

# Advancing Perspectives on Parity-Mode Evolution

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When we submitted our manuscript (Pyron and Burbrink, 2014) on 2 May 2013, I did not anticipate how controversially it would be received, or the magnitude of the response. Articles in this issue (Blackburn, 2015a,b; Duchêne and Lanfear, 2015; Griffith et al., 2015; King and Lee, 2015b; Shine, 2015; Stewart, 2015; Wright et al., 2015) and in other journals (King and Lee, 2015a) have re-examined our data, analyses, and conclusions, drawing a wide range of inferences. Our summary (Pyron and Burbrink, 2015) was written before any of the responses appeared, and merely gives an overview of our original conclusions, with some suggestions for future research. Here, I take a final opportunity to digest the recent responses to Pyron and Burbrink (2014), and offer a complementary perspective. Future studies of parity-mode evolution should consider the following four points:

- 1) It is clear that transitions both from oviparity to viviparity, and any potential reversals from viviparity to oviparity, are physiologically complex and involve a multitude of genetic and developmental changes (Brandley et al., 2012; Blackburn, 2015a; Shine, 2015). This fact should not be overlooked or glossed over by studies attempting to reconstruct these transitions (Lynch and Wagner, 2010; Fenwick et al., 2012; Pyron and Burbrink, 2014; Griffith et al., 2015). Along these lines, we suggested three sources of evidence (genetic, developmental, and physiological) to supplement phylogenetic analyses (Pyron and Burbrink, 2015). I agree that “ancestral state reconstructions require biological evidence to test evolutionary hypotheses” (Griffith et al., 2015), and suggest that:
- 2) Gathering new data along these lines will be important going forward. Pyron and Burbrink (2014) re-analyzed published phylogenetic and natural history data, and the responses in this issue uniformly discuss existing datasets, experiments, and conclusions. Phylogenetic analyses alone cannot resolve this issue, particularly given what we know about the limitations of comparative methods and the exclusion of fossil data from most such studies (Pyron, 2015; Rabosky and Goldberg, 2015). Similarly, the responses in this issue primarily report and discuss existing data and results while extending theoretical models, but without presenting many new data for hypothesized transitions. Thus, it will be crucial for future studies to integrate multiple lines of evidence into evolutionary studies of parity mode. I also suggest that

hypotheses in these future studies should be agnostic to any a priori notions of the likelihood of transitions in either direction, or any pre-conceived notion of the evolutionary history or assumed ancestral state of parity mode. Rather, these can be tested directly. This is particularly important because:

- 3) The widespread inference of earlier origins of viviparity and possible reversals to oviparity requires deeper evaluation and individual refutation. Essentially all phylogenetic analyses for nearly 20 years (deFraipont et al., '96; Lynch and Wagner, 2010; Fenwick et al., 2012; Pyron and Burbrink, 2014) have supported at least some reversals to oviparity, including maximum parsimony, maximum likelihood, and Bayesian inference, across a variety of phylogenies. Even if ancestral-state reconstruction is shown to be potentially biased in general cases (Duchêne and Lanfear, 2015), specific reversals should not be dismissed generally, but should each be examined in detail using the additional data described above. Early nodes in Scincoidea and Serpentes are suggested to be ancestrally viviparous even by Maximum Parsimony, and present a prime candidate for a high-level comparative study using phylogenetic, genetic, developmental, and physiological data across lineages that is agnostic to the assumed ancestral state. Even along the early branches of Squamata, which may actually be oviparous (King and Lee, 2015a,b), there are fossil lizards that are viviparous, suggesting early origins that may influence ancestral-state estimates (Wang and Evans, 2011). Rather than argue that a particular hypothesized reversal to oviparity is unlikely because reversals to oviparity are unlikely generally, strongly supported instances from phylogenetic analyses should be tested directly. In terms of specific cases that could be tested thusly, I suggest that:
- 4) The putative reversals in *Eryx*, *Lachesis*, and *Liolaemus* are immediate and pressing candidates for integrative analysis. While mentioned by several authors in this issue, none of the

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responses dug deep into the three reversals to oviparity that have been hypothesized the most often or most strongly by ancestral-state reconstruction: the snakes *Eryx jayakari* and *Lachesis* (four species), and the lizard *Liolaemus calchaqui*. These taxa are oviparous, and nested deep within otherwise-viviparous clades, requiring numerous additional steps (independent transitions to viviparity) to estimate ancestral oviparity, even when reversals to oviparity are down-weighted (Wright et al., 2015). Most of these species and their close relatives are common in the pet trade and easily available for experiment. These species are prime targets for a study that collects genetic, developmental, and physiological data to corroborate or falsify the existing hypotheses of reversal to oviparity. We outlined such a research program in Pyron and Burbrink (2015): are the eggshells chemically different from other squamates, are the developmental and physiological pathways homologous, etc.? If these three are not found to represent compelling instances of reversal to oviparity, then the traditional paradigm could be considered supported. If they are, however, found to be compelling, the argument from complexity (that reversals to oviparity are unlikely) may be less applicable across the tree, and even more so across deep time.

As we outlined in our previous papers (Pyron and Burbrink, 2014, 2015), models for the evolutionary history of parity mode exist along a continuum from frequent origins of viviparity with no reversals, to an early origin of viviparity with frequent reversals. I agree generally with the other authors that the true history may be closer to the former, and that reversals to oviparity are likely more difficult physiologically and rarer evolutionarily than *de novo* origins of viviparity from oviparous ancestors. I might even also agree that oviparity is more likely the ancestral state of squamate reptiles. However, I suggest that the preponderance of historical evidence suggests the presence of no less than three strongly supported reversals from viviparity to oviparity, with many more (some much earlier in the history of squamates) inferred by most methods. To dismiss these all out of hand is not properly scientific.

Thus, I exhort those with the means and expertise to conduct integrative analyses gathering genetic, developmental, and physiological data to falsify or corroborate the existing phylogenetic hypotheses of reversals, and to do so without assuming a particular history at the start. From this, we can gain a firmer understanding of the possibility or likelihood, or lack thereof, for reversals to oviparity. This can inform further development of a comprehensive and coherent model of parity-mode evolution from organismal to historical scales. Overall, I predict that the true answer is much murkier than any of us would like to believe. Evidence may continue to be ambiguous for the three cases mentioned above. Without additional fossil discoveries, we may always see earlier branches through a glass, darkly for traits such as parity mode. Ultimately, I suggest that reversals might be rare, but they likely have happened; when and where might be harder to pin down, exactly. But over 200

million years of evolutionary history, nearly anything *can* happen, and anything that *can* happen, probably did.

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