gloyd, H. K. (1979). A new generic name for the hundred-pace viper. *Proc. biol. Soc. Wash.* **91,** 963–964.

Greene, H. W. (1970). Modes of reproduction in lizards and snakes of the Gomez Farias region, Tamaulipas, Mexico. *Copeia* **1970,** 565–568.

Greer, A. E. (1966). Viviparity and oviparity in the snake genera *Conopsis, Toluca, Gyalopion,* and *Ficimia,* with comments on *Tomodon* and *Helicops. Copeia* **1966,** 371–373.

Greer, A. E. (1967a). Notes on the mode of reproduction of anguid lizards. *Herpetologica* **23,** 94–99.

Greer, A. E. (1967b). The generic relationships of the African scincid genus *Eumecia. Breviora* (276), 1–9.

Greer, A. E. (1967c). A new generic arrangement for some Australian scincid lizards. *Breviora* (267), 1–19.

Greer, A. E. (1968). Mode of reproduction in the squamate faunas of three altitudinally correlated life zones in east Africa. *Herpetologica* **24,** 229–232.

Greer, A. E. (1970). A new subfamilial classification of scincid lizards. *Bull. Mus. comp. Zool. Harv.* **139,** 151–183.

Greer, A. E. (1974). The generic relationships of the scincid lizard genus *Leiolopisma* and its relatives. *Aust. J. Zool. Suppl.* **31,** 1–67.

Greer, A. E. (1977). The systematics and evolutionary relationships of the scincid lizard genus *Lygosoma. J. nat. Hist.* **11,** 515–540.

Greer, A. E. (1979a). *Eremiascincus,* a new generic name for some Australian sand swimming skinks (Lacertilia: Scincidae). *Rec. Aust. Mus.* **32,** 321–338.

Greer, A. E. (1979b). A phylogenetic subdivision of Australian skinks. *Rec. Aust. Mus.* **32,** 339–371.

Greer, A. E. (1982). A new species of *Leiolopisma* (Lacertilia: Scincidae) from Western Australia, with notes on the biology and relationships of other Australian species. *Rec. Aust. Mus.* **34,** 549–573.

Greer, A. E. (1983). The Australian scincid lizard genus *Calyptotis;* resurrection of the name, description of four new species, and discussion of the relationships. *Rec. Aust. Mus.* **35,** 29–59.

Greer, A. E. and Parker, F. (1967). A new scincid lizard from the northern Solomon Islands. *Breviora* (275), 1–20.

Greer, G. E. and Parker, F. (1968). A new species of *Tribolonotus* (Lacertilia: Scincidae) from Bougainville and Buka, Solomon Islands, with comments on the biology of the genus. *Breviora* (291), 1–16.

Greer, A. E. and Parker, F. (1974). The *Fasciatus* species group of *Sphenomorphus* (Lacertilia: Scincidae): notes on eight previously described species and descriptions of three new species. *Proc. Papua New Guinea Sci. Soc.* **25,** 31–61.

Greer, A. E. and Parker, F. (1979). On the identity of the New Guinea scincid lizard *Lygosoma fragile* Macleay 1877, with notes on its natural history. *J. Herpetol.* **13,** 221–225.

Greer, A. E. and Raizes, G. (1969). Green blood pigment in lizards. *Science, N.Y.* **166,** 392–393.

Griffiths, J. F. (1972). *Climates of Africa.* Vol. 10 in *World Survey of Climatology.* Elsevier, Amsterdam.

Gudynas, E. (1981). Confirmacion de la viviparidas en la "colubra sepia" *Thamnodynastes strigilis* (Serpentes: Colubridae). *C.E.D. Orione Cont. Biol.* **5,** 1–7.

Guillette, L. J., Jr. (1981). On the occurrence of oviparous and viviparous forms of the Mexican lizard *Sceloporus aeneus. Herpetologica* **37,** 11–15.

Guillette, L. J., Jr. (1982a). The evolution of viviparity and placentation in the high elevation, Mexican lizard *Sceloporus aeneus. Herpetologica* **38,** 94–103.

Guillette, L. J., Jr. (1982b). Effects of gravidity on the metabolism of the reproductively bimodal lizard, *Sceloporus aeneus. J. exp. Zool.* **223,** 33–36.

Guillette, L. J., Jr. (1983). Notes concerning reproduction of the montane skink, *Eumeces copei. J. Herpetol.* **17,** 144–148.

Guillette, L. J., Jr., Jones, R. E., Fitzgerald, K. T., and Smith, H. M. (1980). Evolution of viviparity in the lizard genus *Sceloporus. Herpetologica* **36,** 201–215.

Gyi, K. K. (1970). A revision of colubrid snakes of the subfamily Homalopsinae. *Univ. Kansas Publ. Mus. nat. Hist.* **20,** 47–223.

Hardy, G. S. (1977). The New Zealand Scincidae (Reptilia: Lacertilia); a taxonomic and zoogeographic study. *New Zealand J. Zool.* **4,** 221–325.

Hardy, G. S. (1979). The karyotypes of two scincid lizards, and their bearing on relationships in genus *Leiolopisma* and its relatives (Scincidae: Lygosominae). *New Zealand J. Zool.* **6,** 609–612.

Hardy, L. M. (1975). Comparative morphology and evolutionary relationships of the colubrid snake genera *Pseudoficimia, Ficimia,* and *Gyalopion. J. Herpetol.* **9,** 323–336.

Hillenius, D. (1959). The differentiation within the genus *Chamaeleo* Laurenti, 1768. *Beaufortia* **8,** 1–92.

Hoover, E. E. (1936). On the birth of *Constrictor constrictor imperator,* in captivity. *Copeia* **1936,** 62.

Horton, D. R. (1973). "Evolution in the Genus *Mabuya.*" Ph.D. thesis, University of New England (New South Wales, Australia).

Huey, R. B. (1977). Egg retention in some high-altitude *Anolis* lizards. *Copeia* **1977,** 373–375.

Huey, R. B. (1982). Temperature, physiology, and the ecology of reptiles. In *Biology of the Reptilia* (C. Gans and F. H. Pough, eds.). Vol. 12, Academic Press, London, pp. 25–91.

Hughes, B. (1976). Notes on African carpet vipers, *Echis carinatus, E. leucogaster,* and *E. ocellatus* (Viperidae, Serpentes). *Rev. Suisse Zool.* **83,** 359–371.

Ingram, G. and Ehmann, H. (1981). A new species of scincid lizard of the genus *Leiolopisma* (Scincidae: Lygosominae) from southeastern Queensland and northeastern New South Wales. *Mem. Qld. Mus.* **20,** 307–310.

Isemonger, R. M. (1962). *Snakes of Africa, Southern, Central and East.* Nelson, Cape Town.

Jenkins, N. K. and Simkiss, K. (1968). The calcium and phosphate metabolism of reproducing reptiles with particular reference to the adder *(Vipera berus). Comp. Biochem. Physiol.* **26,** 865–876.

Kawamura, Y. (1974). Study of the immunological relationships between venom of six Asiatic *Agkistrodons. The Snake* **6,** 19–26.

Klaver, C. J. J. (1973). Lung-anatomy: aid in chameleon-taxonomy. *Beaufortia* **20,** 155–177.

Klaver, C. J. J. (1977). Comparative lung-morphology in the genus *Chamaeleo* Laurenti, 1768 (Sauria: Chamaeleonidae) with a discussion of taxonomic and zoogeographic implications. *Beaufortia* **25,** 167–199.

Klaver, C. J. J. (1981). Lung-morphology in the Chamaeleonidae (Sauria) and its bearing upon phylogeny, systematics and zoogeography. *Zeitsch. zool. Syst. Evol.* **19,** 36–58.

Klemmer, K. (1968). Lacertidae. In *Grzimek's Animal Life Encyclopedia.* Vol. 6, *Reptiles* (B. Grzimek, ed.). Van Nostrand-Reinhold Co., New York, pp. 284–306.

Kluge, A. G. (1967). Higher taxonomic categories of gekkonid lizards and their evolution. *Bull. Amer. Mus. nat. Hist.* **135,** 1–59.

Koba, K. (1971). Natural history of the habu, *Trimeresurus flavoviridis* (Hallowell). *The Snake* **3,** 75–96.

Koba, K. (1973). The venomous snakes of southeast Asia. *The Snake* **5,** 77–115.

Koba, K., Tanaka, K., Yoshizaki, K., and Nakamoto, E. (1970). Eggs and hatching of the hime-habu, *Trimeresurus okinavensis* Boulenger. *The Snake* **2,** 111–121.

Koba, K., Tanaka, K., Nakamoto, E., and Morimoto, H. (1977). Oviposition of the tokara-habu, *Trimeresurus tokarensis. Acta herpet. Jap.* **4,** 13.

Kochva, E. (1963). Development of the venom gland and trigeminal muscles in *Vipera palaestinae. Acta Anat.* **52,** 49–89.

Kopstein, F. (1938). Ein Beitrag zur Eierkunde und zur Fortpflanzung der Malaiischen Reptilien. *Bull. Raffles Mus.* **14,** 81–167.

Korneva, L. G. (1973). Morphology of female reproductive system in *Vipera lebetina* with special reference to its activity. *Zool. Zhur.* **52,** 85–93.

Kramer, E. and Schnurrenberger, H. (1963). Systematik, Verbreitung und Ökologie der libyschen Schlangen. *Rev. Suisse Zool.* **70,** 453–568.

Kratzer, H. (1968). Zur Fortplanzung von *Vipera lebetina mauritanica. Aqua Terra-Z.* **21,** 380–382.

Landsberg, H. E. and Wallen, C. C. (1977). *Climates of Central and Southern Europe.* Elsevier, Amsterdam.

Lantz, L. A. (1927). Quelques observations nouvelles sur l'herpetologie des Pyrenées centrales. *Rev. Hist. Nat. Appliq.* **8,** 54–61.

Larsen, K. R. and Tanner, W. W. (1975). Evolution of the sceloporine lizards (Iguanidae). *Great Basin Nat.* **35,** 1–20.

Lawson, R. and Dessauer, H. C. (1980). Electrophoretic evaluation of the colubrid genus *Elaphe* (Fitzinger). *Isozyme Bull.* **14,** 83.

Limpus, C. J., Baker, V., and Miller, J. D. (1979). Movement induced mortality of loggerhead eggs. *Herpetologica* **35,** 335–338.

Loveridge, A. (1933). Report on the scientific results of an expedition to the southwestern highlands of Tanganyika territory. VII. Herpetology. *Bull. Mus. comp. Zool.* **79,** 197–416.

Loveridge, A. (1941). Revision of the African lizards of the family Amphisbaenidae. *Bull. Mus. comp. Zool.* **87,** 351–451.

Lydolph, P. E. (1977). *Climates of the Soviet Union.* Vol. 7 in *World Survey of Climatology.* Elsevier, Amsterdam.

McCoy, C. J. (1968). Reproductive cycles and viviparity in Guatemalan *Corythophanes percarinatus* (Reptilia: Iguanidae). *Herpetologica* **24,** 175–178.

McCoy, M. (1980). *Reptiles of the Solomon Islands.* Wau Ecology Institute, Solomons, Handbook No. 7.

McDowell, S. B. (1967). *Aspidomorphus,* a genus of New Guinea snakes of the family Elapidae, with notes on related genera. *J. Zool. (Lond.)* **151,** 497–543.

McDowell, S. B. (1969). Notes on the Australian sea-snake *Ephalophis greyi* M. Smith (Serpentes: Elapidae, Hydrophiinae) and the origin and classification of sea-snakes. *Zool. J. Linn. Soc.* **48,** 333–349.

McDowell, S. B. (1975). A catalogue of the snakes of New Guinea and the Solomons, with special reference to those in the Bernice P. Bishop Museum. Part II. Aniloidea and Pythoninae. *J. Herpetol.* **9,** 1–80.

McDowell, S. B. (1979). A catalogue of the snakes of New Guinea and the Solomons, with special reference to those in the Bernice B. Bishop Museum. Part III. Boinae and Acrochordoidea (Reptilia, Serpentes). *J. Herpetol.* **13,** 1–92.

McDowell, S. B. and Bogert, C. M. (1954). The systematic position of *Lanthanotus* and the affinities of the anguinomorphan lizards. *Bull. Amer. Mus. nat. Hist.* **105,** 1–142.

MacGregor, J. (1975). An observation concerning the incubation period of the eggs of *Opheodrys vernalis. Kentucky Herpetologist* **6,** 181.

Malnate, E. V. (1960). Systematic division and evolution of the colubrid snake genus *Natrix* with comments on the subfamily Natricinae. *Proc. Acad. nat. Sci. Philadelphia* **112,** 41–71.

Mao, S-H., Chen, B-Y., and Chang, H-M. (1977). The evolutionary relationships of sea snakes suggested by immunological cross-reactivity of transferrins. *Comp. Biochem. Physiol.* **57A,** 403–406.

Mao, S. H., Chen, B-Y., Yin, F-Y., and Guo, Y-W. (1983). Immunotaxonomic relationships of sea snakes to terrestrial elapids. *Comp. Biochem. Physiol.* **74A,** 869–872.

Marcellini, D. L. and Davis, S. W. (1982). Effects of handling on reptile egg hatching. *Herp. Rev.* **13,** 43–44.

Marx, H. and Rabb, G. (1965). Relationships and zoogeography of the viperine snakes (Family Viperidae). *Fieldiana, Zool.* **44,** 161–206.

Mell, R. (1929). *Beitrage zur Fauna Sinica. IV. Grundzüge einer Ökologie der chinesischen Reptilien und einer herpetologischen Tiergeographie Chinas.* Walter de Gruyter, Berlin.

Mendelssohn, H. (1963). On the biology of the venomous snakes of Israel. I. *Israel J. Zool.* **12,** 143–170.

Mendelssohn, H. (1965). On the biology of the venomous snakes of Israel. II. *Israel J. Zool.* **14,** 185–212.

Mertens, R. (1964). Neukaledonische Riesengeckos *(Rhacodactylus). Zool. Gart.* **29,** 49–57.

Mertens, R. (1972). Über den Senegal-skink *(Scincus albifasciatus)* und seine Verwandten. *Salamandra* **8,** 117–122.

Minton, S. A., Jr. (1966). A contribution to the herpetology of West Pakistan. *Bull. Am. Mus. nat. Hist.* **134,** 29–184.

Minton, S. A., Jr. (1979). Common antigens in snake venoms. In *Handbook of Experimental Pharmacology. Snake Venoms* (C-Y. Lee, ed.). Vol. 52, Springer-Verlag, Berlin, pp. 847–862.

Mittwoch, U. (1975). Chromosomes and sex differentiation. In *Inter-sexuality in the Animal Kingdom* (R. Reinboth, ed.). Academic Press, New York, pp. 438–446.

Mole, R. H. (1924). The Trinidad snakes. *Proc. zool. Soc. Lond.* **11,** 235–278.

Moll, E. O. and Legler, J. M. (1971). The life history of a neotropical slider turtle, *Pseudemys scripta* (Schoepff), in Panama. *Bull. Los Angeles County Mus. nat. Hist. Sci.* **11,** 1–102.

Montanucci, R. R. (1979). Notes on systematics of horned lizards allied to *Phrynosoma orbiculare* (Lacertilia: Iguanidae). *Herpetologica* **35,** 116–124.

Murphy, G. (1968). Pattern in life history and the environment. *Amer. Natur.* **102,** 391–404.

Muskhelishvili, T. A. (1971). The biology of the reproduction of the asp *Vipera lebetina obtusa* Dw. *Akad. Nauk Gruz. Soobsch.* **62,** 201–203.

Muth, A. (1980). Physiological ecology of desert iguana *(Dipsosaurus dorsalis)* eggs: temperature and water relations. *Ecology* **61,** 1335–1343.

Nakamoto, E. and Sawai, Y. (1982). Observation on egg-laying in the Taiwan-habu, *Trimeresurus mucrosquamatus* (Cantor). *The Snake* **14,** 145–146.

National Fish and Wildlife Laboratory (1978). *Vertebrates of the World,* 2nd Ed. U.S. Fish and Wildlife Service, Gainesville, Florida.

Neill, W. T. (1964). Viviparity in snakes: some ecological and zoogeographical considerations. *Amer. Natur.* **48,** 35–55.

Nickerson, M. A. (1974). Comments on the reproduction of Pope's Pit-viper *(Trimeresurus popeorum)* Smith. *Brit. J. Herpet.* **5,** 451–452.

Nilson, G. and Sundberg, P. (1981). The taxonomic status of the *Vipera xanthina* complex. *J. Herpetol.* **15,** 379–381.

Noble, G. K. and Mason, E. R. (1933). Experiments on the brooding habits of the lizards *Eumeces* and *Ophisaurus*. *Am. Mus. Novitates* (619).

Northcutt, R. G. (1978). Forebrain and midbrain organization in lizards and its phylogenetic significance. In *Behavior and Neurology of Lizards* (N. Greenberg and P. D. MacLean, eds.). U.S. Dept. Health, Education and Welfare, Washington, D.C., pp. 11–64.

Packard, G. C. (1966). The influence of ambient temperature and aridity on modes of reproduction and excretion of amniote vertebrates. *Am. Natur.* **100,** 667–682.

Packard, G. C., Tracy, C. R., and Roth, J. J. (1977). The physiological ecology of reptilian eggs and embryos, and the evolution of viviparity within the class Reptilia. *Biol. Rev.* **52,** 71–105.

Packard, M. J., Packard, G. C., and Boardman, T. J. (1982). Structure of eggshells and water relations of reptilian eggs. *Herpetologica* **38,** 136–155.

Paull, D., Williams, E. E., and Hall, W. P. (1976). Lizard karyotypes from the Galapagos Islands: chromosomes in phylogeny and evolution. *Breviora* (441), 1–31.

Peters, J. A. and Donoso Barros, R. (1970). Catalogue of the neotropical Squamata: Part II, Lizards and amphisbaenians. *Bull. U.S. natl. Mus.* **297,** 1–293.

Peterson, H. W. (1956). A record of viviparity in a normally oviparous snake. *Herpetologica* **12,** 152.

Petzold, H. G. (1968a). Anguidae. In *Grzimek's Animal Life Encyclopedia.* Vol. 6, *Reptiles.* Van Nostrand-Reinhold Co., New York, 307–316.

Petzold, H. G. (1968b). Viperidae. In *Grzimek's Animal Life Encyclopedia.* Vol. 6, *Reptiles.* Van Nostrand-Reinhold Co., New York, pp. 439–484.

Phelps, T. (1981). *Poisonous Snakes.* Blandford Press, Dorset.

Pianka, E. R. and Parker, W. C. (1975). Ecology of horned lizards: a review with special reference to *Phrynosoma platyrhinos*. *Copeia* **1975,** 141–162.

Pienaar, U. de V. (1978). *The Reptile Fauna of the Kruger National Park.* National Parks Board of South Africa, Pretoria.

Pilorge, T. and Barbault, R. (1981). La viviparité chez les lezards: evolution et adaptation. *Acta Oecol., Oecol., Gener.* **2,** 387–397.

Pitman, C. R. S. (1974). *A Guide to the Snakes of Uganda.* Rev. Ed. Wheldon and Wesley, London.

Pope, C. H. (1935). *The Reptiles of China.* American Museum of Natural History, New York.

Pope, C. H. (1961). *The Giant Snakes.* Routledge and Keegan Paul, London.

Porter, W. P. and Tracy, C. R. (1983). Biophysical analyses of energetics, time-space utilization, and distributional limits. In *Lizard Ecology* (R. B. Huey, E. R. Pianka, and T. W. Schoener, eds.). Harvard University Press, Cambridge, Massachusetts, pp. 55–83.

Presch, W. (1969). Evolutionary osteology and relationships of the horned lizard genus *Phrynosoma. Copeia* **1969,** 250–275.

Rage, J. (1982). L'histoire des serpentes. *Pour la Science* (April), 16–27.

Rahn, H. (1939). Structure and function of placenta and corpus luteum in viviparous snakes. *Proc. Soc. exp. Biol. Med.* **40,** 381–382.

Rand, A. S. (1963). Notes on the *Chamaeleo bitaeniatus* complex. *Bull. Mus. comp. Zool.* **130,** 1–29.

Rand, A. S. (1972). The temperatures of iguana nests and their relation to incubation optima and to nesting sites and season. *Herpetologica* **28,** 252–253.

Rankin, P. R. (1978). Notes on the biology of the skink *Sphenomorphus pardalis* (Macleay), including a captive breeding record. *Herpetofauna* **10,** 4–7.

Raw, L. R. G. (1976). A survey of the dwarf chameleons of Natal, South Africa, with descriptions of three new species (Sauria: Chamaeleonidae). *Durban Mus. Novit.* **11,** 139–161.

Raw, L. R. G. (1978). A further new dwarf chameleon from Natal, South Africa (Sauria: Chamaeleonidae). *Durban Mus. Novit.* **13,** 265–269.

Reeve, W. L. (1952). Taxonomy and distribution of the horned lizards, genus *Phrynosoma. Kansas Sci. Univ. Bull.* **34,** 817–960.

Reitinger, F. F. (1978). *Common Snakes of Southeast Asia and Hong Kong.* Heinemann, Hong Kong.

Rieppel, O. (1979). A cladistic classification of primitive snakes based on skull structure. *Z. Zool. Syst. Evol. Fortsch.* **17,** 140–150.

Romer, J. D. (1963). Notes on the white-lipped pit viper, *Trimeresurus albolabris* Gray, in Hong Kong. In *Venomous and Poisonous Animals and Noxious Plants of the Pacific Region* (H. L. Keegan and W. V. Macfarlane, eds.). Macmillan Co., New York, pp. 379–384.

Rossman, D. (1973). Miscellaneous notes on the South American water snake genus *Helicops. HISS News-J* **1,** 189–191.

Rossman, D. A. (1984). *Helicops angulatus* (South American water snake) reproduction. *Herp. Review* **15,** 50.

Rossman, D. A. and Eberle, G. W. (1977). Partition of the genus *Natrix,* with preliminary observations on evolutionary trends in natricine snakes. *Herpetologica* **33,** 34–43.

Roux, J. (1913). Les reptiles de la Nouvelle-Caledonie et des iles Loyalty, Nova Caledonia. In *Rechêrches Scientifiques en Nouvelle Caledonie et aux Iles Loyalty* (F. Sarasin and J. Roux, eds.). Kreidels Verlag, Weisban.

Rustamov, A. K. and Shammakov, S. S. (1967). Ecology of the takyr *Phrynocephalus* (*Phrynocephalus helioscopus helioscopus* Pallas) in Turkmenia. *Zool. Zh.* **46,** 741–748.

Saint Girons, H. (1962). Cycle reproducteur de la vipère a cornes, *Cerastes cerastes* (L.), dans la nature et en captivité. *Bull. Soc. zool. Fr.* **87,** 41–51.

Scherpner, C. (1968). Anniellidae, Xenosauridae. In *Grzimek's Animal Life Encyclopedia.* Vol. 6. *Reptiles* (B. Grzimek, ed.). Van Nostrand-Reinhold, New York, pp. 316–320.

Schetty, P. (1951). Beobachtungen an *Vipera aspis aspis* und *Cerastes vipera*. *Aqua Terra-Z.* **4,** 83.

Schmidt, K. P. and Inger, R. F. (1957). *Living Reptiles of the World.* Hanover House, Garden City, New Jersey.

Schnurrenberger, H. (1958). Het leven van *Aspis cerastes* (Linné) in de vrije natuur. *Lacerta* **16,** 58–60.

Schwaner, T. D. and Dessauer, H. C. (1982). Comparative immunodiffusion survey of snake transferrins focused on the relationships of the natricines. *Copeia* **1982,** 541–549.

Schweizer, H. (1956). Die levante-otter von nordwet-Afrika-*Vipera lebetina mauritanica* (Guichenot). *Aqua Terra-Z.* **9,** 190–193.

Schwerdtferger, W. (1976). *Climates of Central and South America.* Vol. 12. *World Survey of Climatology.* Elsevier, Amsterdam.

Sergeev, A. M. (1940). Researches on the viviparity of reptiles. *Mosc. Soc. Nat. (Jubilee Issue),* 1–34.

Sexton, O. J. and Claypool, L. (1978). Nest sites of a northern population of an oviparous snake, *Opheodrys vernalis* (Serpentes, Colubridae). *J. nat. Hist.* **12,** 365–370.

Shammakov, S. S., Ataev, C. A., and Kamalova, Z. Y. (1973). Ecology of the transcaspian lizard *Phrynocephalus* in the Turkmen SSR. *Ekologiya* **6,** 80–83.

Shcherbak, N. N. (1971). Taxonomy of the genus *Eremias* (Sauria, Reptilia) in connection with the focuses of the desert-steppe fauna development in Palearctic. *Vest. Zool.* **2,** 48–55.

Shine, R. (1977). Reproduction in Australian elapid snakes. II. Female reproductive cycles. *Aust. J. Zool.* **25,** 655–666.

Shine, R. (1978). Propagule size and parental care: the "safe harbour" hypothesis. *J. theor. Biol.* **75,** 417–424.

Shine, R. (1979). Activity patterns in Australian elapid snakes. *Herpetologica* **35,** 1–11.

Shine, R. (1980a). "Costs" of reproduction in reptiles. *Oecologia* **46,** 92–100.

Shine, R. (1980b). Comparative ecology of three Australian snake species of the genus *Cacophis* (Serpentes: Elapidae). *Copeia* **1980,** 831–838.

Shine, R. (1981). The evolution of reptilian viviparity: a review of hypotheses and case-histories. Abstr. for *SSAR-HL Annual Meeting,* Memphis, Tennessee. Circulated 15 January 1981.

Shine, R. (1983a). Reptilian reproductive modes: the oviparity-viviparity continuum. *Herpetologica* **39,** 1–8.

Shine, R. (1983b). Reptilian viviparity in cold climates: testing the assumptions of an evolutionary hypothesis. *Oecologia* **57,** 397–405.

Shine, R. (1984). Ecology of small fossorial Australian snakes of the genera *Neelaps* and *Simoselaps* (Serpentes, Elapidae). *Spec. Publ. Mus. nat. Hist. Univ. Kansas* 10, 173–183.

Shine, R. (1985). Ecological evidence on elapid phylogeny. In *Biology of Australasian Frogs and Reptiles* (G. Grigg, R. Shine, H. Ehmann, eds.). Surrey Beatty, Sydney, in press.

Shine, R. and Berry, J. F. (1978). Climatic correlates of live-bearing in squamate reptiles. *Oecologia* **33,** 261–268.

Shine, R. and Bull, J. J. (1979). The evolution of live-bearing in lizards and snakes. *Am. Natur.* **113,** 905–923.

Smedley, N. (1931). Oviparity in a sea-snake, *Laticauda colubrina* (Schneid). *Bull. Raffles Mus.* **5,** 54–58.

Smith, H. M. (1939). The Mexican and Central American lizards of the genus *Sceloporus*. *Zool. Ser. Field Mus. Nat. Hist.* **26,** 1–397.

Smith, H. M. and Hall, W. P. (1974). Contributions to the concepts of reproductive cycles and the systematics of the *scalaris* group of the lizard genus *Sceloporus*. *Great Basin Nat.* **34,** 97–104.

Smith, H. M. and Taylor, E. H. (1950). An annotated checklist and key to the reptiles of Mexico exclusive of the snakes. *Bull. U.S. Nat. Mus.* **199**, 1–199.

Smith, H. M., Sinelnik, G., Fawcett, J. D., and Jones, R. E. (1973). The occurrence and taxonomic significance of a protracted reproductive season with alternation of ovulation in lizards. *Bull. Canad. Amphib. Rept. Conserv. Soc.* **11**, 1–5.

Smith, M. A. (1930). Ovoviviparity in sea snakes. *Nature, Lond.* **126**, 568.

Smith, M. A. (1935). *The Fauna of British India. Reptilia and Amphibia.* Vol. II, *Sauria.* Taylor and Francis, London.

Smith, M. A. (1943). *The Fauna of British India. Reptilia and Amphibia.* Vol. III, *Serpentes.* Taylor and Francis, London.

Smith, M. A. (1973). *The British Amphibians and Reptiles.* 5th Ed. Collins, London.

Sowerby, A. de C. (1930). IV. The reptiles and amphibians of the Manchurian region. In *The Naturalists in Manchuria.* Tientsin Press, Tientsin, pp. 1–41.

Spawls, S. (1973). Fossorial snake gives live birth. *Bull. East Afr. nat. Hist. Soc., September 1973,* 122.

Spellerberg, I. F. (1975). The grass snake in Britain. *Oryx* **13**, 289–300.

Spellerberg, I. F. (1976). Adaptations of reptiles to cold. In *Morphology and Biology of Reptiles* (A. Bellairs and C. B. Cox, eds.). *Linn. Soc. Symp. Ser.* **3**, 261–285.

Spellerberg, I. F. and Phelps, T. E. (1977). Biology, general ecology and behaviour of the snake, *Coronella austriaca* Laurenti. *Biol. J. Linn. Soc.* **9**, 133–164.

Stebbins, R. C. (1958). A new alligator lizard from the Panamint Mountains, Inyo County, California. *Amer. Mus. Novitates (1883),* 1–27.

Stemmler-Gyger, O. (1965). Zur Biologie der Rassen von *Echis carinatus* (Schneider) 1801. *Salamandra* **1**, 29–46.

Stemmler, O. (1969). Die Sandrasselotter aus Pakistan: *Echis carinatus sochureki* subsp. nov. *Aqua Terra* **6**, 118–125.

Stemmler, O. (1970). Uber den Geburtsvorgang bei einer Sandrasselotter *(Echis carinatus). Salamandra* **6**, 18–25.

Stemmler, O. (1971). Zur Haltung von *Echis carinatus leakeyi* Stemmler und Sochurek 1969, der Kenya-Sandrasselotter (Reptilia, Serpentes). *Zool. Garten N.F., Leipzig* **40**, 200–210.

Stettler, P. H. (1971). *Trimeresurus gramineus* und *T. popeorum* im Terrarium. *Aqua Terra-Z.* **24**, 204–207.

Steward, J. W. (1971). *The Snakes of Europe.* Fairleigh Dickinson University Press, Rutherford.

Stille, W. T. (1954). Observation on the reproduction and distribution of the green snake, *Opheodrys vernalis* (Harlan). *Nat. Hist. Misc. (Chic.)* **127**, 1–11.

Strahm, M. H. and Schwartz, A. (1977). Osteoderms in the anguid lizard subfamily Diploglossinae and their taxonomic importance. *Biotropica* **9**, 58–72.

Street, D. J. (1973). Notes on the reproduction of the southern smooth snake *(Coronella girondica). Brit. J. Herpet.* **4**, 335–337.

Strydom, D. J. (1979). The evolution of toxins found in snake venoms. In *Handbook of Experimental Pharmacology.* Vol. 52. *Snake Venoms* (C-Y. Lee, ed.). Springer-Verlag, Berlin, pp. 258–275.

Stuart, L. C. (1948). The amphibians and reptiles of Alta Verapaz, Guatemala. *Misc. Publ. Mus. Zool. Univ. Mich.* **69**, 1–109.

Sura, P. (1981). Captive breeding of *Elaphe rufodorsata* and *Rhabdophis tigrinus* from the Korean People's Democratic Republic. *Brit. Herp. Soc. Bull.* **3**, 20–24.

Takahashi, K. and Arakawa, H. (1981). Climates of Southern and Western Asia. In *World Survey of Climatology.* Vol. 9, Elsevier, Amsterdam.

Taylor, E. H. (1936). A taxonomic study of the cosmopolitan scincoid lizards of the genus

*Eumeces* with an account of the distribution and relationships of its species. *Univ. Kansas Sci. Bull.* **23,** 1–643.

Taylor, E. H. (1963). The lizards of Thailand. *Univ. Kansas Sci. Bull.* **44,** 687–1077.

Taylor, E. H. (1965). The serpents of Thailand and adjacent waters. *Univ. Kansas Sci. Bull.* **45,** 609–1096.

Telford, S. R., III (1980). Notes on *Agkistrodon himalayanus* from Pakistan's Kaghan Valley. *Copeia* **1980,** 154–155.

Terentev, P. V. and Chernov, S. A. (1965). *Key to Amphibians and Reptiles.* Translation, Israel Program for Scientific Translations, Jerusalem.

Thomas, B. W. (1980). New Zealand Gekkonidae: evolutionary trends and taxa. In *New Zealand Herpetology* (Newman, D. G., ed.). *Occ. Pap. New Zealand Wild. Serv.* (2), 333–337.

Thomas, R. A. and Dixon, J. R. (1976). A re-evaluation of the *Sceloporus scalaris* group (Sauria: Iguanidae). *Southwest. Nat.* **20,** 523–536.

Thompson, J. (1981). A study of the sources of nutrients for embryonic development in a viviparous lizard, *Sphenomorphus quoyii. Comp. Biochem. Physiol.* **70A,** 509–518.

Thompson, J. (1982). Uptake of inorganic ions from the maternal circulation during development of the embryo of a viviparous lizard, *Sphenomorphus quoyii. Comp. Biochem. Physiol,* **71A,** 107–112.

Tinkle, D. W. (1967). The life and demography of the side-blotched lizard, *Uta stansburiana. Misc. Publ. Mus. Zool., Univ. Michigan* **132,** 1–182.

Tinkle, D. W. and Gibbons, J. W. (1977). The distribution and evolution of viviparity in reptiles. *Misc. Publ. Mus. Zool., Univ. Michigan* **154,** 1–55.

Towns, D. R. (1975). Reproduction and growth of the black shore skink, *Leiolopisma suteri* (Lacertilia: Scincidae), in north-eastern New Zealand. *New Zealand J. Zool.* **2,** 409–423.

Tryon, B. W. (1979). Notes on reproduction of the lizard *Cophotis ceylonica. Brit. J. Herpet.* **5,** 845–847.

Underwood, G. (1967). *A Contribution to the Classification of Snakes.* British Museum (Natural History), London.

Underwood, G. (1971). A modern appreciation of Camp's "Classification of the lizards." In *Camp's Classification of the Lizards.* SSAR Facsimile Reprint, pp. 7–17.

Underwood, G. (1979). Classification and distribution of venomous snakes in the world. In *Handbook of Experimental Pharmacology. Snake Venoms* (C-Y. Lee, ed.). Vol. 52, Springer-Verlag, Berlin, pp. 15–40.

Van Devender, T. R. and Howard, C. W. (1973). Notes on natural nests and hatching success in the regal horned lizard *(Phrynosoma solare)* in southern Arizona. *Herpetologica* **29,** 238–239.

Van Devender, T. R. and Van Devender, W. (1975). Ecological notes on two Mexican skinks (genus *Eumeces*). *Southwest. Nat.* **20,** 279–282.

Vessey-Fitzgerald, D. F. (1958). The snakes of northern Rhodesia and the Tanganyika borderlands. *Rhodesian Sci. Assoc. Proc. Trans.* **46,** 17–102.

Visser, J. (1967). First report of ovoviviparity in a southern African amphisbaenid, *Monopeltis c. capensis. Zool. Afric.* **3,** 111–113.

Visser, J. G. J. (1972). Ontogeny of the chondrocranium of the chamaeleon, *Microsaura pumila pumila* (Daudin). *Ann. Univ. Stellenbosch* **47A,** 1–68.

Visser, J. (1975). Oviparity in two South African skinks of the genus *Mabuya,* with notes on hatching. *Zool. Afric.* **10,** 215–217.

Vitt, L. J. and Blackburn, D. G. (1983). Reproduction in the lizard *Mabuya heathi* (Scincidae): a commentary on viviparity in New World *Mabuya. Canad. J. Zool.* **61,** 2798–2806.

Vogel, Z. (1963). *Aus dem Leben der Reptilien.* Verlag Artia, Prag.

Waddick, J. W. and Smith, H. M. (1974). The significance of scale characters in evaluation of the lizard genera *Gerrhonotus, Elgaria,* and *Barisia. Great Basin Nat.* **34,** 257–266.

Wall, F. (1918). A popular treatise on the common Indian snakes. Part 25. *Jour. Bombay nat. Hist. Soc.* **25,** 375–382.

Wall, F. (1921). *Snakes of Ceylon.* Cottle, Colombo.

Wallen, C. C. (1971). Climates of Northern and Western Europe. In *World Survey of Climatology.* Vol. 5, Elsevier, Amsterdam.

Webb, G. J. W., Messel, H. and Magnusson, W. (1977). The nesting of *Crocodylus porosus* in Arnhem Land, northern Australia. *Copeia* **1977,** 238–249.

Webb, R. G. (1968). The Mexican skink *Eumeces lynxe* (Squamata, Scincidae). *Publ. Mus. Michigan State Univ.* **4,** 1–28.

Weekes, H. (1933). On the distribution, habitat and reproductive habits of certain European and Australian snakes and lizards, with particular regard to their adoption of viviparity. *Proc. Linn. Soc. New South Wales* **58,** 270–274.

Weekes, H. C. (1935). A review of placentation among reptiles with particular regard to the function and evolution of the placenta. *Proc. zool. Soc. Lond.* **1935,** 625–645.

Werler, J. E. (1951). Miscellaneous notes on the eggs and young of Texas and Mexican reptiles. *Zoologica* **36,** 37–48.

Werler, J. E. and Keegan, H. L. (1963). Venomous snakes of the Pacific area. In *Venomous and Poisonous Animals and Noxious Plants of the Pacific Region* (H. L. Keegan and W. V. Macfarlane, eds.). Pergamon Press, Oxford, pp. 219–325.

Werner, F. (1930). "Die Lurche und Kriechtiere, Brehm's Tierleben." Bibliographisches Institut, Leipzig.

Werner, Y. L. and Whitaker, A. H. (1978). Observations and comments on the body temperatures of some New Zealand reptiles. *New Zealand J. Zool.* **5,** 375–393.

Whitaker, R. (1978). *Common Indian Snakes. A Field Guide.* Macmillan Co., Delhi.

Willey, A. (1906). Viviparity of *Cophotis ceylanica* and oviparity of *Ceratophora stoddartii. Spol. Zeyl.* **3,** 235–237.

Williams, G. C. (1966). *Adaptation and Natural Selection.* Princeton University Press, Princeton, New Jersey.

Worrell, E. (1963). *Reptiles of Australia.* Angus and Robertson, Sydney.

Yaron, Z. (1972). Endocrine aspects of gestation in viviparous reptiles. *Gen. Comp. Endocrinol. Suppl.* **3,** 663–674.

Zwiefel, R. G. (1960). Reproductive biology of anurans of the arid southwest, with emphasis on adaptation of embryos to temperature. *Bull. Amer. Mus. nat. Hist.* **140,** 1–64.