

EVOLUTION

The evolutionary network of whiptail lizards reveals predictable outcomes of hybridization

Anthony J. Barley^{1,2,*}, Adrián Nieto-Montes de Oca³, Norma L. Manríquez-Morán⁴, Robert C. Thomson²

Hybridization between diverging lineages is associated with the generation and loss of species diversity, introgression, adaptation, and changes in reproductive mode, but it is unknown when and why it results in these divergent outcomes. We estimate a comprehensive evolutionary network for the largest group of unisexual vertebrates and use it to understand the evolutionary outcomes of hybridization. Our results show that rates of introgression between species decrease with time since divergence and suggest that species must attain a threshold of evolutionary divergence before hybridization results in transitions to unisexuality. Rates of hybridization also predict genome-wide patterns of genetic diversity in whiptail lizards. These results distinguish among models for hybridization that have not previously been tested and suggest that the evolutionary outcomes can be predictable.

Understanding why mechanisms of species diversification change across the tree of life remains one of the most challenging endeavors in biology. Recent studies have demonstrated how the strength and pace of mutation, genetic drift, and selection can generate distinct patterns of diversification (1–3). Gene flow through hybridization is arguably the most poorly understood of these primary mechanisms of evolution, despite an increasing appreciation for its importance during speciation (4). This is driven, in part, by the fact that hybridization induces a network structure in evolutionary history that is vastly less tractable to infer than bifurcating phylogenetic history. Therefore, our understanding of speciation in many groups where hybridization is common remains incomplete.

The diversity of hybridization outcomes in nature is substantial. Hybridization is associated with numerous evolutionary phenomena, including genetic introgression, hybrid speciation, lineage fusion, changes in reproductive mode, and polyploidization (5). These distinct biological outcomes have different effects on diversification. For example, hybrid speciation and lineage fusion generate or eliminate species diversity, respectively. Transitions from sexual to unisexual reproduction are also disproportionately associated with hybridization (6). These phenomena have motivated theories to explain the relationship

between hybridization and the evolution of unisexuality and the effects of hybridization on genetic diversity and microevolution (7, 8). However, our understanding of the manner and extent to which the diverse outcomes of hybridization are predictable remains hampered by a lack of empirical data for testing these theoretical models. This is in part caused by a limited number of biological systems that contain replicated examples of each outcome. In this work, we used the North American whiptail lizard (*Aspidoscelis*) to test whether hybridization produces predictable outcomes.

Whiptails include the highest diversity of unisexual lineages among vertebrates. The clade includes >30 sexual species and ~15 recognized unisexual taxa that reproduce by parthenogenesis. Diploid unisexual lineages in this clade are derived from hybridization events between sexual species that form F1 hybrid offspring that reproduce clonally (9). Triploid unisexual lineages are thought to be derived from backcrossing events between diploid unisexual lineages and sexual species. Even before unisexual reproduction was documented in whiptails, the clade was recognized as being “an ideal object lesson in Nature’s way of species-making” because of the notable patterns of phenotypic variation they exhibit across populations (10). However, these patterns of variation and hybridization also produced myriad complications in defining the boundaries between species that have hindered understanding of the group’s systematics and diversification history despite decades of study (9–11). In this work, we study the tree-like and network-like patterns of evolution in *Aspidoscelis* to understand the mechanisms that underlie their divergent outcomes of hybridization.

Using a reduced-representation genomic dataset (tables S1 and S2 and data S1), we inferred patterns of evolutionary history among all the sexual whiptail species (12). Introgression

tests based on the genome-wide frequencies of site patterns detected widespread evidence of nontree-like patterns of evolution (fig. S1 and data S2 and S3). A substantial proportion (~60 to 70%) of the 33 sexual species appears to have been involved in introgressive hybridization events (figs. S2 and S3). Multiple significant tests were detected for several species, which suggests that they have genomes containing introgressed regions from multiple species (data S2 and S3). Phylogenetic network analyses found that patterns of introgressive hybridization among sexual whiptails could largely be captured by ~5 to 13 reticulation edges (figs. S4 and S5). The results across all hybridization analyses were largely congruent. We used admixture graphs to compare introgression hypotheses in the few cases where they were not (figs. S6 and S7 and tables S3 and S4). We detected no evidence of introgressive hybridization between the most distantly related species, even when they occur in sympatry (figs. S2, S4, and S5). Introgressive hybridization appears to have been common even when phenotypic evolution is rapid across populations, as it is in this clade, where ~70% of species encompass multiple, morphologically distinctive subspecies (table S1). Some whiptail subspecies may reflect instances of lineage fusion, where populations that have not diverged sufficiently to develop reproductive isolation come back into contact (13). Several of the inferred hybridization events include species that are morphologically, ecologically, and evolutionarily divergent (figs. S2 and S8). We lack time estimates for the introgression events but suspect that they span a broad range of historical time frames, given the diversity of the introgression patterns (Table 1).

We used phylogenetic network approaches to infer which of the sexual species are the parental ancestors of the hybrid, diploid unisexual lineages [fig. S9; see (12) for a discussion of terminology]. We used population genetics tools to infer the ancestry of the triploid unisexual lineages (fig. S10 and table S5) (12). We identified 11 unisexual lineages that have distinct combinations of genetic ancestry derived from 10 sexual species (table S6). Six of these unisexual lineages are diploid, and two of these appear to have formed multiple times through hybridization. The other five are triploid, and two of these also appear to have been formed multiple times. Within unisexual whiptails, a primary hybrid speciation process always appears to precede speciation by ploidy elevation through genome addition (Fig. 1).

Our ensemble analysis provides a comprehensive view of the patterns and outcomes of hybridization in whiptails, including both introgressive hybridization and hybrid speciation (Table 1 and Fig. 2) (12). The phenomenon

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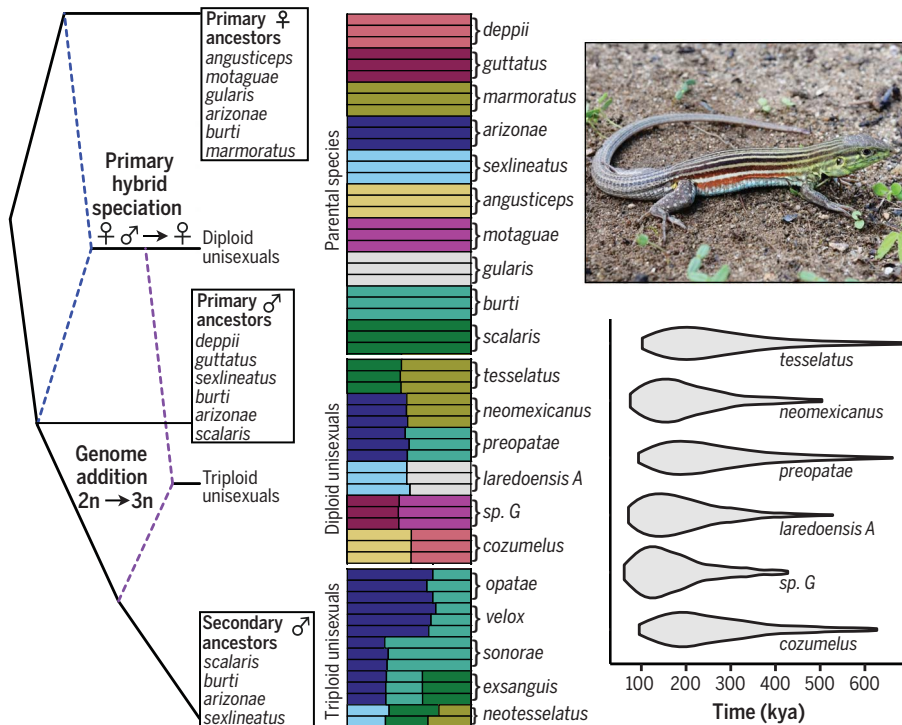


Fig. 1. Summaries of hybrid speciation in unisexual whiptail lizards. Primary hybridization (i.e., a hybridization event between two diploid sexual species that is associated with transition to unisexual reproduction) precedes genome addition (i.e., ploidy elevation) (left). Sexual species associated with each process are indicated. Colored bars in STRUcTURE plot (each representing data for a single lizard) show estimates of the genome-wide proportion of genetic ancestry derived from sexual parental species for each unisexual individual. Violin plots show 95% confidence intervals for formation time estimates of diploid unisexual lineages. kya, thousand years ago. Photo is of *Aspidoscelis deppii*, a sexual species that is both an ancestor of the parthenogenetic lineage *Aspidoscelis cozumelus* and has been involved in introgressive hybridization with *Aspidoscelis guttatus* (photo credit: A.J.B.).

of isolation and lineage divergence followed by secondary contact has occurred repeatedly across broad time scales in *Aspidoscelis*. Consequently, whiptails exhibit many replicated instances of both introgressive hybridization and hybrid speciation, which occurs through transitions in reproductive mode or ploidy elevation. This provides an opportunity to test competing hypotheses explaining the observed association between hybridization and the evolution of unisexuality in vertebrates. Three main hypotheses have been proposed. The phylogenetic constraint hypothesis proposes that particular sexual lineages are inherently predisposed to produce parthenogenetically competent individuals upon hybridization (6). The balance hypothesis predicts that as divergence among hybridizing sexual species increases, the probability that their hybrid offspring will produce unreduced oocytes also increases, allowing for the evolution of unisexual reproduction (14). This is balanced against the increasing likelihood that hybrids will experience impairments in fecundity and/or viability arising from genetic incompatibilities if divergence between their parents is too high. Therefore, this hypothesis predicts that hybridizing lineages that are at intermediate levels of evolutionary divergence produce unisexual offspring, whereas those that are at too low or too high levels lead to sexual offspring or a failed cross, respectively. A further refinement on both of these hypotheses has been called the rare formation hypothesis, in which complex genetic preconditions are necessary to initiate unisexual reproduction in hybrids (15).

These mechanisms are not mutually exclusive, but we see limited evidence for the phylogenetic constraint hypothesis in whiptails. Of the six specific primary hybridization events associated with transitions to parthenogenetic reproduction, only two of the 10 sexual parental species have been involved in more than one of these events (Fig. 2 and table S6). Further, if we model unisexual parental status as a discrete trait on the whiptail phylogeny, we see virtually no evidence of phylogenetic signal (Pagel's $\lambda = 6.6 \times 10^{-5}$; Fritz and Purvis's $D = 0.68$). By contrast, we see conspicuous support for the balance hypothesis. At low levels of divergence, hybridization among sexual whiptail species results only in introgression (Fig. 3A). Only those hybridization events spanning deep levels of evolutionary divergence result in the production of unisexual lineages, and we did not detect evidence of introgression between the parental species of the parthenogenetic lineages. Divergence time estimates between the pairs of sexual parental species that have generated parthenogenetic lineages span a broad range (~15 to 25 million years; fig. S11 and table S7), but these hybridization events have all occurred in the recent past, which suggests that these lineages are

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Table 1. Summary of introgressive hybridization events and their support from alternative analyses.

Posterior probability (PP) for one species in a pair as under reticulation edge in Bayesian analysis, with alternative species as an ancestor. ΔL indicates improvement in likelihood score when focal hybrid node is present in the network. Support for focal hybridization event by *f* branch analysis is indicated by the corresponding Z score. The HyDe column indicates the largest Z score calculation for a test that includes both focal species. Support in best admixture graph model is indicated by an X. Dashes indicate analysis is not applicable (PhyloNet) or introgressive hybridization was not supported by analysis (others).

| Hybridizing species | Admixture graph | PhyloNet (PP) | PhyloNetworks ΔL | <i>f</i> branch | HyDe |
|---|-----------------|---------------|--------------------------|-----------------|------|
| <i>tigris tigris</i> – <i>tigris aethiops</i> | – | 1.0 | – | 10.1 | – |
| <i>deppii deppii</i> – <i>guttatus</i> | X | – | – | 12.3 | 80.2 |
| <i>lineatissimus exoristus</i> – <i>guttatus</i> | X | 1.0 | 3.5 | 10.1 | 73.0 |
| <i>lineatissimus exoristus</i> – <i>cf. deppii infernalis</i> | X | 1.0 | – | 10.5 | 73.0 |
| <i>scalaris scalaris</i> – <i>scalaris colossus</i> | X | 1.0 | 5.0 | 8.3 | 37.1 |
| <i>costatus zweifeli</i> – <i>communis</i> * | X | 1.0 | 6.3 | 11.4 | 31.5 |
| <i>sackii</i> – <i>costatus costatus</i> * | X | 1.0 | 51.2 | 22.8 | 65.4 |
| <i>sackii</i> – <i>parvisocius</i> * | X | 1.0 | 9.4 | 10.3 | 14.0 |
| <i>costatus zweifeli</i> – <i>costatus costatus</i> | X | 1.0 | – | 15.4 | 64.7 |
| <i>mexicanus</i> – <i>motaguae</i> * | X | 1.0 | 51.2 | 5.8 | 58.7 |
| <i>calidipes</i> – <i>costatus zweifeli/communis</i> | X | 1.0 | – | 11.1 | 20.1 |
| <i>scalaris</i> – <i>costatus occidentalis</i> | X | 1.0 | – | 9.6 | 40.9 |

*Phylogenetic discordance between mitochondrial DNA and nuclear DNA datasets in Barley *et al.* (13) also supports these introgressive hybridization events.

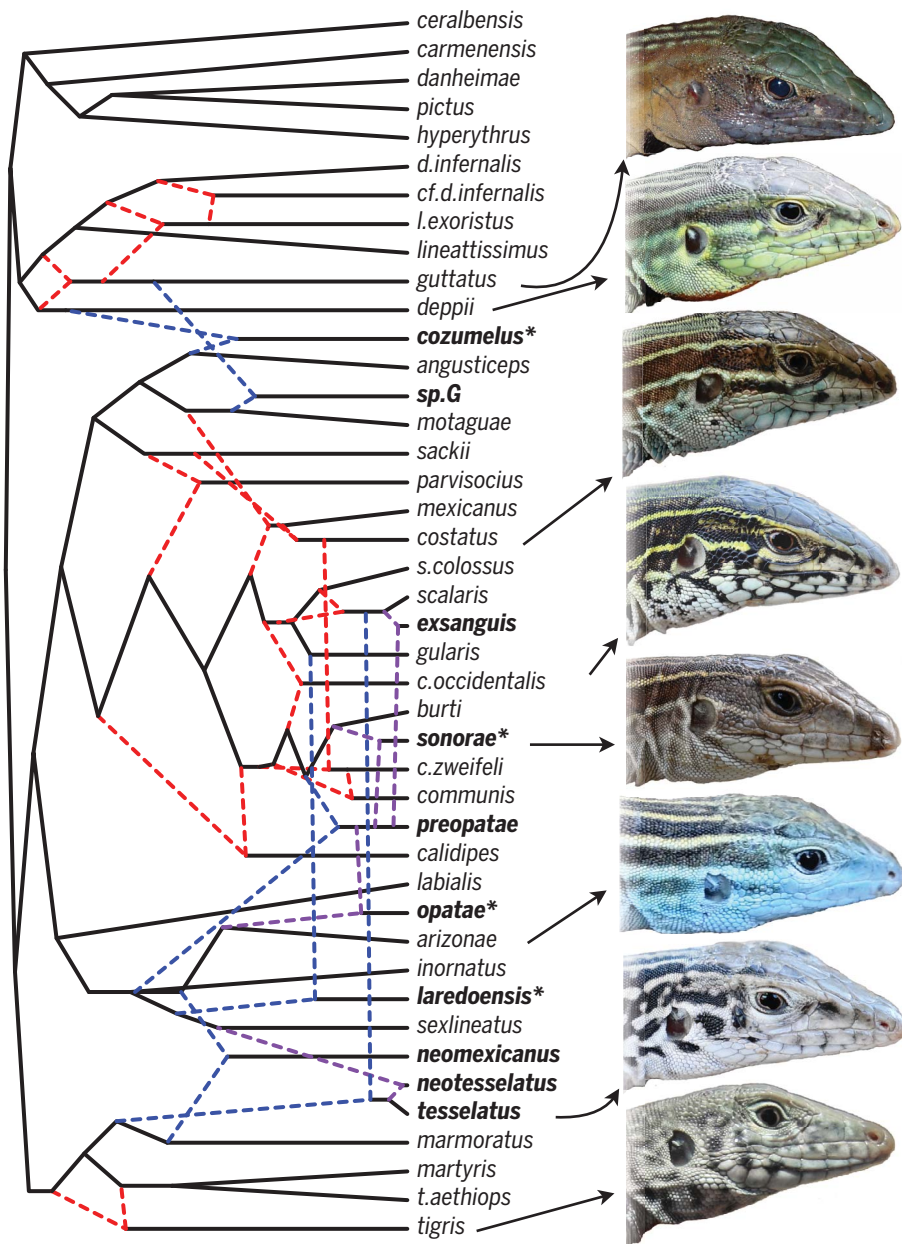


Fig. 2. Evolutionary network history of the whiptails. Red reticulation edges represent introgressive hybridization events between sexual species. Blue reticulation edges denote the evolution of diploid parthenogenetic lineages through the primary hybrid process (Fig. 1). Purple reticulation edges denote the evolution of triploid parthenogenetic lineages through the genome addition process. These edges illustrate instances of hybridization between diploid parthenogenetic lineages and sexual species. Parthenogenetic taxa are indicated in bold. Some of these, indicated by asterisks, have formed multiple times through independent hybridization events between the same sexual species (table S6) (photo credit: A.J.B. and A.N.-M.d.O.).

evolutionarily ephemeral owing to constraints imposed by a lack of genetic recombination (Fig. 1). Finally, we see some evidence in support of the rare formation hypothesis. A limited number of extant unisexual lineages are found in nature compared with the theoretical number of sexual parental combinations whose divergence time falls within this range and whose geographic distributions overlap (6 of 28 combinations). This suggests that specific

genotypic combinations may also be required to induce changes in reproductive mode. This is consistent with laboratory crossing experiments that have had only rare success in producing parthenogenetic lineages (16, 17).

Our results suggest that time since divergence plays a major role in determining the outcomes of hybridization in whiptails, with outcomes switching from introgressive hybridization to hybrid speciation when the diver-

gence time between species exceeds ~10 million years (Fig. 2, fig. S11, and table S7). There is a gap in evolutionary relatedness between pairs of whiptails involved in these two types of hybridization outcomes [between a genetic distance of ~0.0097 and 0.0126 based on the restriction site-associated DNA (RAD)-tag data]. Therefore, it remains an open question whether, within that divergence range, hybridization between pairs of whiptails could conceivably result in either outcome. Predictions of the balance hypothesis are similar to those made by theoretical models of homoploid hybrid speciation that are not accompanied by a transition in reproductive mode (18). This may reflect the importance of particular types of reproductive incompatibilities in both processes that become more likely to arise at intermediate levels of divergence. Incompatibilities in meiosis genes could be necessary to cause transitions from sexual to parthenogenetic reproduction in hybrid individuals (19). In homoploid hybrid speciation, incompatibilities that lead to assortative mating and discrimination against parental populations may be important for initiating reproductive isolation in hybrid populations.

Although patterns regarding the evolution of parthenogenesis and mechanisms of polyploidization appear to be largely conserved in *Aspidoscelis* (Fig. 1), patterns of introgression between species exhibit substantial variation (fig. S2). In their foundational comparative study of speciation, Coyne and Orr (20) have demonstrated that the amount of reproductive isolation between species of *Drosophila* is correlated with their time since divergence. If generalizable, this result predicts that in nature, the amount of introgression between species should be negatively correlated with their time since divergence (21, 22). We expect this relationship because, as species diverge, they should accumulate an increasing number of incompatibilities that both decrease the probability that hybrids can serve as a bridge for gene exchange and increase the probability that introgressed regions will be purged by negative selection over time. Consistent with this prediction, we see a strong negative correlation between the admixture proportion (i.e., the shared proportion of the genome) and the amount of evolutionary divergence that separates two species that have hybridized (Fig. 3B). Within species, allopatric whiptail subspecies show high variability in admixture proportions, with some values similar to those estimated from sister taxa and some much larger (table S8). These results are consistent with a polygenic threshold speciation model, which has garnered support from recent empirical studies (23, 24). Under this model, once two lineages reach a threshold of divergence, Dobzhansky-Muller incompatibilities are typically in sufficient number

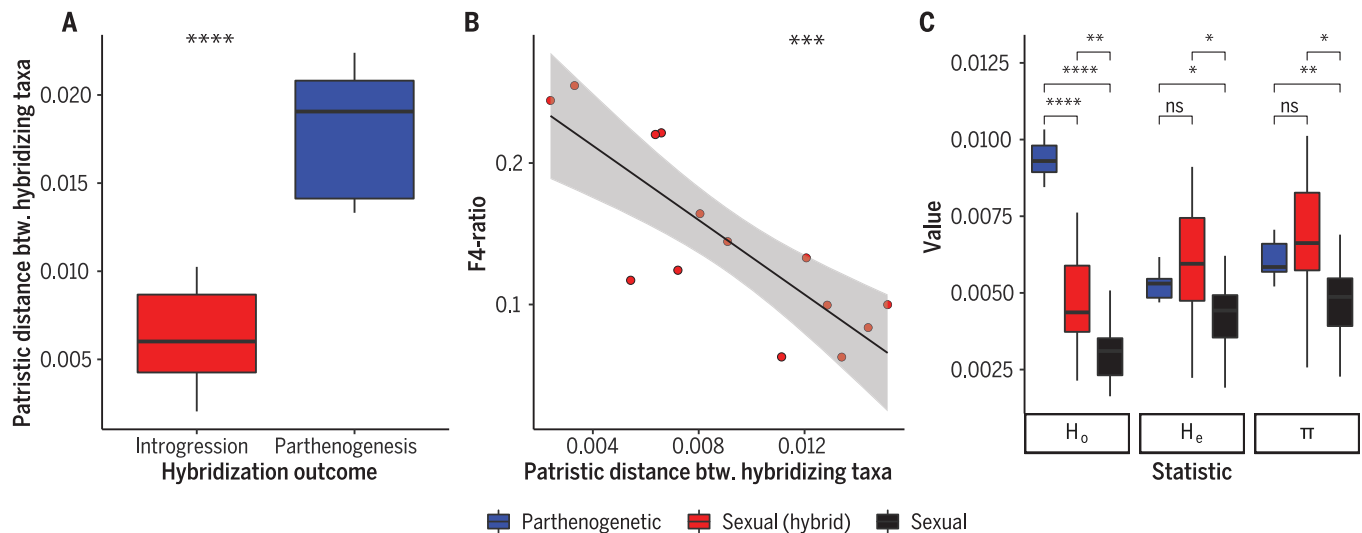


Fig. 3. Illustration of outcomes of hybridization between whiptail lizards.

(A) Hybridization between more closely related sexual species leads to introgression, whereas hybridization between more distantly related sexual species leads to the evolution of parthenogenetic lineages. Box plots are of patristic distances calculated from the posterior distribution of branch lengths separating hybridizing species. (B) For sexual species between which we find strong evidence of introgressive hybridization (Table 1), the amount of the genome that is shared (as estimated by the F4 ratio) is negatively correlated with their time since divergence (here quantified by the patristic distance that separates them). (C) Genome-wide measures of

observed heterozygosity (H_0), nucleotide diversity (H_e), and gene diversity (π) for diploid parthenogenetic lineages and sexual species (see table S9 for data). Because they are clones of F1 hybrids, parthenogenetic lineages have elevated observed heterozygosity compared with that in sexual species. Nucleotide and gene diversity tend to be higher in sexual species that have a hybrid genetic background compared with those that do not, illustrating the role of hybridization as a source of genetic diversity in whiptails. Asterisks indicate significance level for t tests [(A) and (C)] or linear regression with 95% confidence interval (B). **** $P < 0.0001$; *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; ns, not significant.

to begin suppressing introgression. This effect may determine whether sufficient reproductive isolation has evolved to prevent lineage fusion upon secondary contact. Thus, multiple thresholds may be important to speciation and hybridization outcomes in whiptails at different time scales.

Models for speciation with gene flow make contrasting predictions about the effects of hybridization on diversification, including the formation of genomic islands of speciation within the genome, contributions to adaptation and the evolution of new phenotypes, and increasing rates of diversification (3, 25, 26). To examine the effects that hybridization has had on genomic diversity during speciation in whiptails, we compared estimates of observed heterozygosity, nucleotide diversity, and gene diversity between lineages that have been formed by different speciation processes (Fig. 3C and table S9). Parthenogenetic lineages have maintained high levels of observed heterozygosity because they are clones of F1 hybrid offspring. Sexual species with a history of introgressive hybridization frequently have higher estimates of nucleotide and gene diversity than those that do not. These same values in some sexual species even exceed those calculated for the parthenogenetic lineages, which likely reflects these species having had multiple hybrid partners during their evolutionary history.

Causes and consequences of hybridization in whiptails extend beyond the genome and

mode of reproduction. For example, one of the earliest hypotheses to explain the geographic distribution of parthenogenetic lineages proposed that climatic fluctuations during the Pleistocene may have contributed to shifting distributions of species, providing opportunities for secondary contact and hybridization in doing so (14, 27). This idea is consistent with results of an ancestral state biogeographic reconstruction for whiptails, which suggests that many of the parents of parthenogenetic lineages recently dispersed into the areas that they now occupy and where these lineages formed (fig. S12). Hybridization may also play a role in mediating phenotypic evolution. In *Aspidoscelis*, gigantic body size has evolved at least three different times (fig. S13). These giants are associated with some of the strongest (i.e., large D statistics indicating hybridization with multiple species) and most notable (i.e., with evolutionarily divergent species) signals of hybridization in the evolutionary history of the clade (table S10).

Further insights could be gained through comparative studies of other unisexual vertebrates. In *Darevskia* lizards, the specificity of the sexual species involved in the formation of the multiple parthenogenetic lineages and the apparent lack of correlation between gene flow and divergence have been interpreted as support for the phylogenetic constraint hypothesis (28). The evolutionary divergence separating parents of the unisexuals in these

two clades appears to be comparable (table S11). *Cobitis* fishes reproduce by gynogenesis, and crossing data in this group are also consistent with the balance hypothesis (29). The rare formation hypothesis has been a favored explanation in the gynogenetic Amazon molly (*Poecilia formosa*) (30). Age estimates for the unisexual whiptails based on the RAD data are much younger than those for *P. formosa* (median formation times ~160,000 to 250,000 versus ~500,000 generations ago). Resolving the mechanisms that underlie these similarities and differences will help advance our understanding of some of the longest-standing areas of inquiry in biology.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 to S13
Tables S1 to S11
References (33–89)
MDAR Reproducibility Checklist
Data S1 to S3

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Divergent species create distinct hybrids

Hybridization between species is common in many taxa and can lead to a variety of outcomes. Hybrids can backcross with parent lineages, increasing genetic diversity, or they can develop into new species. In squamate lizards, hybridization can create polyploid species with unisexual reproduction (parthenogenesis). Barley *et al.* used North American whiptail lizards, which include 15 recognized unisexual species, as a model system to examine the possible outcomes of hybridization. Phylogenetic analyses showed that divergence time between parents predicts the effects of their hybridization. Hybrid speciation and unisexuality were more common with more time since the parent species diverged from a common ancestor. —BEL

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