LETTER TO THE EDITOR

The Evolution of Viviparity and Placentation Revisted

Most studies on the evolution of viviparity in squamate reptiles have focused on one or more of the following questions: (1) what selective force(s) are involved in the transition from oviparity to viviparity? (2) how does this transition occur (i.e., what changes are involved)? and (3) how and when does placentation evolve? In answer to the first of these questions, most studies have implicated cold climates (at high latitudes or high elevations) as the primary selective force involved [see Shine (1985) for a review]. Recently, in a paper published in this journal, Daniel Blackburn (1995) addressed the latter two of these questions. Specifically, Dr Blackburn tested different evolutionary models (saltation, gradualism, and punctuated equilibrium) for the evolution of viviparity, and questioned whether placentation evolves concurrent with, or subsequent to, the evolution of viviparity.

In this paper, we re-examine these questions. We agree with Dr Blackburn on several main points: that squamate reproductive modes frequently exhibit apparent stasis over long periods of time, that the actual transition from oviparity to viviparity can occur quite rapidly, and that intermediate reproductive forms are relatively rare. However, we disagree, on theoretical grounds, with the manner in which Blackburn chose to couch some of his arguments. We also present further evidence for the existence of evolutionarily intermediate forms from our own studies, which were not published when Dr Blackburn surveyed the literature, and from studies that he apparently overlooked. We first discuss the evolutionary transition from oviparity (the oviposition of shelled eggs early in embryonic development) to viviparity (the retention of developing embryos within the oviducts throughout development), followed by a separate discussion of the evolution of placentation.

Evolution of Viviparity

The evolutionary transition from oviparity to viviparity is essentially an increase in the length of time eggs are retained *in utero* (presumably facilitated by alterations of the hormonal systems that trigger oviposition), such that embryonic development is completed prior to oviposition (Guillette, 1993; Packard *et al*., 1977; Shine, 1985). But how does this transition occur, and what steps (and how many) are involved? To address these questions, Blackburn (1995) proposed and tested three models for this evolutionary transition: saltationist, punctuated equilibrium, and gradualistic.

The saltationist model predicts that the shift from oviparity to viviparity occurs in one step (i.e., macromutation), whereas the other models predict that the transition proceeds through intermediate stages of prolonged egg retention. Thus, saltation is easily distinguishable from punctuated equilibrium and gradualism, and can be tested by searching among extant squamates for the existence of intermediate forms (i.e., oviparity with prolonged egg retention). As noted by Blackburn, such intermediate forms do indeed exist (also see below), and thus, the saltationist model can easily be rejected. However, while the presence of these intermediate forms refutes the saltationist model as a global explanation, Blackburn implies that their absence within specific lineages indicates "non-gradualistic" change (p. 205). He interprets the fact that oviparous *Lacerta vivipara* and *Sceloporus aeneus* (despite having close viviparous relatives) do not exhibit unusually prolonged egg retention as support for the saltationist model. His reasoning is as follows. Both his punctuated and gradualistic models predict intermediate evolutionary stages of prolonged egg retention, yet there are no such intermediates; thus, they must never have existed, and therefore the evolution of viviparity in these lineages must have been saltatory. This conclusion inherently relies on two assumptions: that viviparity arises through cladogenesis, and that the absence of intermediates means that they never existed. However, two alternative interpretations exist that invalidate this conclusion. First, if the transition from oviparity to

viviparity occurred through anagenesis, then the intermediates will have been replaced by their successors, and therefore cannot still exist. Second, even if the transition is cladogenetic, the intermediate forms may simply have gone extinct.

While the saltationist model is clearly inapplicable to the evolution of viviparity, the punctuated and gradualistic models are far more difficult to distinguish. We disagree, on theoretical grounds, with Blackburn's approach of pitting punctuated equilibrium versus gradualistic models in a neontological study of adaptive evolution. We do not challenge the validity of punctuated equilibrium models, but do question, for several reasons, the validity of this dichotomous approach—presenting punctuated equilibrium as a "non-gradualistic" alternative to traditional "gradualistic" models of evolution.

First, the model of punctuated equilibria was proposed to explain patterns in the fossil record, and as a result, is not directly applicable to non-paleontological data. Under the evolutionary model of phyletic gradualism, we would expect paleontological evidence (i.e., fossil series) to show continuous, straight-line evolution. However, this is often not the case; "gaps" in the fossil record are common. Eldredge & Gould (1972) argued that, when combined, the concepts of evolutionary stasis and allopatric speciation explain such gaps in the fossil record. If stasis is common, we expect fossil taxa to frequently show little evolutionary change over relatively long periods of time. However, isolated populations, in a different area from the fossil strata being sampled, may have undergone substantial change during this same time period. An isolated population can diverge significantly, then expand its range and displace its ancestor (or sister taxon). In such a case, the fossil record would show little change over some period of time (stasis), followed by a geologically "instantaneous" transition (punctuation) from the ancestral to the derived form. Indeed, an evolutionary transition may occur through gradualistic processes, and over a long period of time, yet still appear "punctuated" in the fossil record, because the transition occurred somewhere else. We are interested in how the adaptive transition from oviparity to viviparity actually occurs, not how it might appear in the fossil record. Thus, applying the "punctuated versus gradualistic" dichotomy to neontological studies of specific evolutionary transitions (such as the evolution of viviparity) is not appropriate.

Second, Eldredge & Gould (1972) did not propose their theory of punctuated equilibria as a challenge to "gradualism" in general, but simply as an alternative to their specific characterization of "phyletic gradual-

ism", which they defined essentially as slow, constant, uni-directional change (i.e., straight-line evolution). This model of "phyletic gradualism" is not (nor was it intended to be) an accurate characterization of the gradualistic evolution of the modern synthesis (e.g., Futuyma et al., 1981; Levinton, 1988; Templeton & Giddings, 1981), but rather an unrealistic model that is "not consistent with modern evolutionary ideas" (Gould & Eldredge, 1977). Yet, if one starts from the premise that punctuated equilibrium is a "non-gradualistic" alternative to gradualism (as Blackburn did), then one *must* define gradualism as "phyletic gradualism"; thus, in this context, punctuated equilibrium does not pose a challenge to "gradualism" in general, but only to a narrowly defined model of gradualistic evolution. Given the past controversy over punctuated equilibrium as a challenge to gradualism, and the widespread misunderstanding that still exists, we feel that this is a very important point. Some authors (including Dr Blackburn) refer to "punctuated" and "gradualistic" models, without explicitly defining gradualism as "phyletic gradualism". In such cases, it would be easy for readers (especially those unfamiliar with the subject matter) to feel that it was "gradualism" in general that was being tested, rather than only a very narrow subset of the possible gradualistic models. Below, we carefully examine the logic and definitions of punctuated equilibrium and gradualism to illustrate our point.

At the most basic level, evolutionary models must explain three phenomena: (1) the magnitude of individual changes (the size of steps); (2) the rate of change; and (3) the direction of change. Given these components, how can (or simply, can) punctuated and gradualistic models for the evolution of reptilian viviparity be usefully distinguished?

Both the punctuated and gradualistic models predict that the evolution of viviparity proceeds through small, incremental increases in the duration of egg retention, and hence that intermediate forms do occur. Thus, the magnitude of individual changes does not allow us to distinguish between punctuated and gradualistic evolution, and neither does the rate of change. Punctuated equilibrium predicts that changes should appear "rapid" in the fossil record (because they occur in allopatry), but not that the changes actually occur rapidly. Indeed, as Blackburn himself comments, "the pace of evolution during periods of actual change may or may not differ between [punctuated equilibrium and gradualism]" (p. 200). Thus, the rate of actual change does not separate punctuated and gradualistic models. However, punctuated models also predict "periods of evolutionary stasis" (p. 200), over which no change

occurs. Therefore, gradualism must, by default, exhibit "continuous change", since this is the only alternative to stasis.

Thus, it appears that punctuated equilibrium and gradualism can be distinguished on the basis of "stasis" versus "continuous change", but what are the possible definitions of these terms? The most rigorous definition of stasis would entail absolutely no variation in the character of interest over relatively long periods of time. However, as long as a trait (embryo stage at oviposition in this example) exhibits any heritable variation, genetic drift alone will produce a random walk of evolutionary change, probably with frequent reversals of direction (Sheldon, 1993). If we accept that zig-zag evolution of this sort occurs, even during periods of "stasis", we still cannot distinguish stasis from continuous change; to do so, our definitions of these terms must incorporate the direction of change in addition to the rate. Thus, stasis must be defined as no *net* change over relatively long periods of time (this is essentially the definition given by Gould, 1993). To differ from this, gradualism must not only predict continuous change, but continuous change that is entirely (or at least predominantly) in one direction, such that there will be a *net* change over *any* appropriately long period of time. Thus, we have arrived at operational definitions which allow us to distinguish between punctuated and gradualistic models, but what happens when we apply these models, as defined, to the evolution of viviparity?

The restricted definition of gradualism that we must adopt (in order to distinguish gradualistic and punctuated evolution) requires continuous change that is significantly biased in one direction, which is essentially Eldredge & Gould's (1972) definition of "phyletic gradualism". Evolution via phyletic gradualism may or may not actually occur (e.g., Gould & Eldredge, 1993; Levinton, 1988; Wei & Kennett, 1988), but this debate is outside the scope of this paper. We would, however, argue that applying this model of "phyletic" gradualism to the evolution of reptilian viviparity generates a specific evolutionary hypothesis that is unrealistic: through time, a squamate lineage must either continuously flip-flop between oviparous and viviparous reproduction (anagenesis), or continuously give rise to new lineages of the opposite reproductive mode (cladogenesis), which then must either continuously flip-flop or give rise to new lineages of the opposite reproductive mode, which then ... Under this restrictive gradualistic model, we would predict squamate reproductive modes to be evenly distributed along the oviparity–viviparity continuum, but (as noted by

Blackburn, fig. 1) squamate reproductive modes exhibit a bimodal distribution. Thus, we can easily reject phyletic gradualism as a model for the evolution of viviparity (but not as a general evolutionary model). However, rejecting this specific gradualistic model, that is a priori unrealistic, and is generated from a very restricted definition of gradualism, cannot be considered a refutation of gradualism or evidence that viviparity evolves via non-gradualistic processes.

Nonetheless, if we (and Blackburn) reject (phyletic) gradualism, then the process of elimination leaves only the punctuated equilibrium model. Under this model, we predict the following: over much of their geographic ranges, squamate taxa persist through long periods of time without significant *net* change in their mode of reproduction; and viviparity usually arises in small, isolated populations that undergo subsequent range expansions, often displacing the ancestral form. While some evolutionary biologists would likely find this specific model to be very realistic (as we do), most would also consider this to be a *gradualistic* model, *not* a challenge to gradualism.

Despite some disagreement over theoretical issues, our, and Blackburn's, discussion of these evolutionary models does raise some important questions. First, do squamate reproductive modes exhibit stasis, and if so, how prevalent is stasis? We agree with Blackburn's conclusion that reproductive modes can exhibit stasis over relatively long periods of time. For example, several higher taxa of squamates are entirely oviparous (e.g., Teiidae, Pygopodidae) or viviparous (e.g., Xantusiidae, Acrochordidae; see Blackburn, 1982, 1985; Shine, 1985). The most parsimonious explanation for such similarity in reproductive mode throughout many higher taxa is that reproductive mode is phylogenetically conserved, and has changed little since divergence from a common ancestor. Further, the bimodal distribution of reproductive modes suggests that stasis may be predominant. That is, the relative scarcity of intermediate forms suggests that few taxa are currently in transition between oviparity and viviparity. However, intermediate forms are not quite as rare as Blackburn indicates. For example, Blackburn's claim that no single squamate clade exhibits primitive, intermediate, and advanced stages in the evolution of viviparity (p. 201) was premature. Several recent publications (Qualls, 1996; Qualls *et al.*, 1995) document this entire transition among populations of the Australian scincid lizard *Lerista bougainvillii*. Females in some populations lay eggs when embryos are at stages 31–34, females in other populations lay eggs when embryos are at stages 36–39, and females in other

populations are viviparous [staging follows Dufaure & Hubert, (1961)]. A critical component of this example is that both morphological and electrophoretic analyses confirm the conspecific status of these populations (Qualls *et al.*, 1995).

All stages of the transition between oviparity and viviparity are also found in the *sclaris* species group in the genus *Sceloporus*. This is a small group of closely related species in which viviparity has evolved at least twice (Sites *et al.*, 1992). *Sceloporus aeneus* is oviparous and its sister species *Sceloporus bicanthalis* is viviparous (Guillette & Smith, 1985). *Sceloporus scalaris*, the sister species of *S. aeneus* and *S. bicanthalis*, exhibits a range in embryonic stages at oviposition which bridges the entire range between oviparity and viviparity (Mathies & Andrews, 1995). This example is not as compelling as that of *L. bougainvillii*, because the transitions are represented by congeners, but it does, nonetheless, demonstrate the expected intermediate stages.

Blackburn also claims that transitional stages *per se* (oviposition beyond Dufaure and Hubert stage 33; birth or hatching occurs at stage 40) in the length of egg retention are virtually non-existent in any taxon (p. 202–203). Blackburn considers only *Sceloporus scalaris* and *Lacerta vivipara* in this category on the basis of staged embryos and includes *Opheodrys vernalis* on the basis of variable lengths of incubation time. But several other appropriate taxa can be added to this group. *Liolaemus* is a very large genus (∼150 sp.) that contains both oviparous and viviparous taxa. With regards to *Liolaemus scapularis*, Ramirez Pinilla (1994) states "This advanced stage of egg retention (stage 36) could indicate that this species is an egg-retainer like most oviparous *Liolaemus* species (Ramirez Pinilla, 1991)." This, and observations by Espinoza (1994), suggest an abundance of intermediate stages of egg retention may exist in this taxon alone. Another example of intermediate stages of egg retention is provided by the Australian skink *Saiphos equalis*, that lays shelled eggs, which take seven to nine days to hatch, in part of its range and is viviparous in others (Greer, 1989).

When Blackburn surveyed the literature, *S. scalaris* was the one example that he cited of a species with long periods of intra-oviductal development. Our recent studies (Mathies & Andrews, 1995, 1996) provide additional information about the reproductive biology of this species. Females from low elevation populations normally retain eggs to stages 31–33 while females from high elevation populations normally retain eggs to stages 36–37. In both populations, however, the length of egg retention can be extended facultatively when suitable nesting

substrates are not present (Mathies & Andrews, 1996). In fact, females from the low elevation population can extend egg retention to embryonic stage 39 without impairing the developmental rates of embryos or the hatchability of eggs; this suggests that few physiological or morphological obstacles to the evolution of viviparity exist in this taxon. Thus, as Blackburn also points out, the ability to facultatively extend egg retention may facilitate the transition from oviparity to viviparity (Shine & Guillette, 1988).

Second, does the actual transition from oviparity to viviparity occur in allopatry (i.e., in isolated populations)? The available evidence suggests that this is indeed the case. In the three well-studied taxa (cited above), that show variation in reproductive mode among closely related forms, the different forms occur only in allopatry. In *Lerista bougainvillii*, the viviparous form occurs only on offshore islands, and the intermediate oviparous form is restricted to isolated mainland populations (Qualls *et al.*, 1995). The oviparous form of *Lacerta vivipara* is restricted to isolated populations in the extreme southwestern part of the species' range (Heulin *et al.*, 1993). The sister species *Sceloporus aeneus* and *S. bicanthalis* are also allopatric throughout their ranges, with the oviparous form occurring below and the viviparous form above elevations of 3000 m (Camarillo, 1990).

Third, how rapidly does the actual transition from oviparity to viviparity occur? Observations on *Lerista bougainvillii* and *Lacerta vivipara* suggest that this major life-history shift may occur quite rapidly; in both species, the different reproductive forms may have diverged only quite recently. In *L. bougainvillii*, morphological, electrophoretic, and mitochondrial DNA analyses (Qualls *et al.*, 1995; Fairbairn, 1993) all revealed only minimal divergence between the three reproductive forms, and data on sea-level fluctuations suggest that the oviparous and viviparous forms could have been in contact as recently as 10000 years ago (Rawlinson, 1974). Similarly, electrophoretic comparisons (Bea *et al.*, 1990) and experimental hybridizations (Heulin *et al.*, 1989) indicate recent divergence of the oviparous and viviparous forms of *Lacerta vivipara*, which biogeographic analysis suggests may have occurred as recently as "the last quaternary glaciations" (Heulin *et al.*, 1993).

The Evolution of Placentation

Blackburn also addresses whether placentation evolves concurrent with or subsequent to the evolution of viviparity. We agree that this is an important question, but disagree, on several points, with Blackburn's treatment of this issue. First, we disagree with Blackburn's characterization of what he

calls "the traditional gradualistic model" for the evolution of viviparity and placentation, as incorporating three *successive* stages: (1) increased egg retention leading to viviparity, (2) simple placentae that facilitate the exchange of gases and water uptake (lecithotrophy), and (3) placentae that serve for the uptake of organic molecules (placentotrophy). This model is actually a composite of two evolutionary scenarios, which have had a largely independent development in the literature. Most of the papers he cites with reference to this model (Billett *et al.*, 1985; Guillette, 1982; Guillette *et al.*, 1980; Packard *et al.*, 1977; Shine, 1985; Weekes, 1933, 1935) either focus primarily on the evolution of viviparity, or on the evolution of placentation. Further, when these authors discuss both ideas together (often only briefly), they argue that placentation (thinning of the eggshell = step 2) must occur *concurrently* with, rather than subsequent to, the evolution of viviparity (step 1). For example, Weekes (1935) argued that ". . . in the course of evolution [eggs] are laid in more advanced stages of development surrounded by a soft shell, which becomes softer and softer as the time of retention is lengthened" (p. 641); Packard *et al.* (1977) discussed the necessity of a "reduction in calcification and thickness of the eggshell attending the evolutionary transition from oviparity to viviparity" (p. 93); and Guillette (1982) argued "that placentation arose concurrently with viviparity" (p. 1). Thus, Blackburn's gradualistic model is a novel construct, rather than an accurate representation of the views of previous authors, and therefore is essentially a "strawman" set up for rejection.

Further, by linking modes of parity to modes of embryonic nutrition as a necessary linear evolutionary sequence, Blackburn made his gradualistic model for the evolution of viviparity and placentation, as a whole, essentially untestable. As he points out (p. 210), extensive placentotrophy is known in only three squamate clades, while viviparous squamates of 100 or more clades are lecithotrophic. With so few placentotrophic clades in which to search for intermediate forms, a robust test of the third step (and hence the whole) of Blackburn's gradualistic model is not possible. Thus, the evolution of viviparity and the evolution of placentation (in the sense of the transition from lecithotrophy to placentotrophy) are better considered as independent or parallel rather than sequential events.

Second, while the question of whether viviparity and placentation evolve concurrently or sequentially is important, we feel that the traditional definition of a placenta (following Mossman, 1937), as employed by Blackburn, is vague and of limited utility for testing such a specific evolutionary hypothesis. According to Blackburn's description (p. 208) and fig. 2, the presence of a placenta is indicated morphologically by an "approximation of the extra-embryonic membranes to the maternal . . . tissues for physiological exchange" and functionally, by the occurrence of "gas exchange between fetal and maternal circulatory systems". Most squamate embryos spend a significant proportion of development *in utero* and therefore must exchange gases with maternal tissues (i.e., exhibit a functional placenta). Further, this gas exchange must take place via an "approximation" of the extra-embryonic membranes to the maternal tissues (i.e., a morphological placenta), even if they are separated by an eggshell. Even among "placental" viviparous squamates, the extra-embryonic membranes are usually separated from the oviduct by an eggshell, albeit thin (Guillette, 1993; Packard *et al.*, 1977; Weekes, 1935). Under this interpretation, any oviparous squamate could be described as having a crude placenta, with thinner eggshells indicating more advanced placentation. Indeed, the oviducts of oviparous lizards increase in vascularity during gravidity, presumably to facilitate gas and/or water exchange (Guillette & Jones, 1985; Masson & Guillette, 1987). Thus, there is no real dichotomy between placental and non-placental conditions, but rather a continuum of placental function and form. This is analogous to Shine's (1983) argument that oviparity and viviparity should not be considered as a dichotomy, but as opposite ends of a continuum of egg retention. Squamates can only be divided into "placental" and "non-placental" forms if we designate an arbitrary cut-off point (e.g., based on eggshell thickness or rate of gas exchange) along this continuum. Blackburn's attempt to test whether viviparity and placentation evolve concurrently or sequentially illustrates this point.

Blackburn reasons (using Mossman's definition) that, if placentation evolves subsequently to viviparity, then viviparous taxa should exist that do not possess any recognizable placental structures, whereas if the evolution is concurrent, all viviparous species should have morphological placentae. Thus, based on the observation that "every viviparous squamate that has been examined appropriately has been shown to have anatomically recognizable placentae" (p. 208), he concludes that placentation evolves concurrently with viviparity. While we agree with this conclusion, this test is weak. As we have argued previously, all squamates (even oviparous ones) must possess some degree of placentation, but usage of the term "placenta" is limited to, and considered requisite within, descriptions of viviparous taxa. Thus, two

species (one oviparous and one viviparous) could possess equally thin eggshells, but the interface between the fetal and maternal tissues will be called a "placenta" in the viviparous species, whereas the oviparous species will simply be described as possessing a "thin eggshell". Given this bias, Blackburn's observation (p. 208) that "no 'non-placental' viviparous species ever have been observed" is not surprising.

Rather than forcing squamates into this artificial dichotomy of "placental versus non-placental" forms, we believe that it is more informative to search for correlated increases in the duration of egg retention and the degree of placentation. Comparative evidence supports this contention. Viviparous taxa usually possess a thinner eggshell than their closest oviparous relatives, and sometimes produce no eggshell at all (Blackburn, 1993; Guillette, 1993; Packard *et al.*, 1977; Weekes, 1935). Further, of the three lizard species that show intraspecific variation in reproductive mode, all exhibit the predicted negative correlation between egg retention time and eggshell thickness. For example, in *Lerista bougainvillii*, the thickness of the eggshell is negatively correlated with the embryos' developmental stages at oviposition. In the "normal" oviparous form, which oviposits at stages 32 to 33, the eggshell is approximately 23 µm thick; the intermediate form oviposits at stages 35–37 and has a 19 µm eggshell; and the viviparous form has a shell that is only 6 µm thick (see Qualls, 1996). In *S. scalaris*, the low elevation populations, which oviposit at the "normal" time, have thicker eggshells, 27 µm, than the high elevation populations, 19 µm, which retain their eggs longer (Mathies & Andrews, 1995). In *Lacerta vivipara*, the oviparous form has much thicker eggshells, 36 µm, than does the viviparous form, 9 µm, (Heulin, 1990). Additionally, when the egg-laying and live-bearing *L. vivipara* were hybridized, the F1 generation exhibited an intermediate degree of egg retention and produced eggshells of intermediate thickness (Heulin *et al.*, 1992). Thus, a shift in the length of egg retention was accompanied by the predicted shift in eggshell thickness.

Summary

Blackburn's paper raises important issues about the evolution of viviparity and placentation in reptiles. We agree with three of his main conclusions: that the reproductive modes of squamates exhibit apparent stasis over long periods of time, that the actual transition from oviparity to viviparity can occur quite rapidly, and that placentation evolves concurrently with viviparity. However, we disagree with Black-burn's general approach of pitting punctuated equilibrium versus gradualism, his characterization of the "traditional gradualistic model" for the evolution of viviparity and placentation, and some of the arguments he advances in testing the models. While it is evident that the distribution of embryo stage(s) at oviposition is bimodal, we emphasize that the two reproductive modes are linked by well documented intermediate forms. Studies, such as ours, that focus on taxa where reproductive bimodality is known or suspected offer the greatest promise for resolving the questions raised by Dr Blackburn.

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