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The Potential Role of Androgenesis in Cytoplasmic–Nuclear Phylogenetic Discordance

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In many organisms, gene trees based on nuclear markers and those based on cytoplasmic markers (chloroplasts or mitochondria) sometimes indicate quite different relationships among the species being studied (e.g., Rieseberg and Soltis 1991; Rieseberg et al. 1996; Cathey et al. 1998; Bergthorsson et al. 2003; Avise 2004; Croucher et al. 2004; Sullivan et al. 2004; Chan and Levin 2005; Fehrer et al. 2007; Linnen and Farrell 2007). This incongruence is normally attributed to incomplete lineage sorting (when two alleles coalesce prior to speciation and do not track the species phylogeny), introgression (interspecific hybridization followed by unidirectional backcrossing), horizontal gene transfer, or errors in phylogenetic reconstruction.

Although the usual explanations for cytoplasmic–nuclear incongruence are well documented, these explanations are often assumed rather than demonstrated in specific cases. Here, we explore an alternative explanation that may be more prevalent than is currently appreciated. Androgenesis—asexual reproduction of the male nuclear genome—is taxonomically widespread (often at low frequency). When coupled with cross-species capture of maternal gametes, androgenesis results in cytoplasmic–nuclear incongruence in a single generation. Here, we explore expectations for androgenesis as the origin of cytoplasmic–nuclear incongruence and suggest that cases of cytoplasmic–nuclear incongruence should be re-examined to consider the possibility of this mechanism.

OBLIGATE VERSUS SPONTANEOUS ANDROGENESIS

Androgenesis occurs when offspring carry nuclear chromosomes from only the male parent. When the male and female parents represent two different species, offspring of androgenesis have the nuclear genes of the paternal species but usually have the cytoplasmic organelles of the maternal species, a combination hereafter referred to as "cytonuclear mismatch" (e.g., Goodsell 1961; Chase 1963; Abdalla and Hermsen 1972; Pelletier et al. 1987; Horlow et al. 1993; Lee et al. 2005; Hedtke et al. 2008). If evolutionary forces such as drift or selection result in the fixation of this novel genotype within a population, all the nuclear genes in the descendant population will be more closely related to the paternal lineage, whereas the cytoplasmic genes will be more closely related to the maternal lineage (Fig. 1).

Before considering the generality of this mechanism for cytoplasmic–nuclear incongruence, it is important to distinguish 3 types of androgenesis:

1. artificial androgenesis: organisms are manipulated in the laboratory to produce offspring with only paternal nuclear genes, usually by irradiation or treatment with stressors like high heat or chemicals (e.g., Hasimoto 1934; Surani et al. 1984; Datta 2005; Grunina and Recoubratsky 2005; Rapacz et al. 2005; Brown et al. 2006). Artificial androgenesis by definition does not occur in nature and therefore we will not discuss it further.
2. spontaneous androgenesis: offspring with only paternal nuclear DNA are produced at relatively low frequency from parents who normally reproduce sexually. Spontaneous androgenesis has been experimentally observed in both plants and animals, although the frequency of androgenetic offspring varies considerably depending on the particular crosses involved (Table 1).
3. obligate androgenesis (also called paternal apomixis): all offspring inherit only paternal nuclear DNA. Only a few divergent eukaryotic lineages appear to reproduce obligately through androgenesis (Table 1).

Although "obligate" androgenesis produces an obvious source of cytonuclear mismatch, its apparent rarity may limit its applicability as an explanation for this phenomenon. Nonetheless, we argue that "spontaneous" androgenesis is common enough that it should be routinely considered as a possible explanation when nuclear and cytoplasmic histories differ.

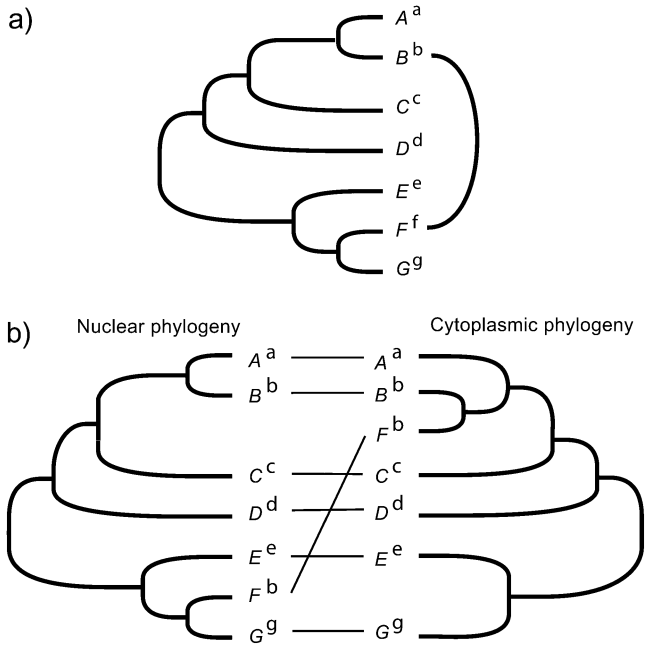

FIGURE 1. Androgenesis can cause phylogenetic discordance between trees built from nuclear versus cytoplasmic markers. Upper case letters indicate the nuclear genome; lower case superscripts indicate the cytoplasmic type. a) Phylogeny detailing relationships between hypothetical species *A*–*G*. There is no initial incongruence between nuclear and cytoplasmic trees. Androgenesis between maternal species *B* and paternal species *F* leads to the capture of cytoplasm from species *B*, depicted by a curved line. b) The spread of the mixed genotype and extinction of cytoplasmic genome f causes incongruence between gene trees; nuclear trees place species *F* as sister to species *G* (as in the initial phylogeny), whereas cytoplasmic markers place species *F* sister to species *B*.

MECHANISMS FOR ANDROGENESIS

For androgenesis to cause cytonuclear mismatch, two steps are necessary: first, the maternal nuclear DNA in the gamete must be lost such that only paternal nuclear chromosomes are inherited and second, these offspring must be able to produce viable gametes.

1. Loss of maternal nuclear DNA: In most animals, female gametes are arrested prior to completion of meiosis II, and gametogenesis finishes only after fertilization (reviewed in Sagata 1996; Greenstein 2005; Madgwick and Jones 2007). The initial axis of orientation of the maternal nuclear genome in both meiosis I and meiosis II is parallel to the cell cortex (Karpen and Endow 1998). In response to intracellular signaling initiated by the sperm, the axis of meiosis is reoriented at fertilization so that it is perpendicular to the cell cortex. The meiotic product that is adjacent to the cell cortex is expelled as a polar body, whereas the maternal genome remaining in the cell fuses with the paternal genome from the sperm. A mutation in the signaling pathway for axis reorientation can result in complete extrusion of the maternal genome as two polar bodies (e.g., see Gard et al. 1995). Cellular extrusion of the entire maternal nuclear genome has been demonstrated through cytological work on two freshwater clam species in the genus *Corbicula* which are obligately androgenetic (Komaru et al. 1998; Ishibashi et al. 2003).

In certain plant species, anthers can spontaneously develop plantlets, and this is mechanistically one form of androgenesis (e.g., Ramanna and Hermsen 1974; Koul and Karihaloo 1977). In androgenetic Tassili cypress trees, ovules contain endosperm but apparently contain no egg cells, and pollen grains appear to go through embryogenesis within the ovule (Pichot et al. 1998; 2008). Androgenetic development directly from pollen grains would not result in cytonuclear mismatch because there are no interactions between gametes of different lineages. However, laboratory crosses of some angiosperms have empirically demonstrated cytonuclear mismatch in those offspring that inherit only paternal nuclear DNA (Goodsell 1961; Chase 1963; Abdalla and Hermsen 1972; Pelletier et al. 1987; Horlow et al. 1993). The mechanism for this is unclear; either the maternal nucleus degenerates (as suggested by Campos and Morgan 1958; Chase 1963; Kindiger and Hamann 1993) or fails to fuse with the paternal nucleus and is lost during the first cellular division after fertilization (as suggested in Goodsell 1961; Chase 1963; Kermicle 1969). Maternal effects can increase the frequency of androgenetic offspring. For example, maize plants homozygous for the maternally expressed indeterminant gametophyte 1 (*ig1*) mutation show high frequencies of androgenetic production (8%: Kindiger and Hamann 1993). One effect of the *ig1* mutation is abnormal maternal microtubule behavior, which results in irregular positioning of the nuclei (Huang and Sheridan 1996); microtubules make up the spindle fibers that pull homologous chromosomes or sister chromatids to opposite sides of the cell. The increase in the proportion of androgenetic offspring in maize plants that carry this mutation may result from this defective microtubule organization. This defect could increase the probability that the maternal genome is lost either during gametogenesis or during the first round of mitotic replication of the embryo.

2. Production of gametes: Gametes usually contain half the DNA of the somatic cells and thus are normally haploid in diploid species. Androgenetic offspring arising from haploid sperm would also be haploid (e.g., Campos and Morgan 1958; Burk 1962; Pelletier et al. 1987; Pichot et al. 2008). However, many plant and animal species either cannot develop or are infertile if haploid. For example, in rainbow trout, fertilization of females with overmature eggs resulted in 100% of offspring being androgenetic, but all were haploids and did not survive to reproduction (Yamazaki 1983). Androgenetic diploid (or polyploid) offspring could very rarely develop as a consequence of polyspermy—fertilization of an egg cell by multiple sperm (as in grass carp: Stanley 1976b). Chromosomal doubling immediately after fertilization (as in *Drosophila*: Komma and Endow 1995) could restore normal ploidy to androgenetic offspring. Fertilization by unreduced sperm can also occur, either following the evolution of unreduced sperm (as in androgenetic *Corbicula*: Komaru and Konishi 1999, and androgenetic *Cupressus dupreziana:* Pichot

TABLE 1. Organisms demonstrated to have reproduced through androgenesis

Organism	Frequency[a]	Evidence[b]	Citation
Spontaneous androgenesis			
Arthropods			
Bacillus rossius-grandii benazzii × *B. benazzi*	0.01	Paternity	Mantovani and Scali (1992)
Bacillus rossius-grandii benazzii × *B. maretimi*	0.18	Paternity	Mantovani and Scali (1992)
Bacillus rossius-grandii benazzii × *B. rossius*	0.13	Paternity	Mantovani and Scali (1992)
Drosophila melanogaster	<0.001 to 0.015	Paternity	Komma and Endow (1995)
Vertebrates			
Cyprinus carpio × *Ctenopharyngodon idella*	0.01	Paternity	Stanley (1976a, 1976b); Stanley and Jones (1976); Stanley et al. (1976)
Angiosperms			
Brassica napus	0.21	Paternity	Chen and Heneen (1989)
Capsicum frutescens	10^{-3}	Paternity	Campos and Morgan (1958)
Nicotiana debneyi × *N. tabacum*	10^{-4} to 10^{-5}	Paternity	Horlow et al. (1993)
Nicotiana debneyi-tabacum × *N. tabacum*	10^{-5} to 10^{-6}	Paternity	Horlow et al. (1993)
Nicotiana digluta × *N. tabacum*	10^{-3}	Paternity	Clausen and Lammerts (1929)
Nicotiana suaveolens × *N. tabacum*	10^{-5}	Paternity	Horlow et al. (1993)
Nicotiana sylvestris-tabacum × *N. sylvestris*	0.0476	Paternity	Clausen and Lammerts (1929); Kostoff (1934)
Nicotiana tabacum	10^{-3} to 10^{-6}	Paternity	Burk (1962); Pelletier et al. (1987); Horlow et al. (1993)
Nicotiana tabacum × *N. langsdorfii*		Paternity	Kostoff (1934)
Petunia hybrida	10^{-4}	Paternity	Singh and Cornu (1976)
Poa arachnifera × *P. secunda*	0.053	Paternity	Kindiger (2004); Kindiger and Wipff (2009)
Poa arachnifera × *P. pratensis*	0.014	Paternity	Kindiger and Wipff (2009)
Poa arachnifera × *P. ligularis*	0.016	Paternity	Kindiger and Wipff (2009)
Solanum verrucosum × *S. tuberosum*	0.09	Paternity	Abdalla and Hermsen (1972)
S. verrucosum × *S. phureja*	0.35	Paternity	Abdalla and Hermsen (1972)
Tripsacum dactyloides × *Zea mays*	1.0	Paternity	Collins and Kempton (1916)
Zea mays	0.009–0.08	Paternity	Goodsell (1961); Chase (1963); Kermicle (1969); Kindiger and Hamann (1993); Belicuas et al. (2007)
Obligate androgenesis			
Arthropods			
Wasmania auropunctata (drones)	1.0	Paternity	Fournier et al. (2005)
Molluscs			
Corbicula australis		Morphology	Byrne et al. (2000)
Corbicula fluminalis		Morphology	Korniushin (2004)
Corbicula fluminea	1.0	Cytological	Ishibashi et al. (2003)
Corbicula leana	1.0	Cytological	Komaru et al. (1998)
Gymnosperms			
Cupressus dupreziana	1.0	Paternity	Pichot et al. (2001)

[a] Frequency reported is the estimated proportion of androgenetic offspring out of all viable offspring when known. It is limited to the crosses done in a given study and does not necessarily reflect the frequency of androgenesis in the species as a whole. A frequency of 1.0 represents obligate androgenesis.

[b] Evidence includes phenotypic or genetic markers indicating only the male parent contributed nuclear genes to the offspring ("paternity"), diagnostic morphological markers ("morphology," specifically biflagellate sperm in the clam genus *Corbicula*), or cytological examination of the fertilization process ("cytological").

and El Maâtaoui 2000) or by rare production of unreduced sperm (as in maize: Chase 1963). Polyploid species could produce sperm, which are reduced, but which are not haploid; for example, a tetraploid species may produce diploid sperm, and androgenetic offspring would also be diploid (as in maize: Chase 1963, and loach: Arai et al. 1995).

ANDROGENESIS AND CYTONUCLEAR MISMATCH

Cytonuclear mismatch (also called mitochondrial or chloroplast capture) occurs when the cytoplasmic organelles of one species are found associated with the nuclear genome of another lineage. Models for cytonuclear mismatch need to provide explanations for two distinct processes: 1) how an individual with the mixed cytonuclear genotype is initially produced and 2) how the novel mixed cytonuclear genotype becomes fixed in a population. Note that this discussion focuses on maternally inherited cytoplasmic organelles. Paternally inherited organelles would not generate phylogenetic conflict through androgenesis, as the nuclear and cytoplasmic genomes would be inherited together and would share the same history.

Generation of a Mixed Cytonuclear Genotype

Androgenesis is not often considered as a mechanism for generating cytonuclear mismatch. Rather, most researchers have suggested that introgression of a maternally inherited cytoplasmic organelle into the nuclear background of another species begins with initial hybridization and exchange of nuclear genes between the two species. Subsequent backcrosses of this hybrid then favor unidirectional nuclear gene flow from the paternal species, with the hybrid as the maternal parent. This could occur through one of the following mechanisms: 1) There is asymmetrical reproductive success (crosses are only successful when one parental lineage is the father and the other is the mother; Rieseberg et al. 1996;

Avise 2004). 2) One or more females colonize a region inhabited by the other species (in plants, pollen from the majority species may swamp out pollen from the minority species; Rieseberg et al. 1996). 3) Hybridization is frequency dependent; females are more likely to mate with heterospecifics if conspecific males are comparatively rare (Chan and Levin 2005). 4) Interactions between cytoplasmic genes from one species and nuclear genes from another give a fitness advantage to the mixed cytonuclear genotype over the paternal species and over nuclear hybrids (Tsitrone et al. 2003). 5) Incompatibilities between nuclear loci select against nuclear hybrids without cytoplasmic interactions (Rieseberg et al. 1996). These mechanisms all require hundreds to thousands of generations to pass before the nuclear genome of the mixed cytonuclear genotype is represented by nuclear alleles from only one of the parental species (Tsitrone et al. 2003; Fig. 2a).

In contrast to the process of introgression via backcrossing described above, androgenesis provides an explanation for how maternal organelles from one species can become associated with the nuclear genome of another in only one generation (Fig. 2b). Spontaneous androgenesis during a hybridization event immediately results in cytonuclear mismatch in the offspring. Cytonuclear mismatch between the paternal nuclear genome and the maternal cytoplasmic genome after spontaneous androgenesis has been empirically demonstrated in laboratory crosses (Goodsell 1961; Chase 1963; Abdalla and Hermsen 1972; Pelletier et al. 1987; Horlow et al. 1993; Kindiger and Wipff 2009). If one of the species were obligately androgenetic, its sperm could utilize the eggs of the other species, once again resulting in cytonuclear mismatch in one generation. This process is the probable cause of incongruence between nuclear and mitochondrial phylogenies of obligately androgenetic clams in the genus *Corbicula* (Lee et al. 2005; Hedtke et al. 2008).

The incongruence between organelle and nuclear gene trees often attributed to hybrid introgression could instead be the product of androgenesis in which the nuclear genome of one species has displaced that of a second during fertilization while retaining maternal cytoplasmic organelles. For example, semigamy—when two gametes fuse without fusion of nuclear genomes—could have functionally caused spontaneous androgenesis in an ancestor of wild cotton (*Gossypium bickii*), replacing the original cytoplasm with that of Sturt's Desert Rose (*G. sturtianum*) and explaining the current incongruence between nuclear and mitochondrial markers (Wendel et al. 1991). However, because the frequency of cytonuclear hybrids may be low, drift or selection need to be invoked to explain why the genotypes of these offspring go to fixation in a population.

Fixation of the Mixed Cytonuclear Genotype after Spontaneous Androgenesis

Models for introgression via backcrossing call for positive selection that favors the novel cytonuclear gene combination or for drift to bring the mixed cytonuclear genotype to fixation (e.g., Rieseberg et al. 1996; Tsitrone et al. 2003). These processes would favor the spread of a mixed cytonuclear genotype regardless of how that genotype was generated—whether through normal sexual hybridization between species or through androgenesis. For example, in hermaphroditic species, fixation due to selection of the mixed cytonuclear genotype after spontaneous androgenesis will follow the conditions described by Tsitrone et al. (2003). In their single-locus model, fixation of the mixed cytonuclear genotype occurs if the mixed cytonuclear genotype has a fitness advantage over both parental cytonuclear genotypes and any nuclear hybrids even when cytoplasmic incompatibilities reduce male fitness.

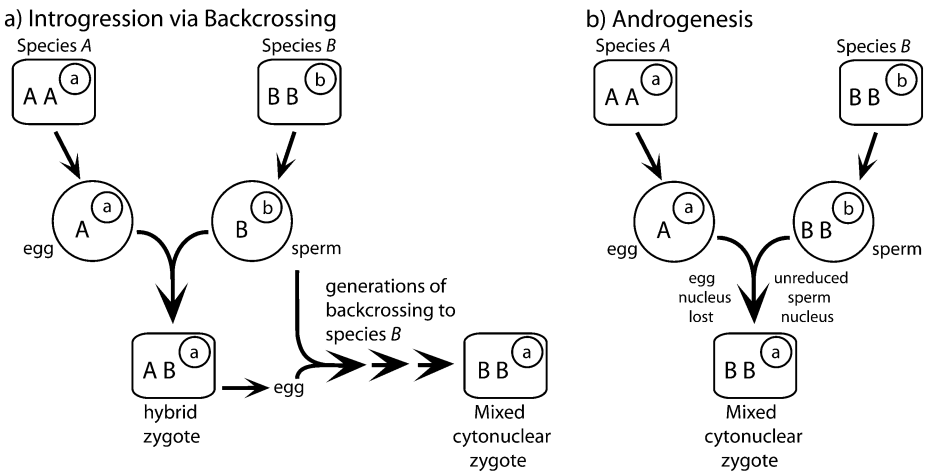

FIGURE 2. Introgression via backcrossing versus androgenesis generating cytonuclear mismatch. Letters in large caps indicate the species' nuclear genome; superscripts indicate the cytoplasmic type. Species *A* serves as the mother and species *B* as the father, and cytoplasmic organelles are maternally inherited. a) Hybridization between two species *A* and *B* creates offspring with nuclear chromosomes from both parents; subsequent backcrossing to species *B* over many generations leads to an individual with the nuclear genome from parent species *B* and the cytoplasmic organelles of species *A*. b) Fertilization of species *A* by species *B* results in offspring with only the paternal nuclear genome. After only one generation, this offspring contains the nuclear genome of parent species *B* and the cytoplasmic organelles of species *A*.

Selection is not required for fixation of a mixed cytonuclear genotype when it is produced through repeated androgenesis. If the mixed cytonuclear state is neutral or slightly disadvantageous, drift could lead to fixation over time. Rapid boom–bust cycles would speed fixation of the mixed cytonuclear genotype within a population. Assume that mixed cytonuclear genotypes are produced through androgenesis each generation at a frequency of 10%. If the population is reduced to a single individual and then recovers, the new population will be fixed for the mixed cytonuclear genotype 10% of the time if it is selectively neutral. If it is not fixed in one generation, another 10% of cytonuclear hybrids will be produced the next generation and the process repeats. But the 10% of the time that it is fixed, both species within that region will become fixed for the same mitochondrial or chloroplast genomes.

Fixation of the Mixed Cytonuclear Genotype under Obligate Androgenesis

If obligate androgenesis arises as a mutation in one species, or as a temporary shift in reproductive mode due to changing environmental conditions, the conditions for the spread to fixation of the mixed cytonuclear genotype are even less restrictive. Because androgenetic individuals have offspring that carry twice as many paternal alleles as sexual offspring, and assuming that fitness between the two species is otherwise equal, androgenesis—and the mixed cytonuclear genotype—will spread (McKone and Halpern 2003). In hermaphroditic species, even if the mixed cytonuclear genotype imparts partial male sterility, a corresponding increase in female fitness is not required for obligate androgenesis to spread unless male fitness is decreased by more than half (McKone and Halpern 2003).

For example, if two genetically isolated species, *A* and *B*, have incompatible nuclear genomes, no (or only sterile) F1 hybrid offspring would be produced. If a mutation for obligate androgenesis arises in species *A*, such that the paternal nuclear DNA fails to fuse with maternal nuclear DNA, and/or blocks or fails to send the signal for meiotic axis reorientation, then it could use maternal gametes from species *B*. The resulting offspring would be like species *A* in every respect except that they would have the cytoplasmically inherited organelles of species *B*. Fitness could be decreased due to cytonuclear incompatibilities between species. Nonetheless, androgenetic individuals could have a far greater overall reproductive output because they can co-opt the female gametes from the other species. The mixed cytonuclear genotype could thus spread quickly because it has become associated with obligate androgenetic reproduction.

If only a single androgenetic individual of species *A* were to disperse into an area occupied by species *B*, and if selfing does not occur, all the paternal offspring of species *A* would have the mixed cytonuclear genotype. In this case, androgenetic individuals would not only have a higher reproductive fitness (because of their ability to capture the maternal gametes of resident individuals) but also have a much greater chance of invading a new area. An obligately outcrossing sexual species would require at least two individuals to invade, whereas an outcrossing androgenetic genotype would require only one, and all its offspring would have the cytonuclear mismatch.

Speed of Capture in a Natural System

In populations of obligately androgenetic *Corbicula*, cytonuclear mismatch through androgenesis has happened rapidly. There are two species of freshwater clams introduced into North American river drainages in the past 80 years (forms A and B; Counts 1981, 1986; cf. *Corbicula leana* and *C. fluminea*; Hedtke et al. 2008). These clams go through regular boom–bust cycles in which large populations are reduced to a very small number of surviving individuals and then quickly return to a large population size (reviewed in McMahon 1999). Across their North American range, the two species are fixed for different nuclear markers, and no heterozygotes between species-specific nuclear alleles have been observed (Hillis and Patton 1982; McLeod 1986; Hedtke et al. 2008). Mixed cytonuclear genotypes occur at low frequency in many populations where the two species are found together, with no evidence of hybridization across nuclear loci (Lee et al. 2005; Hedtke et al. 2008). Cytonuclear mismatch likely arises when the sperm of one species fertilizes the egg of the other species, ejecting the maternal nuclear genome but retaining maternal cytoplasm (Lee et al. 2005; Hedtke et al. 2008). Both species spread to the state of Texas only about 30 years ago (Fontanier 1982), and yet in that short time, populations in at least one river system have captured and become fixed for the mitochondrial DNA of the other species (Hedtke et al. 2008).

When is Androgenesis a Viable Hypothesis for Cytonuclear Mismatch?

Androgenesis occurs in natural systems and can lead to phylogenetic incongruence between nuclear and cytoplasmic markers. But how often does it occur, and in what systems should we look for it? Before attributing any mechanistic explanation for presumed cytonuclear mismatch, phylogenetic error must be ruled out as the cause of gene tree incongruence. If one or more gene trees do not accurately represent the underlying history of that gene, the incongruence between cytoplasmic and nuclear gene trees will not be informative. Phylogenetic error occurs when the model of sequence evolution is inadequate to describe the true evolutionary process and may result in well-supported relationships between species that are not reflective of the true organismal history. Sources of phylogenetic error include long-branch attraction (reviewed in Heath et al. 2008), base-composition bias (see Phillips et al. 2004; Collins et al. 2005), convergence (see Castoe et al. 2009), or insufficient data (see Hillis 1996). For the rest of this

discussion, we will assume that cytoplasmic and nuclear gene trees are well supported by evidence and differences between the two are not simply the result of phylogenetic error. Below we briefly describe conditions that would favor or disfavor androgenesis as an explanation of cytonuclear mismatch.

Effects of Sex Determination System

Spontaneous androgenesis may be a more likely cause of fixed cytonuclear mismatch when species are hermaphroditic (or monoecious) rather than gonochoric (or dioecious). Because all hermaphroditic individuals produce female gametes, a cytonuclear mismatch could be passed on by any offspring formed through androgenesis (and not just females). Partial selfing would further increase the probability that the mismatch would continue in subsequent generations because all offspring produced from selfing would contain the cytonuclear mismatch of their parent.

Dioecious species with chromosomal sex determination and male heterogamety (XX = female, XY = male) could also generate cytonuclear mismatch via spontaneous androgenesis. Females would be produced by either unreduced sperm with two copies of the paternal X chromosome or early chromosomal doubling after fertilization of the egg by an X-bearing sperm. Male offspring would be produced if the fertilizing sperm were unreduced and carried both the X and the Y chromosome from the father or if the fertilizing haploid sperm carried the Y chromosome and chromosomal doubling occurred (YY cyprinids, cichlids, and salmonids are viable; reviewed in Pandian and Kirankumar 2003). However, males would not transmit the cytonuclear mismatch to the next generation (assuming cytoplasmic organelles are maternally inherited). Similarly, haplodiploid systems, in which females are diploid and males are haploid, could only cause cytonuclear mismatch if sperm were unreduced or if chromosomal doubling occurred during the first division of the zygote. Whereas haploid sperm could produce viable haploid males, males would not transfer the cytonuclear mismatch to the next generation.

Spontaneous androgenesis is not likely to produce cytonuclear mismatch in systems with female heterogamety (ZW = female, ZZ = male) and maternal inheritance of cytoplasmic organelles because paternal clones can only be ZZ males, which do not usually transmit mitochondria or chloroplasts to subsequent generations. Androgenesis will also not generate viable offspring in plants and animals with genomic imprinting, as imprinting of sperm chromosomes would potentially cause some necessary genes to have reduced or no expression.

Signals for Introgression via Sexual Hybridization and Backcrossing

The emergence of a mixed cytonuclear genotype can be caused by sexual hybridization and backcrossing (as has been described above). This process has been documented convincingly in *Helianthus*, which is known to hybridize fairly readily between species (e.g., Rieseberg and Brunsfeld 1992; Rieseberg et al. 1999). Current hybridization can be detected through the observation of intermediate morphologies or shared nuclear genes in areas where two species are found in sympatry. Across the nuclear genome, signatures of both species may be present even if hybridization occurred long ago; different nuclear genes may have retained alleles from one parental species or from the other. Sequencing multiple nuclear genes may be helpful in identifying such historical nuclear gene exchange. If the signal for hybrid introgression is still present in the nuclear genome, alleles of some genes would be congruent with the cytoplasmic phylogeny (alleles inherited from the maternal species), whereas alleles at other loci would be incongruent (alleles from the paternal species). In contrast, after androgenesis, there would no indication of mixing between species across the nuclear genome. Difficulty in detecting spontaneous androgenesis may arise in some cases because nuclear hybridization and androgenesis are not necessarily mutually exclusive. In a number of observed cases of spontaneous androgenesis, the mother is a hybrid (e.g., Kostoff 1934; Mantovani and Scali 1992; Horlow et al. 1993), and hybrid nuclear genomes can contain incompatibilities that cause errors in meiotic disjunction (e.g., Tsukii and Hiwatashi 1985; Greig 2009). For this reason, in some systems, ongoing sexual hybridization can actually increase the possibility of spontaneous androgenesis.

Signals for Incomplete Lineage Sorting

Gene phylogenies can differ from one another due to incomplete lineage sorting: if alleles coalesce prior to speciation events, the branching pattern of a particular gene tree can differ from that of the species tree (reviewed and discussed in Maddison 1997). Incomplete lineage sorting is more likely to occur when branches of the species tree are short and population sizes are large (Maddison 1997) and is more likely to be a problem for inferring species relationships among closely related species. Techniques for distinguishing between incomplete lineage sorting and gene flow between species have been developed both within a phylogenetic framework (e.g., Buckley et al. 2006; Meng and Kubatko 2009) and a population genetic framework (without explicitly calculating gene genealogies: Nielsen and Wakeley 2001; Hey and Nielsen 2004). Broadly speaking, if a phylogenetic analysis shows variation between individual nuclear genes, and inferred branch lengths between species are short, incomplete lineage sorting should be considered as a strong contender for causing phylogenetic discordance between nuclear and organellar trees. Techniques developed for inferring species trees using coalescent approaches might be appropriate for further data analysis (e.g., Maddison and Knowles 2006; Edwards et al. 2007; Kubatko et al. 2009; Liu et al. 2009). However, if the incongruence occurs between distantly related taxa, and if multiple nuclear markers

provide consistent estimates of relationships between species, then incomplete lineage sorting is an unlikely explanation.

Empirical Signals for Androgenesis

If evidence for nuclear gene exchange or incomplete lineage sorting is strong, androgenesis can be reasonably discarded as a hypothesis for an observed cytonuclear mismatch. Below we present several questions that should be considered when evaluating androgenesis as a viable generative mechanism for such mismatches. However, the only definitive test for androgenesis in a particular system is to perform paternity analyses.

Do mitochondrial or chloroplast associations follow geographic boundaries?—If spontaneous androgenesis were to occur between two species with multiple overlapping geographic areas, the phylogeographic pattern of cytoplasmic markers could form a mosaic. In areas of sympatry, both species could become fixed for the cytoplasm of one or the other species, even though nuclear alleles remain distinct. For example, in North American *Corbicula*, there are populations where both the two species have become fixed for the same mitochondrial haplotype, even though they remain distinct at nuclear loci (Hedtke et al. 2008). Interestingly, in certain mixed stands of eastern North American white oaks (*Quercus stellata* and *Q. fusiformis*), F1 hybrids are unknown in local populations or occur only at very low frequency. If hybrids are formed, they presumably have reduced fitness, as the species remain distinct without forming hybrid swarms (Muller 1961). However, these mixed stands of highly distinctive oaks can be fixed for the same chloroplast markers, even when no hybridization is apparent at a given sampling location (Whittemore and Schaal 1991). This differs from the pattern observed between several other species of oaks, which also form mixed forests but in which hybrid offspring are frequently detected (e.g., Ferris et al. 1993; Petit et al. 1993; Bacilieri et al. 1996). Although the geographic mosaic seen in *Q. stellata* and *Q. fusiformis* may be due to undetected sexual hybridization in the past, it could also be the result of spontaneous androgenesis.

What is the relative fitness of cytonuclear hybrids compared with parental species?—In polymorphic populations, measurements indicating lower fitness of the mixed cytonuclear genotype relative to the parental genotypes suggests that androgenesis merits consideration. Selection-based models most effectively explain the rapid fixation of the mixed genotype when either the female fitness component or rates of outcrossing are increased (Tsitrone et al. 2003). This fixation is expected when the mixed cytonuclear genotype is generated by either hybrid nuclear introgression or androgenesis. However, if cytonuclear interactions have neutral or slightly deleterious fitness consequences to the female, or no effect on selfing rates, then androgenesis may better explain the spread of the mixed genotype. Obligate androgenesis drives the fixation of cytonuclear mismatch even when the female component to fitness is lowered (McKone and Halpern 2003). In addition, if cytonuclear interactions reduce overall fitness, spontaneous androgenesis followed by fixation due to drift may explain the data better than a selection-based hypothesis, which requires long-term persistence of backcrossing nuclear hybrids. Spontaneous androgenesis would not require maintenance of nuclear hybrids with reduced fitness over many generations within a population to generate the cytonuclear mismatch, as the mismatch would occur in only a single generation. Fixation of the population for the mismatched cytonuclear genotype could then occur through drift, especially if continuing androgenesis repeatedly introduces the mismatched cytonuclear genotype into the population.

Can the species hybridize in the laboratory? What is the relative fitness of the F1 hybrids?—Crosses between plant species that do not form viable nuclear hybrids have produced androgenetic offspring. After pollination, seeds taken from the maternal species germinated into plants with only paternal characteristics, and no maternal characteristics were observed even after several generations of selfing (Collins and Kempton 1916). If species do hybridize, yet the fitness of nuclear hybrids is low, then nuclear hybrids may be unlikely to persist in nature and lead to introgression of organelles from one species to the other.

Do any F1 offspring have only paternal nuclear DNA?—Paternity analyses comparing the nuclear genomes of parents and offspring provide the definitive test for androgenesis (Table 1). In cases for which garden experiments or field paternity analyses are possible, the presence or absence of paternal and maternal markers can be examined in putatively hybrid offspring. For example, spontaneous androgenesis has been detected in laboratory stock crosses in two separate plant genera, mustards (*Brassica*; Chen and Heneen 1989) and teosintes (*Zea*; Chase 1963), and natural populations within each genus have been found with chloroplast–nuclear mismatches (Palmer et al. 1983; Doebley 1989). Spontaneous androgenesis may have generated a genotype with a paternal nuclear lineage and a maternal organelle lineage in these populations.

Further Considerations on Androgenesis in Plants and Animals

Spontaneous and obligate androgenesis are known to occur in both plants and animals. Unlike explanations that rely on introgression via backcrossing, organelle capture by androgenesis provides a simple and an immediate explanation for cytonuclear mismatch. As with other mechanisms, population processes are still needed to explain the spread of a mixed cytonuclear genotype within a population. In organisms with a metapopulation structure characterized by local extirpations and

dispersal, this spread can be explained by stochastic effects of drift and founder events. In the case of invasive species, dispersal into a novel geographic area could also permit rapid fixation of the mixed genotype. Alternatively, the selection-based mechanisms proposed in other models (e.g., Rieseberg et al. 1996; Tsitrone et al. 2003) could also cause the spread of this novel genotypic combination.

Spontaneous androgenesis is well known in laboratory crosses, but the repercussions of these studies on the evolutionary history of wild organisms have been largely ignored. We have focused on the potential effects of androgenesis on phylogenetic discordance, but cytonuclear mismatch through androgenesis may have other impacts on species evolution. For example, reduced male function or male infertility rising from antagonistic interactions between nuclear and organellar genes has been demonstrated in many species (reviewed in Schnable and Wise 1998), sometimes accompanied by a corresponding increase in female function (Lewis 1941). Androgenesis is obviously not the only—or even the main—force driving phylogenetic incongruence between cytoplasmic and nuclear markers in most biological systems, and there are no estimates of how widespread its natural occurrence may be. However, given the known instances of androgenesis across plants and animals, androgenesis should be considered as a potential source of phylogenetic incongruence in systems where nuclear hybrids are not observed. Furthermore, the novel cytoplasmic organelle and nuclear genome combination generated by androgenesis could have important phenotypic effects—either positive or negative—and thus affect the evolutionary trajectory of the species involved.

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