

SQUAMATE REPTILES AS MODEL ORGANISMS FOR THE EVOLUTION OF VIVIPARITY

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ABSTRACT: For over a century, research has been conducted on squamates in order to reveal how viviparity has evolved in mammals and other vertebrates. The recent proliferation of studies has yielded much information on anatomical, physiological, ecological, and evolutionary aspects, allowing a reassessment of squamates as model organisms for the study of viviparity. Strong support for the “squamate model” comes from phylogenetic analyses that have shown that squamates have evolved viviparity with great frequency (> 108 origins), at low taxonomic levels, and in geologically recent times. However, available data also indicate that viviparity has evolved by different chronologies and mechanisms in squamates, fishes, and mammals. Further, generalizations about squamates are difficult to make, given the diverse mechanisms by which they achieve viviparity. Thus, similarities between squamates must be demonstrated empirically, and generalizations should be based on quantitative, phylogenetic analyses of multiple lineages. Explanations for similarities between squamate clades can invoke such concepts as evolutionary constraints, exaptations, and selection pressures, and should distinguish between adaptations, correlated attributes, and features that predate viviparity. However, homocentric assumptions of an orthogenetic transformation towards the eutherian condition should be abandoned, along with untested assumptions that viviparity squamates and mammals is similar. The value of the squamate model ultimately may lie in insights it provides into physiological problems rather than in universality of specific mechanisms that have evolved to meet those problems.

Key words: Animal models; Evolution; Mammals; Placentation; Reproduction; Squamates; Viviparity.

FOR MORE THAN A CENTURY, biologists have studied viviparity in squamate reptiles in hopes of shedding light on the evolution of viviparity in other vertebrates (Giacomini, 1891; Weekes, 1930). The prospects of explaining mammalian evolution, or at least providing general information applicable to non-reptilian species, continues to be offered as a major justification for reptilian studies. Accordingly, the assumption that information is generalizable across higher taxa provides a basis for the “squamate model” for viviparity. However, the fact that viviparity in lizards and snakes has resulted from more than a hundred separate evolutionary transformations (Blackburn, 1999) makes it risky to assume that a single set of functional and evolutionary explanations will suffice for squamates, much less for other viviparous vertebrates. Thus, if the squamate model is to be applied appropriately, we must understand both its potential and its limitations, features that can only be determined by studying multiple clades.

The symposium from which this review emanates has brought together researchers from five continents, representing the most diverse group ever assembled of biologists interested in squamate viviparity. This review summarizes the historical development of the squamate model for viviparity, and evaluates the limitations and potential utility of this model. In addition, this paper considers how and why general explanations should be possible within the order Squamata, given that its lineages have evolved their viviparity independently. A conceptual framework is offered to analyze patterns of similarity that invokes selection pressures, exaptations, and constraints, as well as convergent adaptations that are best able to be analyzed through quantitative, phylogenetic analysis.

DEVELOPMENT OF THE SQUAMATE MODEL

Historical Background

The idea that studies of reproduction in viviparous lizards and snakes can provide insight into mammals and other vertebrates dates to the late 1800s. From studies of viviparous skinks, Haacke (1888) concluded that squamates had evolved viviparity and an

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intimate relationship between fetal–maternal tissues independently of mammals. Ercole Giacomini (1891, 1893, 1906), whose extensive work is seldom read and little-appreciated, noted that placental membranes of lizards show striking parallels to those of mammals, and exceed eutherians in the range of variation. Based on Giacomini's observations, subsequent biologists emphasized that live-bearing squamates are important species for studies of embryology and viviparity (Flynn, 1923; Graham Kerr, 1919).

Claire Hazel Weekes (1927*a, b*, 1929, 1930, 1935) contributed valuably to our understanding of squamate viviparity, through studies of placental histology that established the conceptual basis for all subsequent work in the field. Weekes (1933, 1934) also published comparative studies on the corpus luteum, and analyses of the ecological distribution of viviparous species. Her ideas about parallels between squamates and mammals are particularly relevant in the present context. Harrison and Weekes (1925) proposed that placentas in viviparous squamates and therians evolved in three successive stages—the chorionic placenta, yolk sac placenta, and allanto-placenta. These authors did not identify squamate species representing each of these hypothetical stages. Rather, in accord with Haeckel's (1902) biogenetic law, Harrison and Weekes assumed that the phylogeny of placental organs reflected their ontogeny. In subsequent work, Weekes abandoned this phylogeny, instead emphasizing multiple origins of viviparity and evolutionary transformations between allanto-placental types. By her last work on the subject, Weekes (1935) considered that data on squamates might provide insight into mammal evolution, but without assuming that lineages of the two groups evolved identically. Data on viviparous squamates was deemed relevant to therian mammals because species of the two groups had similar functional problems to solve.

Recognition of ecological implications has played an important role in stimulating research on squamate viviparity. Several early publications noted that viviparity was associated with cold climates of high altitudes and/or high latitudes (e.g., Gadow, 1910; Mell,

1929; Weekes, 1933). This reason given for this association was that environmental conditions had selected for viviparity. However, as later researchers pointed out, a current association does not necessarily indicate the conditions under which viviparity originated, much less a causal relationship (Blackburn, 2000; Packard, 1966; Shine and Bull, 1979). A wide variety of other early studies explored structural and functional aspects of viviparity, including features of placentation, gestation, and parturition (see Blackburn, 1993*a*; Jones and Baxter, 1991; Stewart, 1993, 1997; Yaron, 1985).

Recent Advances

For about 75 years after Giacomini's earliest work, squamate viviparity remained a sort of curiosity—a textbook case of convergent evolution, but a simple phenomenon as compared to that of eutherian mammals. However, by the 1970's, squamate viviparity began to receive increased attention—first from the standpoints of ecology and evolution, and soon thereafter, through anatomical and physiological studies (Blackburn, 2000). Research subsequently proliferated to include descriptive accounts, experimental studies, and theoretical analyses. The reptilian work has been paralleled by extensive research on anamniotes (see reviews by Hamlett et al., 1993; Wake, 1982, 1993; Wourms, 1981; Wourms et al., 1988).

Two conceptual advances contributed importantly to growth of the squamate model for viviparity. The first was the development of life history theory, under which viviparity was viewed as a reproductive strategy that should evolve only when the benefits exceed the costs (Fitch, 1970; Packard et al., 1977; Tinkle et al., 1970; Tinkle and Gibbons, 1977). Accordingly, rather than being viewed as inherently adaptive, reptilian viviparity came to be viewed in terms of pressures, costs, and benefits. The second advance was represented by application of phylogenetic analysis to evolutionary questions. Initially this approach allowed definition of the independent evolutionary origins of viviparity (Blackburn, 1982, 1985; Shine, 1985). This approach has since been applied to a variety of evolutionary questions.

Contemporary Perspectives

Viviparity in squamates has come to be recognized as a complex phenomenon that must be understood in terms of many different aspects. Viviparous reproduction entails anatomical and physiological specializations through which pregnant females maintain their developing embryos, endocrinological features through which ovarian and oviductal function are controlled, and molecular and biochemical specializations associated with embryonic nutrition and maternal-fetal gas exchange. In addition, viviparity has ecological and behavioral implications, given strong evidence that it has evolved in cold climates due to its thermoregulatory benefits (Andrews, 2000; Andrews et al., 1997; Shine, 1983, 1985, 1989, 1995). Finally, viviparity has important evolutionary implications, given its convergent evolution in squamates, chondrichthyans, osteichthyans, urodeles, anurans, caecilians, mammals, and a variety of invertebrate taxa (Hogarth, 1976).

Accordingly, one feature of contemporary research on squamate viviparity is its breadth and diversity, since it ranges from descriptive to experimental work in all relevant areas. Descriptive and experimental work includes studies on structure and function of the oviduct (for reviews see Blackburn, 1998*b*; Girling, 2002) and of placental membranes (Blackburn, 1993*a*; Stewart, 1993; Stewart and Thompson, 2000). Such work also includes research on placental gas exchange (Ingermann, 1992), fetal nutrition and placental transport (Speake and Thompson, 2000; Stewart and Thompson, 2000; Swain and Jones, 1997; Thompson and Speake, 2002; Thompson et al., 2000), and the physiology of gestation and parturition (Jones and Baxter, 1991). Other work has focused on reproductive, physiological, and behavioral ecology (e.g., Andrews et al., 1999; Dunham et al., 1988; Flemming, 1993, 1994; Schwarzkopf and Shine, 1991; Shine and Downes, 1999).

A second feature of current research on viviparity is its multidisciplinary, integrative nature. Instead of defining themselves strictly as anatomists, physiologists, and ecologists, current researchers commonly use whatever techniques are needed for the questions to be answered. For example, some contributors to

our symposium began their careers as field biologists, and retooled themselves to learn sophisticated anatomical and physiological techniques in order to answer functional-evolutionary questions. Further, close collaborations between researchers with diverse approaches are common.

A third characteristic of contemporary approaches to the subject is the use of phylogenetic analyses to clarify evolutionary patterns. This approach has permitted the independent evolutionary origins of reptilian viviparity to be defined and quantified (Blackburn, 1999; Shine, 1985). It also has allowed tests of evolutionary hypotheses about selective pressures, constraints, and historical sequences (Blackburn, 2005*a*; Mendez de la Cruz, 1998; Shine, 1985; Shine and Lee, 1999; Stewart and Thompson, 1996, 2003). A fourth aspect of ongoing research on viviparity is the use of empirical and theoretical work to test evolutionary hypotheses and assumptions. Numerous examples can be cited (e.g., Andrews, 1997, 2000; Andrews et al., 1999; Arrayago et al., 1996; Blackburn, 1995; Heulin et al., 1989, 1991; Qualls and Shine, 1996, 1998; Shine, 1983, 1995; Swain and Jones, 2000; Thompson et al., 2002). As evident from such studies, traditional divisions have broken down between field and laboratory biology, and between descriptive and experimental work—reflecting the integrative nature of current research in the field.

Researchers commonly have justified studies of viviparous squamates on the basis that they provide a model for mammal evolution. Such justification is a frequent feature of the introductions of papers in the primary literature, review articles, and grant proposals (including those of the present author). Interestingly, the conclusions of such papers seldom if ever mention insights applicable to the mammalian situation; rather, such insights are always a promise of future study. Also interesting is the fact that biologists who study mammals never consider that their work is justified because of the information it will provide about reptiles. Studies of mammals apparently have always provided their own justification, given traditional placement of the human species among mammals and as the pinnacle of organismal evolution

(Haeckel, 1899; Ruse, 1996). In any case, the extent to which viviparity in squamates is relevant to mammals (and vice versa) remains to be demonstrated.

POTENTIAL OF THE SQUAMATE MODEL

Squamate reptiles are ideal for studies on viviparity, for at least five major reasons. First, as phylogenetic analysis has demonstrated, viviparity has evolved convergently more than 108 times in the order Squamata, a figure representing 76% of the 141 vertebrate origins now recognizable (Blackburn, 1999, 2005*b*). Thus, viviparity has evolved more frequently in squamates than in all other vertebrates combined. Second, viviparity occurs in about 20% of the extant squamate species (Blackburn, 1985), representing a total of perhaps 1500 species (see EMBL Reptile Data Base for species numbers). In terms of numbers of viviparous species, squamates are second only to the eutherian mammals among vertebrates. Third, in contrast to mammalian viviparity (which arose in the Cretaceous), viviparity in squamates commonly has evolved relatively recently—e.g., in the late Pleistocene (Camarillo, 1990; Heulin et al., 1993). Consequently, good prospects exist for reconstructing the original ecological, morphological, and physiological attributes of lineages in which this pattern has arisen. Fourth, squamate viviparity often has evolved at low taxonomic levels—i.e., the level of genus and species (Blackburn, 1999; Shine 1985); in fact, multiple species have been demonstrated to have both oviparous and viviparous populations (Braña and Bea, 1987; Qualls et al., 1995; Smith and Shine, 1997). As a result we can compare closely-related forms to understand the evolutionary transformation between oviparity and viviparity (e.g., Qualls and Shine, 1998; Stewart et al., 2004*a*). Likewise, experimental studies, including breeding between oviparous and viviparous individuals, show promise in revealing genetic and functional aspects of the transformation (Heulin et al., 1989, 1992).

Fifth, in theory, information on squamates may offer insight into the evolution of viviparity in other vertebrates. Viviparous squamates all have features found in other viviparous vertebrates, such as internal fertil-

ization, Mullerian-duct derivatives (which deposit eggshells and house eggs and fetuses), and such endocrinological features as control of female reproduction via progesterone and estrogenic hormones. Further, squamates, like eutherian mammals, exhibit mechanisms to increase gestation length by changing the timing of parturition, and develop placentas from the chorioallantois and yolk sac, structures that function in gas exchange and water provision (Blackburn, 1993*a*; Stewart, 1993). Yet another feature found among squamates and mammals is an extreme form of placentotrophy, in which placentas supply most of the nutrients for development (Blackburn and Vitt, 1992; Flemming and Blackburn, 2003; Thompson et al., 1999). In fact, some squamate placentas have cellular specializations that are very similar to those of eutherians mammals (Blackburn and Vitt, 2002; Flemming and Branch, 2001; Jerez and Ramirez-Pinilla, 2001, 2003).

LIMITATIONS OF THE SQUAMATE MODEL

Discrepant Evolutionary Sequences

“It is quite evident that the appearance of viviparity with placentation in reptiles is not phylogenetically connected to that of mammals. Nevertheless, the study of its appearance in reptiles can give us information on the path that may have been followed by the ancestors of mammals.” (Bauchot 1965, p. 567; translation by D. Eakins).

The idea that the evolution of squamate viviparity is a valid model for other vertebrates generally assumes that this reproductive pattern has evolved according to a common sequence (Fig. 1). The sequence traditionally invoked for squamates involves at least four separate transitions (Blackburn, 1995). The first step would involve a gradual increase in the length of time developing eggs reside in the maternal oviduct before oviposition, a transition that would culminate in viviparity. At this stage, fetal nutrition would be lecithotrophic; the yolk would provide the nutrients for development, as in oviparous forms. The second step would involve eggshell reduction, leading to evolution of a simple placenta that

Traditional Scenario for Squamate Viviparity

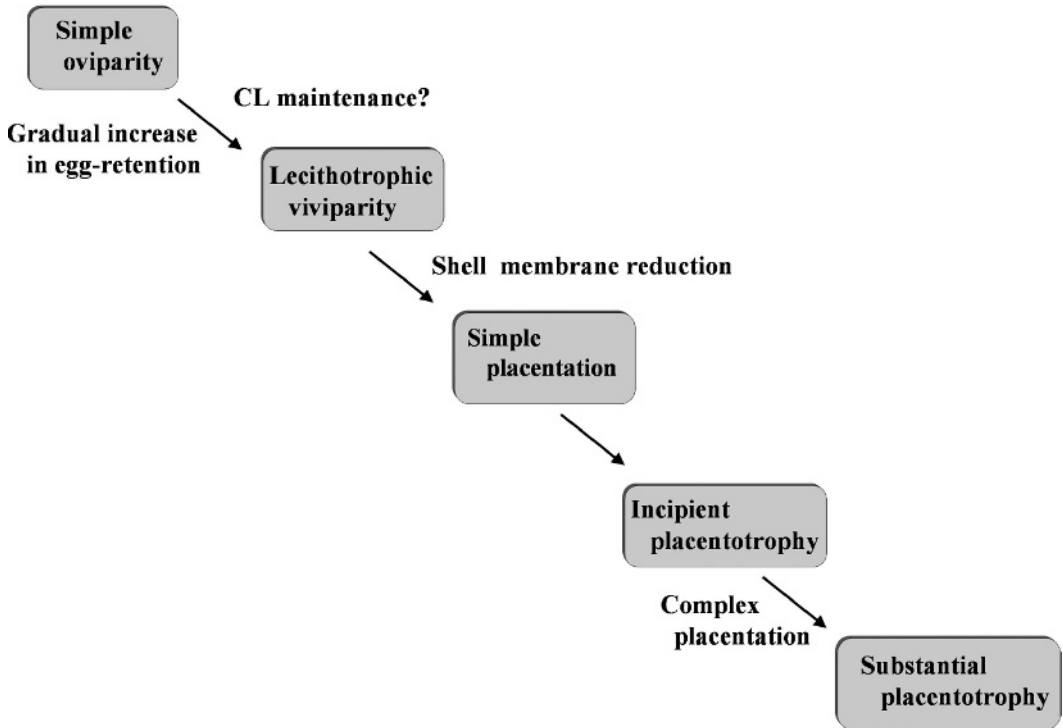


FIG. 1.—Conventional scenario for reproductive evolution in squamate reptiles, involving five successive evolutionary stages. See the text for details.

accomplishes gas exchange. The third step would involve development of incipient placentotrophy, in which yolk supplies are supplemented by small amounts of placental nutrients. Placentotrophy is a type of matrotrophy, the general pattern in which maternal nutrients are supplied to the embryo by non-yolk means (Wourms 1981). In the final stage, a substantial degree of placentotrophy would evolve. Some authors have expanded this scenario by suggesting that the yolk sac placenta predates the chorioallantoic placenta (e.g., Harrison and Weekes, 1925).

A similar sequence has long been accepted for mammals (Huxley, 1888; Lillegraven, 1979; Fig. 2) as well as fishes (Wourms, 1981). Among mammals, monotremes are assumed to represent the putative ancestral condition for extant mammals, a pattern in which females lay developing eggs and supply nutrients for development via the ovulated

yolk. Viviparity is presumed to have evolved through maternal retention of the developing eggs, as described above. The next stage would be characterized by marsupials, with their altricial neonates and yolk sac placentotrophy. Finally, eutherians, with their more precocial offspring and chorioallantoic placentas, would represent the most advanced condition. One problem is that the generalizations implicit in this scenario inaccurately portray mammal diversity. Most eutherians have yolk sac placentas, and many have relatively altricial offspring; further, some marsupials have chorioallantoic placentas (Mossman, 1987). An even more serious problem is that monotremes actually exhibit a very specialized form of oviparity, in which females provide large quantities of nutrients to developing eggs by means of oviductal secretions (Hughes and Carrick, 1978). This pattern of “matrotrophic oviparity” has never

Traditional Scenario for Mammal Evolution

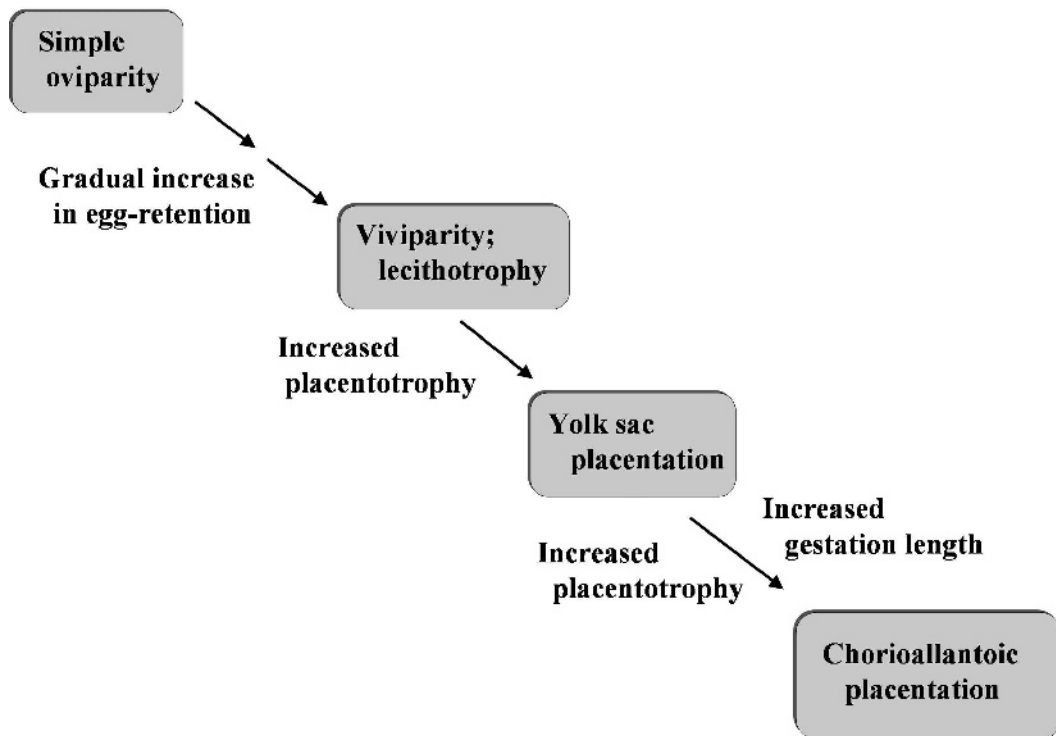


FIG. 2.—The commonly-accepted scenario for reproductive evolution in mammals. Viviparity presumably arose from oviparity as described above for squamates. Placentation and placentotrophy arose in marsupials through evolution of a yolk sac placenta, and were elaborated in eutherians by evolution of a chorioallantoic placenta.

been demonstrated in reptiles or other tetrapods, and is not accounted for in the traditional scenario.

Phylogenetic analyses have offered strong evidence that squamates have not evolved according to the traditional scenario (Fig. 3). Squamate viviparity appears to evolve simultaneously with functional placentas formed from both the yolk sac and chorioallantois, rather than as a separate step. The placentas are formed through eggshell reduction and the resultant apposition of fetal and maternal tissues (Blackburn, 1995); in fact, a degree of eggshell reduction that enhances fetal-maternal exchange can occur in oviparous forms in which females retain developing eggs (Mathies and Andrews, 2000). Further, most species are bimodally distributed between a form of oviparity in which eggs are laid in the limb-bud stage, and a form of viviparity

involving functional placentation. This pattern is more consistent with a punctuated equilibrium model of evolutionary change than a traditional gradualistic model (Blackburn, 1995, 1998c; cf. Qualls et al., 1997). This scenario has been challenged on the grounds that the concept of punctuated equilibrium is meant to apply to extinct taxa as an explanation of gaps in the fossil record. However, punctuational concepts commonly are applied to extant clades, and Gould's (2002, pp. 942–946) adoption of squamate viviparity as an illustrative example confirms that this evolutionary scenario is consistent with the punctuated equilibrium model.

Evidence also indicates that mammals have not evolved in accord with the traditional scenario (Fig. 4). If the matrotrophic oviparity of monotremes is taken as ancestral for the three extant clades (the most parsimonious

Modified Scenario for Squamate Evolution

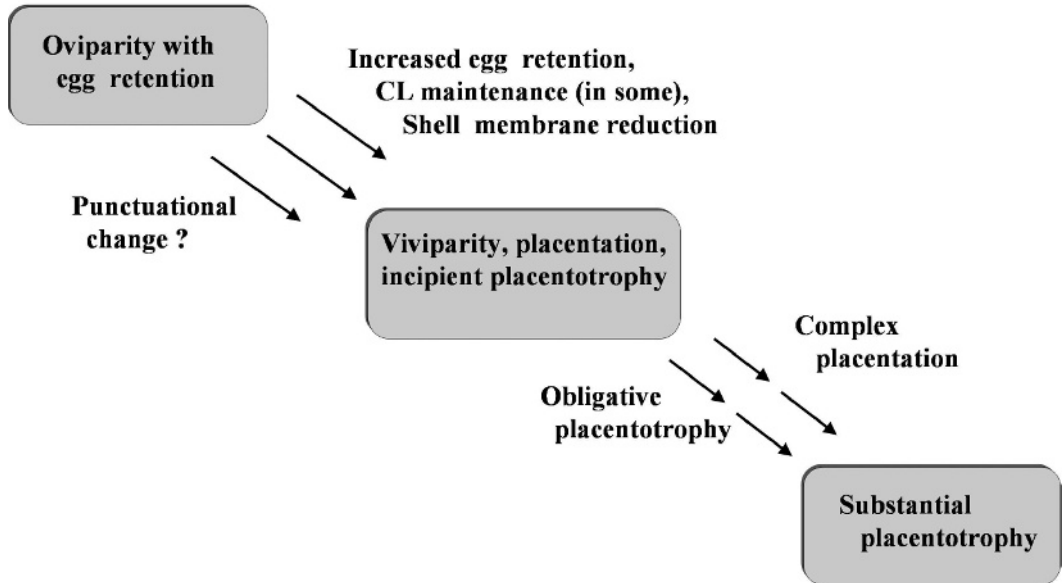


FIG. 3.—Modified scenario for reproductive evolution in squamates. Viviparity has evolved repeatedly (> 100 times), in concert with placentation and incipient placentotrophy. The transition can occur relatively rapidly and at low taxonomic levels, and in accord with a punctuated equilibrium model of change. Substantial placentotrophy and complex placentas evolved at least 4 or 5 times. However, most viviparous squamates have remained relatively lecithotrophic, with incipient placentotrophy.

explanation), then substantial matrotrophy evolved long before viviparity, just the opposite of what has been inferred for viviparous squamates and amniotes (Blackburn, 1992, 1993*b*). In addition, phylogenetic reconstructions (Freyer et al., 2003) suggest that the presence of placentas formed from both the yolk sac and chorioallantois may be ancestral for therians. Furthermore, the evolution of mammalian reproduction appears to have been associated with neonatal miniaturization, with prolongation of gestation arising after the origin of viviparity (see Packard et al., 1989). Moreover, females mammals provide substantial quantities of nutrients via lactation, a pattern that made the evolution of altriciality possible. No such features are found among viviparous squamates.

In sum, broad consideration of patterns of evolution indicates that viviparity and matrotrophy have evolved via entirely different chronologies in squamates, mammals, and amniotes (Blackburn, 1992, 2005*a*; Fig. 5). Whereas matrotrophic oviparity is ancestral

for extant mammals, in squamates, lecithotrophic oviparity (in which the yolk provides nutrients for development) is primitive, and has given rise many times to viviparity with functional placentation. Although evolutionary information about amniotes is sketchy, viviparous fishes appear more likely than amniotes to have followed the traditional chronology outlined above (Blackburn, 2005*a*). Thus, historical sequences derived from the squamate model appear unlikely to extend to other vertebrates, and in particular, not to mammals. The skeptical reader should note that no known squamate—*not one*—exhibits either matrotrophic oviparity (the ancestral pattern for mammals) or aplacental viviparity, the ancestral pattern traditionally assumed for viviparous squamates.

Risks of Higher-level Generalizations

Numerous reproductive similarities of squamate reptiles and mammals make it feasible to compare viviparous representatives of the two groups, including shared features of

Modified Scenario for Mammal Evolution

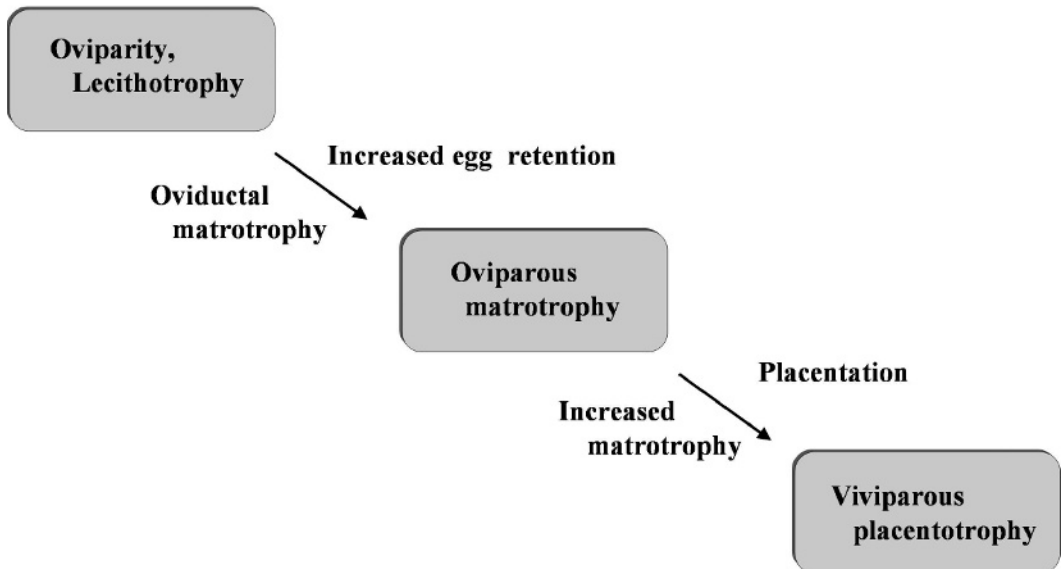


FIG. 4.—Modified scenario for mammalian reproductive evolution. Matrotrophy (in which maternal secretions provide nutrients for development) evolved under oviparous conditions, as seen in monotremes. This pattern arose from lecithotrophic oviparity earlier in therapsid history. Oviparous matrotrophy was followed by evolution of viviparity, placentation, and obligative placentotrophy (as in therians). Some evidence suggests that yolk sac and chorioallantoic placentas evolved simultaneously.

their reproductive tracts and fetal membranes. Many of these similarities are homologues retained from their common ancestors among the terrestrial amniotes; however, others represent convergently-derived attributes. For similarities of both types, risk lies in overlooking distinctive features of these animal groups in the attempt to draw parallels. In fact, viviparous squamates sometimes have been misinterpreted to be similar to mammals, under the assumption that generalizations between the two model systems are valid.

For example, in many eutherians, pregnant females can reabsorb partially-developed embryos (Brambell, 1948; Low 1978). This pattern allows females to modulate reproductive output and to free the uterus of dead or malformed embryos with minimal energetic loss. Such resorption is possible by virtue of the thick glandular endometrium and an invasive form of implantation (Luckett, 1977; Mossman, 1987). Surrounded by vascularized maternal connective tissue, the embryonic

tissues are easily accessible to attack by macrophages and lymphocytes. Many researchers have inferred that such resorption also occurs in squamates, based on observations of degenerating oviductal eggs and embryos. Such inferences fail to consider fundamental differences between female reproductive tracts of eutherians and squamates (Blackburn, 1998*a,b*). The gravid squamate oviduct is an extremely thin-walled tube with little connective tissue, and the epithelial lining is not breached during pregnancy (except in one highly specialized skink: Fleming and Blackburn, 2005); thus, the embryo is not exposed to phagocytic cells. Further, no definitive evidence exists of digestion and absorption of oviductal embryos. In fact, studies of lizard species in which resorption has been suspected have revealed that abortive embryos actually undergo aseptic necrosis, and are extruded by the oviduct (Blackburn et al., 1998, 2003*a*).

Another example of an invalid generalization from mammals is in structure of the yolk

Multiple Scenarios for Evolution of Viviparity and Matrotrophy

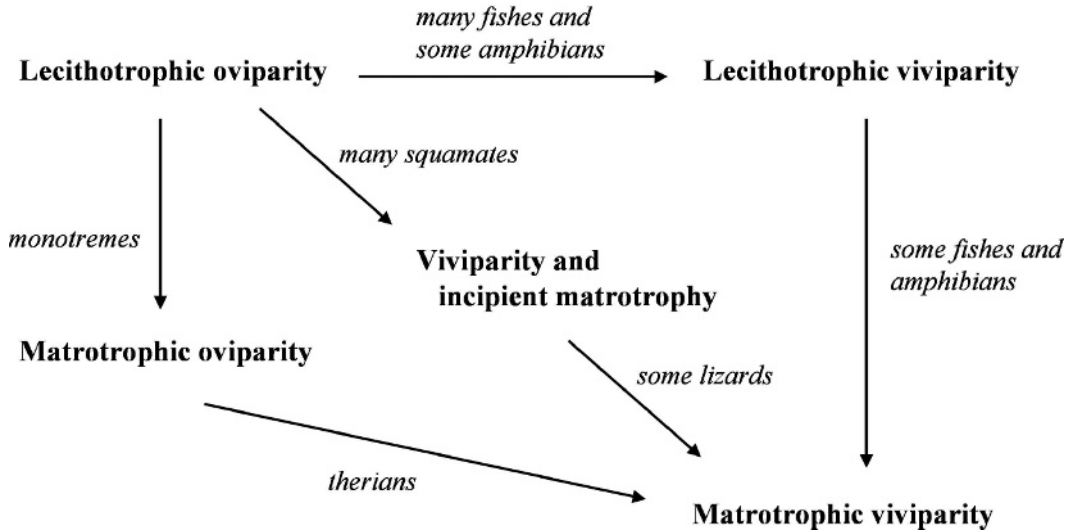


FIG. 5.—Multiple scenarios for reproductive evolution in vertebrates. The historical sequences by which viviparity and matrotrophy have evolved differ markedly among the major taxonomic groups. Note that viviparity and matrotrophy have evolved multiple times among squamates, amphibians, chondrichthyans, and osteichthyans. As noted in the text, placentotrophy of viviparous amniotes is a type of matrotrophy.

sac. In squamates, yolk sac development is unique. It involves formation of an isolated yolk mass and yolk cleft, the latter of which commonly is invaded by the allantois to form an omphalallantoic membrane (Stewart, 1997; Stewart and Blackburn, 1988; Stewart and Thompson, 2000). This pattern has been documented in every squamate to have been described in detail, excepting a few highly-derived skinks with minuscule eggs (Flemming and Blackburn, 2003; Flemming and Branch, 2001; Jerez and Pinilla, 2003). Nevertheless, some sources have failed to recognize the characteristic features of the squamate yolk sac in primary and secondary works (Guillette and Jones, 1985; Guillette et al., 1981; Mossman, 1974) under the mistaken assumption that it is similar to that of mammals. Such work includes species and genera now known to form an omphalallantoic membrane (Johnson, 1993; Stewart et al., 2004a; Villagran Santa Cruz, 1989; Villagran Santa Cruz et al., 2005). Some subsequent research has relied on the misconceptions about yolk sac morphology. These examples

illustrate the risks of generalizing between squamates and mammals, groups with numerous autapomorphies whose most recent common ancestor dates to the Paleozoic. Likewise, generalizations from amniotes are risky as applied to viviparous teleosts, in which gestation can be ovarian; fertilization and hatching can precede ovulation; and maternal nutrients can be absorbed by means of embryonic gills, fin outgrowths, and exteriorized protrusions of the hindgut (see Wourms et al., 1988).

Implications of Squamate Diversity

The idea of a reptilian model often is taken to imply commonality in how squamate viviparity has evolved, including in the mechanisms through which pregnant lizards and snakes gestate, sustain, and give birth to their young. To assume application of the model in this fashion is to presuppose that squamate clades that have evolved viviparity independently have converged on similar or identical adaptations. However, studies on viviparous squamates have revealed considerable diver-

sity in how individual species accomplish reproduction. Such diversity reflects the fact that any given physiological problem can be solved in multiple ways.

Specializations that enhance placental gas exchange offer an illustrative example. The uterine environment is hypoxic, requiring mechanisms to enhance exchange of oxygen between fetal and maternal tissues; in fact, fetal needs for oxygen increase as development proceeds (DeMarco, 1993). In theory, gas exchange could be enhanced by any of the following features: attenuated uterine epithelium, increased uterine vascularity, attenuated chorionic epithelium, increased chorioallantoic vascularity, substantial reduction or loss of the shell membrane, specialized fetal hemoglobin with high oxygen affinity, increased maternal levels of NTP (nucleoside triphosphate) that lower blood oxygen affinity, decreased fetal NTP levels, invasion of the yolk cleft by the allantois, accelerated diminution of the isolated yolk mass, and conversion of the omphalopleure to chorioallantois. Each of these features has been demonstrated in one or more squamate species (for a summary, see Blackburn, 2000). However, no species exhibits them all.

Another example is offered by the diversity of gestational mechanisms. In various mammals and squamates, progesterone from the corpus luteum has been implicated in maintenance of gestation. However, squamate species vary markedly in lifespan of the corpus luteum, progesterone profiles, sources of progesterone, necessity of the CL and progesterone for maintenance of pregnancy, and effects of progesterone on the timing of parturition (Jones and Baxter, 1991; Xavier, 1987; Yaron, 1985). Interspecific diversity is also manifested in many other aspects of viviparity, including details of placental morphology, type of placental nutrient transfer, and level of thermoregulation during pregnancy (see Blackburn, 2000).

Even features that are widespread in viviparous squamates often are accomplished by different mechanisms indicative of alternative evolutionary paths. For example, factors thought to contribute to shell membrane loss in different species include digestion by the chorioallantois, by the omphalopleure,

and by the uterine epithelium, as well as reduced activity of shell glands and expansion of the chorionic vesicle (Blackburn, 1993a, Blackburn and Lorenz, 2003a, b; Jacobi, 1936; Weekes, 1927b). Likewise, although incipient placentotrophy is widespread among viviparous squamates, species differ in which ions are supplied to the fetus, and in whether or not the provision is essential to embryonic development (see Stewart and Thompson, 2000; Thompson et al., 2000). The relationship between obligatory and facultative nutrient provision is a subject of ongoing investigation (Stewart, 1989; Swain and Jones, 2000; Thompson et al., 2000, 2002). Thus, it would be premature to assume a particular evolutionary sequence that is applicable to all clades.

VALUE OF THE SQUAMATE MODEL

The idea that a given animal serves as a heuristic model for other species assumes commonality with respect to relevant attributes and mechanisms. To assume such commonality is reasonable when the shared attributes are plesiomorphic features that predate divergence of the clades in question. Thus, studies of the giant squid axon are relevant to chordates, annelids, and arthropods because the common coelomate ancestor of these organisms had neurons constructed on the same basic plan. Likewise, *Drosophila* serves as a model for understanding genetic features that evolved prior to divergence of protostomes and deuterostomes.

However, when features of interest have resulted from evolutionary convergence, information from a single species is not necessarily applicable to other clades. Accordingly, the fact that viviparity has evolved on numerous occasions in diverse organisms offers a serious challenge to simple application of the "animal model" concept to this reproductive pattern. *A priori*, it would be highly implausible to suppose that more than 140 separate vertebrate clades had evolved viviparity according to the very same evolutionary sequences, structural modifications, physiological mechanisms, and selective pressures. In fact, the assumption that viviparous squamates and anamniotes necessarily have followed the mammalian pattern of evolution

is reminiscent of archaic concepts of orthogenesis, and implies homocentric notions of the inherent superiority of viviparous reproduction and chorioallantoic placentotrophy.

As available evidence shows, therians, squamates, and anamniotes have converged on viviparity through different historical sequences (Fig. 5), and have achieved this pattern of reproduction by means of diverse mechanisms. Furthermore, despite similarities in selective pressures and historical sequences, even squamates exhibit diversity in mechanisms through which viviparity is accomplished. Such diversity ought not be surprising, given that a variety of potential solutions exist to each of the potential problems posed by viviparous reproduction. In addition, such diversity illustrates why studies of one or a few species will not suffice to explain this reproductive pattern.

Given what we know of interspecific diversity, the question now arises: of what value is a squamate model for viviparity; or more specifically, can generalizations be extrapolated from a few squamate species, and if so, under what circumstances? As studies on squamates continue, a preliminary answer is now emerging that incorporates three main principles. The first principle is that the value of the squamate model lies less in its specific elements of predictability, than in the general insights it provides into the problems posed by viviparous reproduction, and the potential means by which these problems can be solved. For example, we can infer from available evidence that intrauterine development poses problems of gas exchange for the developing embryo, problems that become accentuated as gestation proceeds; however, species differ according to how these problems have been met. A second principle is that phylogenetic approaches offer the best way to analyze structural and functional diversity in an evolutionary context. Of particular value are studies and analyses directed towards particular evolutionary transformations, such as the development of placentotrophy (Stewart and Thompson, 2003) and the transition from oviparity to viviparity (Heulin et al., 1989, 1991, 1993; Mathies and Andrews, 2000; Stewart et al., 2004a). For exploration of such transformations, specific clades may

themselves prove ideal, representing "models" that may give insight into other squamate clades.

A third principle is that generalizations about squamate viviparity ultimately should be quantitative in nature, and should draw on as many viviparous clades as possible. In fact, given that species derived from a single origin of viviparity exhibit marked diversity (e.g., see Stewart and Thompson, 2003), multiple representatives should be sampled from individual viviparous clades. Without question, the challenges of understanding more than a few of the 100+ clades of viviparous squamates are daunting. However, researchers can take heart from the progress that has been made in the past two decades, and from the fact that significant questions will remain to be answered for decades to come. If one or two clades were sufficient to explain all viviparous squamates (or amniotes), there would be little need for taxonomically widespread studies of this reproductive pattern. Instead, viviparity is a phenomenon that cries out for extensive study by numerous researchers studying diverse lineages. The phenomenon of reptile viviparity arguably needs an international effort on a scale larger than the Human Genome Project if it is to be fully understood.

CLARIFICATION OF PATTERNS OF SIMILARITY

Given that viviparity in squamates has arisen convergently numerous times, one further challenge is to explain the degree of commonality that does exist between viviparous squamate clades. One perspective would view similarities as results of the aforementioned orthogenetic transformation towards a eutherian (or hominid) style of reproduction. This approach is a manifestation of the *scala naturae* that dominated comparative work through much of the 19th and 20th centuries (Ruse, 1996). A more sophisticated perspective that recognizes that evolution is not goal-directed leads to the question: why is viviparity that has been derived from independent origins of that pattern more similar from one squamate clade to another than to that of mammals and fishes? Or, in what useful sense can we generalize about "viviparous squamates," given that the species in question range from sea snakes to snow

skinks, and from tropical vipers to sub-arctic lacertids?

Explanations for patterns of similarity among squamates will require more study of viviparous forms as well as their oviparous relatives. However, as with questions about the value of the squamate model, answers are beginning to emerge. As products of evolution, structural and functional features are affected by selection pressures, constraints, and exaptations, as well as by the ancestral substrate from which they originated. In theory, therefore, relevant structural and functional similarities between viviparous clades may be of at least three varieties.

The first type of similarity is represented by features that may appear to be adaptations to viviparity, but which actually were present in oviparous squamate ancestors; thus they are consequences of common ancestry, not products of convergence. Such features may include the capacity of fetal membranes to take up calcium (which is widespread in oviparous squamates: Packard and Packard, 1988; Shadrix et al., 1994; Stewart et al., 2004*b*). The ability of fetal membranes to phagocytose extracellular material in oviparous snakes (Blackburn et al., 2005) may be another example. Another feature is the developmental trend in attenuation of the chorionic epithelium. While commonly viewed as a specialization for viviparity that decreases the respiratory diffusion distance, this feature also occurs among oviparous squamates (Blackburn et al., 2003*b*). Yet another example may be the tendency of tissues to vascularize under hypoxic conditions, a feature that could account for increased vascularity of the allantois and uterus under conditions of viviparity. An important point to note is that recognition of such features can require phylogenetic analysis that includes oviparous sister groups and their ancestors (Blackburn, 2005*a*). The need to recognize such features adds impetus to the study of oviparous squamates, which are poorly understood in terms of fetal membrane morphology and physiology, as well as important aspects of reproductive anatomy, physiology, behavior, and ecology.

A second kind of similarity is represented by adaptations to viviparity that evolved from

oviparous features that were well-suited for exaptation. Such features arguably represent parallelisms as opposed to convergences (according to a traditional distinction), since they have arisen through extension of pre-existing characteristics. For example, all viviparous squamates form placentas from the chorioallantois, in apposition to the inner lining of the uterus. As a well-vascularized membrane that functions in gas exchange under oviparous conditions, the chorioallantois is ideally suited for such functions, and for it to have been recruited in each of the 100+ origins of squamate viviparity is not surprising. Indeed, anatomical placentas form from existing structures (the uterus, omphalopleure, and chorioallantois) through simple loss of the eggshell membrane (Packard et al., 1977). Features of this kind include "proto-adaptations" (sensu Gans, 1974) that may be predisposed towards particular new functions by virtue of their structural attributes, including towards functions that are qualitative extensions of their ancestral roles.

A third similarity is represented by true convergences, as evident from their indisputably independent origins in diverse lineages. Squamate viviparity itself can be viewed as a feature of this type. Another example is the use of chorioallantoic placentomes in maternal-fetal nutrient transfer, a feature that has evolved in at least three or four lineages of viviparous lizards (Blackburn, 1998; Fleming and Blackburn, 2003; Stewart and Thompson, 2000, 2003). Why such features are confined to skinks, and always involve the chorioallantois (as opposed to the omphalopleure) is entirely unclear. In general, convergences can be interpreted as products of selective pressures, constraints, and proto-adaptations. Thus, while viviparity may have evolved convergently through similar selective pressures (Shine, 1985), such features as ectothermy, vascularized oviducts, internal fertilization, and egg retention may be considered as features that predisposed squamates towards this pattern. An important, ongoing goal of comparative studies is to clarify the roles of selection pressure, exaptation, and evolutionary constraint in the development of viviparity and the mechanisms through which it is accomplished.

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