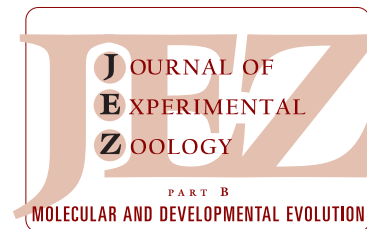


Contrasting Models of Parity-Mode Evolution in Squamate Reptiles



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ABSTRACT

Recent analyses using large-scale phylogenies suggest a radically different history for the evolution of live birth and egg laying in squamate reptiles (lizards and snakes) than traditionally understood. What is the ancestral condition for lizards and snakes? How frequently does live bearing evolve in egg-laying lineages? Can the eggshell ever re-evolve in live-bearing lineages? Answering these fundamental questions about the evolution of key physiological processes will require additional data from genomic, developmental, and fossil data. *J. Exp. Zool. (Mol. Dev. Evol.)* 324B:467–472, 2015. © 2015 Wiley Periodicals, Inc.

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“Which came first, the chicken or the egg?”

“The chicken.”

“What about the egg?”

“Okay, the egg.”

—George Carlin, *When Will Jesus Bring the Pork Chops?*

Among most amniotes, parity mode is a highly conserved trait (Pough et al., 2013). Birds, crocodylians, turtles, and monotreme mammals are strictly oviparous (egg-laying), while metatherian and eutherian mammals are strictly viviparous (live-bearing), with highly developed placentae. In contrast, squamate reptiles exhibit a complex mosaic of oviparous and viviparous species, with ~115 lineages exhibiting viviparity and varying degrees of placentation (Sites et al., 2011). A particular evolutionary scenario, favoring the recent, frequent origin of viviparity from oviparity has traditionally been used as the paradigm to interpret this distribution of parity modes (Blackburn, '99).

In this scenario, squamates were ancestrally oviparous, and the 115 viviparous lineages represent approximately 115 independent origins of viviparity (Lee and Shine, '98). Evidence suggests that viviparity frequently evolves in marginal or unstable climates (particularly temperate areas), where embryo retention promotes initial offspring survival (Shine, '83; Lambert and

Wiens, 2013). This increases maternal costs for reproduction, and thus represents a trade-off when egg mortality is higher (Schwarzkopf and Andrews, 2012). This is not universal, however, as numerous viviparous lineages apparently evolved in tropical areas alongside oviparous species, where climatic effects on egg mortality are seemingly reduced (Tinkle and Gibbons, '77).

A final point in this paradigm is that the evolution of viviparity is irreversible; that oviparity never (or very rarely) re-evolves in viviparous lineages (Blackburn, '99; Shine and Lee, '99). The eggshell has traditionally been considered a “complex” trait that is unlikely to be re-gained, due to the intricate physiological

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mechanisms needed to form and deposit a calcified cuticle, shell, and membranes (Lee and Shine, '98). To summarize, the traditional paradigm for parity-mode evolution in squamates holds that oviparity is the ancestral state, and that viviparity evolution is: (i) recent, and commonly occurs in response to temperate ecological conditions; (ii) frequent, having occurred in ~115 extant lineages; and (iii) essentially irreversible (Blackburn, 2006; Shine, 2014).

In contrast, several lines of evidence suggest that this paradigm is inadequate for a complete understanding of parity-mode evolution in squamates. First, the number of ~115 independent origins is based on pre-phylogenetic hypotheses of squamate relationships, and many of the ~115 lineages now known to form fewer, more inclusive clades (Pyron et al., 2013). This suggests that viviparity evolved earlier in the history of squamates, due to the older age of these more inclusive clades (Schulte and Moreno-Roark, 2010). Related to this point, numerous viviparous lineages are known from the fossil record as early as the Cretaceous, including mosasaurs and other stem diapsids (Wang and Evans, 2011). This suggests that viviparity has been a constant feature throughout the history of squamates, and not solely a recent phenomenon.

Some lizard lineages also present examples of oviparous taxa nested deep within otherwise-viviparous clades, such as Anguidae and Scincidae (Lee and Shine, '98). One study actually suggested that reversal to oviparity was relatively common in numerous lineages, including snakes, anguids, and scincids (de Fraipont et al., '96). That study was criticized, however, because of problems with the datasets and phylogenetic analyses (de Fraipont et al., '99), and most researchers do not typically accept these conclusions (Blackburn, '99; Shine and Lee, '99).

While reversals from viviparity to oviparity seem controversial, there are several taxa for which re-evolution of the eggshell is hard to contest, given that these taxa are a firmly established to be of recent origin and part of larger viviparous clades (Lee and Shine, '98). These include *Eryx jayakari* and *Lachesis* (Lynch and Wagner, 2010; Fenwick et al., 2012), which are both deeply nested within viviparous lineages (Erycidae and Crotalinae). Support for reversal to oviparity is strong given the single best tree for *Lachesis* and for *Eryx* (Lynch and Wagner, 2010; Fenwick et al., 2012), which also lacks an egg tooth that characterizes other oviparous squamates.

If Dollo's Law, suggesting that complex traits are unlikely to re-evolve (Gould, '70), were followed strictly throughout the squamate tree, it would suggest that a large number of viviparity origins (at least five for both *Eryx* and *Lachesis*) would need to have occurred to accommodate oviparous taxa deeply nested within these viviparous clades. A number of comparative studies have demonstrated recently that strict adherence to Dollo's Law is often not supported using model-based phylogenetic tests for the re-evolution of complex traits such as larval stages in frogs and salamanders, shell coiling in limpets, wings in insects, and

mandibular teeth in frogs (Collin and Cipriani, 2003; Whiting et al., 2003; Chippindale et al., 2004; Wiens et al., 2007; Wiens, 2011).

Indeed, violating Dollo's Law seems to be the standard (though certainly not uncontroversial) for the origins of many complex characters in squamates, such as the re-evolution of digits (Kohlsdorf and Wagner, 2006; Brandley et al., 2008; Goldberg and Igić, 2008; Galis et al., 2010; Kohlsdorf et al., 2010), and likely the re-evolution of dangerous venoms distributed throughout Elapidae, Viperidae, Colubridae, Helodermatidae, and other squamates (Fry, 2005; Fry et al., 2006). A host of other untested traits, such as mechanisms necessary for hibernation, gliding, and most types of habitat associations (Sites et al., 2011), are also widely distributed among unrelated lineages, and may also represent "re-evolution" or "re-gain" throughout Squamata. For instance, we do not speak of repeated instances of "re-evolution" of behaviors such as nocturnality or hibernation, despite the fact they were likely present in ancestral lineages, and have been "re-gained" in many extant clades.

We suggest that failing to account for re-evolution of complex traits hampers a proper understanding of rates of character evolution, the influence of the environment on trait selection, the genomic basis for the complex trait expression, and ultimately homology (or the lack thereof) among re-evolved complex traits (Collin and Miglietta, 2008). It is important to note that none of these traits (including oviparity) truly appear to be "re-evolved" in the sense of being obtained *de novo*, but rather it is likely that the raw genetic machinery is being repeatedly and independently co-opted for purposes to which it was previously adapted (Marshall et al., '94; Dingle, 2003), and is thus pre-adapted or exapted for "re-gain" of the associated traits.

Thus, some lingering doubts remain about the traditional paradigm of parity-mode evolution in squamates, given the evidence from the fossil record and some strongly supported reversals to oviparity. Along these lines, we recently presented a new analysis that incorporates a large-scale reconstruction of ancestral parity modes across squamates (Pyron and Burbrink, 2014). We also tested for a relationship between parity mode and diversification rate, and between parity mode and climatic niche. There is a strong relationship between climatic niche and parity mode, where viviparous species typically inhabit areas with lower mean annual temperatures (Hodges, 2004; Lambert and Wiens, 2013). As noted above, this does not explain the origin of all viviparous lineages, given their frequency in the tropics.

There is also a strong relationship between diversification rate and parity mode, as viviparous lineages have high speciation and extinction, and thus low net diversification and high relative extinction (turnover). This indicates that ordinary methods for ancestral-state reconstruction will be misled by the biased representation of states among the extant species. (Maddison, 2006; Paradis, 2008) We accounted for this by estimating

ancestral states using state-dependent methods (Maddison et al., 2007).

Surprisingly, we found strong support for viviparity as the ancestral state of Squamata ~175 Ma, yielding 34 origins of viviparity (including the root), and 59 reversals to oviparity across the history of squamates. Even under maximum parsimony, viviparity originates as early as the stem lineage of Scincoidea (~150 Ma), with at least 12 unambiguous reversals to oviparity across Squamata. Short of enforcing irreversibility, this spans the range of potential models for origin and reversal, and suggests that reversals to oviparity have not been infrequent in Squamata, yielding 0.07–0.34 reversals per million years. This is not common per se, as there are >9500 extant squamates, and still represents fewer changes (93) than the ~115 origins posited by the previous models.

Enforcing a model of irreversibility, we estimated 121 recent origins, as in the traditional paradigm. These models represent opposite ends of a spectrum, ranging from an early origin of viviparity with frequent reversals, to frequent recent origins that are irreversible. Our study is not free from limitations, as we did not consider phylogenetic uncertainty in the SSE analyses or use a phylogeny including all species, and the SSE analyses enforced a single set of transition rates across all lineages, when these seem quite likely to vary considerably among groups. Thus, the true history of parity mode in squamates likely lies somewhere along this continuum, rather than at either extreme.

It seems clear that reversals to oviparity in squamates have happened on a number of occasions. However, we highlight some improvements for future phylogenetic comparative analyses to understand parity evolution in squamates. First, while the tree used in our analyses represents the largest phylogenetic hypotheses for squamates to date, it still includes less than 1/2 of the extant taxa. Including a majority of species is paramount for sampling the diversity of parity states for proper estimation of rate changes and ancestral states. Additionally, sampling more independent loci is important for generating species trees, where distinct gene-histories are accommodated in a coalescent framework to yield better topologies and branch lengths (Edwards and Beerli, 2000; Edwards, 2009). Taxon sampling, topology, and branch lengths are all known to affect comparative analyses (Diaz-Uriarte and Garland, '98; Burbrink and Pyron, 2011), and having credible estimates of all three is important for ancestral character estimation.

We also expect that improved models that incorporate fossil taxa and states, and account for heterogeneous rates of character change throughout the phylogeny, will generally yield a better understanding of parity-mode evolution. Finally, assessing homology of states (e.g., is oviparity homologous throughout Squamata) is important but under studied, and crucial for properly integrating traits and phylogeny. We suggest that the way forward is to incorporate information from physiological,

developmental and genomic studies about the nature of these states, data that remain to be gathered.

It is unlikely that phylogenetic analyses alone will suffice to understand the evolution of parity mode in squamates, particularly with respect to the likelihood, mechanism, and frequency of transitions to and from oviparity. Distinguishing between such hypotheses will now require more detailed species-level data regarding reproduction. The missing egg-tooth of *E. jayakari* provides a key example of this. All egg-laying snakes (but no live-bearing boas) have an egg tooth (a modified tooth projecting out from the maxillary) that facilitates slicing open the leathery eggshell from the inside, so that the neonate can emerge. In contrast, *E. jayakari* lacks this egg tooth, suggesting that oviparity is derived in the species from viviparous relatives that also lack egg teeth, and that this helpful but minor functional trait has not also been regained along with the eggshell. Thus, the main question becomes: how do various lineages representing putative origins of and reversals to oviparity resemble or differ from each other genetically, developmentally, and physiologically?

Numerous studies have examined ecophysiological aspects of parity mode, such as the effects of maternal behavior on incubation temperature, and the effects of these temperatures on offspring survival (Shine, 2002, 2004, 2006). These are likely to continue being a valuable source of data regarding the form, function, and evolution of different reproductive strategies. With respect to specific hypotheses of transition and reversal, we anticipate strong inference can be made via three additional lines of evidence: genetic, developmental, and physiological (Van Dyke et al., 2014).

First, what underlying genetic mechanisms are responsible for the primary functions of eggshell deposition or uterine embryo-retention? What promoter regions or other regulatory complexes are responsible for expressing these genes in various lineages? Most importantly, are the same genomic regions responsible for oviparous or viviparous reproduction (e.g., genes coding for tissues, hormones, and structures related to pregnancy and placenta or eggshells) in different lineages? This seems to be a topic about which little is known at present. If different gene complexes have been recruited for eggshell development in different oviparous lineages that represent putative reversals to oviparity, this would be strong evidence for such reversals.

Conversely, it may be found that the promoter regions or other regulatory complexes responsible for eggshells are simply switched off during the transition to viviparity, but are maintained by selection in a functional or dormant state in the genome of viviparous lineages, and need only be reactivated or re-formulated for the eggshell to be regained. Such a process (re-activation of functional gene-complexes) has been commonly reported as a mechanism for the regain of complex traits in other organisms, such as sex combs in *Drosophila* (Seher et al., 2012),

hand musculature in primates (Diogo and Wood, 2012), and sexuality in oribatid mites (Domes et al., 2007).

Alternatively, if the genes responsible for eggshell development are found in a degraded state in all viviparous lineages, and all oviparous lineages exhibit seemingly homologous functional copies of the same underlying genomic regions, this would be stronger evidence for irreversibility under the traditional paradigm (Zufall and Rausher, 2004), though *de novo* origin of these traits would remain a possibility. Annotated squamate genomes are becoming increasingly available to answer these questions (Alfoldi et al., 2011; Castoe et al., 2013), and transcriptomes from relevant tissues will also likely be helpful for identifying functional genomic regions. Transcriptomic analyses of one viviparous species (*Chalcides*) reveal both homology and convergence in the genetic mechanisms of placentation and pregnancy in mammals and squamates (Brandley et al., 2012). How these vary across species is a crucial next question.

Second, what are the developmental pathways for eggshell formation and calcium deposition among oviparous lineages, and placental formation in viviparous taxa? Little is known comparatively across many species and groups of squamates about the developmental sequence of eggshells or placentae (Blackburn, '93; Blackburn and Flemming, 2007; Blackburn and Flemming, 2009; Stewart and Thompson, 2009). Homogeneity of development within lineages compared to drastically different sequences among lineages representing putative reversals would support hypotheses of eggshell regain. In contrast, heterogeneity of development in viviparous lineages, with high similarity among oviparous lineages, would support the traditional paradigm.

Third, what are the physiological attributes of the major functional traits in different oviparous and viviparous lineages? The egg tooth is a key example of this, and is missing in at least one putative reversal to oviparity (*E. jayakari*). Are there major differences in the structure or composition of eggshells and placentae among lineages representing putative origins of and reversals? Little histological information is available for most lineages (Heulin et al., 2002; Stewart et al., 2010).

If lineages representing putative regains of the eggshell present with drastically different eggshell compositions, this would potentially support hypotheses of reversal. For instance, gecko eggs are very different from other squamates in terms of histology and amino-acid profiles (Sexton et al., 2005). If such differences were common across different lineages, it would support hypotheses of reversal, indicating that the eggshell has re-evolved, and was re-constructed differently each time.

In contrast, if eggshells in all oviparous lineages have the same physiological properties, originate from the same developmental pathways, and are coded for by the same genomic regions, this would cast serious doubt on the hypothesis of frequent reversal. The same is true for placentae, which exhibit several functional

types among viviparous lineages (Stewart and Thompson, 2000), particularly skinks, which have the most complex histories of origin and reversal in our reconstructions. Can different lineages be grouped by unique features of placentation, and do these support hypotheses of frequent reversal or recent origins? Gathering these types of data will be the next step for understanding parity mode evolution in squamates, with explicit reference to how they vary among lineages, and the functional origins of those differences.

In our recent analysis, we presented historical scenarios of parity mode evolution for all major squamates lineages under a variety of models, including strict irreversibility, maximum parsimony, and state-dependent reconstructions. Potential histories range from 121 recent origins of viviparity, to 73 origins and 12 reversals, to 34 origins and 59 reversals. At least 2–5 reversals are already acknowledged as plausible (Lee and Shine, '98; Lynch and Wagner, 2010; Fenwick et al., 2012). Under every method of analysis from Maximum Parsimony to BiSSE, multiple re-gains of oviparity are supported. Thus, it is difficult to reject all of these potential reversals to oviparity, unless one simply states a priori that such reversals are impossible.

These alternative histories offer explicit alternate hypotheses for every major group, that can now be tested directly using more detailed organismal data as described above, including genetic, developmental, and physiological evidence. Phylogenetic analyses alone will not settle these questions. A more detailed and nuanced understanding of squamate reproduction is now needed, with specific reference to comparisons across multiple species in multiple lineages. In addition to potentially settling questions regarding the origin of viviparity and reversal to oviparity, the data gathered will be invaluable to increasing our understanding of parity-mode evolution in general and the functional pathways of vertebrate reproduction.

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