



Invited Reviews and Perspectives

The role of conflict in the formation and maintenance of variant sex chromosome systems in mammals

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Abstract

The XX/XY sex chromosome system is deeply conserved in therian mammals, as is the role of *Sry* in testis determination, giving the impression of stasis relative to other taxa. However, the long tradition of cytogenetic studies in mammals documents sex chromosome karyotypes that break this norm in myriad ways, ranging from fusions between sex chromosomes and autosomes to Y chromosome loss. Evolutionary conflict, in the form of sexual antagonism or meiotic drive, is the primary predicted driver of sex chromosome transformation and turnover. Yet conflict-based hypotheses are less considered in mammals, perhaps because of the perceived stability of the sex chromosome system. To address this gap, we catalog and characterize all described sex chromosome variants in mammals, test for family-specific rates of accumulation, and consider the role of conflict between the sexes or within the genome in the evolution of these systems. We identify 152 species with sex chromosomes that differ from the ancestral state and find evidence for different rates of ancestral to derived transitions among families. Sex chromosome-autosome fusions account for 79% of all variants whereas documented sex chromosome fissions are limited to three species. We propose that meiotic drive and drive suppression provide viable explanations for the evolution of many of these variant systems, particularly those involving autosomal fusions. We highlight taxa particularly worthy of further study and provide experimental predictions for testing the role of conflict and its alternatives in generating observed sex chromosome diversity.

Key words: dosage compensation, mammals, meiotic drive, regulatory evolution, sex chromosomes, sexual antagonism

Introduction

The therian sex chromosomes originated in the common ancestor of marsupial and placental mammals when a transcription factor on an autosome acquired a testis-determining function (Koopman et al. 1991; Potrzebowski et al. 2008; Veyrunes et al. 2008). More than 150 million years later, the ancestral gene content of the X chromosome is largely preserved, whereas progressive suppression of recombination with the X catalyzed massive genetic and structural decay on the Y. Consistent with evolutionarily early degeneration of the Y chromosome, extant placental mammals carry subsets of the same 18 ancestral Y chromosome genes and loss of *Sry* as the first gene in the testis-determining cascade is rare (Bellott et al., 2014; Cortez et al. 2014).

Conflict, whether between the sexes or within the genome, is a widely invoked driver of sex chromosome evolution with a compelling body of theoretical support (Fisher 1931; Charlesworth and Charlesworth 1980; Bull 1983; Rice 1987; Charlesworth 1991; van Doorn and Kirkpatrick 2007; Úbeda et al. 2015; Patten 2018). These conflict-based models apply to any system with genetic sex determination, including mammals. However, the unusual longevity of the mammalian sex chromosomes and the apparent decrepitude

of the Y motivated theoretical focus on stasis (van Doorn and Kirkpatrick 2007; van Doorn 2013) and decay (Charlesworth and Charlesworth 2000; Bachtrog 2008) rather than conflict (but see Blackmon and Brandvain 2017). Even brief intrigue over imminent Y chromosome loss in our own species was quickly dismantled by data showing that Y degeneration had decelerated to a point that made disintegration of the entire chromosome exceedingly unlikely (Aitken and Marshall Graves 2002; Graves 2004; Hughes et al. 2005; Griffin 2012). Given that signatures of conflict have proven hard to demonstrate in relatively young sex chromosome systems where they should be most evident (e.g. Wright et al. 2017; Charlesworth et al. 2021), an ancient sex chromosome system with decelerating decay seems unlikely to provide much insight into conflict-driven evolution. Enforcing this view, the mammalian sex chromosomes are frequently referenced as the evolutionarily stable contrast to systems with recent or recurrent sex chromosome turnover (e.g. van Doorn and Kirkpatrick 2007; Veyrunes et al. 2008; Yoshida and Kitano 2012; Kikuchi and Hamaguchi 2013; Graves 2016).

Here, we argue that the overall conservation of sex-determining pathways and sex chromosome identity in mammals masks both considerable diversity in the genetic and structural features of the sex chromosomes, and

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flexibility in their distribution between the sexes. Much of the variation in mammalian sex chromosome systems was discovered and described by cytologists in the last century (e.g. Fredga 1970; Vorontsov et al. 1980) but remains underrepresented in modern evolutionary genomic studies. In an attempt to close this gap, we enumerate and categorize previously reported variants on the ancestral XX female, XY male system, and evaluate their taxonomic distribution. We discuss the evidence that conflict—between the sexes or within the genome in the form of meiotic drive—played a major role in the evolution of these variant sex chromosome systems. We close with a brief discussion of non-conflict-based models for sex chromosome evolution.

Although humans are not discussed herein, this is a paper about the diversity of sex chromosomes and sex determination in mammals and is therefore broadly relevant to the diversity of sexual and gender identities in our own species. We aim to use inclusive language (e.g. avoiding terms like “feminizing” and “masculinizing”) but found it hard to write about sex chromosome evolution without using the terms “male” and “female,” thus enforcing a binary view of sex. In this, we sacrifice inclusivity for the sake of simplicity. We emphasize, however, that the diversity of sex chromosome genotypes in mammals provides a strong argument against both the immutability of chromosomal sex, and the non-intersection of “male” and “female” developmental pathways (e.g. Nelson and Kriegsfeld 2017).

Methods

Data collection

We generated an initial list of mammals with variant sex chromosomes using literature reviews on the topic (Fredga 1970; Vorontsov et al. 1980; Romanenko and Volobouev 2012; Saunders and Veyrunes 2021). Once we identified species of interest, we searched mammalian karyotype datasets (Pardo-Manuel de Villena and Sapienza 2001; Graphodatsky et al. 2020) for evidence of variant sex chromosomes in other members of their respective genera or families. We also searched the literature for additional species with variant sex chromosome systems using Google Scholar, with the search terms “novel sex chromosomes mammals,” “sex chromosome fusion mammals,” “sex autosome translocation mammals,” “sex chromosome rearrangement mammals,” “sex chromosome loss mammals,” and iterations thereof replacing “mammals” with families and genera of interest. We retained only species for which a published karyotype could be sourced but did not otherwise evaluate the strength of evidence supporting each of the sex chromosome variants we cataloged. Species names were brought into alignment with the Mammal Diversity Database v1.11 (2023). Monotremes were excluded because their sex chromosomes are independently derived relative to Theria (Veyrunes et al. 2008). We note that restricting ourselves to published karyotypes inevitably means that we will undercount the number of variant sex chromosome systems in some taxa. For example, all members of the tribe Tragelaphini (spiral-horned antelopes) are inferred to have the same Y-autosome fusion, but karyotype data is not available for all species (Rubes et al. 2008). The degree to which different families have been studied and cytogenetically characterized is also likely to be inconsistent, due to variation in the level of scientific interest in a taxon and the availability of specimens.

Taxonomic distribution of variant sex chromosomes

The number of species with novel sex chromosome systems varies between mammalian lineages, but it is unclear whether these variants are over- or underrepresented in a given taxon. Most examples of mammalian species with variant sex chromosomes, especially those that are not sex-autosome fusions, are found in rodents (Saunders and Veyrunes 2021). However, as Rodentia comprises the largest order of mammals, this pattern may be simply a function of species richness. To compare the rates at which novel sex chromosome configurations arise in mammalian families, we used the *ratebytree* function (Revell et al. 2018) in the *R* package *phytools* v1.5.1 (Revell 2012). We sampled 100 trees from the posterior distribution of the node-dated mammal phylogeny from Upham et al. (2019) and provided the *ratebytree* function with family-level subsets and character codes indicating whether or not each species had an XX/XY system. We included all families comprised of three or more species with at least one novel sex chromosome configuration and one XX/XY system. *ratebytree* fits two Mk models (Lewis 2001); one where all trees have the same transition rate, and another where transition rates can vary between trees (Revell 2012). The two models are compared with a log-likelihood ratio test. We first fit a unidirectional model where the transition rate from variant systems to XX/XY is set to zero. This should reflect the biological reality that no transitions from a variant system to the ancestral XX/XY configuration have been observed. This allowed us to infer whether the rate at which novel sex chromosomes evolve varies significantly between families and whether the inferred rate is sensitive to tree topology. We additionally fit both the unidirectional model and an equal rates model to the maximum clade credibility tree from Upham et al. (2019), the results of which are reported in Supplementary Table 1. We note that, because some families are closely related (e.g. Cricetidae and Muridae) and may share the same rate due to common ancestry, the inferred rates are likely not independent. Furthermore, the inferred rates do not account for different categories of sex chromosome variants that evolved within genera, as in *Tokudaia* (Ryūkyū spiny rats) and *Ellobius* (mole voles).

Species were assumed to be XX/XY unless published evidence of a variant sex chromosome system could be found. However, erroneously labeling species as XX/XY due to lack of available evidence for a variant sex chromosome system could inflate estimated transition rates. Conversely, if a species incorrectly assigned XX/XY is closely related to other species assigned XX/XY (correctly or incorrectly) then rates will be deflated. Because restricting the entire analysis to species with known sex chromosome systems would introduce a family-specific sampling bias that would distort the relative rates between families, we evaluated the effect of XX/XY assignment uncertainty by limiting our analysis to species with published sex chromosome karyotypes from three families with high estimated transition rates: Atelidae, Bovidae, and Herpestidae.

Results

Categorizing variant sex chromosome systems

We identify nine broad categories of variant sex chromosomes in mammals (Table 1), accounting for 152 species in 58

Table 1. Variant sex chromosomes in 152 therian mammals based on published karyotypes. Taxonomy follows the Mammal Diversity Database v1.11 (2023).

Order	Family	Species	2n		Sex chromosomes		Variant system	Refs
			♀	♂	♀	♂		
Afrosoricida	Tenrecidae	<i>Echinops telfairi</i>	40	40–41	XX	XY, XY ₁ Y ₂	Unknown ^a	Borgaonkar (1967), Fredga (1970)
		<i>Tragelaphus oryx</i>	32	31	X ₁ X ₁ X ₂ X ₂	X ₁ X ₂ Y	Y-A fusion	Rubes et al. (2008)
Artiodactyla	Bovidae	<i>Tragelaphus angasi</i>	56	55	X ₁ X ₁ X ₂ X ₂	X ₁ X ₂ Y	Y-A fusion	Fredga (1970); Rubes et al. (2008)
		<i>Tragelaphus derbianus</i>	32	31	X ₁ X ₁ X ₂ X ₂	X ₁ X ₂ Y	Y-A fusion	Rubes et al. (2008)
		<i>Tragelaphus eurycerus</i>	34	33	X ₁ X ₁ X ₂ X ₂	X ₁ X ₂ Y	Y-A fusion	Rubes et al. (2008)
		<i>Tragelaphus imberbis</i>	38	38	XX	XY	X-A and Y-A fusions ^b	Rubes et al. (2008)
		<i>Tragelaphus scriptus</i>	34	33	X ₁ X ₁ X ₂ X ₂	X ₁ X ₂ Y	Y-A fusion	Rubes et al. (2008)
		<i>Tragelaphus spekii</i>	30	30	XX	XY	X-A and Y-A fusions ^b	Rubes et al. (2008)
		<i>Tragelaphus strepsiceros</i>	32	31	X ₁ X ₁ X ₂ X ₂	X ₁ X ₂ Y	Y-A fusion	Fredga (1970), Rubes et al. (2008)
		<i>Boselaphus tragocamelus</i>	46	46	XX	XY	X-A and Y-A fusions	Gallagher et al. (1998)
		<i>Antelope cervicapra</i>	30–32	31–33	XX	XY ₁ Y ₂	X-A fusion ^c	Vassart et al. (1995); Cernohorska et al. (2012)
		<i>Eudorcas rufifrons</i>	58	58	XX	X ₁ X ₂ Y ₁ Y ₂	X-A and Y-A fusion ^c	Vassart et al. (1995); Cernohorska et al. (2015)
		<i>Eudorcas thomsonii</i>	58	58	XX	X ₁ X ₂ Y ₁ Y ₂	X-A and Y-A fusion ^c	Vassart et al. (1995); Cernohorska et al. (2015)
		<i>Gazella bennettii</i>	49–52	49–52	XX	XY ₁ Y ₂	X-A fusion ^c	Kumamoto et al. (1995)
		<i>Gazella dorcas</i>	30	31	XX	XY ₁ Y ₂	X-A fusion ^c	Efron et al. (1976)
		<i>Gazella gazella</i>	34	35	XX	XY ₁ Y ₂	X-A fusion ^c	Efron et al. (1976)
<i>Gazella leptoceros</i>	32	33	XX	XY ₁ Y ₂	X-A fusion ^c	Efron et al. (1976)		
<i>Gazella marica</i>	30–32	31–33	XX	XY ₁ Y ₂	X-A fusion ^c	Kingswood and Blank (1996)		
<i>Gazella spekei</i>	32	33	XX	XY ₁ Y ₂	X-A fusion ^c	Efron et al. (1976)		
<i>Gazella subgutturosa</i>	30	31	XX	XY ₁ Y ₂	X-A fusion ^c	Efron et al. (1976)		
<i>Nanger dama</i>	38–40	38–40	XX	XY ₁ Y ₂	X-A fusion ^c	Cernohorska et al. (2012)		
<i>Nanger granti</i>	30	31	XX	XY ₁ Y ₂	X-A fusion ^c	Efron et al. (1976)		
<i>Nanger soemmerringii</i>	34–39	34–39	XX, X ₁ X ₁ X ₂ X ₂	XY, XY ₁ Y ₂ , X ₁ X ₂ Y	X-A and Y-A fusions ^{c,d}	Steiner et al. (2015)		
Cervidae	<i>Elaphodus cephalophus</i>	46–48	47–48	XX	XY, XY ₁ Y ₂	X-A fusion ^c	Shi (1981), Zhang et al. (1983), Cao et al. (2005)	
		42–50	43–51	XX	XY ₁ Y ₂	X-A fusion	Duarte et al. (2008), Abril et al. (2010), Aquino et al. (2013)	
Carnivora	Herpestidae	<i>Mazama nemoriuaga</i>	68	69	XX	XY ₁ Y ₂	X-A fusion	Fiorillo et al. (2013)
		<i>Mazama rufina</i>	52	53	XX	XY ₁ Y ₂	X-A fusion	Peres et al. (2021)
		<i>Muntiacus crinifrons</i>	6	7	XX	XY ₁ Y ₂	X-A fusion	Zhou et al. (2008), Yin et al. (2021)
		<i>Muntiacus feae</i>	12–14	14	XX	XY ₁ Y ₂	X-A fusion	Soma et al. (1987), Tanomtong et al. (2005)
		<i>Muntiacus muntjak</i>	6	7	XX	XY ₁ Y ₂	X-A fusion	Würster and Benirschke (1970)
		<i>Atilax paludinosus</i>	36	35	X ₁ X ₁ X ₂ X ₂	X ₁ X ₂ Y	Y-A fusion	Fredga (1977)
		<i>Herpestes ichneumon</i>	44	43	X ₁ X ₁ X ₂ X ₂	X ₁ X ₂ Y	Y-A fusion	Fredga (1972)
		<i>Herpestes pulverulentus</i>	40	39	X ₁ X ₁ X ₂ X ₂	X ₁ X ₂ Y	Y-A fusion	Fredga (1972)

Table 1. Continued

Order	Family	Species	2n	Sex chromosomes	Variant system	Refs
		<i>Herpestes sanguineus</i>	42	X ₁ X ₁ X ₂ X ₂	Y-A fusion	Fredga (1972)
		<i>Uroa auropunctata</i>	36	X ₁ X ₁ X ₂ X ₂	Y-A fusion ^f	Fredga (1972), Murata et al. (2016a)
		<i>Uroa brachyura</i>	36	X ₁ X ₁ X ₂ X ₂	Y-A fusion	Fredga (1972)
		<i>Uroa edwardsii</i>	36	X ₁ X ₁ X ₂ X ₂	Y-A fusion	Fredga (1972)
		<i>Uroa fusca</i>	36	X ₁ X ₁ X ₂ X ₂	Y-A fusion	Fredga (1972)
		<i>Uroa urua</i>	36	X ₁ X ₁ X ₂ X ₂	Y-A fusion	Fredga (1972)
Chiroptera	Phyllostomidae	<i>Carollia brevicauda</i>	20	XX	X-A fusion	Pieczarka et al. (2005), Noronha et al. (2009)
		<i>Carollia castanea</i>	20	XX	X-A fusion	Tucker and Bickham (1989)
		<i>Carollia perspicillata</i>	20	XX	X-A fusion	Yonenaga et al. (1969), Noronha et al. (2009)
		<i>Carollia subrufa</i>	20	XX	X-A fusion	Tucker and Bickham (1989)
		<i>Ametrida centurio</i>	30	XX	X-A fusion	Gardner (1977)
		<i>Ardops nicholli</i>	30	XX	X-A fusion	Greenbaum et al. (1975)
		<i>Ariteus flavescens</i>	30	XX	X-A fusion	Greenbaum et al. (1975)
		<i>Artibeus fimbriatus</i>	30	XX	X-A fusion	Pinto et al. (2012)
		<i>Artibeus jamaicensis</i>	30	XX	X-A fusion	Baker (1967)
		<i>Artibeus lituratus</i>	30	XX	X-A fusion	Yonenaga et al. (1969), Noronha et al. (2009)
		<i>Artibeus obscurus</i>	30	XX	X-A fusion	Pieczarka et al. (2013)
		<i>Artibeus planirostris</i>	30	XX	X-A fusion	Noronha et al. (2010)
		<i>Chiroderma villosum</i>	26	XX	X-A and Y-A fusion	Gomes et al. (2016)
		<i>Dermanura azteca</i>	30	XX	X-A fusion	Baker (1973)
		<i>Dermanura cinerea</i>	30	XX	X-A and Y-A fusion ^g	Baker (1973), Noronha et al. (2010)
		<i>Dermanura phaeotis</i>	30	XX	X-A and Y-A fusion	Hsu et al. (1986)
		<i>Dermanura tolteca</i>	30	XX	X-A fusion	Pinto et al. (2012)
		<i>Dermanura watsoni</i>	30	XX	X-A and Y-A fusion	Baker and Bickham (1980)
		<i>Mesophylla macconnelli</i>	22	X ₁ X ₁ X ₂ X ₂	X-A and Y-A fusions	Gomes et al. (2016)
		<i>Platyrrhinus incarum</i>	30	XY	X-A and Y-A fusion	Baker (1973)
		<i>Platyrrhinus lineatus</i>	30	XY	X-A and Y-A fusion	Baker and Bickham (1980)
		<i>Platyrrhinus vittatus</i>	30	XY	X-A and Y-A fusion	Varella-Garcia et al. (1989)
		<i>Phyllops falcatus</i>	30	XX	X-A fusion	Greenbaum et al. (1975)
		<i>Uroderma bilobatum</i>	42	XX	X-A and Y-A fusion	Noronha et al. (2010)
		<i>Uroderma magnirostrum</i>	36	XX	X-A and Y-A fusion	Noronha et al. (2010)
		<i>Vampyressa pusilla</i>	24	X ₁ X ₁ X ₂ X ₂	X-A and Y-A fusions	Gardner (1977)
		<i>Vampyressa thylene</i>	24	X ₁ X ₁ X ₂ X ₂	X-A and Y-A fusions	Baker (1973)
		<i>Vampyriscus bidens</i>	26	XX	X-A and Y-A fusion	Baker (1973)
		<i>Vampyriscus brocki</i>	24	XX	X-A and Y-A fusion	Baker (1973)
		<i>Vampyrodes caraccioli</i>	30	XX	X-A and Y-A fusion	Baker (1973)

Table 1. Continued

Order	Family	Species	2n	Sex chromosomes	Variant system	Refs		
Diprotodontidae	Pteropodidae	<i>Epomophorus crypturus</i>	36	XX	XO	Y loss	Peterson and Nagorsen (1975), Denys et al. (2013)	
		<i>Epomophorus gambianus</i>	36	XX	XO	Y loss	Peterson and Nagorsen (1975), Denys et al. (2013)	
Diprotodontidae	Rhinolophidae	<i>Epomops buettikoferi</i>	36	XX	XO	Y loss	Denys et al. (2013)	
		<i>Epomops franqueti</i>	36	35-36	XX	XO, XY	Haiduk et al. (1980), Denys et al. (2013)	
		<i>Rhinolophus morio</i>	32	X ₁ X ₂ X ₂ X ₂	X ₁ X ₂ Y ₁ Y ₂	Y-A fusion ^b	Volleth et al. (2015)	
		<i>Wallabia bicolor</i>	10	XX	XY ₁ Y ₂	Y fission	Toder et al. (1997)	
Eulipotyphla	Macropodidae	<i>Lagorchestes conspicillatus</i>	16	X ₁ X ₁ X ₂ X ₂	X ₁ X ₂ Y	Complex fusions ⁱ	Martin and Hayman (1966), Hayman and Sharp (1981)	
		<i>Sorex antinorii</i>	24	XX	XY ₁ Y ₂	X-A fusion	Zima et al. (1998), Biltueva et al. (2011), Bulatova et al. (2019)	
Primates	Aotidae	<i>Sorex araneus</i>	20-33	XX	XY ₁ Y ₂	X-A fusion	Zima et al. (1998), Biltueva et al. (2011), Bulatova et al. (2019)	
		<i>Sorex arcticus</i>	28	XX	XY ₁ Y ₂	X-A fusion	Zima et al. (1998), Biltueva et al. (2011), Bulatova et al. (2019)	
		<i>Sorex asper</i>	32	XX	XY ₁ Y ₂	X-A fusion	Zima et al. (1998), Biltueva et al. (2011), Bulatova et al. (2019)	
		<i>Sorex coronatus</i>	22	XX	XY ₁ Y ₂	X-A fusion	Zima et al. (1998), Biltueva et al. (2011), Bulatova et al. (2019)	
		<i>Sorex daphnaeodon</i>	26-28	27-29	XX	XY ₁ Y ₂	X-A fusion	Zima et al. (1998), Biltueva et al. (2011), Bulatova et al. (2019)
		<i>Sorex granarius</i>	36	37	XX	XY ₁ Y ₂	X-A fusion	Zima et al. (1998), Biltueva et al. (2011), Bulatova et al. (2019)
		<i>Sorex maritimensis</i>	28	29	XX	XY ₁ Y ₂	X-A fusion	Zima et al. (1998), Biltueva et al. (2011), Bulatova et al. (2019)
		<i>Sorex satunini</i>	24	25	XX	XY ₁ Y ₂	X-A fusion	Zima et al. (1998), Biltueva et al. (2011), Bulatova et al. (2019)
		<i>Sorex tundrensis</i>	30-41	30-41	XX	XY ₁ Y ₂	X-A fusion	Zima et al. (1998), Biltueva et al. (2011), Bulatova et al. (2019)
		Peramelemorphia	Thylacomyidae	<i>Macrotilis lagotis</i>	18	XX	XY ₁ Y ₂	X-A fusion
<i>Phataginus tricuspis</i>	114			X ₁ X ₁ X ₂ X ₂	X ₁ X ₂ Y	Y-A fusion ⁱ	Houck et al. (2023)	
Pilosa	Choloepodidae	<i>Choloepus didactylus</i>	53-65	X ₁ X ₁ X ₂ X ₁	X ₁ X ₂ Y	Y-A fusion ^k	Dobigny et al. (2005)	
		<i>Choloepus hoffmanni</i>	49	X ₁ X ₁ X ₂ X ₂	X ₁ X ₂ Y	Y-A fusion ^k	Corin-Frederic (1969)	
Primates	Aotidae	<i>Aotus azarae</i>	50	X ₁ X ₁ X ₂ X ₂	X ₁ X ₂ Y	Y-A fusion	Menezes et al. (2010)	
		<i>Aotus nigriceps</i>	50	X ₁ X ₁ X ₂ X ₂	X ₁ X ₂ Y	Y-A fusion	Menezes et al. (2010)	
Primates	Atelidae	<i>Alouatta arctoidea</i>	44	X ₁ X ₁ X ₂ X ₂	XY ₁ Y ₂	X-A and Y-A fusions	Steinberg et al. (2014)	
		<i>Alouatta belzebul</i>	50	X ₁ X ₁ X ₂ X ₂	X ₁ X ₂ Y	Y-A fusion	Armada et al. (1987), Steinberg et al. (2014)	
		<i>Alouatta caraya</i>	52	X ₁ X ₁ X ₂ X ₂	X ₁ X ₂ Y ₁ Y ₂	Complex fusions ^l	Mudry et al. (2001), de Oliveira et al. (2002), Solari and Rahn (2005), Steinberg et al. (2014)	

Table 1. Continued

Order	Family	Species	2n	Sex chromosomes	Variant system	Refs
		<i>Alouatta guariba</i>	46–50	XX, X ₁ X ₂ X ₃ X ₁ X ₂ X ₃ X ₃ X ₁ X ₂ X ₃ Y ₁ Y ₂	Complex fusions ^l	Mudry et al. (2001), de Oliveira et al. (2002)
		<i>Alouatta macconnelli</i>	47–49	X ₁ X ₂ X ₃	Complex fusions ^m	Mudry et al. (2001), de Oliveira et al. (2002), Steinberg et al. (2014)
		<i>Alouatta palliata</i>	54, 56	XX, X ₁ X ₂ X ₃	Complex fusions	Solari and Rahn (2005), Steinberg et al. (2014)
		<i>Alouatta pigra</i>	58	X ₁ X ₂ X ₃	Complex fusions	Steinberg et al. (2008), Steinberg et al. (2014)
		<i>Alouatta sara</i>	48–51	X ₁ X ₂ X ₃	Y-A fusion ^m	Minezawa et al. (1985), Stanyon et al. (1995), Steinberg et al. (2014)
		<i>Alouatta seniculus</i>	44–49	X ₁ X ₂ X ₃	Complex fusions ⁿ	Lima and Seauñez (1991), Solari and Rahn (2005), Steinberg et al. (2014)
		<i>Alouatta ululata</i>	50	X ₁ X ₂ X ₃	Y-A fusion	Viana et al. (2015)
Callitrichidae		<i>Callimico goeldii</i>	46	X ₁ X ₂ X ₃	Y-A fusion	Dumas et al. (2007)
Cercopithecidae		<i>Trachypithecus cristatus</i>	44	X ₁ X ₂ X ₃	Y-A fusion	Bigoni et al. (1997)
		<i>Dicrostonyx torquatus</i>	45–46	XX, XX*, X*Y	Oocyte-promoting X ^o	Gileva (1980), Fredga (1988), Romanenko et al. (2016), Saunders and Veyrunes (2021)
Rodentia		<i>Ellobius alaicus</i>	52	XX	Y loss, X duplication	Matveevsky et al. (2017)
		<i>Ellobius fuscocapillus</i>	36	XX	Sry amplification	Matveevsky et al. (2017), Bakloushinskaya and Matveevsky (2018)
		<i>Ellobius lutescens</i>	17	XO	Y loss ^p	Matthey (1953), Matveevsky et al. (2017)
		<i>Ellobius talpinus</i>	54	XX	Y loss, X duplication	Matveevsky et al. (2017)
		<i>Ellobius tancrei</i>	54	XX	Y loss, X duplication	Matveevsky et al. (2017)
		<i>Lasiopodomys mandarinus</i>	47–52	X ₁ X ₂ X ₃ , X ₁ YX ₃ X ₁ X ₂ X ₃	Y loss, complex fusions ^o	Gladkikh et al. (2016), Romanenko et al. (2020), Roy (2021)
		<i>Microtus cabrerae</i>	54	XX, XY	Sry amplification ^r	Modi (1987), Burgos et al. (1988), Marchal et al. (2003)
		<i>Microtus oregoni</i>	17–18	X ^m X ^p	X-Y fusion ^s	Couger et al. (2021)
		<i>Myopus schisticolor</i>	32	XX, XX*, X*Y	Oocyte-promoting X ^t	Gropp et al. (1976), Herbst (1978), Akhverdyan and Fredga (2001)
		<i>Akodon azarae</i>	38	X ₁ X ₂ X ₃ , X ₁ X ₂ Y ₁ Y ₂	Oocyte-promoting X ^u	Hoekstra and Edwards (2000), Lisanti et al. (2000), Bianchi (2002)
		<i>Akodon boliviensis</i>	40	XX, XX*, X*Y	Oocyte-promoting X ^u	Hoekstra and Edwards (2000), Bianchi (2002)
		<i>Akodon kofordi</i>	40	XX, XX*, X*Y	Oocyte-promoting X ^u	Hoekstra and Edwards (2000), Bianchi (2002)
		<i>Akodon lutescens</i>	34	XX, XX*, X*Y	Oocyte-promoting X ^u	Hoekstra and Edwards (2000), Bianchi (2002)
		<i>Akodon mollis</i>	22	XX, XX*, X*Y	Oocyte-promoting X ^u	Bianchi and Merani (1984), Hoekstra and Edwards (2000), Bianchi (2002)
		<i>Akodon montensis</i>	24	XX, XX*, X*Y	Oocyte-promoting X ^u	Hoekstra and Edwards (2000), Bianchi (2002)
		<i>Akodon subfuscus</i>	40	XX, XX*, X*Y	Oocyte-promoting X ^u	Hoekstra and Edwards (2000), Bianchi (2002)
		<i>Akodon torques</i>	24	XX, XX*, X*Y	Oocyte-promoting X ^u	Hoekstra and Edwards (2000), Bianchi (2002), Jiménez et al. (2013)
		<i>Akodon varius</i>	40	XX, XX*, X*Y	Oocyte-promoting X ^u	Bianchi and Merani (1984), Hoekstra and Edwards (2000), Bianchi (2002)

Table 1. Continued

Order	Family	Species	2n	Sex chromosomes	Variant system	Refs
		<i>Deltamys kempi</i>	38	X ₁ X ₁ X ₂ X ₂	Y-A fusion ^v	(Sbalqueiro et al. 1984) Castro et al. (1991), Sbalqueiro et al. (1984), Ventura et al. (2011)
		<i>Oecomys auyantepui</i>	64	XX	X-A fusion	Oliveira da Silva et al. (2022)
		<i>Salinomys delicatus</i>	18	XX	X-A fusion	Lanzone et al. (2005), Lanzone et al. (2011)
		<i>Reithrodon typicus</i>	28	XX	X-A and Y-A fusions, Y loss ^w	Ortells et al. (1988)
Echimyidae		<i>Lonchothrix emiliae</i>	64	XX	X-A fusion	Dias de Oliveira et al. (2019)
		<i>Proechimys goeldii</i>	16, 24	XX	X-A fusion	Rodrigues da Costa et al. (2016)
		<i>Proechimys longicaudatus</i>	16, 28	XX	X-A fusion	Amaral et al. (2013)
			28–30			
Muridae		<i>Acomys ngurui</i>	59, 60	XX, XO	Unknown ^s	Castiglia et al. (2007), Castiglia and Annesi (2012), Saunders and Veyrunes (2021)
		<i>Mus minutoides</i>	18, 34	XX, XX*, X*Y	Oocyte-promoting XY	Britton-Davidian et al. (2012), Veyrunes et al. (2007), Veyrunes et al. (2010)
		<i>Mus musculoides</i>	18	XX	X-A fusion	Veyrunes et al. (2004)
		<i>Mus triton</i>	30, 32	XX, XX*, X*Y, XO	Oocyte-promoting X, Y loss ^z	Jottrand-Bellomo (1988), Veyrunes et al. (2007)
		<i>Tokudaia muenninki</i>	44	XX	X-A and Y-A fusion ^{am}	Murata et al. (2012), Murata et al. (2016a)
		<i>Tokudaia osimensis</i>	25	XO	Y loss	Nakamura et al. (2007)
		<i>Tokudaia tokumoshimensis</i>	45	XO	Y loss	Nakamura et al. (2007)
		<i>Vandeleuria oleraceus</i>	29	X1X1X2	X fission	Raman and Sharma (1976)
		<i>Gerbillus gerbillus</i>	42	XX	Complex fusions ^{ab}	Viegas-Péquignot et al. (1982), Wahrman et al. (1983), Aniskin et al. (2006)
		<i>Gerbillus hesperinus</i>	58	XX	Complex fusions ^{ab}	Viegas-Péquignot et al. (1982)
		<i>Gerbillus floweri</i>	40	XX	Complex fusions ^{ab}	Aniskin et al. (2006)
		<i>Gerbillus nigeriae</i>	72–74	XX	Complex fusions ^{ab}	Viegas-Péquignot et al. (1982)
		<i>Gerbillus occidius</i>	40	XX	Complex fusions ^{ab}	Aniskin et al. (2006)
		<i>Gerbillus pyramidum</i>	38	XX	Complex fusions ^{ab}	Wahrman et al. (1983)
		<i>Gerbillus tarabuli</i>	40	XX	Complex fusions ^{ab}	Aniskin et al. (2006)
		<i>Taterillus arenarius</i>	30	XX	Complex fusions ^{ac}	Dobigny et al. (2004)
		<i>Taterillus gracilis</i>	36	XX	Complex fusions ^{ac}	Dobigny et al. (2004)
		<i>Taterillus petteri</i>	18	XX	Complex fusions ^{ac}	Dobigny et al. (2004)
		<i>Taterillus pygargus</i>	22	XX	Complex fusions ^{ac}	Dobigny et al. (2004)
		<i>Taterillus tranieri</i>	14	XX	Complex fusions ^{ac}	Dobigny et al. (2004)
Zapodidae		<i>Napaeozapus insignis</i>	72	X ₁ X ₁ X ₂	X deletion ^{ad}	Whitaker and Wrigley (1972)
		<i>Zapus princeps</i>	71–72	XX, XO	Unknown ^{ae}	Meylan (1968), Hart et al. (2004)

Table 1. Continued

- ^aSome males have a second, smaller Y, and both Ys are acrocentric. This does not appear to be from sex-autosome fusion, or fission (Fredga 1970).
- ^bAll species in Tringelaphini have the same Y-autosome fusion, though no data exist for *T. bixtoni* or *T. sylvaticus*. In *T. imberbis* and *T. spekti*, the remaining autosome in the pair has also fused to the X (Rubes et al. 2008).
- ^cWe included in this table only species with a published karyotype that could be located and definitively assigned to a taxon. In *E. ruffifrons* and *E. thomsoni*, the X and Y have each translocated to different autosomes—each species both display X-5 and Y-16 translocations. An X-A translocation is suspected to be synapomorphic for all members of *Antelope*, *Eudorcas*, *Gazella*, and *Nanger* (Cernohorska et al. 2015). *Ellibius albionotata*, *E. rufina*, and *E. tilonura*, are presumed to have the same sex chromosome configuration as *E. ruffifrons*, given their previous status as subspecies.
- ^dIn *N. soemmerringii*, both Y- and X-autosome translocations exist, both separately and together.
- ^eIn *E. cephalophus*, both XY and XY₂Y₁ males exist. Additionally, both the X and Y are polymorphic due to large heterochromatin expansions (Cao et al. 2005).
- ^f*Urva ianatica* was recently split from *U. auropunctata* and is suspected to have the same Y-A fusion (Fredga, 1972), but no confirmed male karyotype has been published.
- ^g*Dermianuina cinerea* has an XY₁Y₂ system in Central America (Baker 1973), but a fusion between the Y and the unpaired autosome has led to South American populations having an XXXY system (Noronha et al. 2010; Gomes et al. 2016).
- ^hIn *R. morio*, the ancestral Y has fused to 15p through a swap translocation (Volleth et al. 2015). Thus, 15q has become Y₂ and the homologous 15 is X₂.
- ⁱWhile *L. conspiciillatus* appears to have a simple Y-A fusion, it is in actuality the result of three successive fusions: the X to an autosome, the Y to the homologue of that autosome, and then the other end of the Y to a second autosome.
- ^jIn *Phataginus tricuspis*, a species of pangolin, the Y chromosome has fused with male 2n = 113 and female 2n = 114. *Phataginus tricuspis* has the second highest reported 2n among mammals (Houck et al. 2023).
- ^kSome oocyte-producing *Choloepus hoffmanni* individuals are XO in somatic cells (Corin-Frederic 1969; Dobigny et al. 2005).
- ^lSome populations of *A. araya* are still XXXY (Steinberg et al. 2014). The X₂ appears to derive from two fused autosomes, with parts of both having been translocated to Y₁, and one of which also forms Y₂.^mIn addition to individuals with XXXY sex chromosomes, there are two variant cytotypes of *A. guariba* (Stemberg et al. 2014). 1: *A. g. guariba*, 2n = 50/49. 2: *A. g. fusca*, 2n = 46/45.
- ⁿThe differences in 2n are due to microchromosomes.
- ^o2n of *D. torquatus* can vary further due to the presence of B chromosomes. Both the X and Y chromosomes have experienced autosomal translocations. Romanenko et al. (2016) describe a male with X₁X₂Y, where X₁ has a second autosomal translocation.
- ^pIn *E. latescens*, Y loss is independent from that seen in other *Ellibius* (Bakloushinskaya and Marveevsky 2018).
- ^qIn *L. mandarinus*, one small acrocentric is called Y, but it appears to be the result of an X-autosome translocation. The ancestral Y and its genes—including *Sry*—have not been located. X₁ is polymorphic, and the X₂ is remarkably small. X₁ results from a translocation between X₁ and X₂, and has been suggested to be oocyte-promoting (Roy 2021).
- ^rOnly one population of *M. cabrae* has been found with XY females, which were fertile (Burgos et al. 1988). In all members of the species, there are multiple pseudogenized copies of *Sry* on the X and Y. This species, as well as *M. agrestis*, *M. chrotorrhinus*, *M. epiroticus*, and *M. transcaasicus*, have giant, polymorphic, heterochromatin blocks on the sex chromosomes (Marchal et al. 2003).
- ^sIn *M. oregoni*, females: 2n = 17 (somatic) and 18 (germline), with only X^m. Males: 2n = 18 (somatic) and 17 (germline), with X^m and X^r (Ohno et al. 1963, 1966; Couger et al. 2021).
- ^tIn *M. schisticolor*, both the X and Y have experienced fusion to autosomes. Populations show a female-biased sex ratio and frequent chromosome number deviations (2%); XO females, X*YY females XX*Y females (all fertile) and XX*Y males (sterile) (Gropp et al. 1976). There exist individuals from Siberia with 2n = 34 (Kozlovskij 1986).
- ^uSome *Akodon* species have XXXY, and the variant configuration has been proposed to have multiple origins (Hoekstra and Edwards 2000; Bianchi 2002), the multiple origin hypothesis needs to be reexamined (see Ortiz et al. 2009). *Akodon azarae* has additional X chromosome polymorphisms.
- ^vPopulation-specific variation has been described for 2n in *D. kempi* and for the structure of the X (Castro et al. 1991).
- ^wIn *R. typicus*, X-autosome translocations have occurred in separate populations. The Argentine population is suggested to have the ancestral sex chromosome karyotypes. In Brazil and Uruguay, the X-autosome translocations are identical. Banding patterns between the Brazilian Y and its Uruguayan counterpart suggest heterochromatin has been lost. Ortells et al. (1988) conclude that the ancestral Y chromosome has therefore been lost in the Uruguayan form, but it is possible that heterochromatin has been lost instead.
- ^xThe exact system of *A. ngarui* is unclear, but it appears that they are XXXY but with chromosomal variants that are gonadosomatic mosaics. Variant females are XO, and males are XO and XY in somatic cells but XY in the germ line (Castiglia et al. 2012; Saunders and Veyrunes 2021).
- ^yIn *M. minutoides*, chromosome 1 has fused to both the X and Y. Some populations have further rearrangements, including whole-arm reciprocal translocations with X* and another autosome (Veyrunes et al. 2007, 2010).
- ^zMost *M. triton* individuals have an oocyte-promoting X* system; however, Jottrand-Bellormo (1988) identified a population in Burundi that is XO/XO.
- ^{aa}In *Tokudaia*, two out of three species have experienced Y-loss and lack *Sry* entirely (Murata et al. 2010). However, in *T. mueminki*, Y-derived genes have been translocated onto the ancestral X- and Y-chromosomes fused with autosomes (Murata et al. 2012, 2016a). Zoo-FISH analysis with mouse probes suggested each neo-sex chromosome is fused with an autosome homologous to mouse autosomes 11 + 16 (Murata et al. 2012). *Tokudaia mueminki* has over 70 pseudogenic copies of *Sry* (Murata et al. 2010), and both sex chromosomes are giant on account of large heterochromatin blocks (Murata et al. 2012).
- ^{ab}All members of *Gerbillius* in our dataset appear to share X- and Y- autosome translocations, and X chromosomes are morphologically variable between taxa (Viegas-Péquignot et al. 1982; Ndiaye et al. 2016). In *G. gerbillus*, a second autosome was translocated onto an X chromosome. *Gerbillus floweri* is considered synonymous with *G. perpallidus* following Ndiaye et al. (2016).
- ^{ac}In tateilms with variant sex chromosomes, the X is fused to two autosomes. The Y is also fused to an autosome, and part of it has translocated to the X (Dobigny et al. 2004).
- ^{ad}*Napaeozapus insignis* X chromosomes are polymorphic, with a large X (X₁) comprising about 13% of the haploid genome and the smaller X₂ seemingly derived from a large deletion (Whitaker and Wrigley 1972).
- ^{ae}Females with both XX and XO co-occur, but the underlying mechanism is unknown.

genera and 20 families with published karyotypes (Fig. 1). These numbers are certainly conservative as many species of mammals remain unkaryotyped and we exclude taxa inferred to have variant sex chromosomes but lacking cytogenetic confirmation. Moreover, population-level variation in sex chromosome configuration (e.g. Ortells et al. 1988; Ventura et al. 2011) is presumably underestimated. As a rough benchmark for the sampling breadth of mammal karyotypes, the Atlas of Mammalian Chromosomes (Graphodatsky et al. 2020) contains approximately 1,100 karyotypes out of the almost 6,500 species of mammals (Burgin et al. 2018). The three most common categories involve fusions between one or more sex chromosome and autosomes. Such rearrangements are thought to be highly deleterious and so should be rare (Ashley et al. 2002; Barasc et al. 2012; White et al. 1998; but see Charlesworth and Charlesworth 1980; Guerrero and Kirkpatrick 2014). While we use the general term fusion, most of these cases are Robertsonian translocations (Schubert and Lysak 2011). Three categories are represented by only one or two species each: X-Y fusion and X- or Y-fission. Finally, we identify three categories that involve modification of ancestral sex-determining pathways: gene amplification, Y chromosome loss, and oocyte-promoting X (X^*) chromosomes.

Rate estimation

Under our simplified approach of assigning sex chromosomes as either variant or not, we find evidence of family-specific differences in rate of variant sex chromosome evolution (Fig. 2; Supplementary Table 1). Under an equal rate model on the maximum clade credibility tree (Upham et al. 2019), the highest transition rates were found in Zapodidae (5.6411), Atelidae (0.1347), and Aotidae (0.1000), while the lowest rate was in Cercopithecidae (0.0030), a family with 125 species of which one has variant sex chromosomes. Zapodidae's obviously elevated rate relative to other families is likely an overestimate stemming from the small number of species in the family (five species, two of which have variant sex chromosome systems). After repeating the analysis without Zapodidae, we found that family-specific rates still show a better fit than a common-rate model (Equal rate model. Likelihood ratio: 80.4501. $P = 0$). The unidirectional rate model, which should be more biologically realistic, also found family-specific rates to fit better than a common-rate (Likelihood ratio: 96.4545. $P = 0$). While the order of families from highest to lowest rate is mostly the same, the three fastest rates in the unidirectional model are inferred in Atelidae (0.0827), Herpestidae (0.066), and Zapodidae (0.0629)—note that Zapodidae has an inferred rate far more in line with the other families than under the equal rate model. When examining the distribution of rates from across the set of 100 credible phylogenies, the inferred transition rates are inconsistent in the five families with the highest rates, whereas most families of mammals have low inferred rates that are stable across different tree topologies (Fig. 2). Thus, our results suggest that mammal families have lineage-specific rates at which they acquire variant sex chromosomes. While most variant sex chromosome systems are found in rodents, this does not correspond to higher inferred transition rates in families within Rodentia.

Restricting the analysis to species with published sex chromosome karyotypes in Atelidae, Bovidae, and Herpestidae (Supplementary Fig. 1; Supplementary Table 2), had different effects on each family that reflect gaps in both sampling

completeness in the phylogeny used and our knowledge of sex chromosome karyotypes. For Herpestidae, the estimated distribution of transition rates was reduced but remained qualitatively high relative to other families (Fig. 2; Supplementary Fig. 1). The inferred transition rates for Bovidae were also lower, which is likely a consequence of species that would be XX/XY but are missing from the phylogeny. The biggest difference in estimated transition rates between our two approaches was seen in Atelidae, in which the removal of taxa with unconfirmed sex chromosome karyotype lead to a much lower estimated transition rate—though still higher than the majority of families in the analysis with all species included—and a narrower range of estimated rates. Taken together, these results reinforce the difficulties in estimating accurate rate values without comprehensive sex chromosome karyotypes and given topological uncertainty in phylogenies. Despite our two approaches yielding inconsistent specific transition rate estimates, both suggest that several families of mammals show elevated transition rates from XX/XY chromosomes to variant sex chromosome systems.

Our model neglects additional parameters that are worthy of future consideration. For example, different families are likely to have their own baseline rate of chromosome fusion and fission, which would naturally influence the rate of sex-autosome fusions. Similarly, chromosome morphology (Blackmon et al. 2019) and the number of chromosomes in a karyotype (Anderson et al. 2020) will directly impact the probability that a given fusion involves a sex chromosome. The rate at which chromosome fusions accumulate is also likely influenced by generation time. However, high transition rates in taxa with very different generation times (i.e. primates and rodents) suggest minimal effects of this parameter on the current dataset.

Discussion

Review of the literature on mammalian sex chromosomes revealed over 150 species with variant sex chromosome systems. Analysis of the distribution of these variants across therian mammals indicates that a propensity for sex chromosomes to diverge from the traditionally ultra-stable XX/XY configuration is taxonomically widespread. Here, we consider the evolution and maintenance of representative systems in light of two types of conflict: between the sexes and within the genome in the form of meiotic drive. We begin with a brief summary of the conflict-based models for sex chromosome evolution and then discuss the major types of variant sex chromosome systems in turn. In closing, we outline non-conflict-based models for sex chromosome evolution, with particular focus on a recently proposed model that emphasizes the role of regulatory divergence in the origin of heteromorphic sex chromosomes (Lenormand et al. 2020; Lenormand and Roze 2022).

Models of conflict-driven sex chromosome evolution

What drives the evolution of suppressed recombination between homologous chromosomes? This is the question that all models for the evolution of heteromorphic sex chromosomes are obliged to address. Nearly a century ago, Fisher interpreted the excess of Y chromosome-linked color genes in guppies (*Poecilia reticulata*) as a consequence of

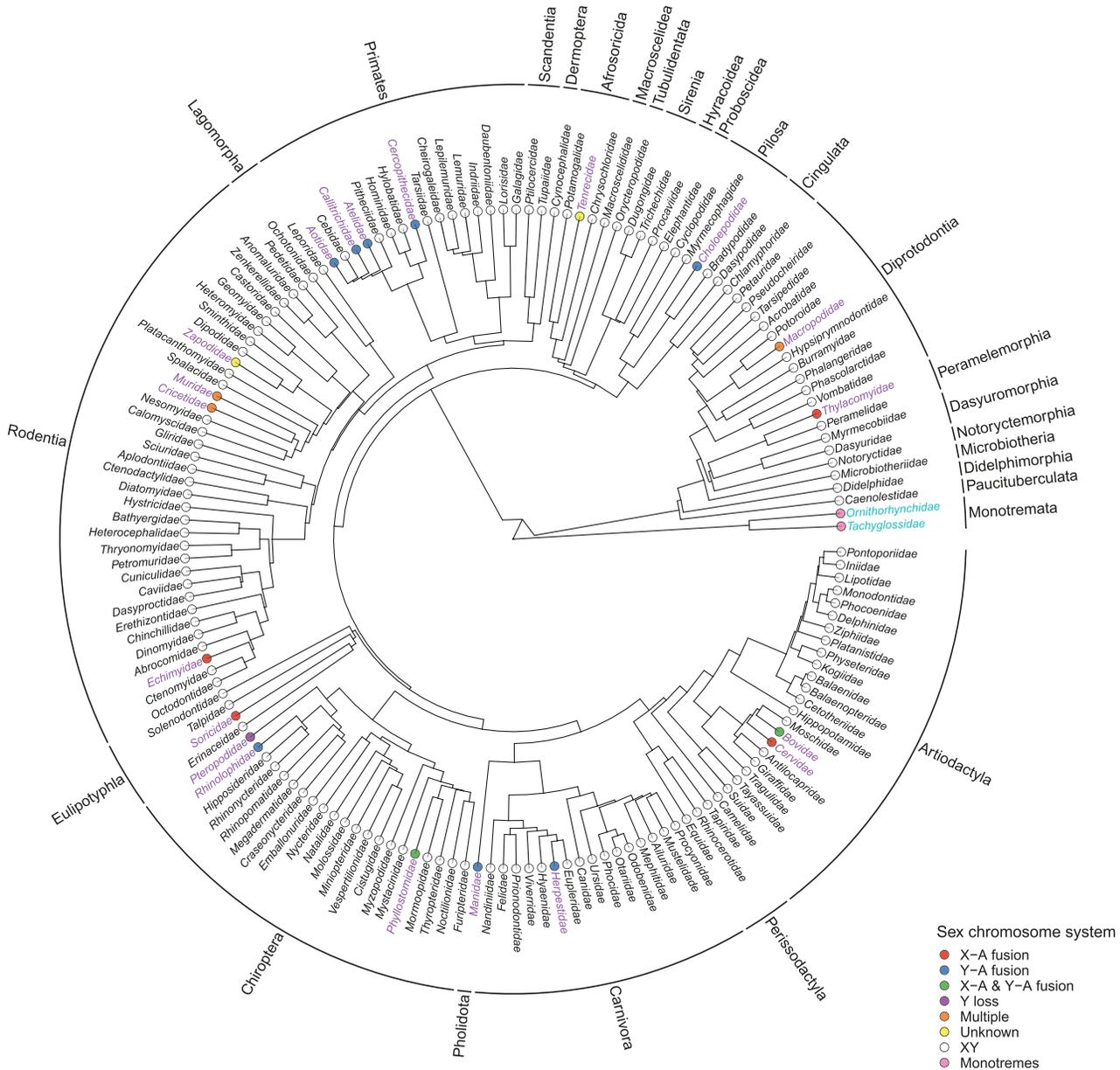


Fig. 1. Family level phylogeny of Mammalia, with families containing species that have variant sex chromosomes indicated by purple text. Monotremes are in blue to denote the independent origin of their sex chromosomes relative to therian mammals. The categories of sex chromosome system found in each family are indicated by colored circles on the tips.

selection to limit sexually selected genes to the sex they benefit (Fisher 1931). This hypothesis seeded an elegant body of theory on the role of sexual conflict in sex chromosome evolution (Charlesworth and Charlesworth 1980; Bull 1983; Rice 1987; Charlesworth 1991; van Doorn and Kirkpatrick 2007). The key features of these models are, 1) linkage between a sex-determining locus and one or more sexually antagonistic loci (loci that benefit one sex but harm the other), and 2) selection for suppressed recombination that restricts the interval to the sex it benefits, thereby resolving intralocus sexual conflict. The presence or gain of additional sexually antagonistic loci on the same chromosome favors recombination suppression over a larger interval, ultimately leading to sex-limitation of an entire chromosome (Charlesworth 1991). Importantly, these models apply equally well to the origin of new sex chromosomes, and to neo-sex chromosome systems,

in which an autosomal fusion to an existing sex chromosome generates a new sex-linked part of the genome. In both cases, gene movement to the Y chromosome resolves male-benefit sexual antagonism whereas the asymmetric distribution of X chromosomes between males and females makes the X a predicted hotspot for recurrent bouts of sexually antagonistic evolution (Rice 1984).

Novel sex-determining loci and sex chromosome configurations may also achieve fixation through meiotic drive, the biased transmission of a locus (Pardo-Manuel de Villena and Sapienza 2001; Kozielska et al. 2010). Meiotic drive *sensu stricto* manifests during oogenesis where the structural features of a chromosome, such as its centromere (Chmátal et al. 2014; reviewed in Clark and Aker 2021; Kumon and Lampson 2022; Talbert and Henikoff 2022), may aid in its transmission to the ovum rather than the polar body (Rhoades 1942;

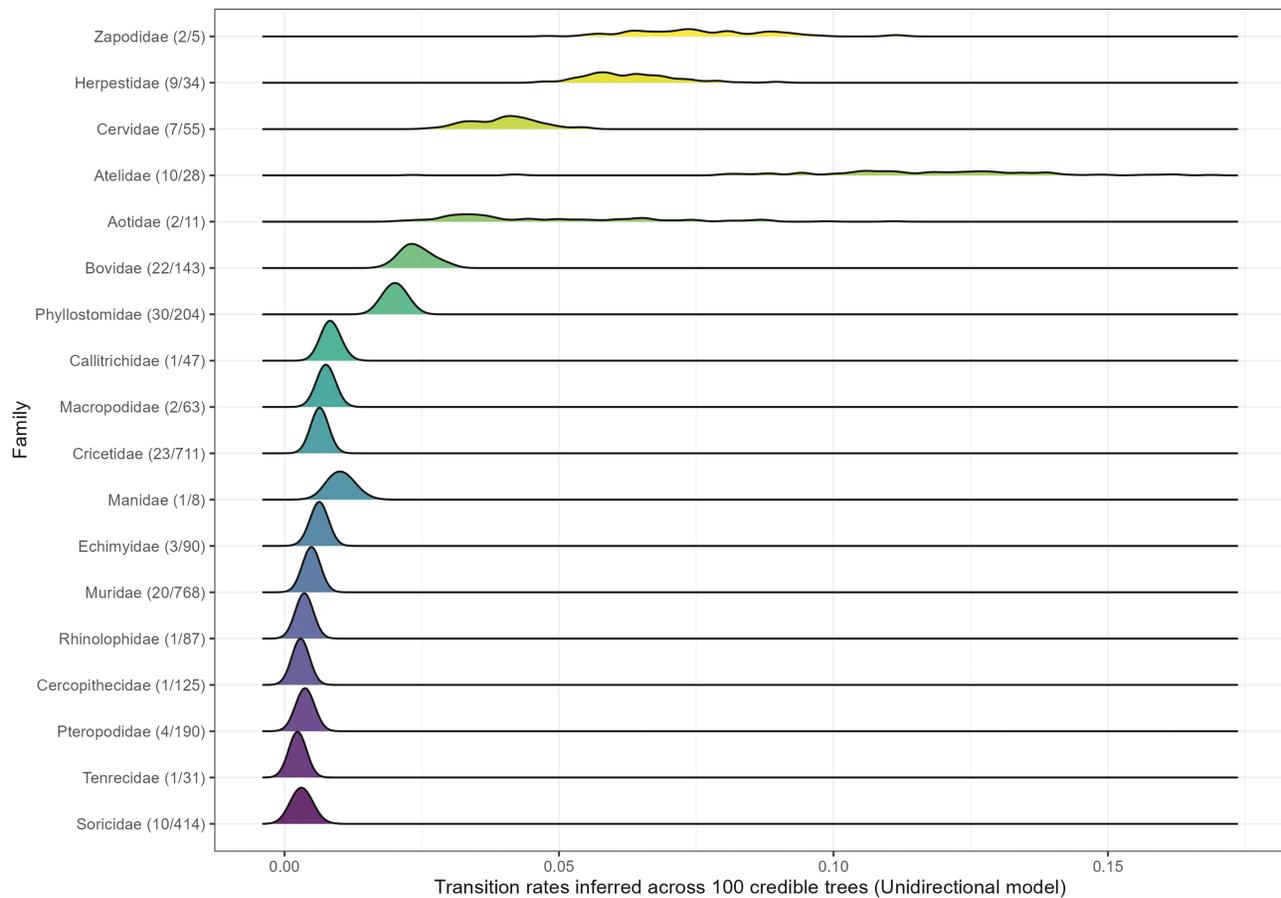


Fig. 2. Density plot showing the inferred transition rate from XX/XY to a variant sex chromosome system in families of mammals. Rate distributions are inferred by fitting a unidirectional model to 100 trees sampled from the posterior distribution of Upham et al. (2019). Numbers in brackets after family names indicate the number of species with variant sex chromosome systems as a fraction of the total number of species in the family that are present in the phylogeny. Two families of therian mammals with variant systems are excluded: Choloepodidae (2/2) and Thylacomyidae (1/1). Results from fitting both the equal rates and unidirectional rate models to the maximum clade credibility tree from Upham et al. (2019) are reported in Supplementary Table 1.

Sandler and Novitski 1957). More generally, the term has come to apply to any form of non-Mendelian inheritance, including malsegregation or non-disjunction of the nondriving locus, or the death of sperm lacking the driver (Presgraves et al. 1997). As meiotic drivers are selfish elements whose biased transmission tends to impose steep fitness costs (Fishman and Saunders 2008; Lindholm et al. 2016), genomic responses that restore equilibrium by suppressing the driver are expected, as are further mutations to “strengthen” the force of drive, leading to cycles of conflict (Jaenike 1999; Hall 2004). This is especially true for sex chromosomes, which are more likely to develop drivers than autosomes (Frank 1991; Hurst and Pomiankowski 1991), and where failure by the genome to respond to drive can lead to extinction from warped sex ratios and the elimination of one sex (Hamilton 1967; Jaenike 2001; Holman et al. 2015). Depending on the fitness cost of a driving X, an autosome that acquires a new sex-determining locus may invade (Werren and Beukeboom 1998; Kozielska et al. 2010), a mechanism that has been proposed in two mole species, *Talpa europaea* and *T. occidentalis* (McVean and Hurst 1996). We exclude these from our dataset as there is no associated change in sex chromosome configuration, but XY individuals of both species have testes and XX individuals possess ovotestes, which have both a typically functioning ovarian section and a testicular section (Jiménez et al. 2023).

Drivers are often associated with structural variants (Charlesworth and Hartl 1978; Jaenike 2001; Lyon 2003) and changes in chromosome morphology (Pardo-Manuel de Villena and Sapienza 2001; Yoshida and Kitano 2012), which facilitates the reduced recombination necessary to form heteromorphic sex chromosomes. Beyond the proposed role of meiotic drive in the origin of sex chromosomes (Úbeda et al. 2015), it has been invoked to explain shifts in karyotype morphology (Pardo-Manuel de Villena and Sapienza 2001; Blackmon et al. 2019) and, by extension, the evolution of neo-sex chromosomes (Yoshida and Kitano 2012) and other variant sex systems (Helleu et al. 2015).

X-autosome and Y-autosome fusions

The most common forms of variant sex chromosomes in mammals are those resulting from fusions between a sex chromosome and an autosome. These fusions, which are achieved primarily by Robertsonian translocation (Schubert and Lysak 2011), account for 79% of all our observations (Table 1). Typically, an X-autosome fusion generates an XY_1Y_2 sex chromosome system, with Y_2 representing the remaining unfused autosomal homolog, whereas Y-autosome fusions lead to an X_1X_2Y condition (Fig. 3a). In therian mammals with published karyotypes, we identified 49 species

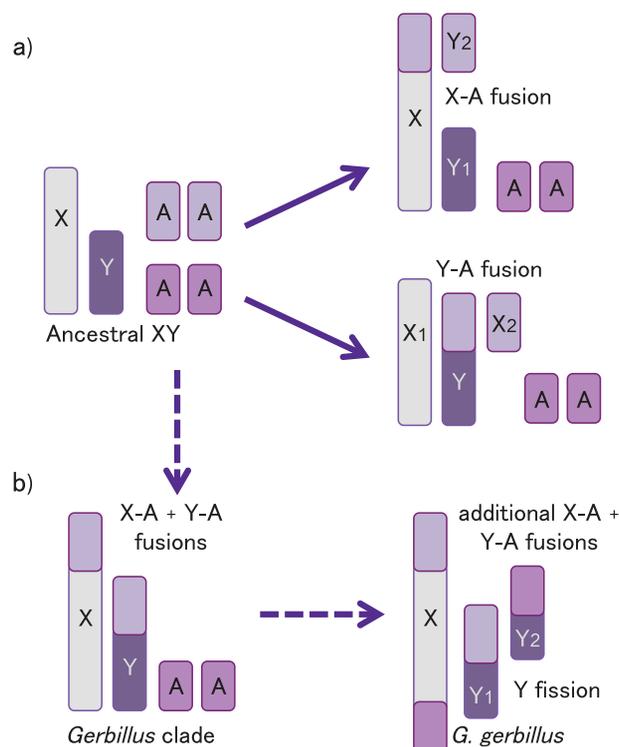


Fig. 3. Outcomes of sex chromosome-autosome fusions in mammals. a) An X-autosome fusion produces an XY_1Y_2 system; a Y-autosome fusion produces an X_1X_2Y system. b) The fusion of a homologous pair of autosomes to both X and Y explains the large sex chromosomes of gerbils in the clade, *Gerbillus* (*sensu* Ndiaye et al. 2016). In *G. gerbillus*, a second pair of autosomes are fused to the X and Y, and fission of the ancestral part of the Y chromosome produced an XY_1Y_2 system (Wahrman et al. 1983). Dashed lines indicate that transitional sex chromosome states were likely involved. A, autosome.

across 21 genera with an X-autosome fusion, 27 species across 13 genera with a Y-autosome fusion, and 44 species in 20 genera with both X- and Y-autosome fusions. Of the 54 unique genera, 18 had only X-autosome fusions and 10 had only Y-autosome fusions.

Several mechanisms have been proposed to explain the fixation of sex-autosome fusions. Classic theory predicts that sexually antagonistic loci on an autosome are released from constraint by translocation to either the X or Y (Charlesworth and Charlesworth 1980; Rice 1984). More recently, it was suggested that meiotic drive can fix sex-autosome translocations when chromosome morphology biases transmission rate (Yoshida and Kitano 2012). This preferential transmission of one chromosome morphology over another is termed meiotic polarity. Genetic drift (Lande 1985) and autosomal loci with heterozygote advantage (Charlesworth and Wall 1999) may also contribute.

Single sex-autosome fusions.

Some of the best-known examples of X-autosome translocations in mammals are those of shrews in the genus *Sorex*, which exhibits remarkable inter- and intra-specific karyotype variation (Bulatova et al. 2019). Ten species of *Sorex* are united by a large metacentric X chromosome, formed by the fusion of the X to a similarly sized autosome (Sharman 1956). In the best studied of these 10 species, *S. araneus*, the ancestral and autosomal arms of the

large X show distinct behaviors reflecting their origins. The arm derived from the ancestral X exhibits X inactivation in females and, during male meiosis, pairs to the ancestral Y much earlier than the autosomal arm pairs to its Y_2 homolog (Pack et al. 1993). Biased transmission of metacentrics through increased spermatocyte survivability has been documented for both autosomes and the X chromosome in *S. araneus* (Searle et al. 1986; Wyttenbach et al. 1998; Fedyk and Chętnicki 2007). Borodin et al. (2019) suggest that this biased transmission stems from disruption to the telocentrics, with uneven asynapsis between the heteromorphic chromosomes.

Based on existing karyotype data (Fredga 1972; Murata et al. 2016b), the Y-autosome translocation within the mongoose family (Herpestidae) presumably has two independent origins, one in the common ancestor of *Urva* and *Atilax* and another in *Herpestes*. While $2n$ (the diploid number of chromosomes) is otherwise conserved in *Urva* and *Atilax*, autosomes in *Herpestes* have undergone further rearrangement. In *Herpestes* the ancestral Y arm of the fused sex chromosome is readily identifiable (Fredga 1972), but in the *Urva* and *Atilax* groups the Y translocation has only recently been identified (Murata et al. 2016b) on account of its miniscule size (Fredga 1965; Raman and Nanda 1982). Mirroring the pattern in shrews, the ancestral Y portion is at the distal end of an autosome, and in spermatogenesis both the ancestral X and X_2 only associate with their respective homologs during pachytene (Murata et al. 2016b).

In contrast, the black muntjac (*Muntiacus crinifrons*), which has an X-autosome fusion, exhibits a large inversion on the Y_2 that limits recombination with the autosomal arm of the fused X (Yang et al. 1995). While the X-autosome fusion is shared with two other muntjac species (Wurster and Benirschke 1970; Soma et al. 1987), the inversion is unique to *M. crinifrons* (Yang et al. 1995). Strikingly, the *M. crinifrons* Y_2 shows patterns of degeneration similar to a typical Y chromosome (Zhou et al. 2008), making it an ideal system for studying the origins of Y chromosomes (e.g. Yin et al. 2021). X-autosome fusions are also observed in the tufted deer (*Elaphodus cephalophus*), a close relative of muntjacs that is polymorphic for the ancestral XX/XY and an XY_1Y_2 system, and is characterized by large, variable heterochromatin expansions on the sex chromosomes (Shi et al. 1991; Cao et al. 2005).

Secondary sex-autosome fusions.

Karyotype diversity is a long-recognized feature of Bovidae, a family characterized by numerous Robertsonian translocations between autosomes. Furthermore, X chromosomes may vary in centromere position, heterochromatin domains, and by which autosomes they are fused to (Robinson et al. 1998; Robinson and Ropiquet 2011). Two bovid lineages possess contrasting variant sex chromosomes, with members of tribe Tragelaphini sharing a Y-autosome translocation as a synapomorphy (Rubes et al. 2008), and species within the genera *Antilope*, *Eudorcas*, *Gazella*, and *Nanger* being united by a shared X-autosome fusion (Cernohorska et al. 2015). Furthermore, both lineages contain a small number of species in which the unmodified sex chromosome has also fused to an autosome. In *Eudorcas* gazelles, the *E. thomsoni* X and Y are each fused to homologs of the same chromosome, giving the appearance of an $XX/$

XY sex chromosome system, whereas the *E. rufifrons* X and Y are fused to different autosomes (Vassart et al. 1995; Cernohorska et al. 2015).

But wait, there's more! Complex sex-autosome fusions.

Some karyotypes appear particularly prone to rearrangements involving the sex chromosomes, which could indicate multiple bouts of sex chromosome drive and subsequent resolution. Two genera of rodents in Gerbillinae, *Gerbillus* and *Taterillus*, are prime examples. Several species of *Gerbillus* have markedly large sex chromosomes, as the X and Y have each fused to one homolog in a pair of autosomes (Fig. 3b; Viegas-Péquignot et al. 1982; Aniskin et al. 2006). The giant X of *Gerbillus gerbillus* is distinguished by a second autosomal fusion, whereas the two Y chromosomes in this species are the product of Y fission; both carry part of the original Y fused to a different autosome (Fig. 3b; Wahrman et al. 1983). Similarly, in *Taterillus*, West African species are differentiated from their East African relatives by a pair of autosomes translocated to both sex chromosomes, as well as a second autosomal translocation to the opposite end of the X (Volobouev and Granjon 1996; Dobigny et al. 2002). The ancestral sex chromosomes are separated from their autosomal arms by large, species-specific expansions of heterochromatin (Dobigny et al. 2004).

A similar pattern is observed in the spectacled hare-wallaby (*Lagorchestes conspicillatus*). Its unusual sex chromosome constitution, $X_1X_1X_2X_2/X_1X_2Y$, looks similar to a Y-autosome fusion, but is in fact the result of three rearrangements of unknown order (Martin and Hayman 1966; Hayman and Sharp 1981). Two homologs in an autosomal pair are fused to both the X and Y, the latter of which has fused to a second autosome and occupies the centromeric region of the resulting compound chromosome. There is no association between the ancestral X and Y components of the compound chromosomes during male meiosis (Hayman and Sharp 1981).

Within primates, sex-autosome translocations are a feature of three genera of Platyrrhine monkeys: *Aotus*, *Callimico*, and *Alouatta*. Species with variant sex chromosomes in *Aotus* and *Callimico* have simple Y-autosome translocations (Dumas et al. 2007; Menezes et al. 2010), but the more distantly related howler monkeys (*Alouatta*) display population-specific variation in sex chromosome karyotype and at least two independent Y-autosome translocation events (Lima and Seuánez 1991; de Oliveira et al. 2002; Solari and Rahn 2005; Steinberg et al. 2014). Curiously, the two Y-autosome fusions have each led to loss of autosomal material in some species, while in others this material is presumed to remain as microchromosomes (Steinberg et al. 2014). Meiotic drive is among the recently proposed explanations for this remarkable sex chromosome diversity, although available data are insufficient to support any particular hypothesis (Steinberg et al. 2022). Whereas the XX/XY system is highly conserved in Catarrhine monkeys, a single species (*Trachypithecus cristatus*) has been identified with a reciprocal translocation between the Y and an autosome (Bigoni et al. 1997). Difficulties in obtaining specimens notwithstanding, these primates are prime candidates for understanding the dynamics of sex-autosome fusions.

Phyllostomid bats exhibit a staggering amount of sex chromosome diversity. The genus *Carollia* is united by an X-autosome fusion (Baker et al. 1989; Pieczarka et al. 2005; Noronha et al. 2009). Within the subfamily Stenodermatinae, a series of rearrangements between autosomes and sex chromosomes are

suspected. *Artibeus* fruit bats are characterized by fusion of an autosome to the distal end of a metacentric X, as are their close relatives in the genus *Dermanura* (Baker 1973; Noronha et al. 2010; Rodrigues et al. 2003). To add to this complexity, some species of *Dermanura* and South American populations of *D. cinerea* have an additional Y-autosome fusion, restoring the appearance of an XX/XY system (Baker 1973; Hsu et al. 1986; Noronha et al. 2010). This same X-autosome translocation is found in other genera in the Vampyressina group, which can be broadly distinguished by a Y-autosome fusion with two alternate morphologies (Gomes et al. 2016). The composite Y is either acrocentric, as seen in *Platyrrhinus*, *Vampyrodes*, *Vampyriscus*, and *Chiroderma*, or metacentric, as in *Uroderma* (Pieczarka et al. 2013; Gomes et al. 2016). Furthermore, a second autosome has translocated to the metacentric composite Y in *Mesophyla*, and the autosomal arm of the composite X has fissioned in *Vampyressa* (Gomes et al. 2016).

Many of these genera are speciose and only a small subset of species have been karyotyped, so genus-level descriptions may well fail to capture the extent of sex-linked variation. Moreover, most of the sex chromosome diversity of phyllostomid bats is only described at the karyotypic level. Comparative genomics would likely uncover undescribed sex chromosome variants in this group, and would advance understanding of the mechanisms and evolutionary consequences of such lability in sex chromosome structure.

A final example of note is the naked-soled conyrat (*Reithrodon typicus*), a South American cricetid rodent. Sex chromosomes vary geographically in this species; Argentinian populations have standard XY chromosomes whereas Brazilian populations harbor distinct X- and Y-autosome fusions. Uruguayan populations appear to share the X-autosome fusion with the Brazilian form but have apparently lost the ancestral Y chromosome (Freitas et al. 1983; Ortells et al. 1988). However, given the limitations of cytogenetic visualization techniques of the time, whether the Y is truly lost or was too small to be detected (e.g. after a reduction in heterochromatin content), remains an open question. Crosses between geographic karyomorphs of *R. typicus* would be useful for investigating the meiotic fates of different sex chromosome morphologies and their role in speciation.

Just why are there so many sex-autosome fusions?

Sex-autosome fusions in mammals are associated with a suite of deleterious effects, including meiotic malsegregation and sterility, the silencing of autosomal genes by X inactivation, and conflicting replication times (White et al. 1998; Ashley 2002). Sex-autosome fusions are nonetheless clearly tolerated in many species where these ill effects are presumably mitigated. This is likely achieved by the physical separation of the two chromosome arms through the accumulation and expansion of heterochromatin (as in taterills; Dobigny et al. 2004) or other highly repetitive elements (as in *Mus minutoides*; Veyrunes et al. 2004; Colomina et al. 2017) such as telomeres and centromeres. It stands to reason that if meiotic polarity in a species favors metacentric chromosomes, then sex-autosome fusions may become fixed in spite of their deleterious potential.

Models of sexually antagonistic selection predict that Y-autosome fusions should be more common than X-autosome fusions (Charlesworth and Charlesworth 1980), though this

may require both deleterious fusions and biased mutation rates or sex ratios (Pennell et al. 2015). While Y-autosome fusions are more common in both fish (Kitano and Peichel 2012) and reptiles (Pennell et al. 2015), both X and Y sex-autosome fusions are similarly common in mammals (White 1973; Yoshida and Kitano 2012; Table 1).

Centromere drive and meiotic polarity provide compelling explanations for the emergence and maintenance of sex-autosome fusions in mammals. Highly repetitive sequences, particularly at centromeres, are associated with biased segregation during oogenesis (Pardo-Manuel de Villena and Sapienza 2001; Didion et al. 2015; Iwata-Otsubo et al. 2017). The probability that a chromosome preferentially segregates to the egg rather than the polar body appears to be a function of centromere strength, where greater strength refers to the centromere's ability to recruit more kinetochore proteins and associations with spindle fibers (Chmátal et al. 2014; Akera et al. 2017; Iwata-Otsubo et al. 2017; Kumon et al. 2021). The number and strength of centromeres can therefore be modified by the fusion and fission of chromosomes (Chmátal et al. 2014). In a taxon where meiotic polarity favors metacentrics but the X chromosome is telocentric, one X may gain a transmission advantage over its homolog by forming a metacentric via fusion to an autosome (Yoshida and Kitano 2012). As in Chmátal et al. (2014), relative centromere strength can be quantified by staining for centromeric and microtubule-recruiting proteins.

Y-autosome fusions would presumably be unaffected by centromere strength as the meiotic spindle is symmetric during spermatogenesis (i.e. both products of both divisions are retained). However, given that Y chromosomes may tolerate fusion well (Cech and Peichel 2016), Y-autosome fusions could still accumulate in karyotypes with telocentric autosomes. Indeed, X-autosome fusions are found in mammalian species with primarily metacentric karyotypes while Y-autosome fusions occur in species with more telocentric chromosomes (Yoshida and Kitano 2012).

Meiotic drive during spermatogenesis may also favor sex-autosome fusions. As postulated in *S. araneus* (Borodin et al. 2019), partial and uneven asynapsis between a metacentric and a pair of telocentrics can systematically lead to differential germ cell death. Where this occurs in the heterogametic sex, sex-autosome fusions should be associated with biased sex ratios. From the perspective of an autosome fused to the X chromosome, meiotic polarity allows it to benefit by reaching the egg more frequently or by being in the rarer sex if the Y is driving (Bull and Charnov 1988).

While sex-autosome fusions do not appear to change the underlying mechanisms of sex determination, they exhibit a degree of diversity that is underappreciated in mammals. Given the lineage-specific, and in some cases population-specific, nature of meiotic polarity, it seems unlikely that either spermatogenic or oogenic drive can wholly explain the maintenance of sex-autosome translocations. Genera like *Gerbillus*, *Tragelaphus*, and *Dermanura*, in which all species share a sex-autosome fusion and some have acquired an additional sex-autosome fusion, provide ideal systems with which to identify signatures of meiotic drive. If meiotic drive underlies the fixation of sex-autosome fusions, taxa with serial, complex fusions may reflect cycles of repeated drive and suppression as sex chromosomes vie for transmission. While driving elements are notoriously difficult to observe without access to crosses between divergent populations, their influence on deleterious

sex-autosome fusions could be inferred from biased sex ratios and signatures of selective sweeps (Didion et al. 2016). In the case of centromere drive, one would expect to see reduced variation around driving centromeres (Hurst 2022), and the association of X-autosome fusions with metacentric karyotypes and Y-autosome fusions with telocentric karyotypes (Yoshida and Kitano 2012). The mechanisms behind centromeric drive are increasingly well understood (reviewed in Kumon and Lampson 2022), and long read sequencing technologies should make it feasible to assemble centromeric regions more accurately and interrogate the repetitive sequences therein. Identification of differences in centromere size and rate of repeat evolution in taxa with both ancestral X and Y chromosomes and sex-autosome fusions, such as members of *Alouatta* (Steinberg et al. 2014) and phyllostomid bats (Gomes et al. 2016), would be suggestive of meiotic drive.

X and Y fission

In addition to sex-autosome fusions, X_1X_2Y or XY_1Y_2 sex chromosome systems can theoretically also be the product of sex chromosome fission, as seen in some insects (Blackmon et al. 2017). However, fissions appear to be substantially rarer in mammals. We identified three described instances of sex chromosome fission: Y fission in the lesser Egyptian gerbil (*G. gerbillus*; Wahrman et al. 1983; see above and Fig. 3b) and the swamp wallaby (*Wallabia bicolor*; Toder et al. 1997), and X fission in a population of the Indomalayan long-tailed climbing mouse (*Vandeleuria oleraceus*; Sharma and Raman 1972). In *W. bicolor*, chromosome painting revealed that autosomal material had fused to both the ancestral X and Y chromosomes, followed by a fission of the Y chromosome within the pseudoautosomal region, forming an XX/X_1Y_2 system (Toder et al. 1997). In contrast, while *V. oleraceus* is canonically XX/XY (Prakash and Aswathanarayana 1976), apparent fission of the X chromosome in the north Indian subspecies *V. o. oleraceus* has yielded an $X_1X_1X_2/X_1X_2Y$ configuration (Sharma and Raman 1972; Raman and Sharma 1976; Romanenko and Volobouev 2012).

In a meiotic drive framework, fissioned sex chromosomes should stem from the same processes as fused sex chromosomes; in a population where meiotic polarity favors telocentrics, a metacentric chromosome could preferentially bias its own transmission through fission (Yoshida and Kitano 2012). While this holds true for autosomes (Pardo-Manuel de Villena and Sapienza 2001; Blackmon et al. 2019), sex chromosome fission in mammals is comparatively rare. Fissions may be rarer in general because both fragments need to maintain functional centromeres. Moreover, the fact that *W. bicolor* has an otherwise metacentric karyotype (Toder et al. 1997) suggests that meiotic drive would favor the maintenance of metacentric sex chromosomes, especially as the fission was preceded by sex-autosome fusions. The pattern is similar in *G. gerbillus*; primarily metacentric autosomes and two sex-autosome fusions followed by a sex chromosome fission (Wahrman et al. 1983). However, *V. oleraceus* has an evenly mixed karyotype of metacentrics and telocentrics (Prakash and Aswathanarayana 1976), which could suggest a recent shift in meiotic polarity.

Y-loss and X-Y fusions

Complete loss of the Y chromosome is rare in mammals (Table 1) and should involve transfer of at least some

ancestral Y genes to the X, turnover in sex-determining loci, or both. The *Tokudaia* group has three spiny rat species, two of which (*T. tokunoshimensis*, *T. osimensis*) are XO/XO (Honda et al. 1978; Endo et al. 2008). The Okinawa spiny rat (*T. muenninki*) is XX/XY, with neo-X and neo-Y chromosomes resulting from sex-autosome fusions, and several autosomal genes on the neo-Y show signs of degeneration (Murata et al. 2015). Whereas *T. tokunoshimensis* and *T. osimensis* have lost *Sry* (Arakawa et al. 2002), in *T. muenninki* *Sry* is amplified to over 70 mostly pseudogenized copies (Murata et al. 2010).

Of the five species of *Ellobius* mole voles, one (*E. fuscopallidus*) retains the ancestral XX/XY system. *Ellobius lutescens* has lost the Y and is XO/XO. While most ancestral Y-linked genes, including *Sry*, are not detected in *E. lutescens* (Just et al. 2007; Matveevsky et al. 2017), at least two have been translocated to the X chromosome (Mulugeta et al. 2016). The remaining three species (*E. alaicus*, *E. talpinus*, and *E. tancrei*) also lack the Y chromosome but are XX/XX (Matveevsky et al. 2017; Bakloushinskaya and Matveevsky 2018). In *E. talpinus*, the two X chromosomes appear to be homologous in that they share identical G-banding patterns and are fully synapsed in oogenesis (Kolomiets et al. 2010). However, X chromosome synapsis in spermatogenesis is incomplete in *E. talpinus* and *E. tancrei* (Kolomiets et al. 2010; Matveevsky et al. 2016; Gil-Fernández et al. 2021). The lone X in *E. lutescens* is unpaired during meiosis (Kolomiets et al. 1991).

The mandarin vole, *Lasiopodomys mandarinus*, is an unusual case that maintains a neo-Y chromosome in the apparent absence of either the ancestral Y chromosome, or translocation of *Sry* to the X (Chen et al. 2008; Gladkikh et al. 2016). It remains to be determined whether the ancestral Y is truly lost or is an undetected part of the neo-Y. Four karyomorphs have been identified (Wang et al. 2003): $X_1YX_3X_3$ individuals produce sperm, while $X_1X_2X_3$, X_2YX_3 , and $X_1X_1X_3X_3$ individuals produce eggs. *Lasiopodomys mandarinus* is widely distributed (Tai et al. 2001) and is a model system for studying sociality, paternal care, and monogamy (e.g. Tai et al. 2001; Jia et al. 2009), making it ideal for studying crosses between karyomorphs. Crossbreeding and chromosome painting experiments by Romanenko et al. (2020) lead to the suggestion that X_2 , which is formed by a translocation between X_1 and X_3 , is oocyte-promoting. These crosses also revealed biased transmission of sex chromosomes (Romanenko et al. 2020). Roy (2021) ascribed this to Y chromosome drive and a sex-ratio adjusting imprinting mechanism, though recent models suggest this is only plausible when drive is much weaker than that observed in *L. mandarinus* (Saunders et al. 2022).

Finally, the unusual sex chromosome constitution of the creeping vole (*Microtus oregoni*) was described over 50 years ago (Matthey 1956; Ohno et al. 1963, 1966). Detailed cytological studies revealed that both sexes are gonosomic mosaics, meaning that the diploid number differs between somatic and germline cells (Ohno et al. 1963, 1966). Females carry one X in the soma but mitotic non-disjunction in the germline results in all oocytes transmitting an X (Ohno et al. 1966). Males were described as XY in the soma but YO in the germline (Ohno et al. 1963). However, recent genomic analysis in *M. oregoni* revealed additional sex chromosomal twists (Couger et al. 2021). Despite substantial differences in size, both sex chromosomes are largely X-derived and both carry a full complement of Y-derived genes due to ancestral X-Y fusion. X chromosome dosage

in somatic cells is reversed between the sexes, such that X chromosome inactivation occurs in XX males but not in XO females. Surprisingly, there is no evidence for differential degeneration of ancestral Y genes shared between the two chromosomes, despite the fact that the larger X is only transmitted through females. Notably, both X chromosomes carry multiple functional copies of *Sry* (Couger et al. 2021); the mechanism by which fertile ovaries develop remains to be determined.

These systems represent case studies in Y chromosome loss or reconfiguration and, to varying degrees, the translocation of sex-determining loci to the X chromosome. Recent work in *Drosophila affinis* provides a model under which such radical changes in sex chromosome identity and function might result from meiotic drive (Ma et al. 2022). In *D. affinis*, a driving X chromosome (X^{SR}) initially produces female-biased sex ratios by increasing Y chromosome non-disjunction such that sperm are either aneuploid with no sex chromosome or carry X^{SR} . Unlike most *Drosophila*, *D. affinis* males that lack a Y chromosome are viable, and so XO and $X^{SR}O$ males can persist. Because X^{SR} -carrying sperm are inviable, $X^{SR}O$ individuals only produce males, thus restoring sex-ratio parity (Ma et al. 2022). It is straightforward to imagine a similar chain of events in mammals, whereby Y chromosomes are lost in response to meiotic drive. *Ellobius*, with XX, XY, and XO males, is a particularly appealing system for testing for signs of X-linked drive and evaluating the costs of rescuing vs. sacrificing the Y chromosome. *Tokudaia* provide a system for contrasting possible fates of the Y chromosome and its genes (Murata et al. 2016a), but the restricted distribution and endangered status of spiny rat species make them difficult study organisms.

The fluidity of Y chromosomes

If sexual conflict is a primary driver of the evolution of heteromorphic sex chromosomes, Y chromosomes should be havens for male-benefit genes, released from the sexually antagonistic constraints of a genome shared with females. Moreover, if male-limited evolution in *Drosophila* can negatively affect female development after just 30 generations (Rice 1998), surely a chromosome that has been male-limited for many millions of generations should be toxic in a female developmental environment. From this perspective, the fact that there are at least 14 species of mammals in which some Y-bearing individuals are fertile females, and at least seven more in which previously Y-linked genes are permanently embedded in the shared genome (Table 1), is quite remarkable. We consider these two flavors of “shared-Y” systems in turn and identify open questions in both.

Oocyte-promoting X chromosomes: driving or driven to it?

Polymorphic sex chromosome systems have multiple independent origins in arvicoline, sigmodontine, and murine rodents (Table 1). Although the details vary between species, one or more X chromosome variant (designated X^*) that promotes ovarian development in Y-bearing individuals is common to all (Fagundes et al. 2000; Hoekstra and Edwards 2000; Ortiz et al. 2009; Veyrunes et al. 2010). Consequently, at least three sex chromosome genotypes produce females (XX, XX^* , and X^*Y), and females that carry X^* produce an excess of daughters. Considering that selection should act against strongly biased sex ratios (Hamilton 1967), and that

an expected 25% of X*Y females' gametes will be lost due to YY inviability, the independent establishment and maintenance of X* chromosomes in multiple species is puzzling.

Crossing experiments and mathematical modeling in a subset of species point to a central role for meiotic drive in the establishment of X*, thus providing at least partial solutions to this puzzle. In both the African pygmy mouse (*M. minutoides*) and the Arctic lemming (*Dicrostonyx torquatus*), Y chromosome drive in males is evident in crosses to females that do not carry X* (Gileva 1987; Saunders et al. 2022; see also Bull and Bulmer 1981; Bulmer 1988). Added twists include apparent reversal of male Y chromosome drive in African pygmy mouse crosses with X*Y females ("conditional drive," Saunders et al. 2022), and Y chromosome elimination from the germline in X*Y wood lemming (*Myopus schisticolor*) females (Fredga et al. 1972).

Does Y chromosome drive explain the establishment of X*? In other words, are these oocyte-promoting X chromosomes an adaptive compensatory response to male-biased sex ratios? Or are X* chromosomes themselves drivers that gain advantage by neutralizing Y chromosomes (e.g. Bull and Bulmer 1981)? The highly female-skewed sex ratio in wood lemmings (Bengtsson 1977) that results from complete transmission bias of X* over Y seems consistent with the latter interpretation (but see McVean and Hurst 1996). However, in a population genetic model for the history of X* in the African pygmy mouse, an oocyte-promoting X or a driving Y evolve first with equal probability (Saunders et al. 2022). Finally, the fact that X*Y females out-reproduce females with two X chromosomes in at least three species (African pygmy mouse, Saunders et al. 2014; wood lemming, Fredga et al. 2000, 2005; Azara's grass mouse [*Akodon azarae*], Espinosa and Vitullo 1996) suggests that selection contributes to the maintenance, and possibly the establishment, of X*.

X-Y integration: when sex chromosomes collide

In contrast to polymorphic X* systems, in which some egg-producing individuals thrive in the presence of a Y chromosome, at least nine species carry Y to X translocations that are likely fixed at the species level. The scale of these translocations from the male-limited genome ranges from X-linked copies of *Sry* in Cabrera's vole (*Microtus cabrerai*), to intervals that contain multiple Y-derived genes in mole voles (*Ellobius*) and Ryūkyū spiny rats (*Tokudaia*), to X chromosomes that carry most or all of the gene content of the ancestral Y in the creeping vole (*M. oregoni*) (Bullejos et al. 1997; Arakawa et al. 2002; Murata et al. 2012, 2016a; Mulugeta et al. 2016; Matveevsky et al. 2017; Bakloushinskaya and Matveevsky 2018; Couger et al. 2021). Whereas the ancestral Y chromosome is retained in Cabrera's vole and in one mole vole and one spiny rat species (*E. fuscocapillus* and *T. muenninki*, respectively), the other mole voles and spiny rats, and the creeping vole, have all lost an independently segregating Y chromosome.

It is hard to envision a role for either natural selection or sexually antagonistic selection in the fixation of any of these variant systems. The transfer of Y chromosome genes to the shared genome must always precede loss of the entire chromosome, so an initial benefit to males seems unlikely. Meanwhile, females are exposed to the outcome of long-term evolution in a male developmental environment without the proposed compensatory effects of a Y-neutralizing X*

chromosome. In the Transcaucasian mole vole (*E. lutescens*), the four Y-derived genes detected to date appear to have male-limited expression, suggesting active suppression in female genomes (Mulugeta et al. 2016). However, at least two Y-derived genes in the creeping vole are expressed in both sexes (Couger et al. 2021) and the genes and tissues evaluated in both studies are too limited to exclude the possibility of additional expression in females. Multi-tissue transcriptome data in these and other "shared Y" species will be essential to understanding the short term evolutionary response of female genomes to male-limited evolution. As to gaining insight into the processes that moved these systems from their ancestral to present day states, parameterization of mathematical models with species-specific empirical data (e.g. Saunders et al. 2022) is a promising approach.

Other avenues for future work

First, there is currently little support for sexual conflict as a primary driver of Y chromosomal transitions into the shared genome. However, many of the systems described above have increased opportunity for intralocus sexual conflict, in some cases potentiated by newly evolved asymmetries in the distribution of sex chromosomes between the sexes. For example, in all systems with oocyte-promoting X* chromosomes, the Y chromosome spends part of its time in female environments. Assuming that the effects of previously male-limited genes on female fertility are neutral at best, does relaxed selection in females increase the frequency of Y haplotypes that reduce male fitness? Population genetic tests for Y-linked differentiation between XY males and X*Y females would be a logical first step to addressing this question. Species with among population differences in the frequency of X* (e.g. *M. minutoides*, Veyrunes et al. 2013) provide natural experiments in which the effect of females on Y chromosome evolution could be calibrated to the frequency of X*.

Second, the X-linked mutations that promote ovarian development in Y-bearing individuals have yet to be identified in any species. Just as in the origin of a new sex-determining locus on an autosome, local suppression of recombination between X* and the original X could facilitate the accumulation of female-benefit alleles on X*. Intriguingly, the X* chromosomes of *M. minutoides* and *M. schisticolor* each carry a cytologically visible deletion and inversion relative to the ancestral X (Liu et al. 2001; Veyrunes et al. 2010). The inverted intervals likely hold the key to the oocyte-promoting effect of X* chromosomes in these species.

Master switch or tuning knobs?

Loss of *Sry*, the transcription factor that initiates testis development in most XY individuals, is convincingly demonstrated in just six species in our dataset: the mandarin vole (*Lasiopodomys mandarinus*), two species of Ryūkyū spiny rat (*Tokudaia tokushimensis* and *T. osimensis*), and three species of mole vole (*E. tancrei*, *E. talpinus*, and *E. lutescens*). In all three genera, long-term efforts to find an alternative "master switch" for testis development eliminated several genes as probable candidates but found none that were (Just et al. 2007; Wang et al. 2009; Chen et al. 2011; Kuriowa et al. 2011). However, a recent landmark study in *T. osimensis* identified a small (17 kb) male-limited duplication on the same autosome as *Sox9*, the direct target of *Sry* in the testis-determining cascade (Terao et al. 2022). The duplicated

interval contains a *cis*-regulatory element that, when bound by a yet to be identified transcription factor, upregulates *Sox9* (Terao et al. 2022). Whereas there is more work to be done to map the complete molecular pathway of testis development in *T. osimensis*, the study is groundbreaking in identifying a new sex-determining locus, and therefore a newly arisen sex chromosome, in a mammal.

We will probably never know whether selection to limit sexually antagonistic alleles to the sex they benefit drove recombination suppression around *Sry* on the proto-Y chromosome of therian mammals. But the case of *T. osimensis* provides an opportunity to test the classic model for sex chromosome evolution (e.g. Fisher 1931; Charlesworth 1991) in real time. Given the increasing feasibility of producing chromosome-level genome assemblies with long read sequencing, we anticipate that discoveries of sex-limited intervals in other mammals with variant sex chromosomes will be forthcoming. The other *Sry*-less spiny rat, *T. tokushimensis*, is a particularly strong candidate. The fact that the new activator of testis development in *T. osimensis* is a *cis*-regulatory element is yet another illustration of the power of small regulatory changes to shift evolutionary trajectories (e.g. Wray 2007; Wittkopp and Kalay 2012), in this case facilitating the loss of an entire chromosome.

Does *nothing* in sex chromosome evolution make sense except in light of conflict?

As evidence for sexual antagonism as the primary driver of suppressed recombination on sex chromosomes remains scarce (Wright et al. 2016), non-conflict hypotheses as to why sex chromosomes evolve have received increased attention. Neutral processes, such as drift, neutral divergence (Ironsides 2010; Ponnikas et al. 2018; Jeffries et al. 2021), and heterozygote advantage (Ponnikas et al. 2018; Jay et al. 2022), have been proposed as avenues by which rearrangements capture sex-determining alleles and become fixed in a population. Sex-specific selection, specifically where ecological factors act to influence sex-limited traits, can impact sex chromosome evolution (Meisel 2022). Local adaptation can also shape what alleles get fixed in a population by favoring linkage through suppressed recombination (Guerrero and Kirkpatrick 2014; Meisel 2022). Recently, a non-conflict model driven by regulation of gene expression was developed, in which degeneration and dosage compensation coevolve, and proto-sex chromosomes diverge, shortly after the initial inversion event that captures a sex-determining allele (Lenormand et al. 2020; Lenormand and Roze 2022). Subsequent sexually antagonistic effects result from dosage compensation required by the heterogametic sex to regulate gene expression and not a sex-specific optimum as is invoked by the sexual conflict model of sex chromosome evolution.

The stage at which dosage compensation evolves is different between the contemporary sexual conflict model (Wright et al. 2016) and the regulatory divergence model of sex chromosome evolution (Lenormand et al. 2020; Lenormand and Roze 2022). In a sexual conflict framework, dosage compensation occurs after recombination has been suppressed and as a consequence of Y (or W) genes that have degenerated because of the lack of recombination between non-homologous sex chromosomes (Charlesworth 1978; Disteche 2012). In contrast, dosage compensation is the cause of suppressed recombination in the regulatory divergence model as regulatory

regions continually evolve to balance the expression of Y- and X-linked alleles and maladaptive recombinants are selected against. Examining variant sex chromosome systems could provide insights into the early stages of sex chromosome evolution, particularly to determine whether or not dosage compensation plays a primary role in suppressing recombination between proto-sex chromosomes. In the Okinawa Island spiny rat, *T. muenninki*, the neo-X and neo-Y do not harbor any apparent chromosomal rearrangements between them, yet there is suppressed recombination (Murata et al. 2015, 2016a). The lack of rearrangements could provide key insights into how regulatory evolution, particularly dosage compensation, could maintain suppressed recombination between the diverging sex chromosomes. In *T. osimensis*, a new autosomal sex-determining locus is exhibiting signs of sex-specific regulatory divergence (Terao et al. 2022). Given that cytogenetics shows that the autosome harboring the sex-specific region has yet to degenerate in the male-limited interval compared to its autosomal homolog (Koyabashi et al. 2007, 2008; Nakamura et al. 2007), it could be fruitful to compare levels of gene expression between this male-limited interval and its autosomal homolog. Reduced expression on the male-specific interval in the absence of degeneration would provide preliminary evidence for the regulatory divergence model.

More broadly, the non-conflict regulatory evolution model predicts dosage compensation should evolve concurrently with low levels of degeneration in early stages of sex chromosome evolution (Muyle et al. 2022). While studies that examine both regulatory evolution and coding sequence degeneration in young sex chromosomes are currently lacking, there is evidence that gene-silencing can facilitate Y degeneration in *Drosophila* (Zhou and Bachtrog 2012) and that Y degeneration is a progressive process in some *Rumex* species with young sex chromosomes (Beaudry et al. 2017). Much of our understanding about the role of Y degeneration and dosage compensation in eutherian sex chromosomes comes from ancient systems (Charlesworth 1996; Disteche 2012), but focusing on the regulatory processes in variant eutherian sex chromosome systems provides the opportunity to observe a more recent slice of evolutionary time. Even with the opportunity to study sex chromosomes at early stages, it can be difficult to come to a single conclusion (e.g. Charlesworth et al. 2023; Fong et al. 2023). We look forward to seeing what the large number of variant sex chromosomes in mammals may add to our understanding of sex chromosome evolution.

Conclusions

Here, we emphasize the role of genomic and sexual conflict in the evolution of variant sex chromosome systems, with meiotic drive and sexual antagonism acting as the primary forces underlying the emergence and fixation of variants. Mammalian sex chromosomes and sex-determining mechanisms clearly have the potential to vary dramatically, and the true extent of that variation is severely understudied outside of select taxa (e.g. Steinberg et al. 2014; Romanenko et al. 2020; Saunders et al. 2022). Several sex chromosome variants are population specific, and further efforts to cytologically describe mammal species are necessary lest we risk missing variation assumed to be absent. Because the majority of variant systems we cataloged are characterized at the cytological level only, it is entirely possible that genomic evaluation of less-studied

systems will reveal sex-linked variation that was invisible to cytology. Indeed, the advent of long read genomics offers new opportunities to detect signs of conflict in centromeres and repetitive elements, and even to reveal new sex-determining mechanisms (e.g. Peichel et al. 2020; Couger et al. 2021). We have highlighted systems that would be ideal for collaborative work between cytologists, genomicists, and theoreticians to unpack the evolution of sex chromosomes. Finally, having shown the extent to which norms and “rules” around mammalian sex chromosomes are bent and broken, we encourage consideration of more precise and inclusive language in describing these systems.

Supplementary material

Supplementary material is available at *Journal of Heredity* online.

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Author Contributions

Jonathan Hughes (Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Validation, Visualization, Writing – original draft, Writing – review & editing), German Lagunas-Robles (Conceptualization, Data curation, Investigation, Writing – original draft, Writing – review & editing), and Polly Campbell (Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Supervision, Visualization, Writing – original draft, Writing – review & editing)

Data Availability

All supporting data and code are available on GitHub (https://github.com/jjh359/2023_conflict_review) and will be preserved on Dryad.

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