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# Evolutionary Origins of Viviparity in the Reptilia.
# I. Sauria

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**Abstract.** Reproductive mode data were extracted piecemeal from the literature and superimposed over currently accepted phylogenies to permit estimation of the minimum frequencies with which viviparity (live-bearing) has evolved in lizards, as well as to facilitate analysis of factors hypothesized to influence this evolution. Viviparity has arisen on at least 45 separate occasions in the Sauria. Each of these origins is pinpointed phylogenetically as far as is now possible. Of these origins, 22 have occurred in the Scincidae, ten in the Iguanidae, five in the Anguidae, two each in the Lacertidae and Gekkonidae, and one each in the Chamaeleontidae, Xantusiidae, Agamidae, and Cordylidae. Further origins may be detected in the Scincidae, Iguanidae, and Diploglossa as phylogenetic relationships are elucidated. Over 19 % of the saurian species are live-bearing, and about 2/3 of the viviparous species are skinks.

Most of the sub-generic saurian origins of viviparity have occurred in cold climates, possibly as an adaptation to facilitate maternal thermoregulation of the developing embryos. Phylogenetic distributions of these origins are consistent with hypotheses that genetic sex-determination of the male-heterogametic type as well as a tendency towards egg retention preadapt a lineage for viviparity. Evolution of the live-bearing mode may be constrained by temperature-dependent sex determination, female heterogamety, and formation of highly calcified eggshells.

## Introduction

It has long been apparent that the viviparous (live-bearing) reproductive mode has been achieved on multiple occasions in vertebrate history. Viviparity has arisen in the squamate reptiles more frequently than in all other vertebrate groups combined (Blackburn, 1981), suggesting the Squamata to be an ideal group for studying the evolution of live-bearing. Recent advances in the morphology and physiology of non-mammalian viviparity have created the need for a phylogenetic framework within which the diversity of adaptations can be interpreted, and evolutionary trends and transformations can begin to be recognized. Such a framework can also provide a means of analyzing the various factors that have been hypothesized to preadapt and constrain lineages in the evolution of viviparity (e. g., see Blackburn, 1981, Bull, 1980; Mittwoch, 1973, 1975; Packard et al., 1977; Shine and Bull, 1979; Williams, 1966; Wourms, 1977).

The present work derives from an extensive and long-term synthesis of the literature on saurian reproduction and systematics, and constitutes the second in a proposed series of papers seeking to analyze vertebrate viviparity from an evolutionary standpoint. The purposes of this paper are as follows: 1) to pinpoint the evolutionary origins of viviparity, 2) to enumerate the minimum frequencies with which viviparity has evolved in each major lineage, 3) to summarize the evidence upon which these conclusions are based to facilitate future refinement as further information accumulates, and 4) to examine some of the factors which may influence the relative frequencies with which viviparity has arisen. It is expected that this work will provide a basis for interpreting and analyzing the considerable reproductive diversity in reptiles which is currently being documented in my laboratory and elsewhere. It is hoped that this paper will stimulate others to investigate the fascinating and significant phenomenon of reptilian viviparity.

## Terminology

Although reptilian reproductive modes have traditionally been classified as "oviparous", "viviparous", and "ovoviviparous", there has been little consensus on the proper usage of these terms. Viviparity is often defined as the ability to give birth to live young, but some restrict use of the term to cases where the mother supplies (non-yolk) nutrients during gestation, reserving the term "ovoviviparity" to instances of live-bearing in which the embryo derives all of its nutrients from yolk. Alternatively, others use the presence or absence of a shell membrane as the criterion for whether a live-bearer should be classified as viviparous or ovoviviparous. Still others apply the term "ovoviviparity" to all cases of egg retention, regardless of whether offspring are ultimately deposited as eggs or living young.

BUDKER (1958) and HOAR (1969) have shown that the distinction between viviparity and ovoviviparity is artifical and impractical in fish, and their arguments have been widely accepted. I follow the majority of recent workers on vertebrate reproductive modes in classifying organisms as either "oviparous" (egg-laying) or "viviparous" (live-bearing) regardless of the form in which nutrients for development are supplied. This system is widely applicable and upholds a biologically meaningful distinction.

## Materials and Methods

Systematic and reproductive data were gathered piecemeal from the literature Each species was classified as oviparous or viviparous as discussed above. Because much of the literature on lizard reproduction is widely scattered and difficult to obtain, of considerable value were reviews by BAUCHOT (1965), BÖHME (1981), FITCH (1970), GUILLETTE et al. (1980), GREER (1967a, 1970a, 1974, 1977), TINKLE and GIBBONS (1977), and WEEKES (1935). In all cases original sources were consulted to ensure consistency of terminology, because semantic confusion has sometimes led to discrepancies.

Reproductive mode data were superimposed over the appropriate most widely accepted generic, familial, or subordinal phylogenies. Species for which reproductive information was unavailable were assumed to exhibit the reproductive mode of their closest known relatives to ensure the most parsimonious interpretation. To avoid circularity, phylogenies which relied heavily upon reproductive mode data were avoided whenever possible. Oviparity was assumed to represent the primitive saurian condition, from which viviparity irreversibly evolves (see Fitch, 1970). A separate origin for viviparity was recorded only when the closest relatives of a monophyletic viviparous taxon or group of taxa are oviparous. Discrepant systematic interpretations seldom influenced reconstruction of the history of reproductive modes; however, in such cases the most parsimonious interpretations were adopted to ensure that the resultant estimates were conservative.

The method is best illustrated by means of an example. Reproductive bimodality (the presence of both oviparity and viviparity) in a monophyletic taxon indicates that viviparity antedated derivation of that taxon, and has evolved at least once in that group. The minimum frequency with which viviparity has evolved in a family can be determined by enumerating the number of lowest-level monophyletic taxa (e. g., genera, subgenera, species groups) in which reproductive bimodality exists. Thus four bimodal genera in a family indicate a minimum of four independent origins for viviparity. Should one of these genera contain two bimodal subgenera, a total of five origins would be indicated within the family. Should one further genus in the family be shown to consist entirely of viviparous species, a further origin of viviparity would be recorded only if the closest living relatives of that genus were oviparous.

## Results

Each known origin of viviparity is described below, along with the major supporting evidence. For further information, the reader is referred to the sources cited.

**Iguanidae.** The reproductive habits of this large family of predominately New World lizards are relatively well known. Six genera contain live-bearing species, and there have been a minimum of ten separate origins of viviparity within the family.

Most *Phrynosoma* are egg-layers. Viviparous horned lizards include *douglassi* (Goldberg, 1971; Stebbins, 1954), *ditmarsi* (Lowe and Howard, 1975), *brac~~c~~onnierii* (Montanucci, 1979), and presumably *orbiculare* (Fitch, 1970). These four live-bearing species constitute a closely related group (Presch, 1969; Montanucci, 1979), and therefore must be assumed to represent derivatives from a common viviparous ancestor.

Reproductive modes in *Sceloporus* have recently been summarized by Guillette et al. (1980). Of the 68 species, 28 are viviparous. The live-bearers fall into four species groups (as defined by Smith, 1939; Cole, 1978; Thomas and Dixon, 1976): the *formosus, grammicus, torquatus,* and *scalaris* groups. According to Smith's (1939) phylogeny, as modified by more recent work (Cole, 1970, 1971a, b, 1978), viviparity must have arisen separately in each of these four groups. The *scalaris* group contains three species, the viviparous *goldmani*, the oviparous *scalaris*, and *aeneus*, a species which has been demonstrated to exhibit viviparity and oviparity in different parts of its range (Smith and Hall, 1974; Thomas and Dixon, 1976; Guillette, 1981). Thus two separate origins for viviparity are exhibited by the *scalaris* group, bringing the total for the genus to five.

Most of the *Liolaemus* for which reproductive data are available are live-bearing (Donoso-Barros, 1966). The taxonomy of the genus is still in the alpha state (Duellman, 1979a:409), and thus more than one origin for the viviparous mode cannot be detected at present.

Viviparity has also arisen independently in the basiliscine *Corytophanes*, for but one of the three species (*pericarinatus*) is live-bearing, the others being egg-layers (ALVAREZ DEL TORO, 1960; FITCH, 1970; McCOY, 1968). *Phymaturus* is a monotypic live-bearing genus (DONOSO-BARROS, 1966). A widely accepted iguanid phylogeny (reprinted by PAULL et al., 1976) suggests that the viviparity of *Phymaturus* has arisen independently of other members of the family. One further origin is indicated in the genus *Ctenoblepharis* (sensu CEI, 1979). *C. nigriceps* is viviparous, and *reichei* (previously referred to *Phrynosaura*) is oviparous. (Note that *jamesi* has been referred to *Liolaemus* by CEI, 1979).

**Agamidae.** This large family, generally regarded as the Old World counterpart to the Iguanidae, is almost entirely oviparous. The highly arboreal *Cophotis ceylanica* is well known to be viviparous (WILLEY, 1906; SMITH, 1935). *Phrynocephalus* is widely reported to be oviparous (MINTON, 1966; RUSTAMOV and SHAMMAKOV, 1967; TERENT'EV and CHERNOV, 1949), and claims of viviparity in the genus remain unconfirmed. Both BOULENGER (1890) and SMITH (1935) reported that this desert-living genus is "said to be viviparous". SMITH (1935:228) noted that females may contain two embryos in a "well-advanced state of development", and further stated that "how far development proceeds before the young are born is not known". These statements suggest that SMITH employed the term "viviparity" to include cases of oviparous egg retention, an archaic usage in favor among certain researchers of his day. In absence of evidence to the contrary, *Phrynocephalus* is regarded here as oviparous, with viviparity having made but one appearance in the family Agamidae.

**Gekkonidae.** Over 98 % of the species in this large cosmopolitan family are oviparous. Viviparity is found in three closely related genera of the Diplodactylinae endemic to New Zealand, *Naultinus, Heteropholis,* and *Hoplodactylus* (McCANN, 1955), and has recently been discovered in *Rhacodactylus* (BARTMANN and MINUTH, 1979), a diplodactyline genus which also includes oviparous members (ROUX, 1913; MERTENS, 1964). This distribution most likely represents two gekkonid origins of the live-bearing mode.

**Xantusiidae.** All species of night lizards are believed to be viviparous. Origins of this New World family are uncertain. Although some workers have noted certain similarities to the scincomorphs (MILLER, 1966; ETHERIDGE, 1967; WEVER, 1978) or teiids (BEZY, 1972), considerable evidence has accumulated indicating that their true affinities lie with the gekkonids and pygopodids (WALLS, 1942; McDOWELL and BOGERT, 1954; HOFFSTETTER, 1962; SAVAGE, 1963; GABE and SAINT-GIRONS, 1965; 1969; SAINT-GIRONS, 1967; UNDERWOOD, 1971; NORTHCUTT, 1978). On this basis it is probably safe to assume that adoption of the viviparous mode occurred within the xantuisid basal stock after its divergence.

**Anguidae.** MESZOELY (1970) and SULLIVAN (1979) have recognized three extant subfamilies in the Anguidae. Reproductive modes have been summarized by GREER (1967) and FITCH (1970). Reproductive bimodality in each of the subfamilies indicates multiple origins of viviparity in the family.

Viviparity has apparently arisen once in the Anguinae and once in the Gerrhonotinae. Of the anguine genera, *Ophisaurus* is oviparous (CONANT and DOWNS, 1940; McCONKEY, 1954; POPE, 1929) and the monotypic *Anguis* is viviparous (SMITH, 1935). Viviparous gerrhonotines include *Gerrhonotus* subgenus *Barisia* (STEBBINS, 1958; FITCH, 1970) and *Abronia* (SMITH and ALVAREZ DEL TORO, 1963; SMITH and WILLIAMS, 1963; Werler, 1951), whereas the subgenus *Gerrhonotus* is oviparous (Greer, 1967). Undetected gerrhonotine origins for viviparity are possible, especially considering that reproductive mode was one of the features used by Stebbins (1958) in recognition of the subgenera of *Gerrhonotus*.

Live-bearing members of the Diploglossinae include *Ophiodes, Sauresia, Wetmorena* (Greer, 1967), *Celestes* (Strahm and Schwartz, 1977), and some but not all *Diploglossus* (Barbour and Ramsden, 1919; Greer, 1967; Mertens, 1939; Schmidt and Inger, 1957; Taylor, 1956). According to Strahm and Schwartz (1977), *Ophiodes* and *Celestes* arose separately from a pro-*Diploglossus* stock, *Celestes* in turn giving rise to *Sauresia* and *Wetmorena*. Thus, viviparity has probably evolved separately in the lines leading to *Ophiodes* and *Celestes*, as well as within *Diploglossus*. A minimum of three origins of the live-bearing mode are indicated for the subfamily, bringing the total for the Anguidae to five.

**Anniellidae.** This family is represented by a single genus of limbless burrowers well known for their viviparous habits (Miller, 1964). *Anniella* is probably of anguine origin (McDowell and Bogert, 1954; Bezy et al., 1977). Therefore, the viviparous mode of this genus cannot be assumed to have arisen independently of the Anguidae.

**Xenosauridae.** As presently conceived, this small family consists of two genera (McDowell and Bogert, 1954; Haas, 1960; Costelli and Hecht, 1970) of anguid derivation (Camp, 1923; Hecht and Costelli, 1969; Northcutt, 1978). Viviparity has been documented for the Mexican *Xenosaurus* (Alvarez del Toro, 1960; Fritts, 1966), but the reproductive habits of the monotypic *Shinisaurus* of China are unknown. Xenosaurids may be derived from a gerrhonotine stem (McDowell and Bogert, 1954). Thus, like the viviparity of the Annielidae, xenosaurid live-bearing may have had its origins within the Anguidae.

**Lacertidae.** All genera of this Old World group have oviparous species, but two genera also include live-bearing members. Viviparity is exhibited by at least one *Eremias* (Terent'ev and Chernov, 1949) and by many, if not all, *Lacerta vivipara* (see Tinkle and Gibbons, 1977, for a review of the reported reproductive bimodality in this species). Viviparity within these two genera clearly indicates dual origins of that mode within the Lacertidae.

**Cordylidae** (including Gerrhosauridae). As currently conceived, this family includes the subfamilies Gerrhosaurinae and Cordylinae (McDowell and Bogert, 1954; Olmo and Odierna, 1980). Oviparity is exhibited by all gerrhosaurines (FitzSimons, 1943; Loveridge, 1942; 1953). Although the cordylines are widely reported to be totally viviparous (FitzSimons, 1943; Fitch, 1970; Goin et al., 1978), *Platysaurus* is certainly oviparous (Broadley, 1974, 1978). At present it can be concluded that viviparity has arisen at least once in the family; more origins may be revealed as intergeneric relationships are elucidated.

**Scincidae.** Saurian viviparity has reached a pinnacle in this large family. Most viviparous lizards are skinks, and the most complex and effective reptile placentae known are included herein (Bauchot, 1965; Blackburn et al., 1981; Cate-Hoedmaker, 1933; Luckett, 1976; Weekes, 1930, 1935). Extensive work by Greer has done much to elucidate phylogenetic relationships and reproductive modes within the family. Greer's (1970a, 1974, 1977, 1979b) division of the Scincidae into four subfamilies is followed here. At present, 22 separate origins for the live-bearing mode are known for the family.

Because further information is likely to reveal other origins of viviparity, the available phylogenetic and reproductive mode data are considered here in some detail. The origins of skink viviparity are summarized by taxonomic group in Table 1.

**Table 1.** Minimum number of evolutionary origins of viviparity in the Scincidae. Classification follows Greer (1970a, 1974, 1977, 1979b). See text for details.

| Taxon | Minimum no. of origins |
|---|---|
| Scincinae | 3 |
| Feyliniinae | – |
| Acontinae | – |
| Lygosominae: | |
| Egernia grp. | 2 |
| Eugongylus grp. | 2 |
| Sphenomorphus grp. | 9 |
| Other Lygosominae | 6 |
| Total Lygosominae | 19 |
| Total Scincidae | 22 |

*Scincinae:* The Scincinae is a large cosmopolitan group immediately ancestral to the other skink subfamilies (Greer, 1970a). Known reproductive data bear out Greer's (1970a: 167) contention that only in *Eumeces* have reproductive modes been shown to cross (generic) taxonomic boundaries. Three origins for viviparity are known.

Oviparity is exhibited by *Nessia* (Smith, 1935), *Neoseps* (Telford, 1959), and *Scincus* (Arnold and Leviton, 1977). Viviparous genera include *Chalcides* (Giacomini, 1891, 1906; Kehl and Combescot, 1955; Mosauer, 1935), *Melanoseps* (Greer, 1970b), *Proscelotes* (Barbour and Loveridge, 1928: 166; FitzSimons, 1943: 205; Greer, 1970b), *Scelotes* (Barbour and Loveridge, 1928: 167; FitzSimons, 1943; Pienaar and FitzSimons, 1966), *Brachymeles* (Taylor, 1922), and *Typhlacontias* (Laurent, 1964). *Melanoseps, Scelotes*, and *Typhlacontias* are closely related (Greer, 1970b) and thus presumably represent one origin of the viviparous mode. Relationships within the other Old World Scincinae remain unclear.

Viviparity has apparently arisen at least twice within the scincine genus *Eumeces*. Reproductive modes are known for for most of the major species groups distinguished by Taylor (1935). Live-bearing is confined to the *lynxe* group (Tanner, 1958; Taylor, 1935; Werler, 1951), the *brevirostris* group (Axtell, 1960; Legler and Webb, 1960), and *E. copei* (Van Devender and Van Devender, 1975) of the *anthracinus* group. According to Taylor's (1935) phylogeny, the *lynxe* and *brevirostris* species groups are not closely related, and their common ancestor was oviparous. The position of *E. copei* is in some doubt (Taylor, 1935: 49). Viviparity has thus arisen at least twice in the genus, once each in the lines leading to the *lynxe* and *brevirostris* groups.

*Feyliniinae and Acontinae:* As far as is known, these small limbless African skinks are viviparous. Live-bearing acontines include *Typhlosaurus* (Brain, 1959; Broadley, 1968) and *Acontias* (FitzSimons, 1943: 244). The feyline *Feylinia* may also exhibit this mode (de Witte, 1953; Greer, 1970a). Both of these subfamilies are derived from the Scincinae (Greer, 1970a). In view of the widespread taxonomic and geographic distribution of scincine viviparity, the live-bearing of these subfamilies may have originated in the Scincinae. Independent origins of this reproductive mode cannot be assumed.

*Lygosominae:* Most of the origins of viviparity in the Scincidae have been in this large diverse subfamily, with 19 origins now known. Division of the Lygosominae follows GREER (1974, 1977, 1979b).

The *Egernia* group consists of four genera. Both *Egernia* and *Tiliqua* are viviparous (COGGER, 1975, RAWLINSON, 1971; WAITE, 1929; WEEKES, 1929; WORRELL, 1964), as is the monotypic *Corucia* (Blackburn, pers. obs.). All *Tribilonotus* are oviparous with the exception of the live-bearer *T. schmidti* (GREER and PARKER, 1968a; ROUX, 1930). Like other members of the genus, *schmidti* exhibits a variety of unique specializations which precludes immediate ancestry to other members of the *Egernia* group; specializations include volar pores, abdominal glands, and a single functional oviduct (GREER and PARKER, 1968a; PARKER, 1940; ROUX, 1930). Viviparity has probably arisen once in *Tribilonotus* and at least once in the line leading to the other genera of the group.

The *Eugongylus* group consists of two subgroups, the *Eugongylus* subgroup and the *Lampropholis* subgroup. The latter contains only oviparous forms, including *Carlia* (COGGER, 1975; GREER, 1975, 1976a), *Cophoscincopus* (GREER, 1974), *Geomyersia* (GREER and PARKER, 1968b), *Lampropholis* (CLARKE, 1965; GREER and KLUGE, 1980; WORRELL, 1964), *Menetia* (GREER, 1980; RAWLINSON, 1971), and *Panaspis* (*sensu* PERRET, 1975) (FITZSIMONS, 1943: 238; FUHN, 1972; LOVERIDGE, 1942; PERRET, 1973). Semantic confusion may have led recent reviewers to cite LOVERIDGE (1936, 1942) as authority for the presence of viviparity in *Leptosiaphos* (= *Panaspis*, in part). LOVERIDGE recorded his observations of hatching in (*Siaphos*) *kilimensis* (1936: 325) and (*Lygosoma*) *meleagris* (1942: 353). Of *graueri*, LOVERIDGE (1942: 351) reported finding females "in all stages of pregnancy", a phrase he employed in reference to both oviparous and viviparous species, including the egg-layer *meleagris* (LOVERIDGE, 1936: 325). I am unaware of any substantiated evidence of viviparity in *Panaspis* (*sensu stricto*) or elsewhere in the *Lampropholis* subgroup.

Most of the genera of the *Eugongylus* subgroup are oviparous, including *Anotis* (RAWLINSON, 1971), *Cryptoblepharus* (MCGREGOR, 1904), *Emoia* (GREER, 1968a), *Eugongylus* (GREER, 1967c), and *Morethia* (COGGER, 1975). Only *Leiolopisma* (*sensu* GREER, 1974, 1979b; see also HARDY, 1977) exhibits both modes of reproduction. Most *Leiolopisma* for which data are available are viviparous, including *aeneum* (BARWICK, 1959), *festivum* (MCCANN, 1955), *nigriplantare* (= *zelandica*) (BARWICK, 1959), *ornata* (= *Sphenomorphus pseudornatus;* see HARDY, 1977) (MCCANN, 1955), *palfreymani* (COGGER, 1975), *spenceri* (RAWLINSON, 1971), and a variety of placental forms studied by WEEKES (1927a, b, 1929, 1930, 1935) and HARRISON and WEEKES 1925), including *entrecasteauxi, metallicum, ocellata, pretiosum,* and *"weeksae"*. (RAWLINSON 1974b doubts the correct identification of this last form and suggests it to be an as yet undescribed species. Note also the alternative placement of some of these species by HARDY, 1977, and RAWLINSON, 1974b). The only known oviparous *Leiolopisma* seem to be *suteri* (WHITAKER, 1968) and *trilineatum* (RAWLINSON, 1974a). (GREER, 1974, has referred to oviparous *delicata* and *mustelinum* to *Lampropholis.*)

Reconstruction of the evolutionary history of reproductive modes in the genus *Leiolopisma* indicates a minimum of two origins for the viviparous mode. Phylogenies presented by HARDY (1977, 1979) require separate origins of live-bearing in the *palfreymani – spenceri – aeneum – ornatum* lineage and in the line leading to other *Leiolopisma*. Reproductive bimodality in *Leiolopisma* of both New Zealand and Tasmania was interpreted by SHINE and BULL (1979) as evidence for separate origins of live-bearing on those two islands. However, considerable biogeographic and systematic evidence indicate that the species of these two islands represent multiple invasions rather than monophyletic lineages (BULL and WHITAKER, 1975; HARDY, 1977; RAWLINSON, 1974a).

The *Sphenomorphus* group contains more origins for viviparity than the other groups of Scincidae, as indicated by the high amount of intrageneric reproductive bimodality. Oviparous genera include *Ctenotus* (COGGER, 1975; RANKIN and GILLAM, 1979), *Eremiascincus* (GREER, 1979a), and *Saiphos* (BUSTARD, 1964; COGGER, 1967). Known viviparous genera include *Hemiergis* (COPLAND, 1945; SMYTH and SMITH, 1968; WEEKES, 1929), *Isopachys* (= *Ophioscincus*, in part) (TAYLOR, 1963), and *Trophidophorus* (INGER and GREENBERG, 1966; SMITH, 1935). Genera containing both oviparous and viviparous species include *Ablepharus* (FUHN, 1969, 1970), *Anamolopus* (SHINE and BULL, 1979; COGGER, 1975), *Lerista* (GREER, 1967b, 1979d; RAWLINSON, 1971, 1974a), *Lipinia* (BRONGERSMA, 1942: 45; BROWN and ALCALA, 1956; BROWN and FEHLMAN, 1958; GREER, 1974; OLIVER and SHAW, 1953), *Lobulia* (GREER, 1974), *Prasinohaema* (GREER, 1974), *Scincella* (*sensu* GREER, 1974) (JOHNSON, 1953; SMITH, 1935), and two of the species groups of the genus *Sphenomorphus*, the *fasciatus* species group (BUSTARD, 1964; GREER, 1973, 1979c; GREER and PARKER, 1967a; WORRELL, 1964) and the *variegatus* species group (*sensu* GREER, 1967b; 1974) (ALVAREZ DEL TORO, 1960; GREENE, 1969; FITCH, 1970).

The remaining lygosomine skinks are *Lygosoma* and its allies. Oviparous genera include *Apterygodon* (GREER, 1970c), *Dasia* (DERANIYAGALA, 1953; SMITH, 1935), *Lamprolepis* (GREER, 1970; HEDIGER, 1934), and *Macroscincus* (GREER, 1976; PERACCA, 1891a, b). Two genera exhibit reproductive bimodality, *Lygosoma* and *Mabuya*. GREER (1977) redefined *Lygosoma* and summarized its reproductive modes. He concluded that viviparity may have evolved twice in the genus, once in the line leading to *tannae* and *mabuiiforme*, and once in the line leading to *vinciguerrae* and *laeviceps*. Multiple origins are also apparent in *Mabuya*. According to HORTON'S (1974) phylogenies, viviparity has evolved four times in the genus, twice in Asia (*aurata* and *multifasciata* lineages) and twice in Africa (the *striata* complex and the *brevicollis – megalura* line). Further work on the genus may be necessary to confirm these relationships and to determine whether independent origin of viviparity has occurred in the live-bearing *Mabuya* of the New World, and the~~ir~~ derivative *Eumecia*.

**Other families.** Viviparity has not been reported in the remaining families of lizards. The following are believed to include only egg-layers: Teiidae (BELLAIRS, 1970; FITCH, 1970), Pygopodidae (COGGER, 1975; KLUGE, 1976a), Varanidae (FITZSIMONS, 1943; MINTON, 1966), Dibamidae (DOWLING and DUELLMAN, 1974–1978), and Helodermatidae (ALVAREZ DEL TORO, 1960; FUNK, 1966). Reproduction in the monotypic Lanthanotidae is poorly known.

## Discussion

Superimposition of reproductive and phylogenetic data indicates that viviparity has evolved on a minimum of 45 separate occasions in the Sauria. This constitutes about 44 % of the origins of viviparity known to have occurred in vertebrate history (BLACKBURN, 1981, in prep.). As Table 2 shows, the saurian origins are distributed discontinuously throughout the suborder. About 1/2 (22) of the known saurian origins of viviparity have occurred in the Scincidae, and another 1/3 (15) of them have been in the Iguanidae and Anguidae, leaving only eight origins scattered among the remaining 14 families. Undetected origins seem likely, particularly in the Scincidae, the diploglossan anguinomorphs, and possibly the Cordylidae and the iguanid genus *Liolaemus*. Over 19 % of the lizard species are viviparous, and about 2/3 of these live-bearing species are skinks. The percentage of live-bearing species in each family varies considerably.

The approximate geographic location for many of the origins of viviparity can be inferred from present species distributions. As Table 3 shows, these origins exhibit a worldwide distribution, with a preponderance of them occurring in the Australo-Pacific region, an area where skinks are particularly abundant.

Although a complete analysis of the factors influencing the evolution of viviparity is beyond the scope of this paper, a few of the hypotheses particularly relevant to lizards shall be considered. Presumably, the frequency with which viviparity has evolved in a reproductively bimodal taxon is a function of some or all of the following factors: the size of the taxon, the operating selection pressures, and the degree to which the taxon is evolutionarily preadapted for viviparity. Although these factors may exert a collective influence, they shall be considered individually for the purpose of analysis.

**Table 2.** Minimum number of evolutionary origins of viviparity in the Sauria. All estimates are based upon current knowledge of reproductive modes and phylogenetic relationships. Data on sex determination mechanisms are derived from KING (1977) and BULL (1980). Egg retention data is from SHINE and BULL (1979). Numbers of species and genera are from DUELLMAN (1979b).

| family | origins of viviparity | genera | species | viviparous species | egg retention | sex determination mechanisms |
|---|---|---|---|---|---|---|
| Iguanidae | 10 | 55 | 608 | 14 % | yes | XX/XY |
| Agamidae | 1 | 36 | 320 | < 1 % | rare[a] | TSD |
| Chamaeleontidae | 1 | 2 | 88 | 17 % | no | ? |
| Gekkonidae | 2 | 86 | 733 | 1 % | no | ZZ/ZW; TSD |
| Pygopodidae | – | 6 | 29 | – | no | XX/XY |
| Xantusiidae | 1 | 4 | 14 | 100 % | – | ? |
| Teiidae | – | 38 | 198 | – | no | XX/XY |
| Lacertidae | 2 | 27 | 210 | 1 % | rare[a] | ZZ/ZW |
| Cordylidae | 1 | 10 | 54 | 39 % | no | ? |
| Scincidae | 22 | 85 | 1029 | 43 % | yes | XX/XY |
| Dibamidae | – | 2 | 4 | – | no | ? |
| Anguidae | 5 | 6 | 74 | 69 % | yes | ? |
| Xenosauridae | – | 2 | 4 | 100 % | – | ? |
| Anniellidae | – | 1 | 2 | 100 % | – | ? |
| Helodermatidae | – | 1 | 2 | – | ? | ? |
| Varanidae | – | 1 | 30 | – | no | ZZ/ZW |
| Lanthanotidae | – | 1 | 1 | – | no | ? |
| Total Sauria | 45 | 363 | 3307 | 19.8 % | | |

[a] reported in only one genus

**Table 3.** Geographic distribution of saurian origins of viviparity. Approximate sites of origin are inferred from present species distributions.

| Region | Minimum no. of origins |
|---|---|
| Nearctic | 6 |
| Neotropical | 7 |
| Unclassified New World | 4 |
| Palearctic | 4 |
| Ethiopian | 5 |
| Oriental | 1 |
| Australo-Pacific | 12 |
| Unclassified Old World | 4 |
| Other | 2 |
| Total | 45 |

**Taxon size:** If (primitively) oviparous groups were equally preadapted for viviparity and subject to equivalent selective pressures, the number of origins of the live-bearing mode would merely reflect the size of that group. Table 2 indicates that this is generally not the case. Although absence of viviparity in the Helodermatidae and Dibamidae may relate to the small size of these families (only one out of six saurian genera contain live-bearing species), this explanation cannot account for the scarcity or absence of viviparity in such large groups as the Teiidae, Lacertidae, Agamidae, and Gekkonidae. Nor can the relative frequencies with which viviparity has evolved in the Scincidae and Anguidae be attributed solely to size of these families. Clearly other factors are involved.

**Selection pressures:** As a reproductive strategy, viviparity may be associated with a variety of possible advantages and disadvantages (for recent reviews see TINKLE and GIBBONS, 1977; SHINE and BULL, 1979; GUILLETTE et al., 1980). Only individual cost-benefit analyses will reveal the extent to which a factor is operative in each case. Nonetheless, a few major generalities are possible.

The selective agent most frequently hypothesized as leading to the evolution of viviparity in reptiles is cold climate. A commonly invoked explanation is that viviparity allows favorable thermoregulation of developing embryos by the mother. Many studies have suggested that there is a higher proportion of viviparous species in the cooler climates of high altitudes and latitudes (e.g. GREENE, 1970; GREER, 1968c; GUILLETTE et al., 1980; PACKARD, 1966; TINKLE and GIBBONS, 1977; but, see SHINE and BERRY, 1978). Although some of these authors have interpreted this distribution as an indication that viviparity has evolved under cold conditions, this correlation need not imply a causal relationship; a higher proportion of live-bearers in cold environments may merely represent differential survival rather than indicating the conditions under which viviparity actually arose. These ideas have been discussed by TINKLE and GIBBONS (1977) and PACKARD et al. (1977), among others.

SHINE and BULL (1979) argued that species derived from relatively recent (= subgeneric) origins of viviparity are likely to be found in ecological conditions similar to those under which live-bearing actually evolved. Their data suggest that at least 82 % of the sub-generic saurian origins of live-bearing distinguished by them have occurred in cold climates[1]. The methodology of the present analysis allows a more precise phylogenetic, geographic, and ecological definition of each of the origins of viviparity, and also includes data from generic and supra-generic taxonomic levels. Assuming that the ecologies of species derived from recent origins of viviparity reflect the environments within which this mode was adopted, at least 68 % of the sub-generic origins of viviparity have occurred in cold climates. Ecological data are lacking for most of the remaining sub-generic origins, although aridity may have played an important role in the two origins in *Lygosoma* (GREER, 1977: 525). Thus, I support SHINE and BULL's contention that cold environments have favored the evolution of viviparity and suggest that the majority of the known sub-generic origins can be so explained. Similar inferences are warranted for some of the higher level origins in which the derivate species have retained a restricted distribution in cold environments, including the iguanid *Phymaturus*, the anguid *Anguis*, and the live bearing geckoes of New Zealand.

The fact that viviparity frequently evolves in cold environments provides a plausible explanation for the large number of origins in widespread groups such as the Iguanidae,

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[1] My analysis indicates that a number of these "origins" actually represent polyphyletic groupings. Our data also differ in many other respects; e.g., I am skeptical of the evidence for viviparity in *Sceloporus variabilis* (see TINKLE and GIBBONS, 1977) and *Leptosiaphos* (see above), I have located no evidence that live-bearing *Phrynocephalus* are found in cold climates, etc.

Scincidae, and Anguidae, and the absence of viviparity in families not well represented in cold environments (e.g., Varanidae and Heloderm~~itade~~atidae). However such an explanation is insufficient to account for its scarcity in such ecologically diverse families such as the Gekkonidae, Teiidae, Lacertidae, and Agamidae. The taxonomic distribution of viviparity suggests that evolutionary preadaptations and constraints may play at least as important a role in determining the frequencies with which viviparity evolves as do environmental factors.

**Preadaptations and constraints:** Of the various sets of preadaptations and constraints which have been suggested to influence the evolution of viviparity in vertebrates (see BLACKBURN, 1981), the three most plausible for the Sauria are 1) proclivity towards egg retention, 2) type of eggshell, and 3) mode of sex determination.

1) PACKARD et al. (1977) presented a widely accepted theoretical model in which an increase in the length of time the eggs reside in the oviduct can constitute an initial step towards the evolution of live-bearing. As a consequence of an evolutionary trend towards increase in the duration of egg retention, considerable development may precede oviposition. The culmination of this trend is a non-nutritive viviparity involving in utero hatching (the "ovoviviparity" of some authors). The selective pressures for egg retention may be similar to those for simple viviparity, for both phenomena are correlated with cold climates (see SHINE and BULL, 1979); thus, egg retention may allow embryonic development to proceed at optimum temperatures due to maternal thermoregulation.

If, as generally supposed, egg retention is an intermediate stage in the development of live-bearing, one might expect that taxonomic groups in which viviparity has frequently evolved would be those in which egg retention has often appeared. Conversely, taxa lacking egg retention of even a moderate duration could be predicted to have seldom or never evolved viviparity. The literature on egg retention (see SHINE and BULL, 1979, for references) upholds this correlation (see Table 2). The Scincidae and Iguanidae, the families in which most of the saurian origins of viviparity have occurred, are the families in which egg retention is taxonomically most widespread. Furthermore, egg retention is rare or absent in families with little or no viviparity; for example it has never been reported in such major groups as the Gekkonidae, Teiidae, Varanidae, and Pygopodidae, and has been observed in but one species of Agamidae and one genus of Lacertidae *(Lacerta).*

Given that egg retention. like viviparity, is adaptive in cold climates, it is difficult to explain its absence in large oviparous families common in such environments. One possibility is that herpetologists have merely overlooked egg retention in these families; this seems unlikely, if for no other reason than that these families are well represented in the herpetological literature. Alternatively, certain disadvantages of egg retention (e.g., decrease in fecundity, increase in mortality) may outweigh its potential advantages in these taxa; however, it is difficult to conceive how these factors would produce such striking discontinuities at familial levels. A possible explanation is that certain groups are more predisposed than others towards egg retention, and thus viviparity. No doubt, egg retention ability is heritable. Unfortunately, little is known about the chain of events occurring between ovulation and oviposition (or parturition) other than the likelihood that posterior pituitary hormones induce oviduct contractions (LA POINTE, 1977; GUILLETTE, 1979). Nor is the alteration of the mechanism of oviposition by which egg retention is accomplished currently understood; presumably such disruption could operate at the level of the oviduct, the hypophysis, or both. It could prove most illuminating, therefore, to compare the mechanisms of oviposition of wholly oviparous families such as the Teiidae with those of reproductively bimodal families in which viviparity is common (e.g., Iguanidae).

2) The theoretical model presented by PACKARD et al. (1977) suggests that because gas exchange is probably the major problem of intra-uterine existence, the transition to viviparity involves evolutionary reduction in the thickness and degree of calcification of the eggshell as a means of decreasing the diffusion distance between fetal and maternal blood vessels. This trend towards thinner eggshells seems feasible for an egg-retaining squamate in which the shell's major function, protection of the embryo, is either postponed or supplanted. However, in some reptiles, the eggshell performs an additional function. Whereas the eggshells of crocodilians and many turtles are hard and heavily impregnated with calcium deposits, the shells of most other squamate eggs are parchment-like and thinly calcified (BELLAIRS, 1970). PACKARD et al. pointed out that in contrast to squamates in which the yolk constitutes the major store of calcium for the developing embryo, turtles and crocodiles use the heavily calcified shell as the source of developmental calcium. These authors suggested that crocodilians and turtles lack the evolutionary potential for viviparity, perhaps due to an inability to accomplish eggshell reduction without depriving the embryo of its calcium source. In view of this suggestion, it is interesting to note that those squamate groups which produce heavily calcified eggshells, the dibamidae (BOULENGER, 1912; LOVERIDGE, 1945) and the large gekkonid subfamilies Sphaerodactylinae and Gekkoninae (BUSTARD, 1968; WERNER, 1972), are entirely oviparous. The only viviparous geckoes belong to the Diplodactylinae (*sensu* KLUGE, 1967), a small primitive subfamily whose oviparous members lay parchment-shelled eggs (BUSTARD, 1968) as do oviparous representatives of other reproductively bimodal taxa. Further evaluation of the hypothesis requires additional information as to the source of developmental calcium in dibamids and advanced geckoes; JENKINS and SIMKISS (1968) suggested that the yolk contains sufficient calcium for development in the gekkonine *Hemidactylus turcicus,* despite its highly calcified shell[2].

There is an alternative reasion why a capacity for producing highly calcified eggshells might be incompatible with viviparity. Shell membranes of viviparous squamates commonly thin and/or degenerate during gestation, particularly in later stages when metabolic demands are increased (WEEKES, 1935; pers. obs.). A highly calcified shell would clearly prevent significant gas exchange in utero. Thinning of the shell in dibamids and (most) geckoes would require suspension of shell mineral deposition and/or an additional mechanism for substantial uterine calcium resorption; difficulty in accomplishing these would select against egg retention.

3) Sex determination has been reviewed by BULL (1980), MITTWOCH (1973), and OHNO (1967; 1979). In temperature-dependent sex determination (TSD), the temperature at which development takes place during a certain "sensitive period" controls whether the offspring becomes male or female. This mode contrasts with genotypic

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[2] This conclusion is based primarily upon one specimen; data for a second specimen are equivocal.

(chromosomal) sex determination (GSD) in which the sex of the offspring is fixed by the genotype. GSD operates through either a male heterogametic (XX–XY) or a female heterogametic (ZZ–ZW) system.

Bull (1980) hypothesized that TSD might be incompatible with viviparity because maternal incubation of all embryos under similar thermal conditions could lead to a skewed sex ratio. If this proposal is correct, viviparity would be expected to evolve preferentially in lineages exhibiting alternative modes of sex determination. Furthermore, the time interval of egg retention would never be expected to overlap the period during which sex determination occurs. There are a number of theoretical objections to this hypothesis, but their validity remains untested (Blackburn, ms.). Nonetheless, it is interesting to note that TSD has only been demonstrated in species of Agamidae and Gekkonidae (see Bull, 1980, for references), groups in which there have been exceptionally few origins of viviparity; moreover, all origins for viviparity have occurred in taxa distantly related to those shown to exhibit TSD. It is also known that TSD does not operate in *Lacerta viridis* (Raynaud and Pieau, 1972), a congener to the live-bearer *L. vivipara*. Evaluation of Bull's hypothesis in lizards requires extensive information on the origins of viviparity, the distribution of TSD, and the timing of saurian sensitive periods; the last two of these are still poorly known.

Mittwoch (1967, 1973, 1975) suggested that male heterogamety was required for mammalian viviparity because male embryos would need a Y chromosome to counter the potentially feminizing effects of maternal hormones upon their sexual differentiation. In contrast, she suggested, female heterogamety is possible in birds because the oviparous avian embryo is isolated from the maternal hormonal environment well before sexual differentiation occurs. If this argument is valid, male heterogamety could preadapt a lineage for viviparity and/or egg retention, whereas female heterogamety could constrain it from evolving these reproductive modes. This hypothesis can be evaluated by testing the prediction that viviparity has evolved more frequently in lineages exhibiting male heterogamety than in those with female heterogamety.

Heterogamety is only detectable as visible chromosomal heteromorphism in its more advanced stages; less differentiated sex chromosomes may not be visibly distinct (Ohno, 1967; Bull, 1980). Nonetheless, the impracticality of techniques used in anamniotes renders chromosome morphology the chief criterion of heterogamety in reptiles. In a family for which non-GSD is primitive, male and female heterogamety should evolve with approximately equal frequencies. If a group exhibits multiple origins of heteromorphism of but one type (e.g., male), this may represent parallel derivation from a single underlying heterogametic condition. For example, most of the iguanids examined have no visible sex chromosomes, yet on each of the occasions in which heteromorphism has evolved, it has been of the male (XX-XY) type (see Gorman, 1973; King, 1977). A likely explanation for this apparent parallelism is that male heteromorphism is primitive for the family. Sex chromosomes have been observed in seven families of lizards, and each of these families exhibits but one type of GSD. For the present analysis, heterogamety is assumed to have evolved at or near familial taxonomic levels in lizards. The Gekkonidae are the only family for which this assumption is known to be invalid; GSD has been demonstrated in two genera of the Gekkoninae and TSD in a representative of the Eublepharinae (Bull, 1980), suggesting that sex determination mechanisms may differ at or below the subfamilial level.

As Table 2 shows, the distribution of GSD and reproductive modes is consistent with the prediction that viviparity should evolve preferentially in lineages exhibiting male heterogamety. Most of the origins of viviparity have occurred in two families with male heterogamety, the Scincidae and the Iguanidae. Moreover, families with female heterogamety, including the Lacertidae, Varanidae, and Gekkonidae, have seldom or never evolved viviparity. Furthermore, the live-bearing gekkonids belong to a subfamily but distantly related (Kluge, 1967) to those with female heterogamety. On the other hand, female heterogamety has been demonstrated in both of the live-bearing genera of Lacertidae.

The taxonomic distribution of viviparity in the Sauria is consistent with hypotheses invoking the evolutionary constraints imposed by female heterogamety, TSD, highly calcified eggshells, and egg retention ability. However, full evaluation of these hypothese will require further information on egg retention mechanics, embryonic calcium sources, and sex determination mechanisms in lizards lacking sex chromosomal heteromorphism. Consideration of the general applicability of these hypotheses to other vertebrates is deferred to a forthcoming paper.

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Insert to page 188:

Chamaeleontidae. Viviparity in the Old World chameleons is confined to two closely related species groups of Chamaeleo (Hillenius, 1959, 1963; Klaver, 1973, 1979). These live-bearers constitute the East African bitaeniatus group (Bustard, 1965, 1966; Hillenius, 1959; Loveridge, 1923, 1959; Rand, 1963) and the South African pumilis (= Microsaura) group (Atsatt, 1953; Bustard, 1955, 1966; Hillenius, 1959). Viviparity seems, therefore, to have evolved but once in the family.