



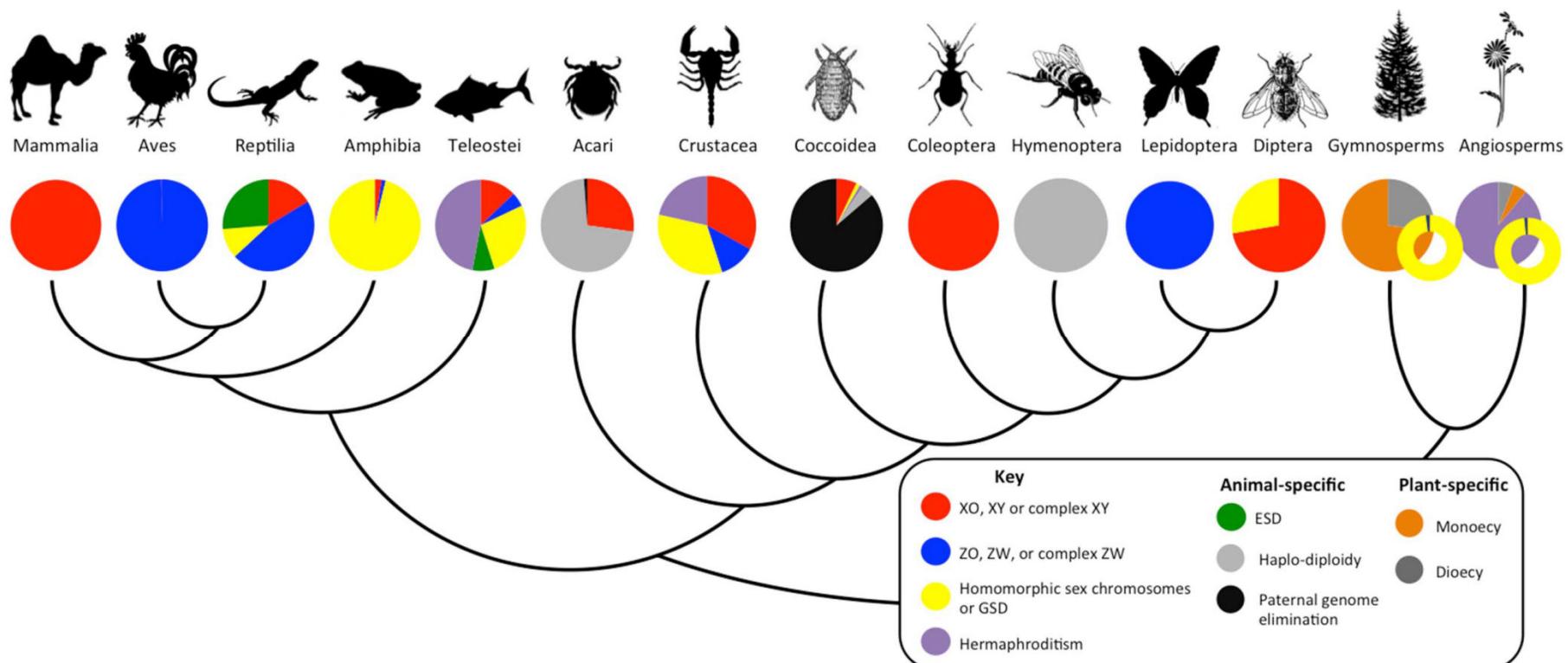
**Детерминация пола у
млекопитающих без Y хромосомы:
загадка слепушонок рода *Ellobius***

Ирина Баклушинская

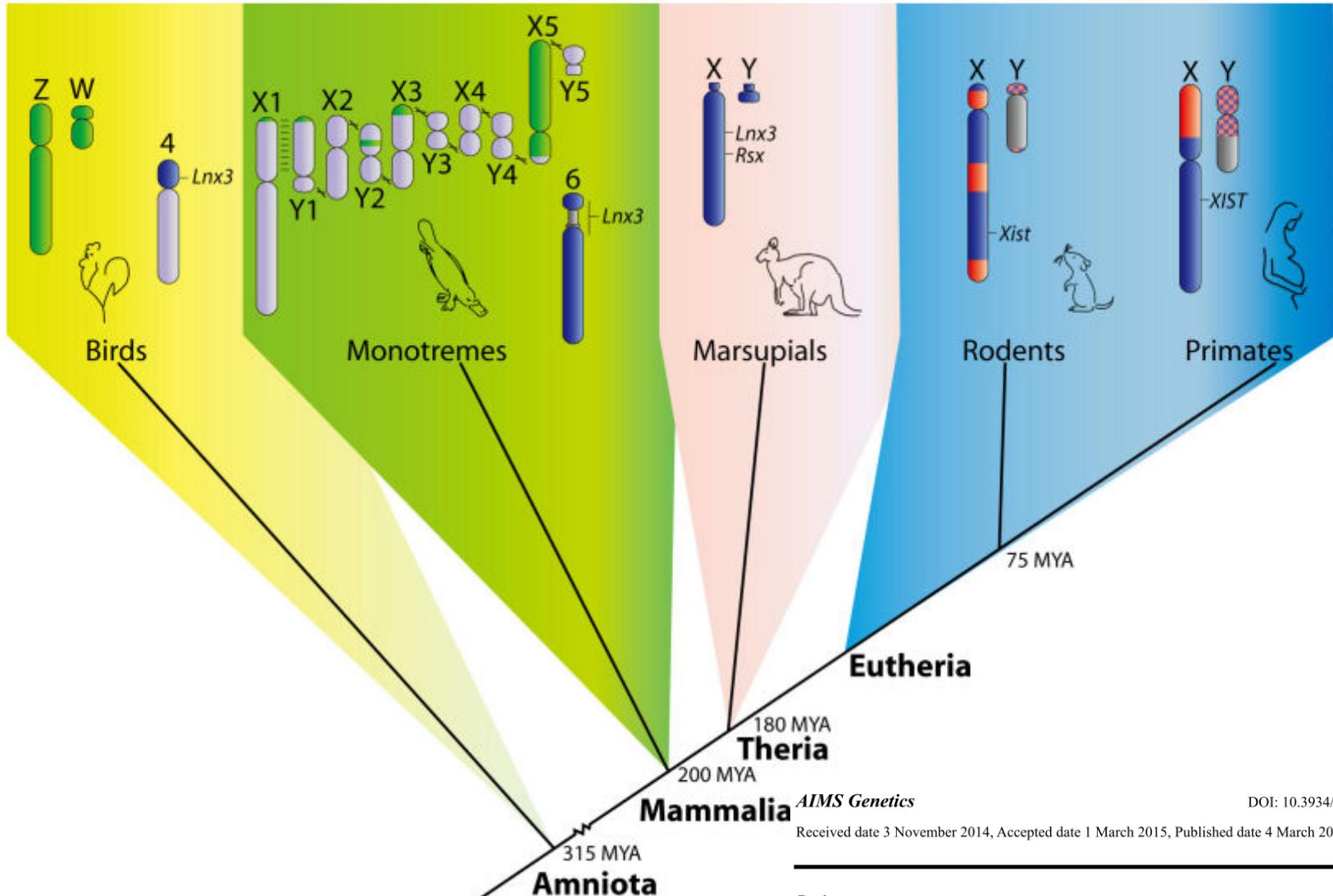
Essay

Sex Determination: Why So Many Ways of Doing It?

Doris Bachtrog^{1*}, Judith E. Mank², Catherine L. Peichel³, Mark Kirkpatrick⁴, Sarah P. Otto⁵,
Tia-Lynn Ashman⁶, Matthew W. Hahn⁷, Jun Kitano⁸, Itay Mayrose⁹, Ray Ming¹⁰, Nicolas Perrin¹¹,
Laura Ross¹², Nicole Valenzuela¹³, Jana C. Vamosi¹⁴, The Tree of Sex Consortium¹



Половые хромосомы млекопитающих



Received date 3 November 2014, Accepted date 1 March 2015, Published date 4 March 2015

DOI: 10.3934/genet.2015.2.110

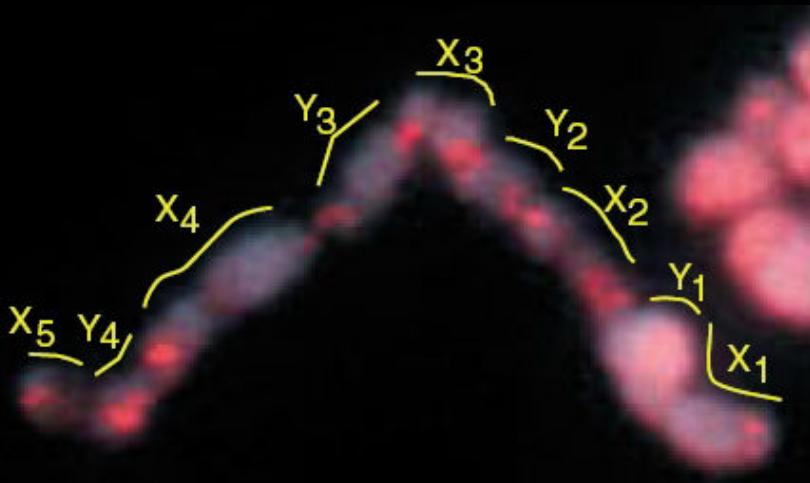
Review

Imprinted X chromosome inactivation: evolution of mechanisms in distantly related mammals

Shafagh A. Waters * and Paul D. Waters



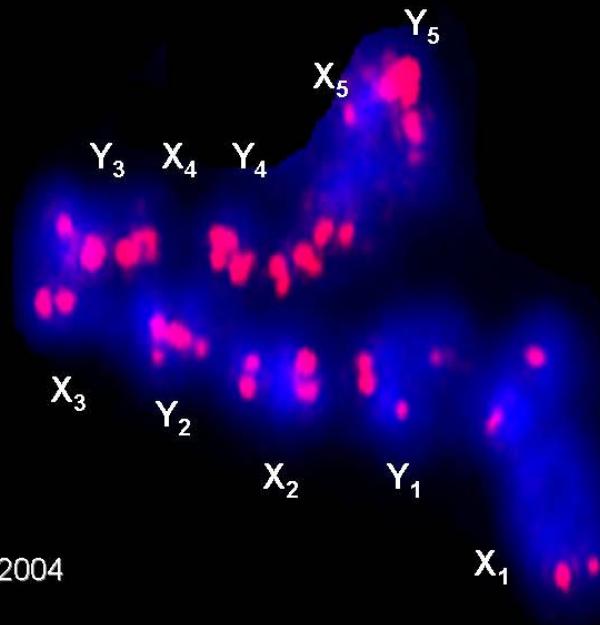
Echidna sex chromosomes



Rens et al., 2007



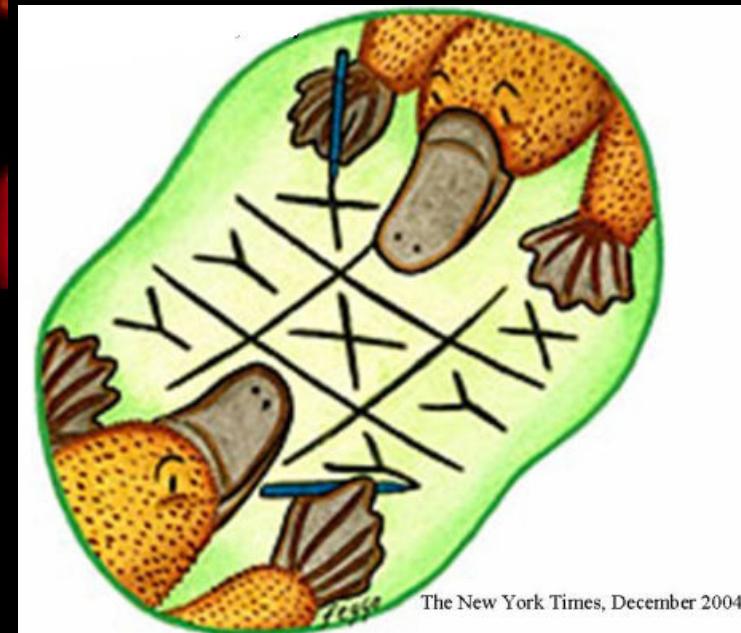
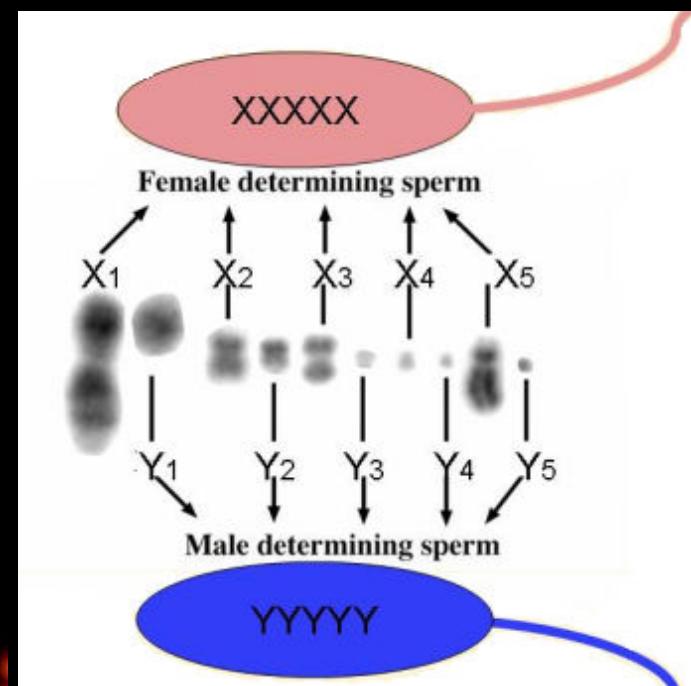
Platypus sex chromosomes - 5X + 5Y



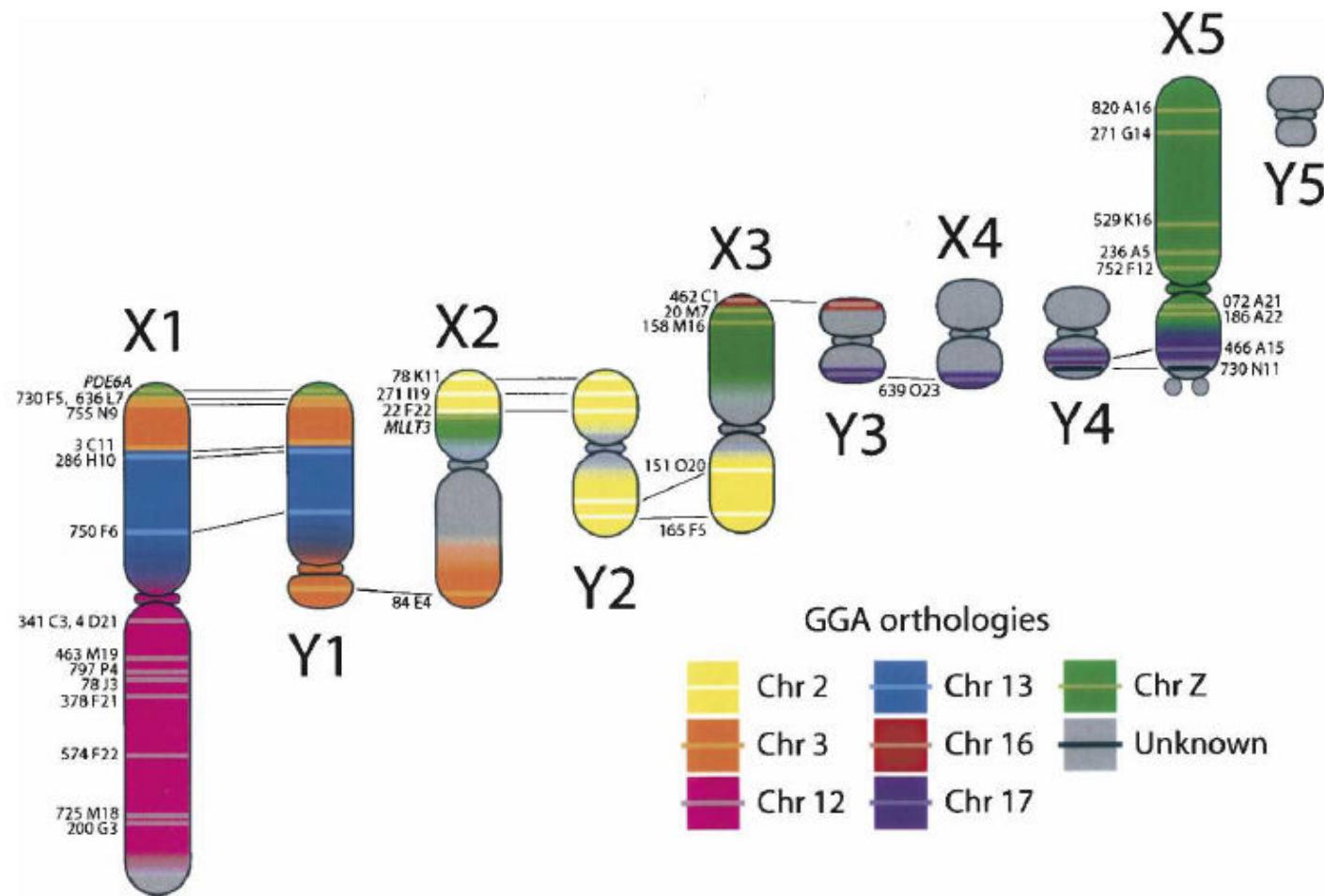
Grützner et al 2004

Половые хромосомы утконоса в мейозе

Platypus male meiosis



Структура половых хромосом утконоса



Гомология с фрагментами хромосом курицы,
линии соединяют гомологичные участки псевдоаутосомных районов

Veyrunes et al., 2008



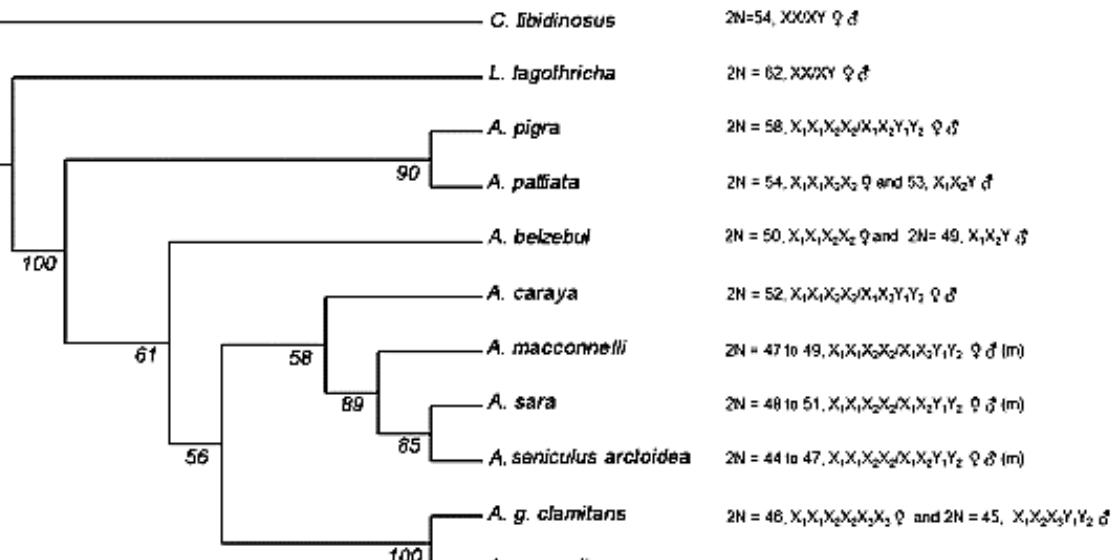
© 2011 Bart van Dorp

Alouatta guariba guariba

Multiple sex chromosome systems in howler monkeys (Platyrrhini, Alouatta)

Eliana Ruth Steinberg¹, Mariela Nieves¹, Marta Dolores Mudry¹

Species	2N	Sex Chromosome Systems
<i>A. belzebul</i>	♀50 ♂49	X ₁ X ₁ X ₂ X ₂ /X ₁ X ₂ Y
<i>A. s. seniculus</i>	♀♂47 to 49†	XY
<i>A. s. stramineus</i>	♀♂47 to 49†	X ₁ X ₁ X ₂ X ₂ /X ₁ X ₂ Y ₁ Y ₂
<i>A. s. arctoidea</i>	♀44 ♂45†	X ₁ X ₁ X ₂ X ₂ /X ₁ X ₂ Y ₁ Y ₂
<i>A. sara</i>	♀♂48 to 51†	X ₁ X ₁ X ₂ X ₂ /X ₁ X ₂ Y
	♀♂50	X ₁ X ₁ X ₂ X ₂ /X ₁ X ₂ Y ₁ Y ₂
<i>A. macconnelli</i>	♀♂47 to 49†	X ₁ X ₁ X ₂ X ₂ /X ₁ X ₂ Y ₁ Y ₂
<i>A. caraya</i>	♀♂52	XX/XY
		X ₁ X ₁ X ₂ X ₂ /X ₁ X ₂ Y ₁ Y ₂
<i>A. palliata</i>	♀♂56	XX/XY
	♀54 ♂53	X ₁ X ₁ X ₂ X ₂ /X ₁ X ₂ Y
<i>A. pigra</i>	♀♂58	X ₁ X ₁ X ₂ X ₂ /X ₁ X ₂ Y ₁ Y ₂
<i>A. guariba guariba</i>	♀50 ♂49	XX/XY
	♂49	X ₁ X ₂ Y
	♀50♂49	X ₁ X ₁ X ₂ X ₂ X ₃ / X ₁ X ₂ X ₃ Y ₁ Y ₂
<i>A. guariba clamitans</i>	♀46 ♂45	XX/XY
		X ₁ X ₁ X ₂ X ₂ /X ₁ X ₂ Y ₁ Y ₂
		X ₁ X ₁ X ₂ X ₂ X ₃ / X ₁ X ₂ X ₃ Y ₁ Y ₂
<i>A. nigerrima</i>	♀50	XX
<i>A. coibensis</i>	ND	ND



Независимое происхождение множественных половых хромосом

**sex is typically determined by
X and Y chromosomes**

myth

**sex is controlled by one
master-switch gene**

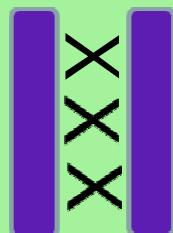
Sex chromosome differentiation

Muller, 1914
Ohno, 1967

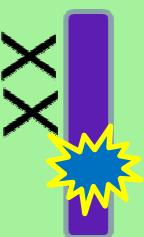
degeneration of Y

differentiation
of sex chromosomes

acquire sex
determining
locus



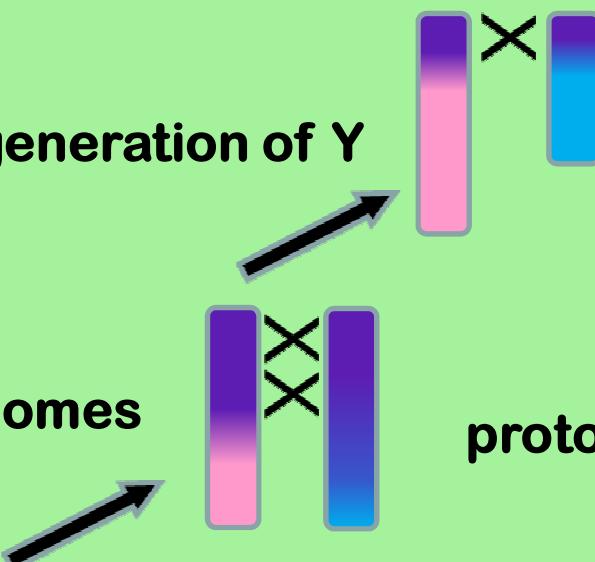
Homologous chromosomes
(autosomes)



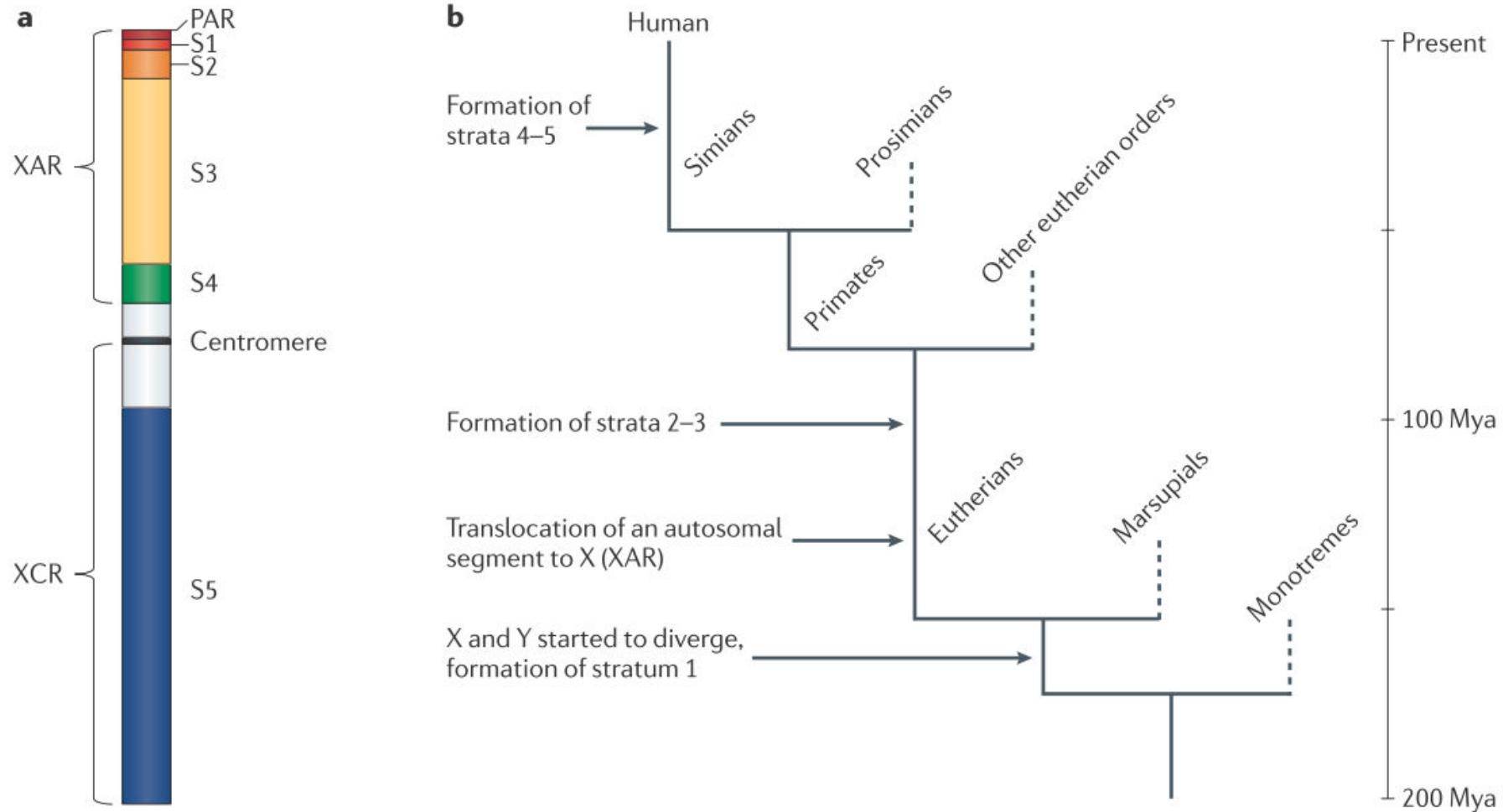
recombination suppression

Sry

sex-determining region Y



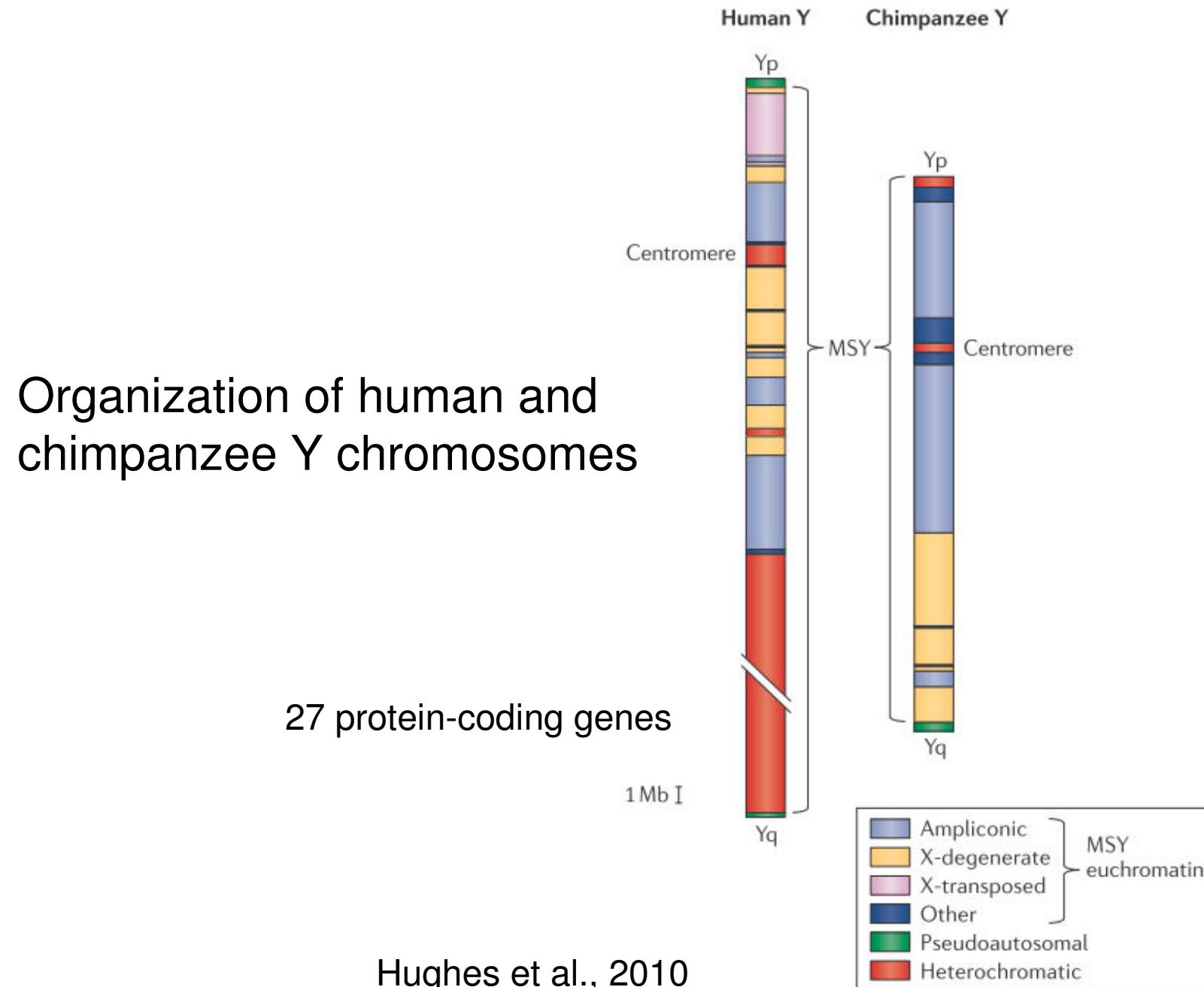
Evolutionary history of the human X chromosome



Organization of human and chimpanzee Y chromosomes

27 protein-coding genes

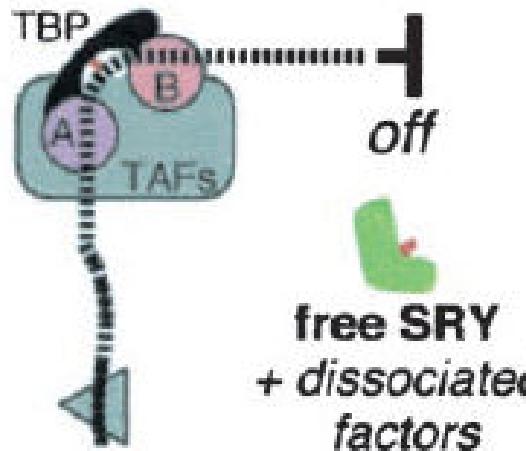
1 Mb I



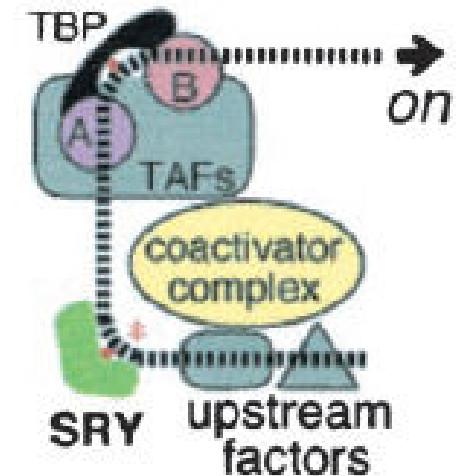
Hughes et al., 2010

SRY, Sex-determining Region on the chromosome Y

Sinclair et al., 1990, Koopman et al., 1991



SRY on
→
SRY off



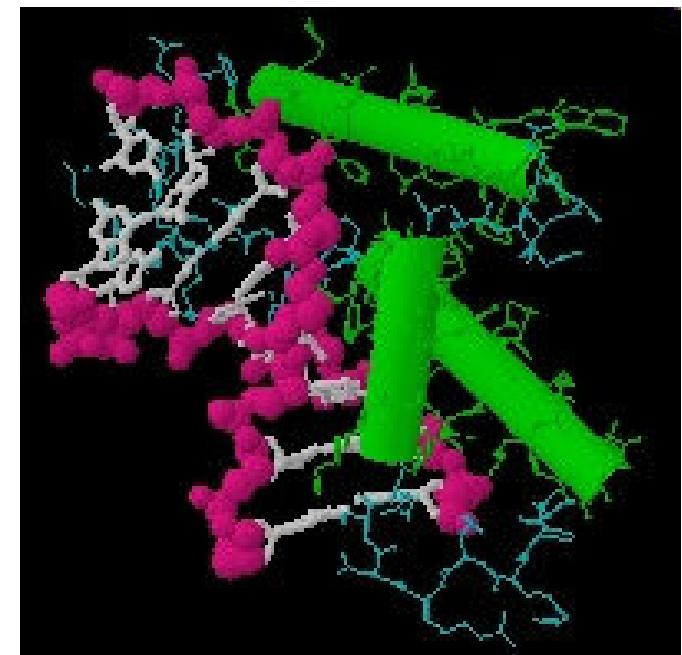
Функция *SRY* – регуляция экспрессии генов
половопределяющего каскада

справа: активация транскрипции

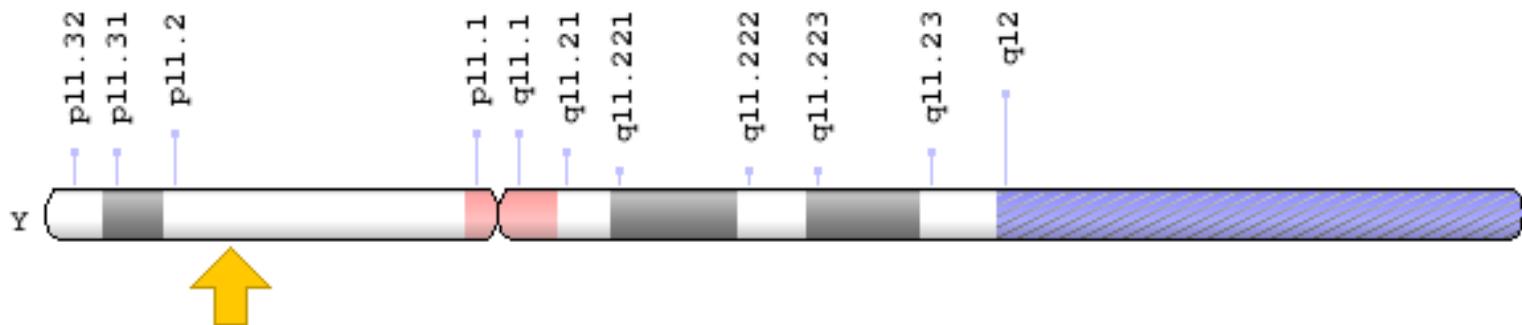
происходит при связывании продукта *SRY*
с определенным районом ДНК, *SRY*
изгибает ДНК особым образом, что
позволяет собраться комплексу активатор-
коактиватор

слева: нет связывания, не образуется
протеиновый комплекс и комплекс
активатор-коактиватор

Ukiyama et al., 2001

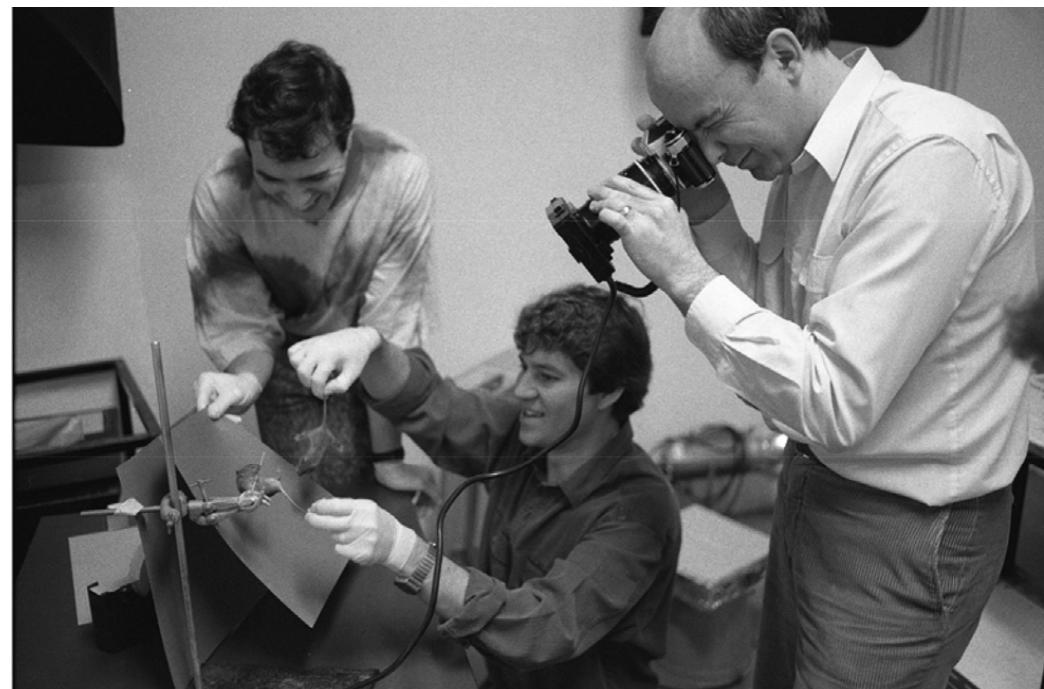


<https://ghr.nlm.nih.gov/gene/SRY#location>



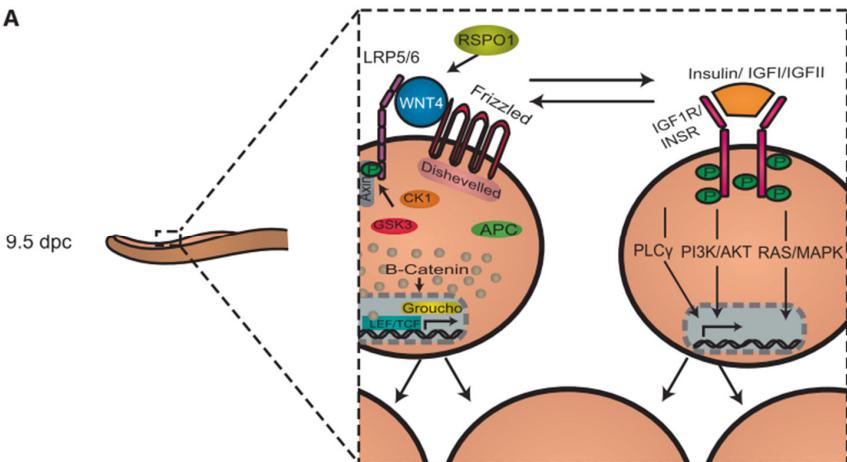
Cytogenetic Location:
Yp11.2, which is the short
(p) arm of the Y
chromosome at position
11.2

Molecular Location: base
pairs 2,786,855 to
2,787,741 on the Y
chromosome (Homo
sapiens Annotation
Release 109,
GRCh38.p12) (NCBI)



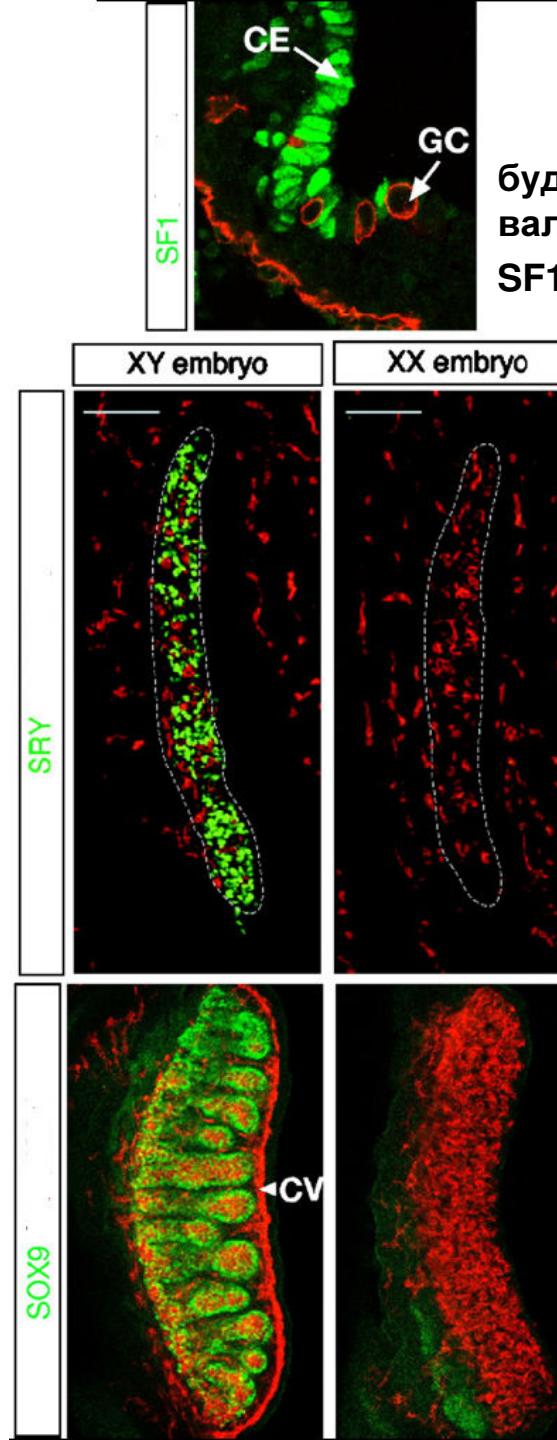
Nigel Vivian, Robin Lovell-Badge, Peter Koopman

A



Экспрессия генов каскада детерминации пола на ранних стадиях эмбрионального развития

Polanco, Koopman, 2007



10.5 dpc

будущие гонады
валик
SF1-positive cells

11.5 dpc

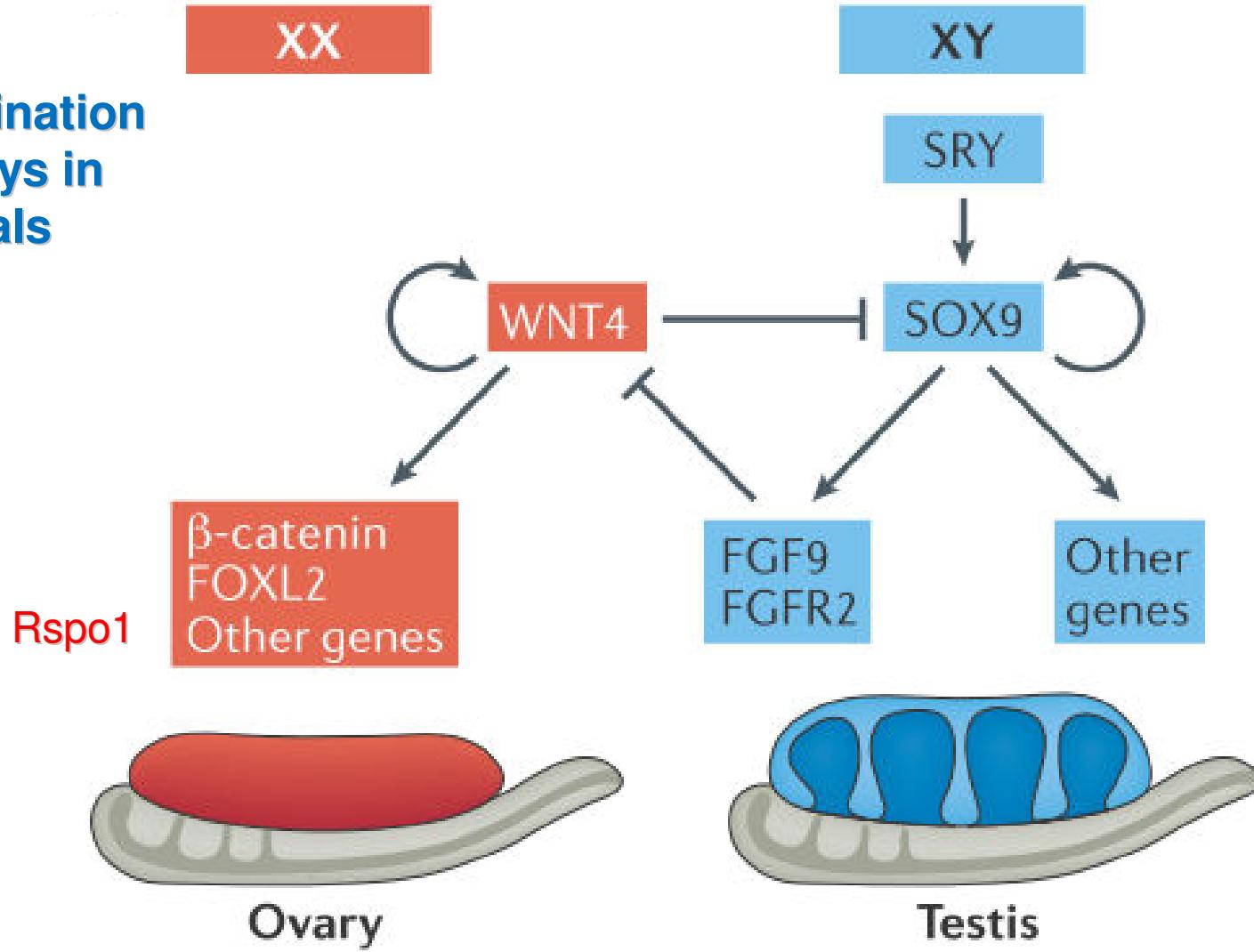
бипотенциальные гонады имеют сходную морфологию, стадия маркируется по факту миграции ППК

Gata4/Fog2 и WT1+KTS активируют экспрессию *Sry* в XY гонадах

12.5 dpc

после up-регуляции
Sox9 морфология
мужских гонад
меняется,
появляются
семенные тяжи и
целомическая
полость (CV)

sex determination pathways in mammals



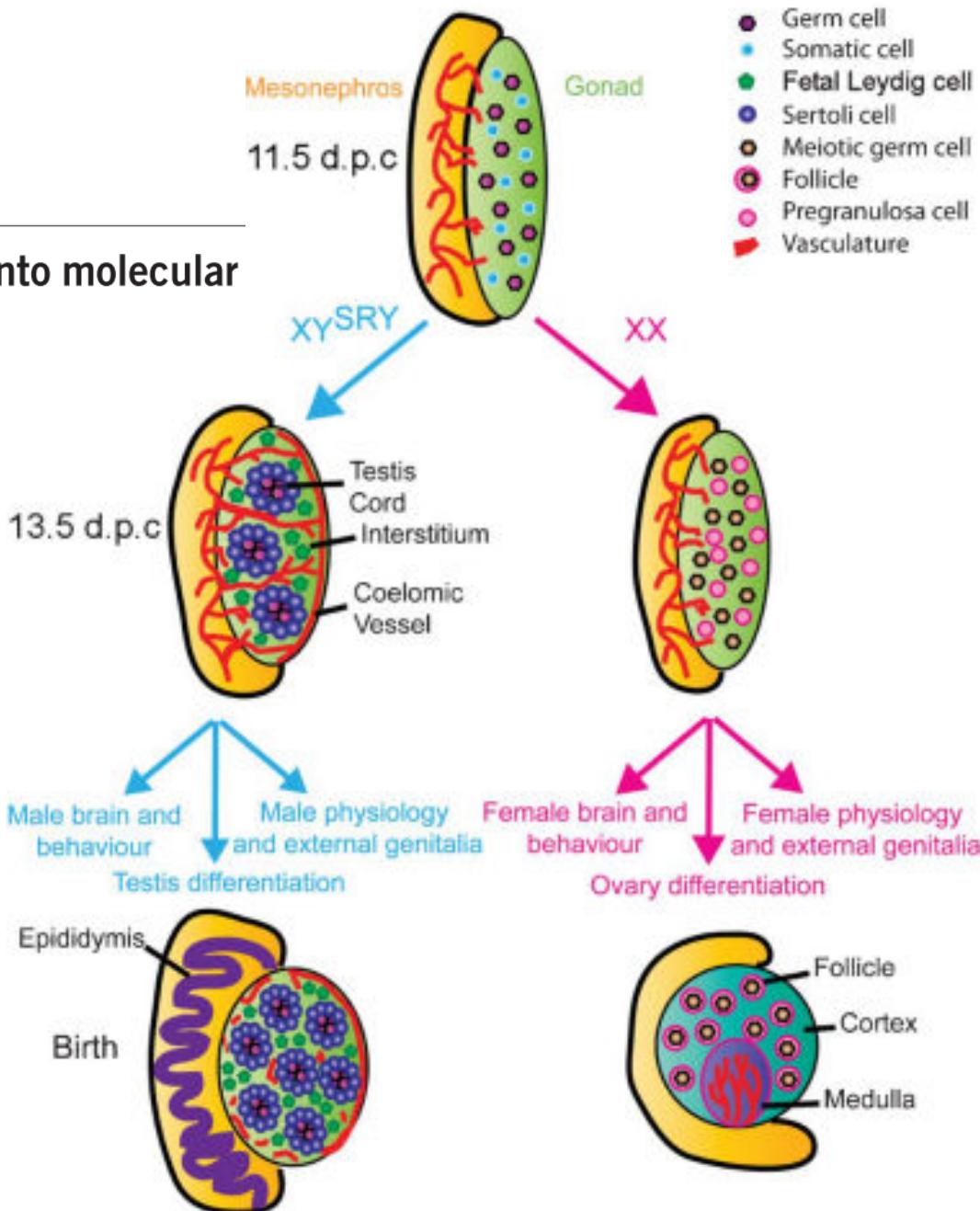
Vertebrate sex determination:
evolutionary plasticity of a
fundamental switch 2017

REVIEW

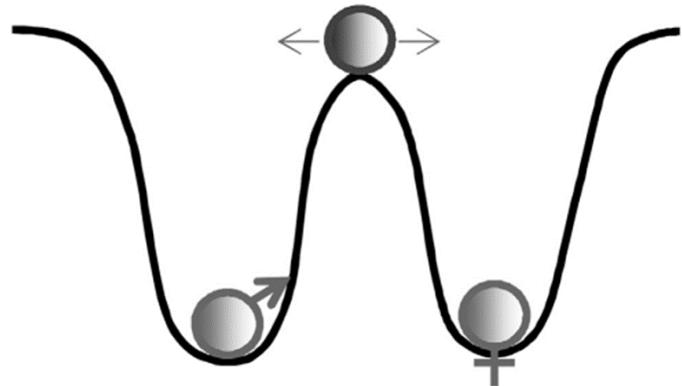
Male sex determination: insights into molecular mechanisms

Kathryn McClelland, Josephine Bowles and Peter Koopman

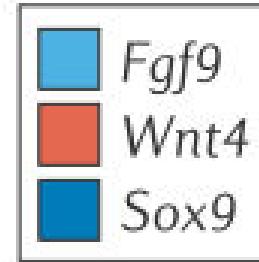
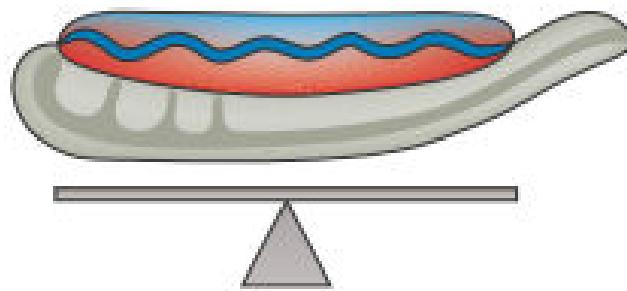
sex determination: early development



balance



Female-biased transcriptome, nearly identical in XX and XY gonads



Vertebrate sex determination:
evolutionary plasticity of a
fundamental switch

Evolution of sex determination = transcriptional evolution

DEVELOPMENTAL DYNAMICS 242:307–319, 2013

SPECIAL ISSUE REVIEWS-A PEER REVIEWED FORUM

Transcriptional Evolution Underlying Vertebrate Sexual Development

Nicole Valenzuela,* Jennifer L. Neuwald, and Robert Lierman

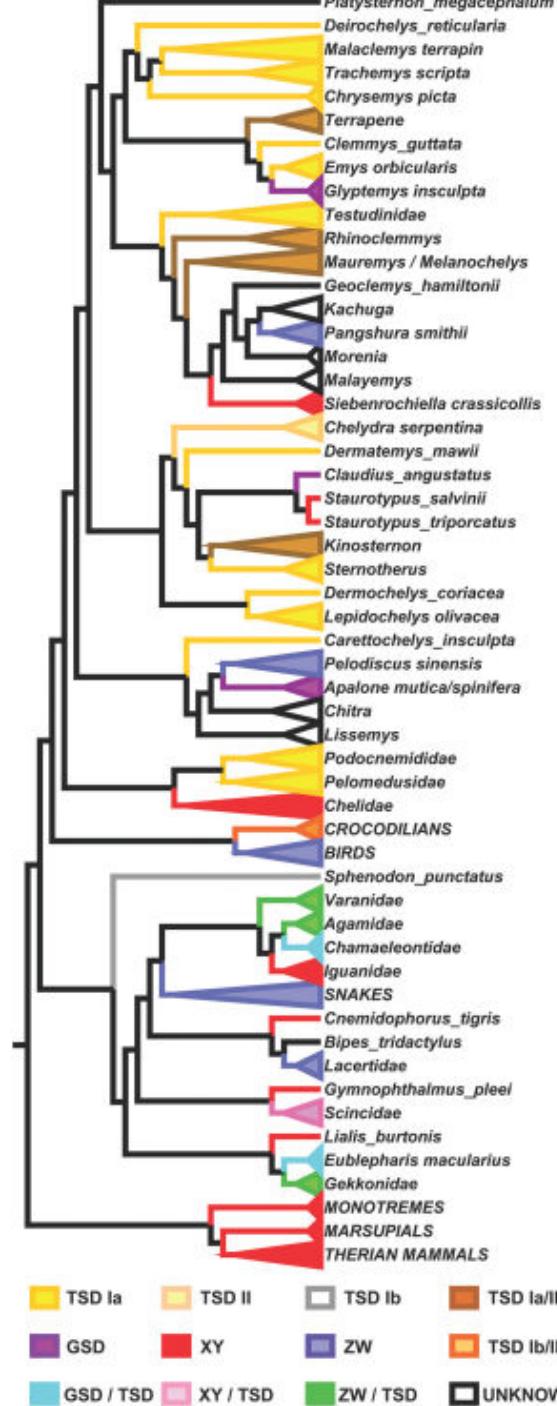
CBX2 (chromobox homolog 2)

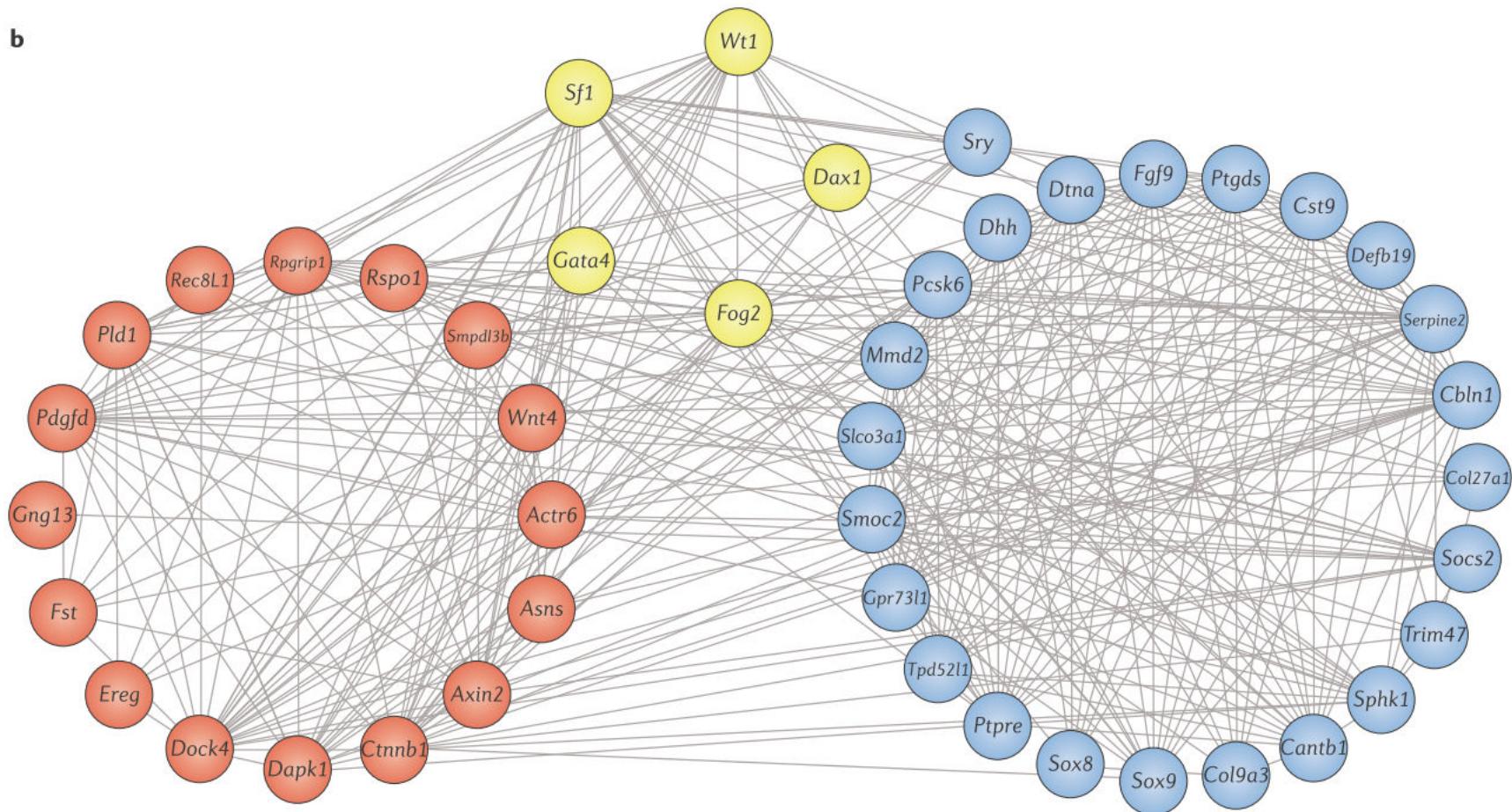
Chromatin modifacaton

upregulation of male-related genes SRY, SOX9, SF1
negatively regulates female-related FOXL2

Sox9 male-biased and Aromatase female-biased
expression appear ancestral and virtually conserved
throughout vertebrates

epigenetics
small RNA



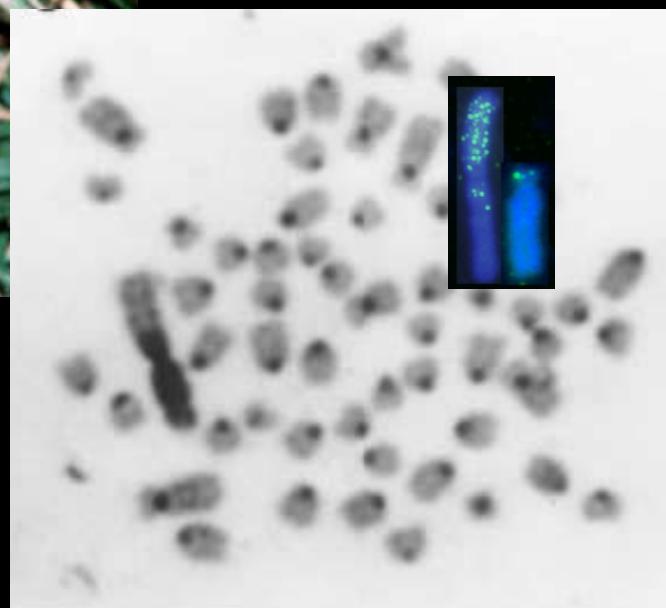
b

Vertebrate sex determination: evolutionary plasticity of a fundamental switch



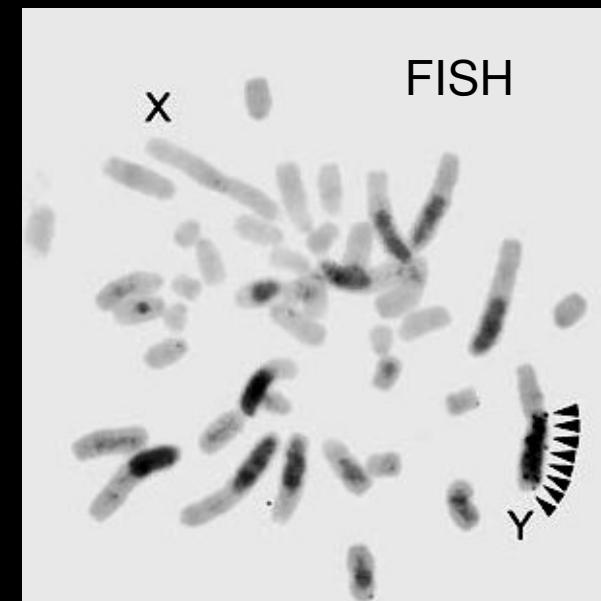
Исключения из правил

Слишком много Sry



Microtus cabrerae
гигантские половые хромосомы
у самцов и самок присутствуют несколько
копий *Sry* (псевдогена) + фрагменты L1 и LTR
ретроэлементов на X и Y

Marchal et al., 2008



Tokudaia muenninki
24 копии *Sry* (псевдогена)
только на Y
Murata et al., 2010

нет Y нет *Sry*



Ellobius lutescens

Ellobius lutescens $2n=17$ X0 ♀, ♂
E. tancrei $2n=54-30$ NF=56 XX ♀, ♂
E. talpinus $2n=54$, NF=54 XX ♀, ♂

Just et al. Nat. Genet., 1995



Tokudaia osimensis

Tokudaia osimensis $2n=25$, X0 ♀, ♂
T. tokunoshimensis $2n=45$, X0 ♀, ♂



Fragment of Y was translocated to the X
Arakawa et al., 2002; Kuroiwa et al., 2010

Rodentia
Cricetidae
Arvicolinae



Ellobius tancrei

genus ***Ellobius***

subgenus ***Bramus***

Ellobius fuscocapillus

2n=36, XY ♂ XX ♀

Ellobius lutescens

2n=17, XO ♀, ♂



Ellobius lutescens

subgenus ***Ellobius***

Ellobius talpinus

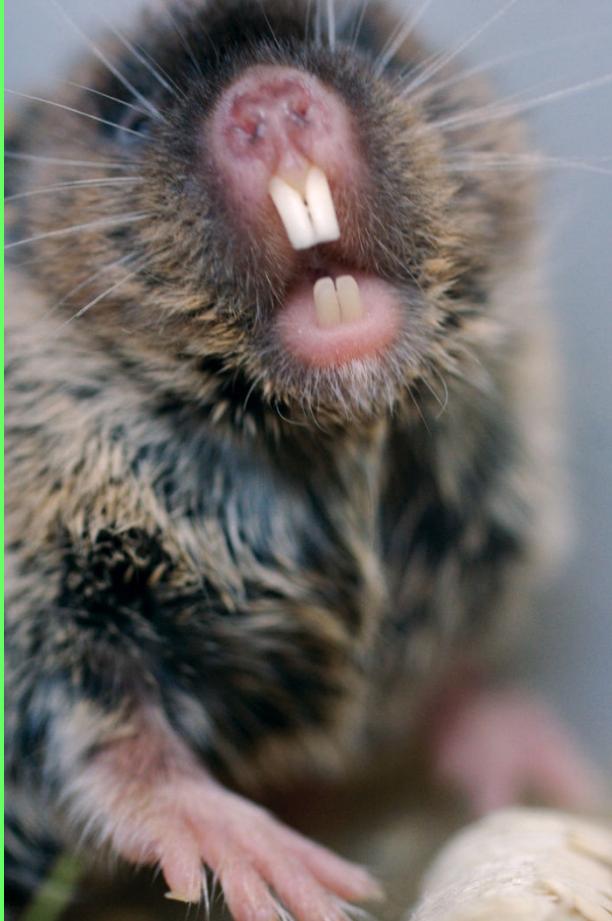
2n=54, NF=54, XX ♀, ♂

Ellobius tancrei

2n=54-30, NF=56, XX ♀, ♂

Ellobius alaicus

2n=52-48, NF=56, XX ♀, ♂



Subterranean Arvicolinae

Ellobius lutescens



Ellobius tancrei

конвергенция



Fukomys anselli



Ellobius lutescens

Ellobius tancrei





Фото С. Черенкова www.rusbiophoto.com

резцы

ARKIVE
www.arkive.org



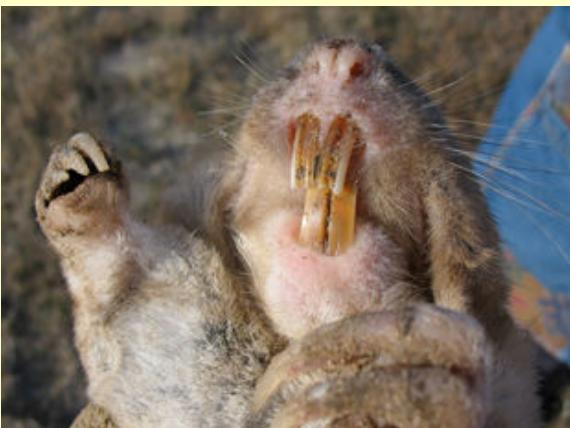
Fukomys anselli



Tachyoryctes macrocephalus



туко-туко *Ctenomys*



цокор Geomys



Spalacopus

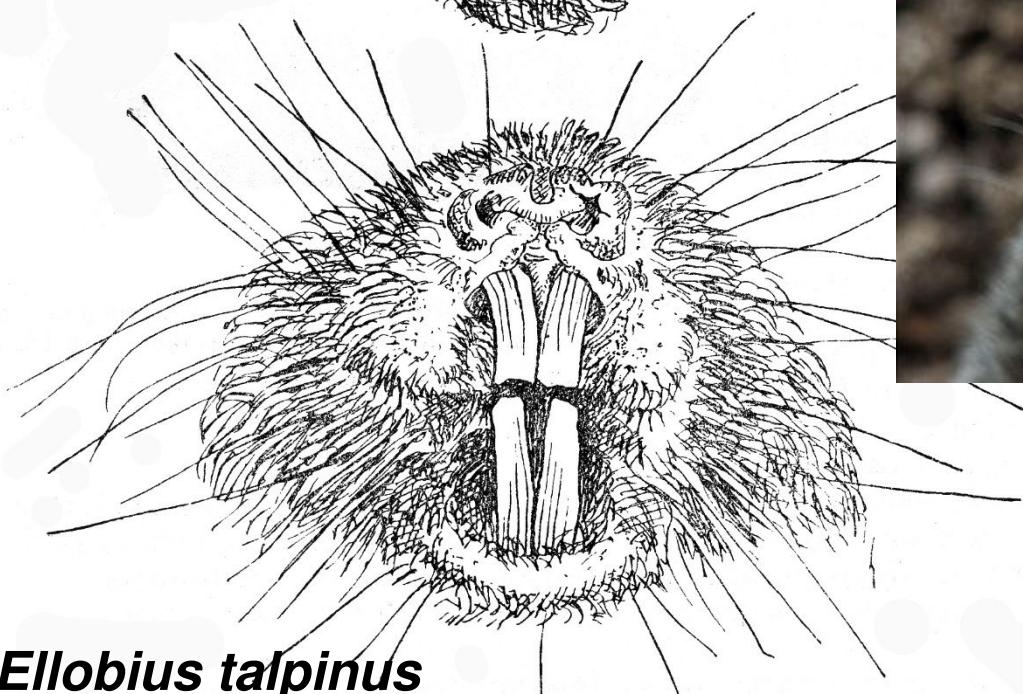


голый землекоп
Heterocephalus glaber

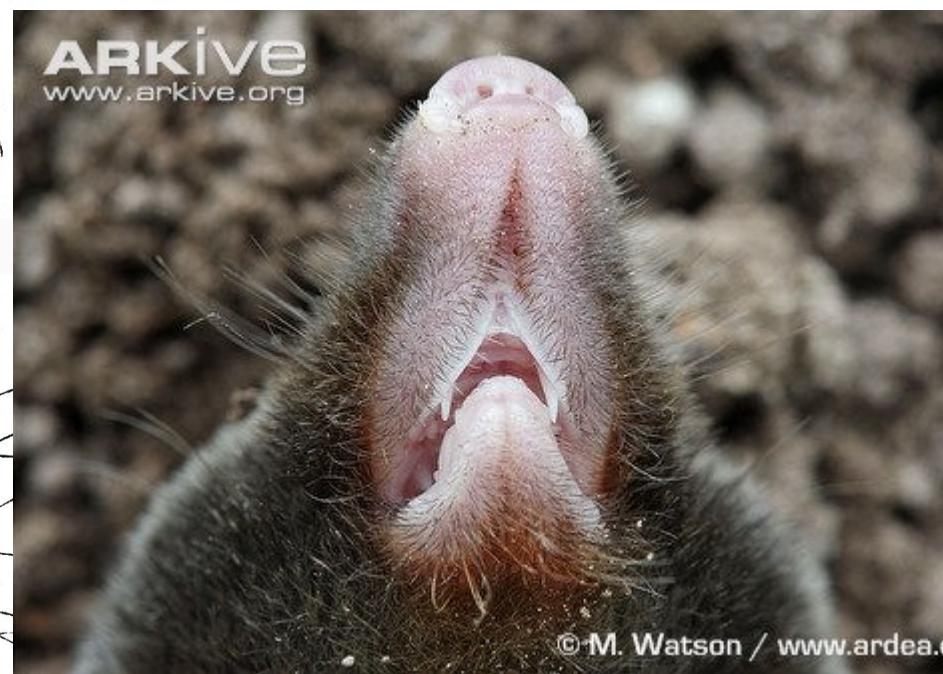
С.И. Огнев



*Prometheomys
schaposchnikovi*



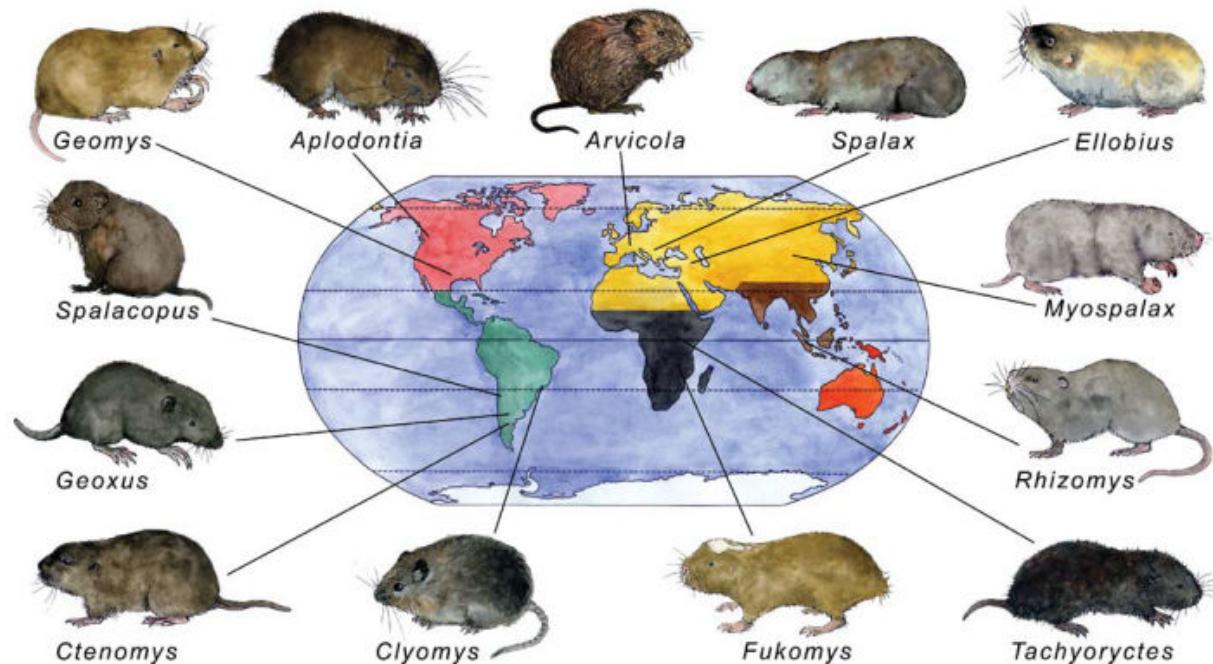
Ellobius talpinus



© M. Watson / www.ardea.co.uk

крот

Euarchontoglires



250 современных видов грызунов
38 родов, 6 семейств

Suborder	Family Subfamily	Genus
Hystricognatha	Bathyergidae Bathyerginae	<i>Bathyergus</i> <i>Cryptomys</i> <i>Fukomys</i> <i>Georychus</i> <i>Heliophobius</i> <i>Heterocephalus</i>
	Heterocephalinae Octodontidae Octodontinae	<i>Ctenomys</i> <i>Pithanotomys</i> <i>Spalacopus</i>
	Echimyidae Heteropsomyinae	<i>Carterodon</i> <i>Clyomys</i> <i>Euryzygomatomys</i>
Myomorpha	Muridae Arvicolinae	<i>Arvicola</i> <i>Ellobius</i> <i>Hyperacrius</i> <i>Microtus</i> <i>Prometheomys</i> <i>Aepeomys</i> <i>Akodon</i> <i>Blarinomys</i> <i>Chelemys</i> <i>Euneomys</i> <i>Geoxus</i> <i>Kunisia</i> <i>Notiomys</i> <i>Eospalax</i> <i>Myospalax</i> <i>Nannospalax</i> <i>Spalax</i> <i>Cannomys</i> <i>Rhizomys</i> <i>Tachyoryctes</i>
	Sigmodontinae	
	Myospalacinae	
	Spalacinae	
	Rhizomyinae	
	Geomyidae Geomyinae	<i>Geomys</i> <i>Orthogeomys</i> <i>Pappogeomys</i> <i>Thomomys</i> <i>Zygogeomys</i> <i>Aplodontia</i>
Sciuroomorpha	Aplodontidae	

Box 1

Classification of social and breeding systems encountered in subterranean rodents

Solitary

Burrow system is occupied by a single adult animal, mother cares for her offspring alone, young disperse after weaning.

Social

Burrow system is occupied by at least two adult animals.

**Colonial (communal),
polygynous,
± cooperatively breeding**

Typically, more than one female breeds in a colony simultaneously; nest-mates may or may not cooperate.

**Familial,
monogynous
(monogamous),
cooperatively breeding**

Typically, only one female breeds. Dispersal of the offspring is delayed; as long as they live in the parental nest they do not reproduce; they help in foraging, extending, maintaining and defending the burrow system and looking after younger siblings.

Eusocial

Most of the offspring never disperse and are lifelong nonbreeding helpers.

ЭВОЛЮЦИЯ ЭУСОЦИАЛЬНОСТИ	
цена	ограничение размножения, инбридинг
плюсы	устойчивые пищевые ресурсы, защита от хищников
ПОДДЕРЖАНИЕ ЭУСОЦИАЛЬНОСТИ	
цена	ограничение размножения (1% - голые землекопы, 8% - дамарский землекоп)
плюсы	непрямые последствия: kin selection, устойчивые пищевые ресурсы, защита от хищников



Contents lists available at ScienceDirect

Mammalian Biology

journal homepage: www.elsevier.com/locate/mambio

Original Investigation

Evolutionary association between subterranean lifestyle and female sociality in rodents

Antonina V. Smorkatcheva^{a,*}, Vladimir A. Lukhtanov^b

2013

J Ethol
DOI 10.1007/s10164-013-0392-y

ARTICLE

Delayed dispersal in the Zaisan mole vole (*Ellobius tancrei*): helping or extended parental investment?

2014

A. V. Smorkatcheva · A. R. Kumaitova



Canadian Journal of Zoology
Revue canadienne de zoologie

Make haste slowly: reproduction in the Zaisan mole-vole, *Ellobius tancrei*

A. V. Smorkatcheva, A. R. Kumaitova, K. V. Kuprina

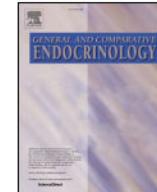
2015



Contents lists available at ScienceDirect

General and Comparative Endocrinology

journal homepage: www.elsevier.com/locate/ygcen



Fathers and sons: Physiological stress in male Zaisan mole voles, *Ellobius tancrei*



Antonina V. Smorkatcheva^{a,*}, Ekaterina Yu. Kondratyuk^b, Ivan A. Polikarpov^a

Mammalian Biology 88 (2018) 144–150



Contents lists available at ScienceDirect

Mammalian Biology

journal homepage: www.elsevier.com/locate/mambio



Original investigation

Does sire replacement trigger plural reproduction in matrifilial groups of a singular breeder, *Ellobius tancrei*?



Antonina V. Smorkatcheva*, Kristina V. Kuprina

RESEARCH ARTICLE

2018

Reproduction and mortality rates in ecologically distinct species of murid rodents

Eugene Novikov  · Ekaterina Kondratuk · Tatiana Titova · Pavel Zadubrovsky ·
Inna Zadubrovskaya · Mikhail Potapov · Olga Potapova · Ludmila Proskurnyak ·
Galina Nazarova

Biogerontology
DOI 10.1007/s10522-017-9723-7

2017

RESEARCH ARTICLE

Reproduction, ageing, and longevity in two species of laboratory rodents with different life histories

Eugene Novikov  · I. Zadubrovskaya · P. Zadubrovskiy · T. Titova

УСПЕХИ СОВРЕМЕННОЙ БИОЛОГИИ, 2013, том 133, № 1, с. 98–108

УДК 599.32

ЭКОЛОГО-ЭВОЛЮЦИОННЫЕ ПРЕДПОСЫЛКИ АНОМАЛЬНОЙ ПРОДОЛЖИТЕЛЬНОСТИ ЖИЗНИ У ПОДЗЕМНЫХ ГРЫЗУНОВ

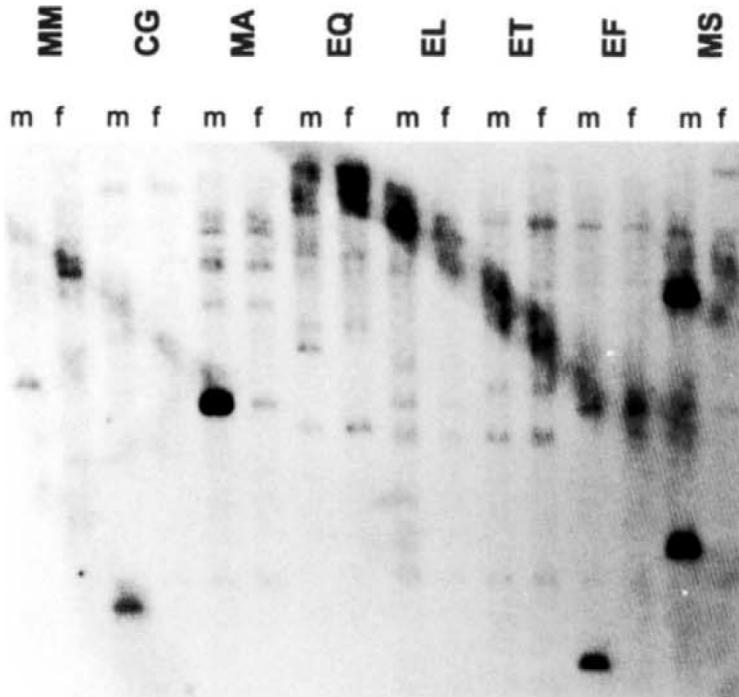
© 2013 г. Е.А. Новиков¹, Г. Бурда^{2,3}







Absence of Sry in species of the vole *Ellobius*



Walter Just

Wolfgang Rau

Walther Vogel

Dept. of Medical Genetics, University of Ulm, Albert-Einstein-Allee 11, D-89081 Ulm, Germany

Mikhail Akhverdian

Institute of Zoology, National Academy of Sciences, Republic of Armenia, Sevak str.7, 375 044 Yerevan, Armenia

Karl Fredga

Dept. of Genetics, University of Uppsala, Box 7003, S-75007 Uppsala, Sweden

Jennifer A. Marshall Graves

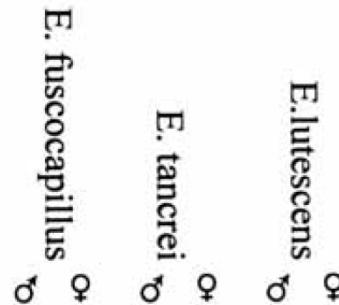
School of Genetics and Human Variation, La Trobe University, Bundoora, Victoria 3083, Australia

Elena Lyapunova

N.K. Koltsov Institute of Developmental Biology, Russian Academy of Sciences, Vavilov str. 26. 117 334 Moscow, Russia

HincII

E. lutescens and *E. tancrei* lost ZFY



Cytogenet Cell Genet 80:214-221 (1998)

Cytogenetics and Cell Genetics

Sex determination in *Ellobius lutescens*: The story of an enigma

W. Vogel, S. Jainta, W. Rau, C. Geerkens, A. Baumstark, L.-S. Correa-Cerro, C. Ebenhoch, and W. Just

Sex determination in *Ellobius lutescens*: The story of an enigma

W. Vogel, S. Jainta, W. Rau, C. Geerkens, A. Baumstark, L.-S. Correa-Cerro,
C. Ebenhoch, and W. Just

Vogel *et al.* (1998)

Если у слепушонок нет *Sry*, то,
вероятно, пол детерминируется
каким-то геном/мутантным аллелем
гена, который обычно
экспрессируется после *Sry*.

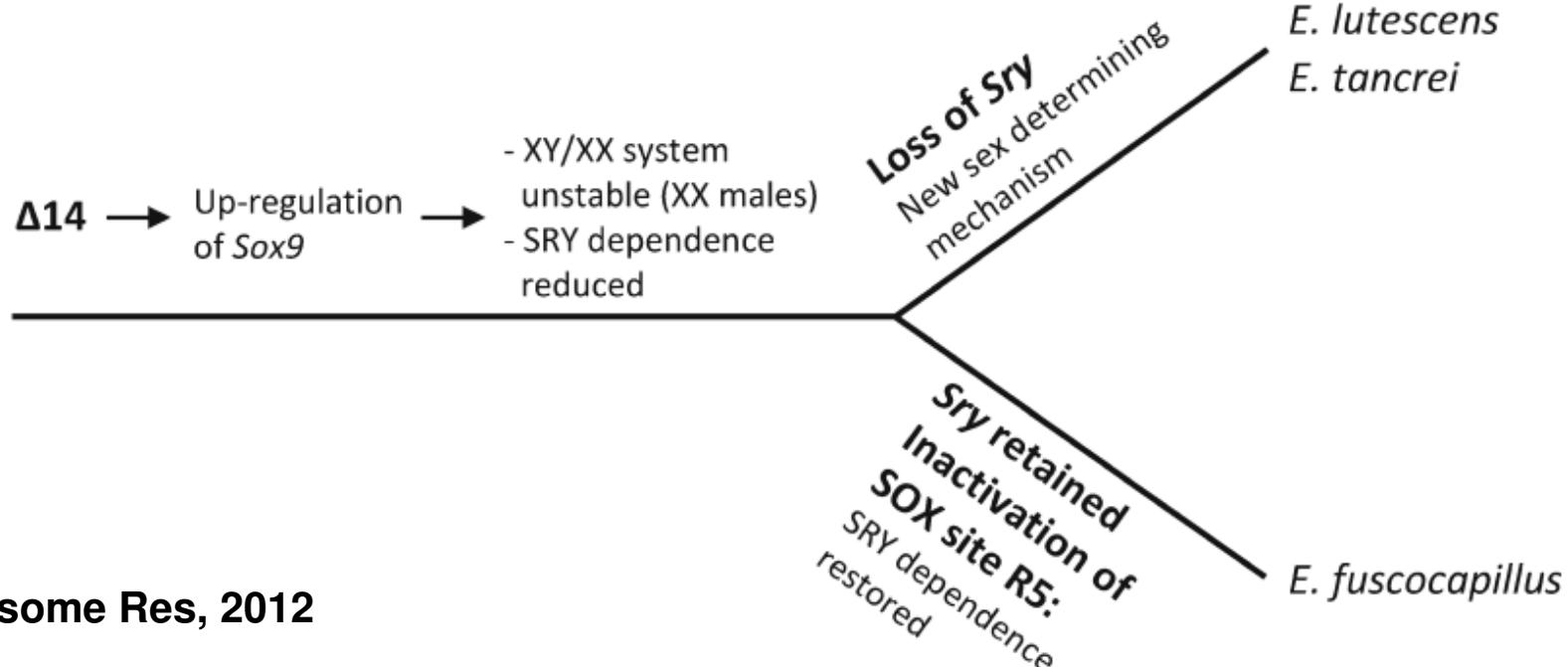


Sox9 gene regulation and the loss of the XY/XX sex-determining mechanism in the mole vole *Ellobius lutescens*

Stefan Bagheri-Fam · Rajini Sreenivasan ·
 Pascal Bernard · Kevin C. Knower ·
 Ryohei Sekido · Robin Lovell-Badge ·
 Walter Just · Vincent R. Harley



	SOX/TCF	SOX (R5)	SOX/TCF	GATA
Human	CCTTTGTT CCTAA -- CCTGGGCAG-TATGGAGAAAAAACAAATACCTT	CCTTTGTT	CAGAAACTGTGGGAATCTGAAAGGTAGGATTCTGCTCTCCAGATAAGAGCTGGCAG	
Mouse	CCTTTGTT CCTAA -- CCTGGGCAG-TTTTCACAAAATAACAAATGCCTT	CCTTTGTT	CAGAAACT-TTAGGGCTAAGAAAGAGAAGACTCC-ACTCTCGCA	GATAAGGGCTGGCAG
Rat	CCTTTGTT CCTAA -- CCTGGGGGGTTTCACAAAATAACAAATACCTT	CAGAAACT-TTGGGACTAAGAAAGGTACAATCC-TCTCTCCCAGATAAGGGCTGGCAG		
<i>E. lut</i>	CCTTTGTT CCTAT -- CCTGGGCAG-TTTTCACAAAATAACAAATAC-TTCC		--GGCTAAGAAAGGA-GACTCT-CCTCTCCCAGATAAGGGAGGAAG	
<i>E. tanc/talp</i>	CCTTTGTT CCTAA -- CCTGGGCAG-TTTTCACAAAATAACAAATAC-TTCT		--GGCTAAGAAAGGA-GACTCT-CCTCTCCCAGATAAGGGTGGAG	
<i>E. fusc</i>	CCTTTGTT CCTAG -- GCTGGGCAG-TTTTCACAAAATAACAAATAC-TTCT		--GGCTAAGAAAGGA-GACTCT-CCTCTCCCAGATAAGGGTGGAG	
Opossum	CCTTTGTT CCTAA -- TCTGCTCAG-TTTTAGAAAAACAAATACCTT	CAGAAACT	--GGCTAAGAAAGGA-GACTCT-CCTCTCCCAGATAAGGGTGGAG	
Platypus	CCTTTGTT CCTAA -- CCTACGTTG-CTTGGAAAGGGTAACAATACCTCCTT	CAGCCCCCTGCCAGGAGACTGAAAGGTAGGACTCTGTGAGATAAGAGCTGGCAG		
Chicken	CCTTTGTT CTCAA -- GCTTGGC (85bp)	AAGGTAAACAATACATCCTTCAGGCACTGCCAAAG-----	--CCCTACTCAAGCCCACCTCCGATAAGAGCTGGCAG	
Lizard	CCTTTGTT ACTAA -CCTGTGC (58bp)	GGGAATACARTAGGTCTTTCAGGCTGTGCCAAGC-----	--TTCTTCTCAAGCCCTCTCAGATAAGCGCTGGCAG	
Frog	CCTTTGTT CCGCTCCTGGCTA-TACTGC-TCGGTACRACATACCTG	CATTCAAGCTGTGCCAAGCAGCACACGACGTACCC	-----ACCAGTGT-AGATAAGAGTAGGCAG	
	*****	**	*****	*****
			*	*****



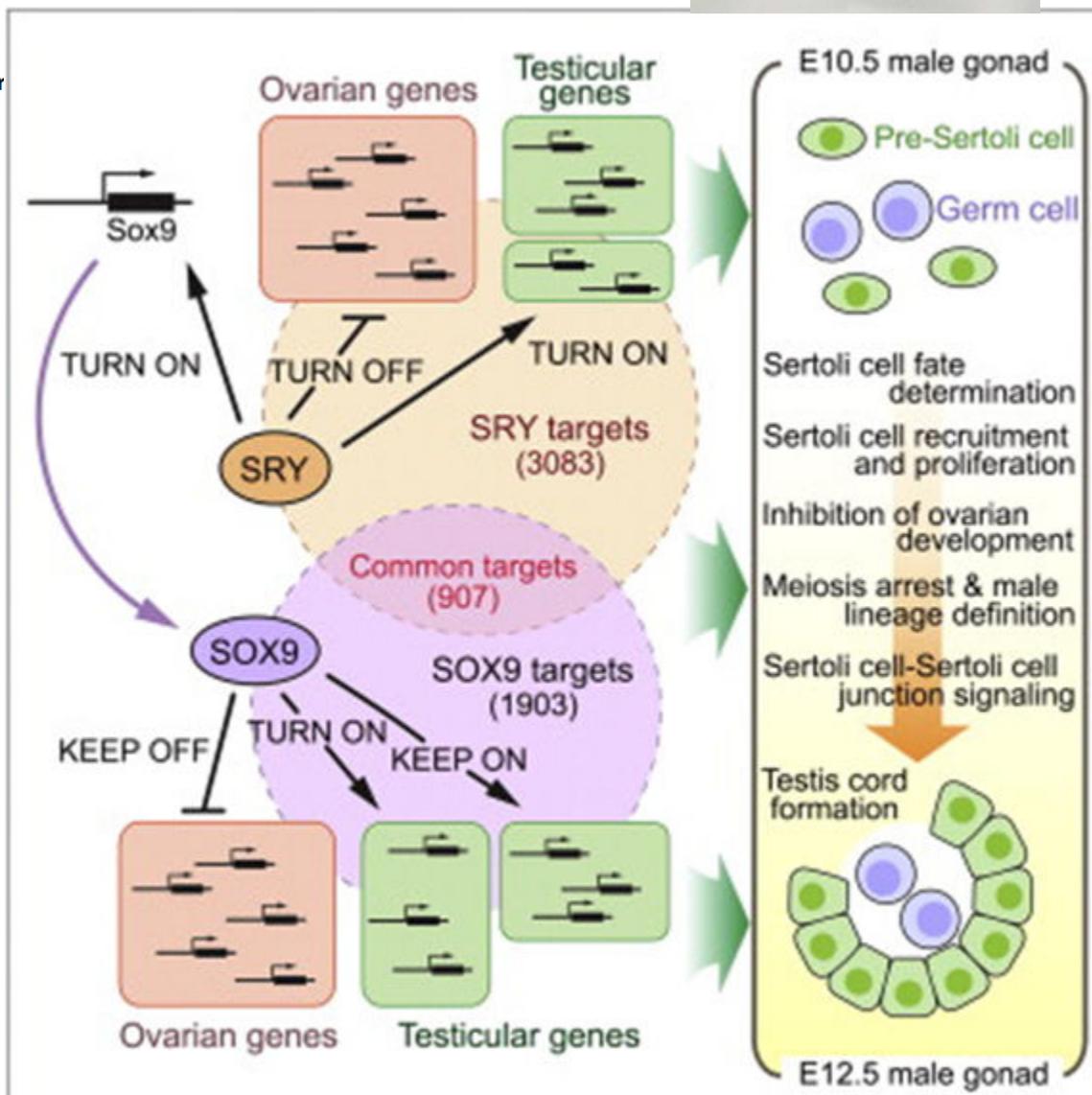


Mutations in the Testis-Specific Enhancer of SOX9 in the SRY Independent Sex-Determining Mechanism in the Genus *Tokudaia*

Ryutaro Kimura¹, Chie Murata^{2✉a}, Yoko Kuroki^{3✉b}, Asato Kur

SRY proteins bind to the testis-specific enhancer of SOX9 (TES) with SF1 to upregulate SOX9 expression in undifferentiated gonads of XY embryos of humans and mice. The core region within TES, named TESCO, is an important enhancer for mammalian sex determination

TESCO of *Tokudaia* has no enhancer activities





OPEN

Molecular mechanism of male differentiation is conserved in the SRY-absent mammal, *Tokudaia osimensis*



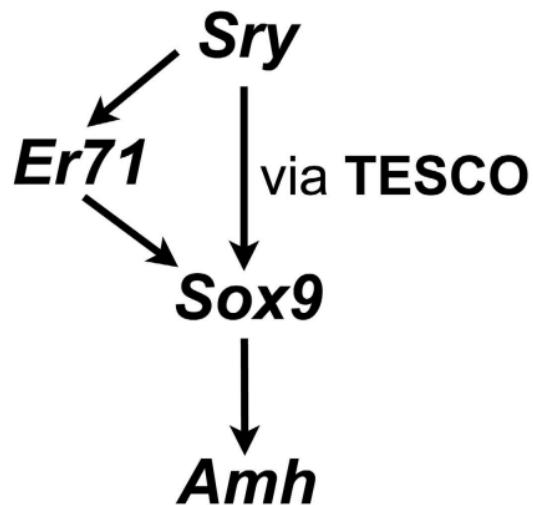
Received: 16 June 2016

Accepted: 16 August 2016

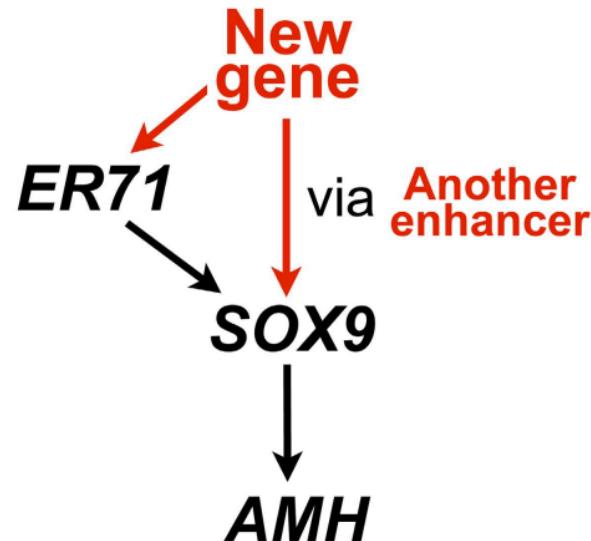
Published: 09 September 2016

Tomofumi Otake¹ & Asato Kuroiwa^{1,2}

Mouse
(Most placenta mammals)



Amami spiny rat
(*T. osimensis*, 2n=25, XO/XO)



The ER71 protein belongs to the ETS transcription factor family and is testis-specifically expressed in adult mice



OPEN

Molecular mechanism of male differentiation is conserved in the SRY-absent mammal, *Tokudaia osimensis*



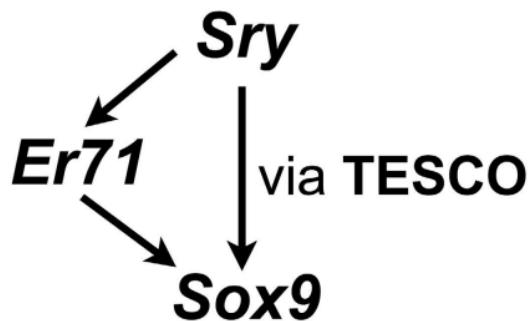
Received: 16 June 2016

Accepted: 16 August 2016

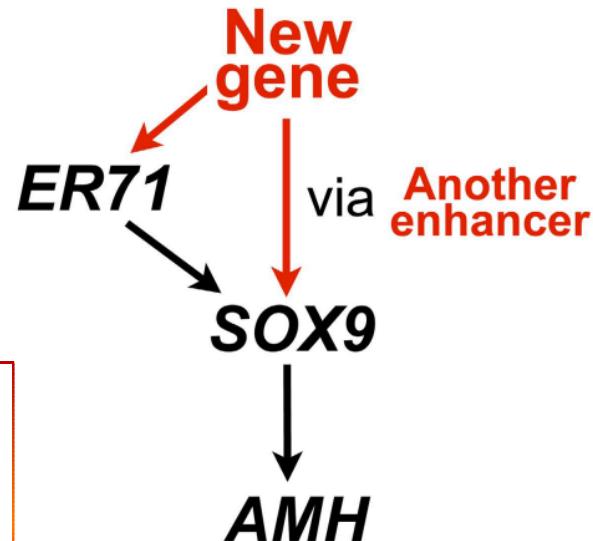
Published: 09 September 2016

Tomofumi Otake¹ & Asato Kuroiwa^{1,2}

Mouse
(Most placenta mammals)



Amami spiny rat
(*T. osimensis*, 2n=25, XO/XO)



SEX DETERMINATION

Sex reversal following deletion of a single distal enhancer of *Sox9*

Nitzan Gonen¹, Chris R. Futtner², Sophie Wood¹, S. Alexandra Garcia-Moreno², Isabella M. Salamone^{2*}, Shiela C. Samson^{1†}, Ryohei Sekido^{3‡}, Francis Poulat⁴, Danielle M. Maatouk^{2§||}, Robin Lovell-Badge^{1§¶}

Exclusion of *SOX9* as the Testis Determining Factor in *Ellobius lutescens*: Evidence for Another Testis Determining Gene Besides *SRY* and *SOX9*

Annette Baumstark,* Mikhail Akhverdyan,† Angela Schulze,* Ingrid Reisert,‡
Walther Vogel,* and Walter Just*



Review Article

Sexual
Development

Sex Dev 2007;1:211–221
DOI: 10.1159/000104771

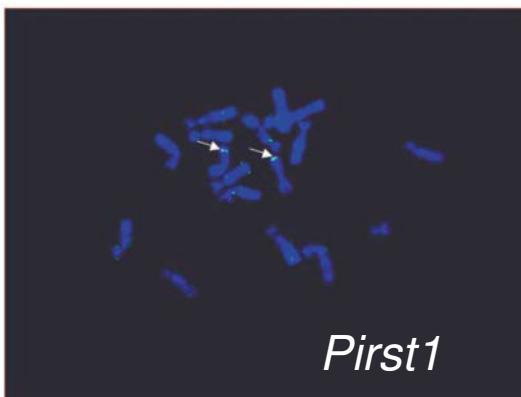
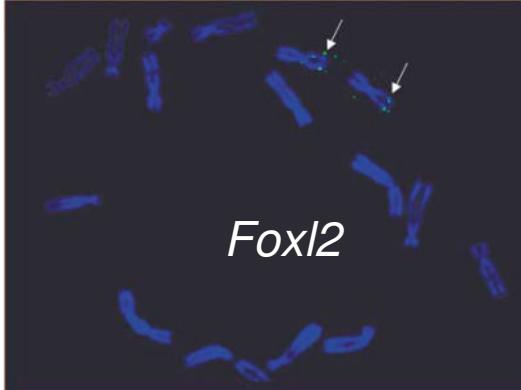
Characterization of *Pisrt1/Foxl2* in *Ellobius lutescens* and exclusion as sex-determining genes

Annette Baumstark,¹ Horst Hameister,¹ Mikhayil Hakhverdyan,²
Irina Bakloushinskaya,³ Walter Just¹

Ellobius lutescens: Sex Determination and Sex Chromosome

W. Just^a A. Baumstark^a A. Süß^a A. Graphodatsky^b W. Rens^c N. Schäfer^a
I. Bakloushinskaya^d H. Hameister^a W. Vogel^a

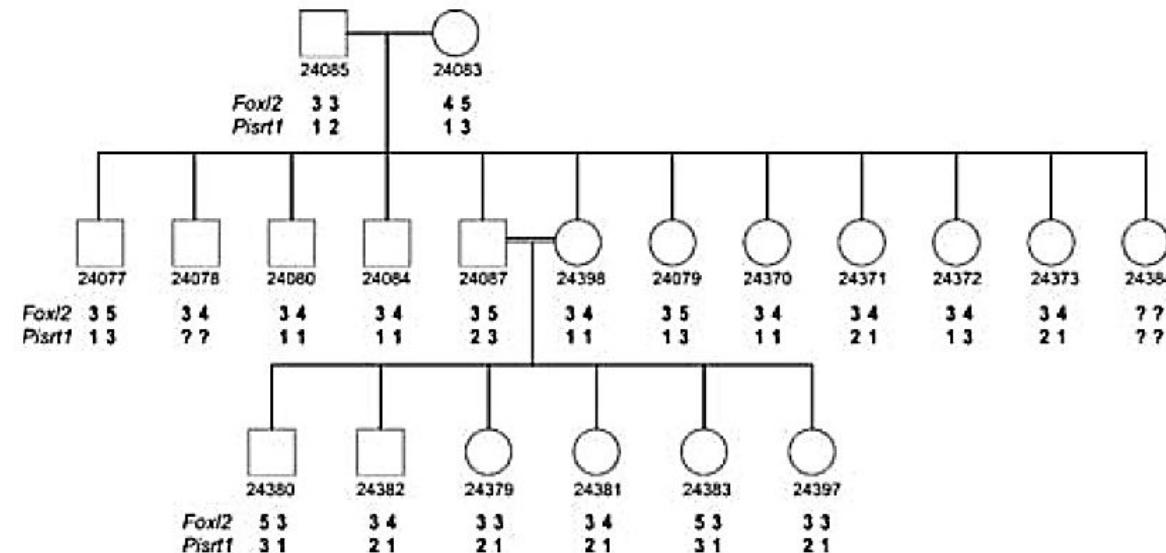
- Firstly, polymorphic/biallelic markers were searched, and then screened in at least three generations families of mole voles.
The same strategy was used in mole voles for the main genes of sex determination network:
- ***SOX9, SF1, Sox3, Atrx, Nr0b1, Ar, Nr5a1, Foxl2/Pisrt1, Dmrt1***
(Baumstark *et al.*, 2001; 2005; Just *et al.*, 2002, 2007).
No one demonstrated co-segregation of marker alleles with sex of animals.
- A primary sex determining function was excluded for all mentioned genes in *E. lutescens* and *E. tancrei*, species with X0 or XX sex chromosomes in males and females.



Fluorescence in situ hybridization with the isolated *Foxl2* phagemid or the *Pisrt1* phagemid to metaphase spreads of *E. lutescens* chromosomes ($2n = 17$). The signals map to the same region on chromosome 8.

Characterization of *Pisrt1/Foxl2* in *Ellobius lutescens* and exclusion as sex-determining genes

Annette Baumstark,¹ Horst Hameister,¹ Mikhayil Hakhverdyan,²
Irina Bakloushinskaya,³ Walter Just¹



Genotypes of *E. lutescens* animals after marker analysis at the *Foxl2* and *Pisrt1* loci. The pedigree shows the three-generation family with 20 animals. Animals with identical genotypes but with different sex, e.g., 24084 (male) and 24398 (female) exclude sex-specific haplotypes as well as animals with different genotype but same sex (e.g., males 24084 and 24087; females 24079 and 24371). The third generation, which was obtained by inbreeding, shows some animals with identical sex but different genotypes (e.g., 24381 and 24383).

Genomes of *Ellobius* species provide insight into the evolutionary dynamics of mammalian sex chromosomes

Eskeatnaf Mulugeta,^{1,2} Evelyne Wassenaar,¹ Esther Sleddens-Linkels,¹ Wilfred F.J. van IJcken,³ Edith Heard,² J. Anton Grootegoed,¹ Walter Just,⁴ Joost Gribnau,¹ and Willy M. Baarens¹



Genome Research

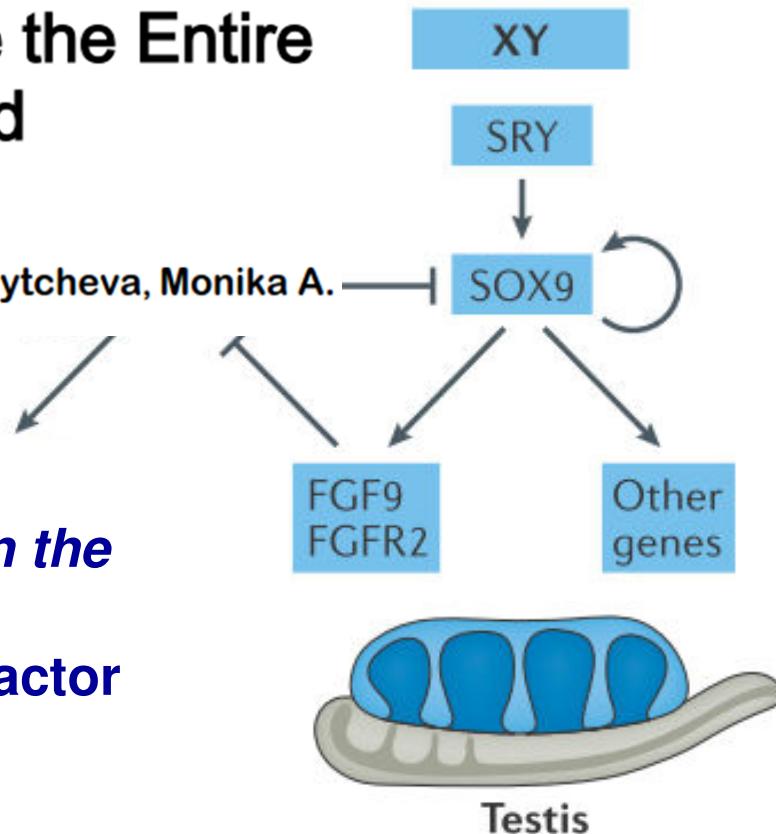


	<i>M. musculus</i>		<i>R. norvegicus</i>		<i>E. lutescens</i>		<i>E. talpinus</i>	
	X	Y	X	Y	X	Y-derived	X	Y-derived
Ancestral	Zfx	Zfy1+2	Zfx	Zfy1+2	Zfx	Zfy	Zfx	Zfy
	Uba1	Uba1y	Uba1	Uba1y	Uba1	-	Uba1	
	Kdm5c	Kdm5d	Kdm5c	Kdm5d	Kdm5c	-	Kdm5c	-
	Eif2s3x	Eif2s3y	Eif2s3x	Eif2s3y	Eif2s3x	Eif2s3y	Eif2s3x	Eif2s3y
	Kdm6a	Uty	Kdm6a	Uty	Kdm6a	-	Kdm6a	-
	Tspy12	Tspy-ps	Tspy12	Tspy1	Tspy12	-	Tspy12	-
	Ddx3x	Ddx3y	Ddx3x	Ddx3y	Ddx3x	-	Ddx3x	-
	Usp9x	Usp9y	Usp9x	Usp9y	Usp9x	Usp9y	Usp9x	-
	Sox3	Sry	Sox3	Sry	Sox3	-	Sox3	-
	Rbmx	Rbmy(mc)	Rbmx	Rbmy(mc)	Rbmx	-	Rbmx	-
Added	Slx (mc)	Sly (mc)	-	-	-	-	-	-
	Spin2 (mc)	Ssty (mc)	Spin2 (mc)	Ssty(mc)	Spin2	Ssty	Spin2	Ssty
	Srsx (mc)	Srsy (mc)	-	-	-	-	-	-
	1700012L04Rik	Gm6026/Gm16501	-	-	-	-	-	-
	Rbm31x* (1)	Rbm31y (2)	Rbm31x*	-	Rbm31x	-	Rbm31x	-
		Prssly		-		-		-
		Teyorf1		-		-		-

Two Y Genes Can Replace the Entire Y Chromosome for Assisted Reproduction in the Mouse

Yasuhiro Yamauchi, Jonathan M. Riel, Zoia Stoytcheva, Monika A. Ward*

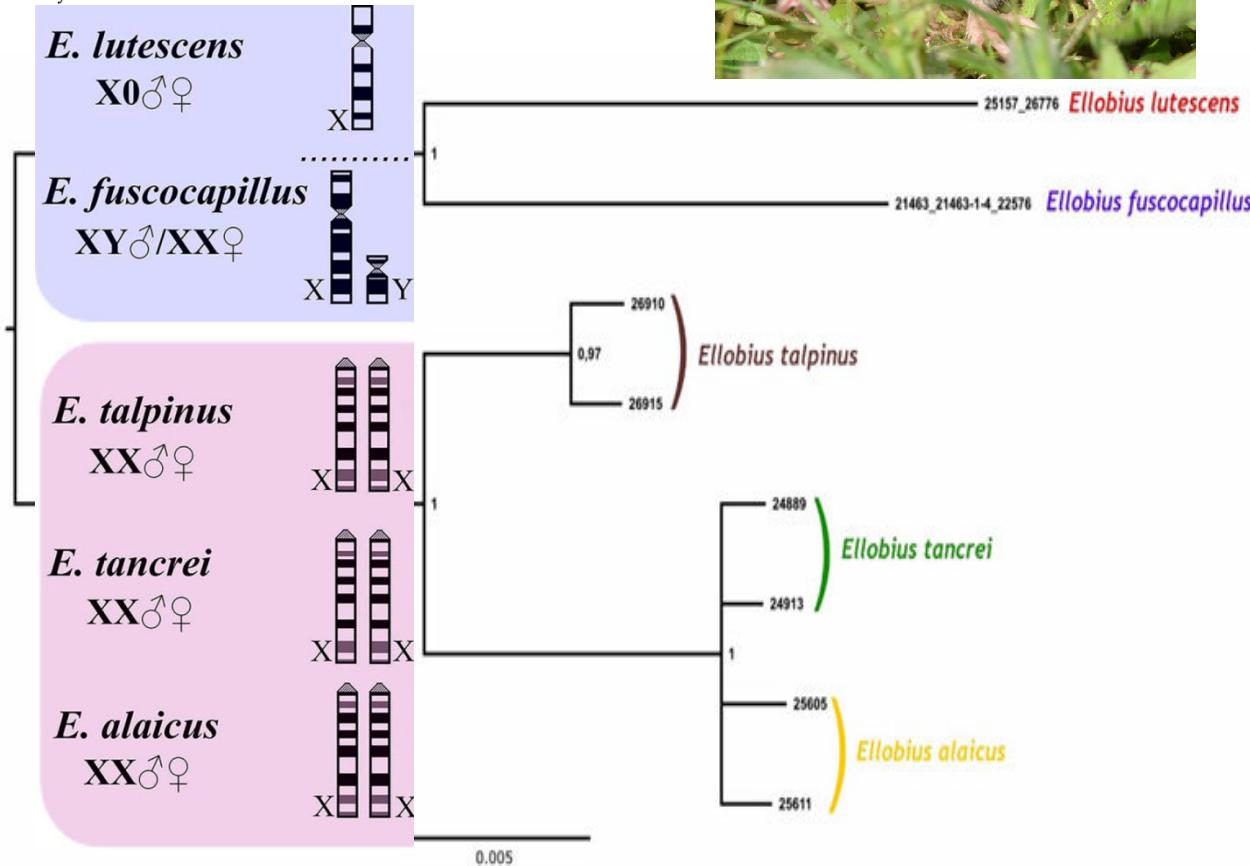
testis determinant factor
Sry Sex-determining Region on the chromosome Y
spermatogonial proliferation factor
Eif2s3y



Article

Chromosomal Evolution in Mole Voles *Ellobius* (Cricetidae, Rodentia): Bizarre Sex Chromosomes, Variable Autosomes and Meiosis

Sergey Matveevsky ^{1,*} , Oxana Kolomiets ¹, Alexey Bogdanov ², Mikhayil Hakhverdyan ³ and Irina Bakloushinskaya ² 



Sry / Eif2s3y

No *Sry*

Eif2s3y is maintained in male and female genomes

Fragments of the *Sry* and *Eif2s3y* are maintained in male and female genomes

No *Sry*

Eif2s3y is maintained in male and female genomes

Evolution of sex determination = transcriptional evolution

DEVELOPMENTAL DYNAMICS 242:307–319, 2013

SPECIAL ISSUE REVIEWS-A PEER REVIEWED FORUM

Transcriptional Evolution Underlying Vertebrate Sexual Development

Nicole Valenzuela,* Jennifer L. Neuwald, and Robert Lierman

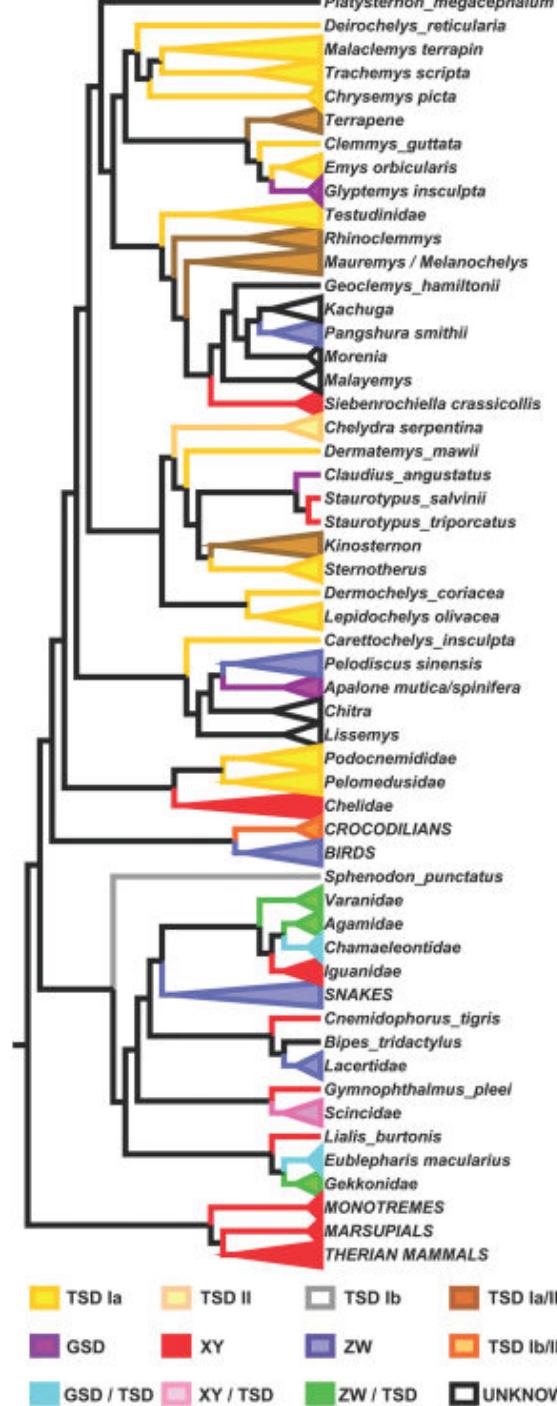
CBX2 (chromobox homolog 2)

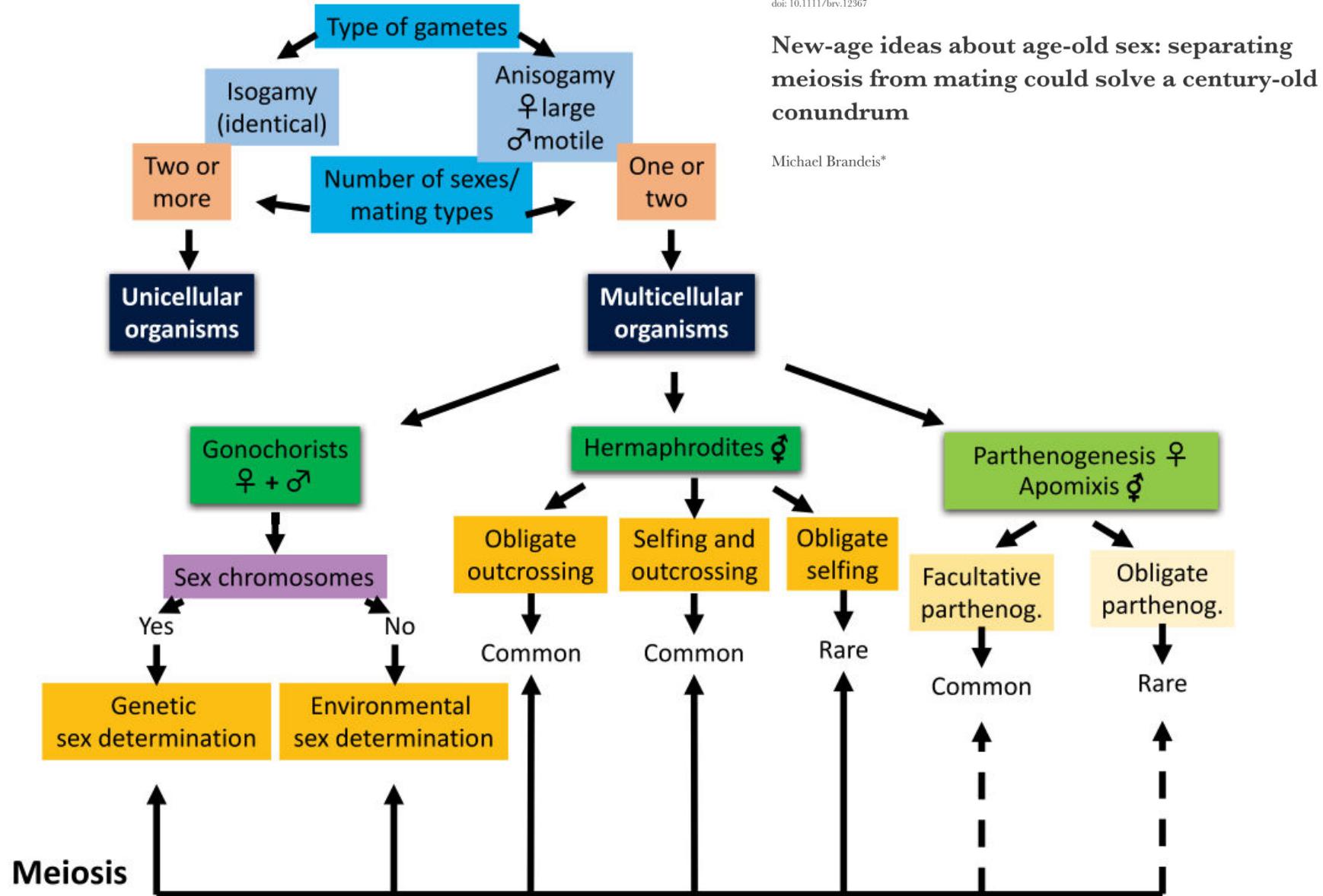
Chromatin modifacaton

upregulation of male-related genes SRY, SOX9, SF1
negatively regulates female-related FOXL2

Sox9 male-biased and Aromatase female-biased
expression appear ancestral and virtually conserved
throughout vertebrates

epigenetics
small RNA

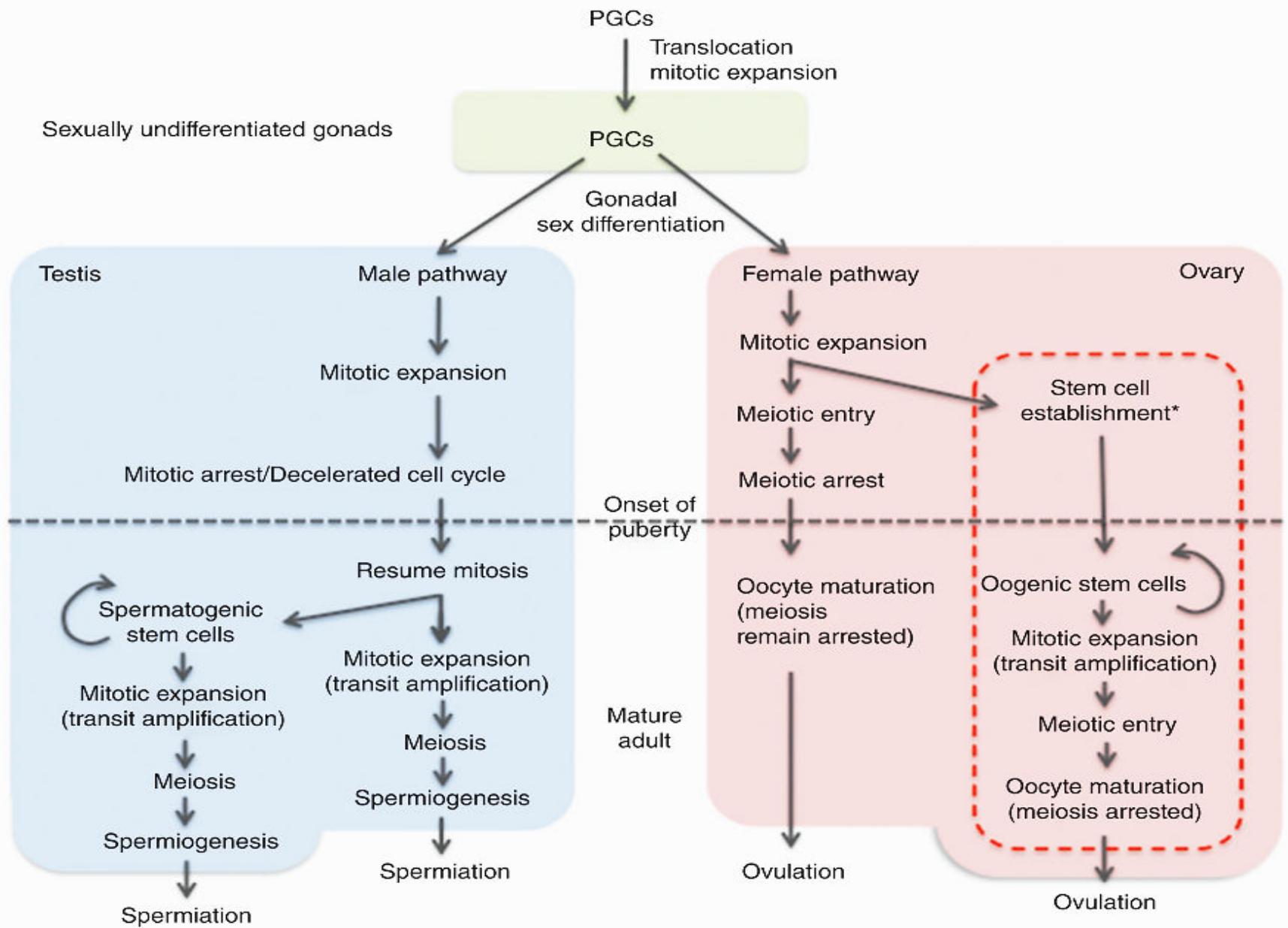




New-age ideas about age-old sex: separating meiosis from mating could solve a century-old conundrum

Michael Brandeis*

Meiosis is highly conserved and rigid, mating is extremely varied and flexible

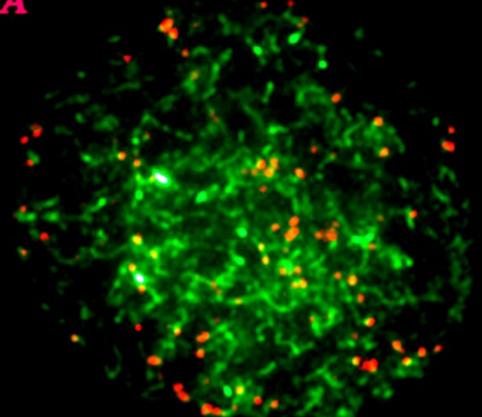


Focus Article

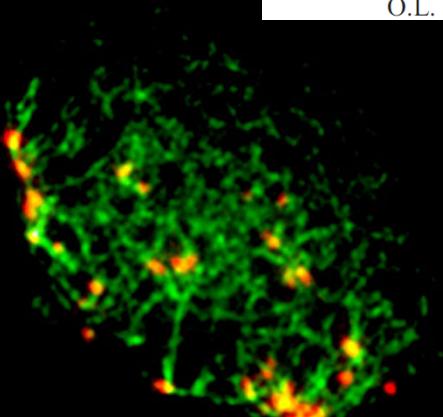
From cyst to tubule: innovations in vertebrate spermatogenesis



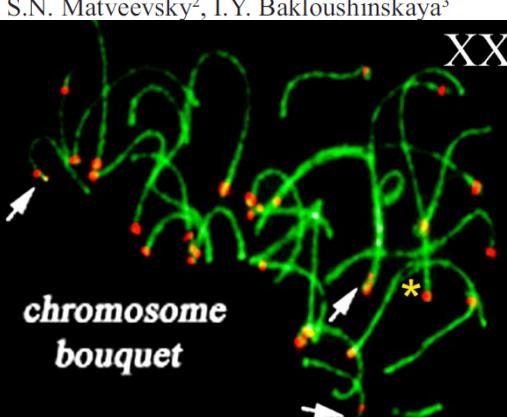
Ellobius talpinus, females

SCP3
ACA

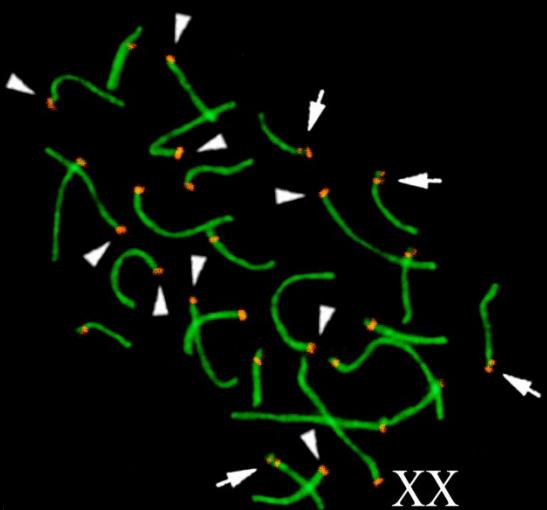
preleptotene



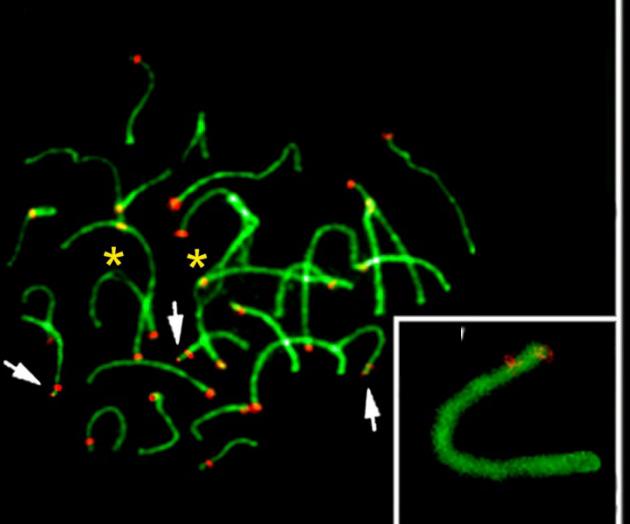
early zygotene



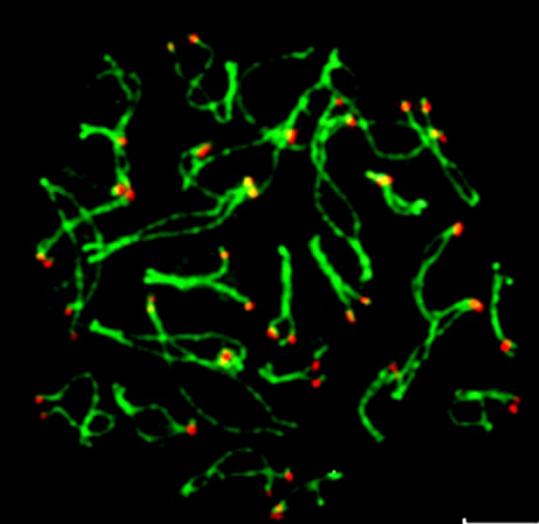
early pachytene



middle pachytene



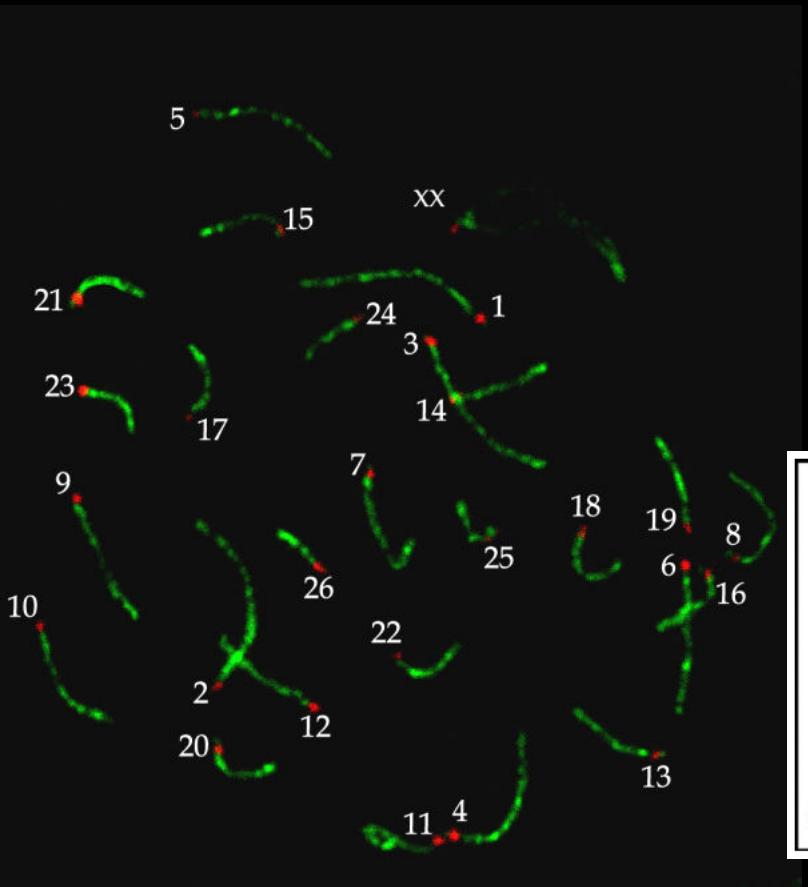
early diplotene



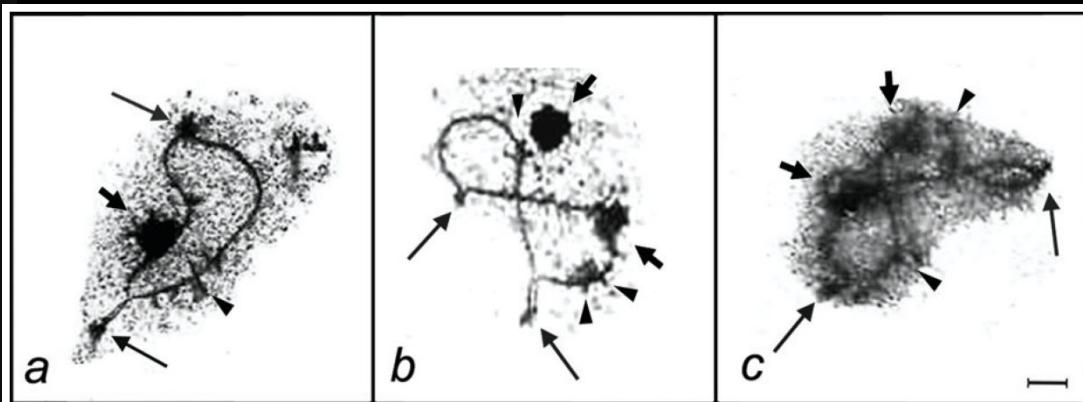
middle diplotene

Sexual dimorphism in prophase I of meiosis in the Northern mole vole (*Ellobius talpinus* Pallas, 1770) with isomorphic (XX) chromosomes in males and females

O.L. Kolomiets¹, S.N. Matveevsky², I.Y. Bakloushinskaya³



E. talpinus, males



a - late zygotene. A closed sex bivalent with short paratelomeric SC fragments and extensive zone of asynapsis between the axial elements of XX chromosomes.

b - pachytene. Two electron-dense nucleolus-like bodies at each of XX chromosomes axes.

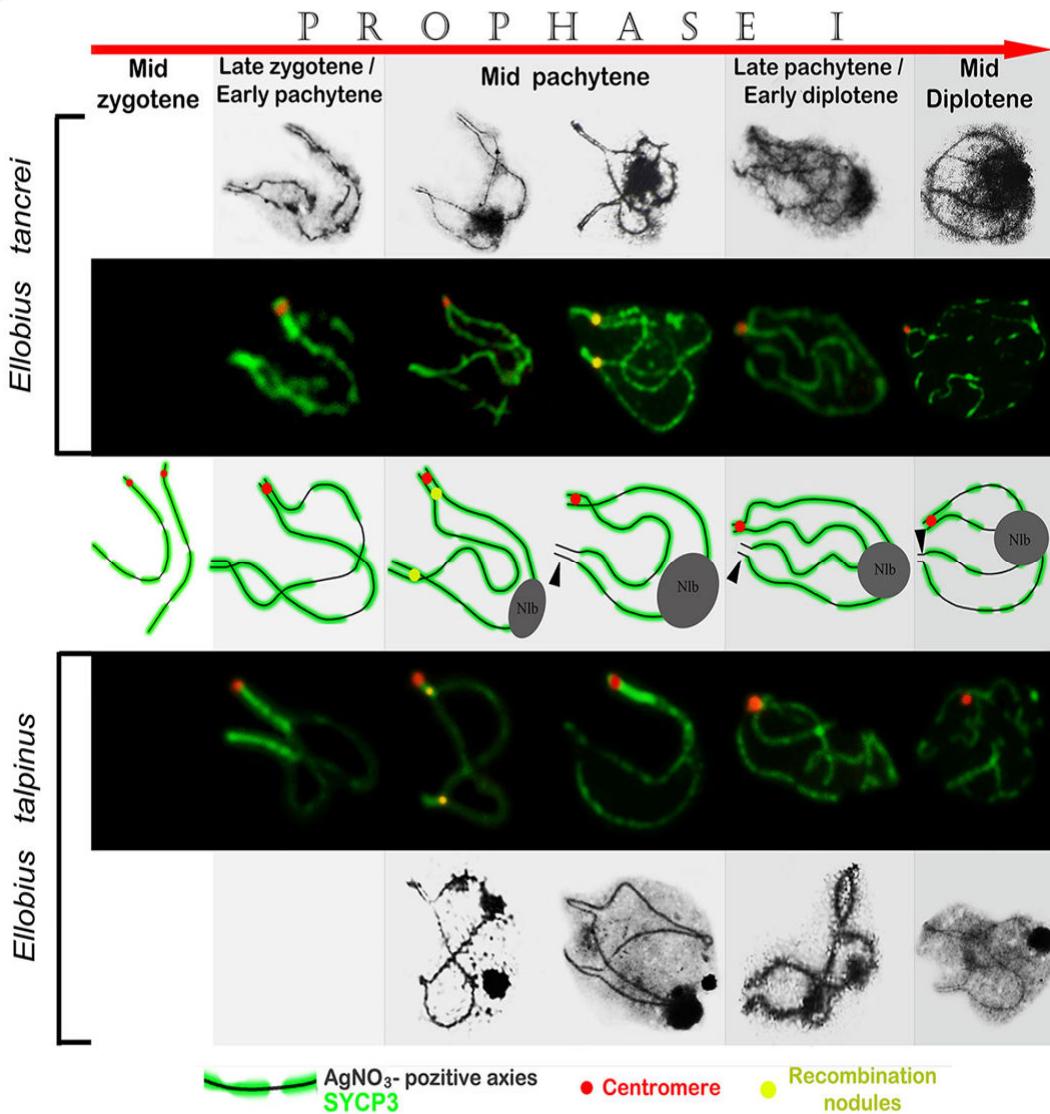
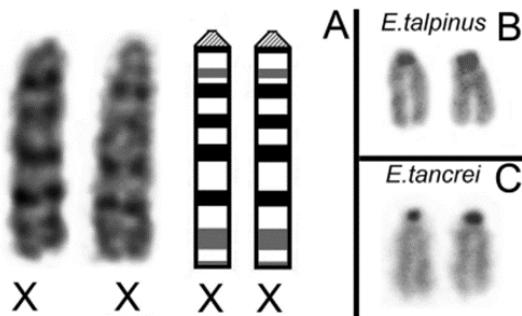
c - diplotene. The compact sex bivalent has a complicated configuration and is surrounded by a “cloud” of electron-dense material.

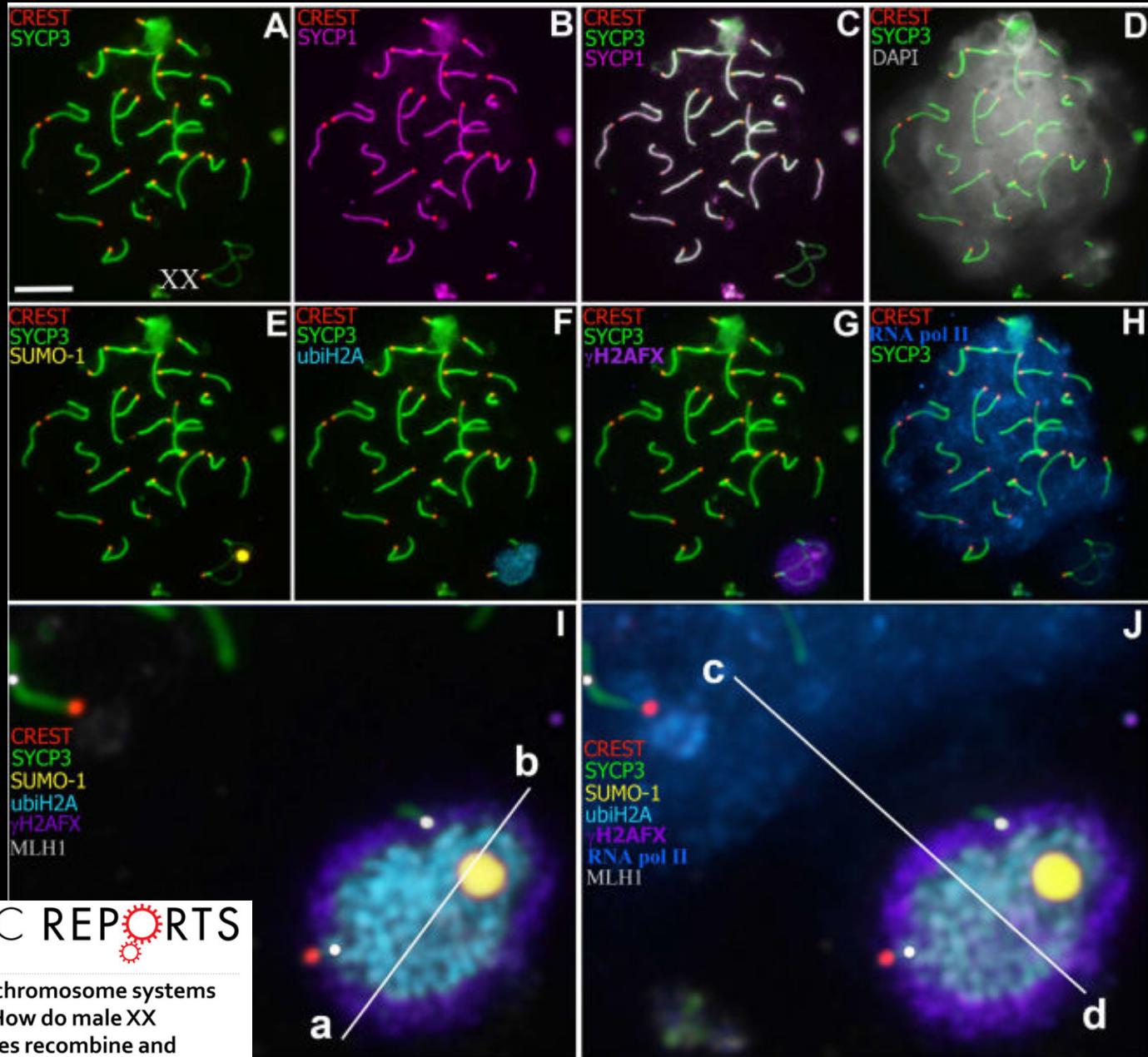
OPEN

Unique sex chromosome systems in *Ellobius*: How do male XX chromosomes recombine and undergo pachytene chromatin inactivation?

Received: 26 February 2016
 Accepted: 27 June 2016
 Published: 18 July 2016

Sergey Matveevsky¹, Irina Bakloushinskaya² & Oxana Kolomiets¹





E. talpinus, male

SCIENTIFIC REPORTS

OPEN

Unique sex chromosome systems in *Ellobius*: How do male XX chromosomes recombine and undergo pachytene chromatin inactivation?

Received: 26 February 2016
Accepted: 27 June 2016
Published: 18 July 2016

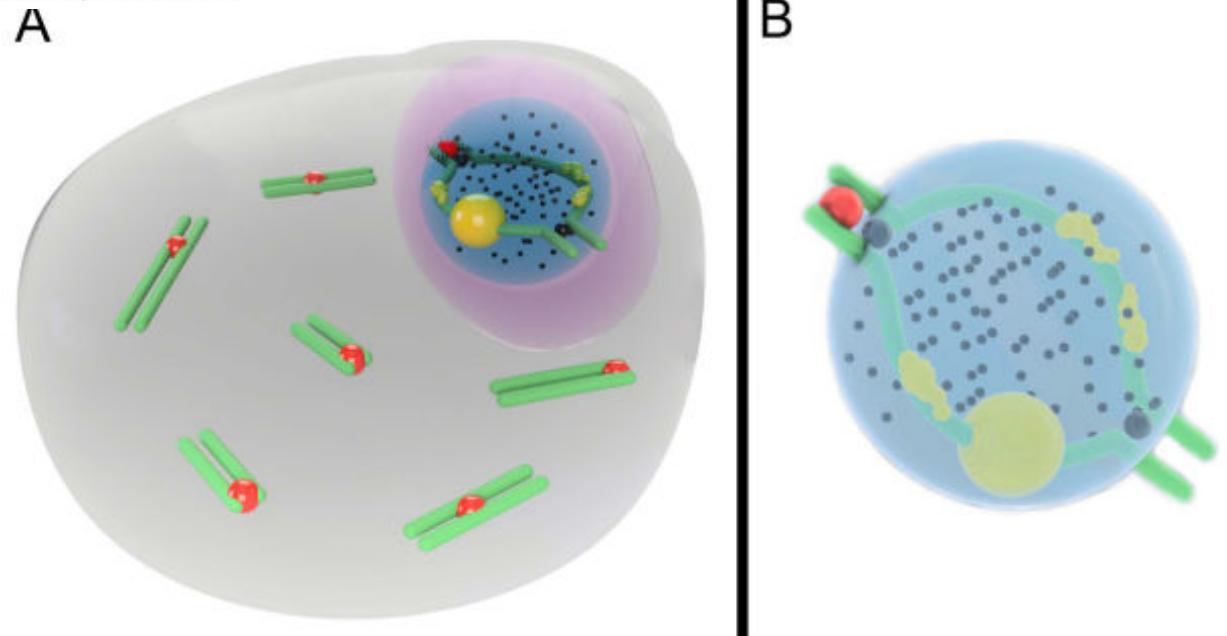
Sergey Matveevsky¹, Irina Bakloushinskaya² & Oxana Kolomiets¹

OPEN

Unique sex chromosome systems in *Ellobius*: How do male XX chromosomes recombine and undergo pachytene chromatin inactivation?

Received: 26 February 2016
 Accepted: 27 June 2016
 Published: 18 July 2016

Sergey Matveevsky¹, Irina Bakloushinskaya² & Oxana Kolomiets¹

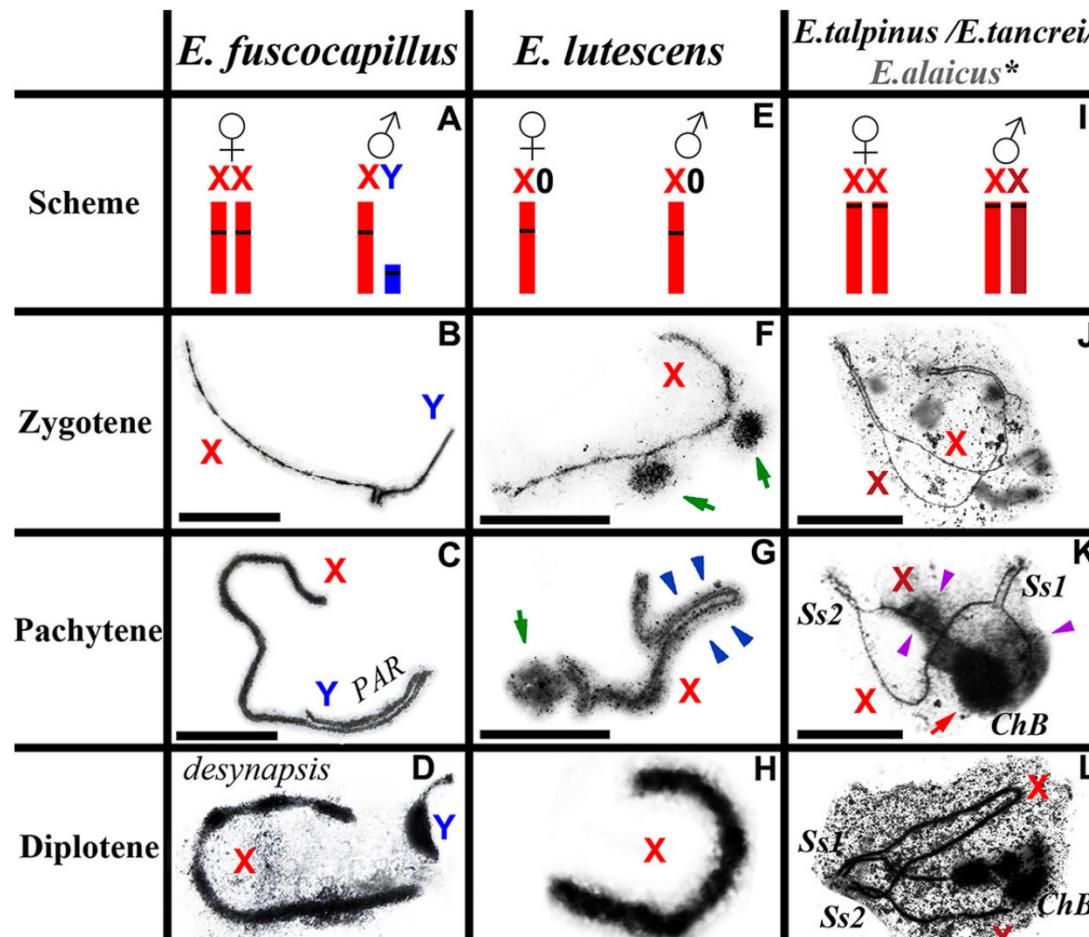


Schematic illustration of male *Ellobius* MSCI (meiotic sex chromosome inactivation)

A pachytene spermatocyte (A) and a sex (XX) bivalent (B) of a mole vole are shown.

The sex (XX) chromosomes form a sex body on the periphery of the nucleus. The chromatin of the sex body undergoes reorganization. MSCI markers have different distributions: SUMO-1 (yellow), ATR (black dots), ubiH2A (blue), H2AFX (violet). SUMO-1 marks a small nucleolus-like body of the meiotic XX. ATR and ubiH2A are localized in the asynaptic area of the sex bivalent. γ H2AFX covers the entire XX bivalent. MLH1 signals are shown only for the sex chromosomes (black balls). The red balls indicate centromeres.

Ellobius male sex chromosomes behaviour in meiotic prophase I



genes

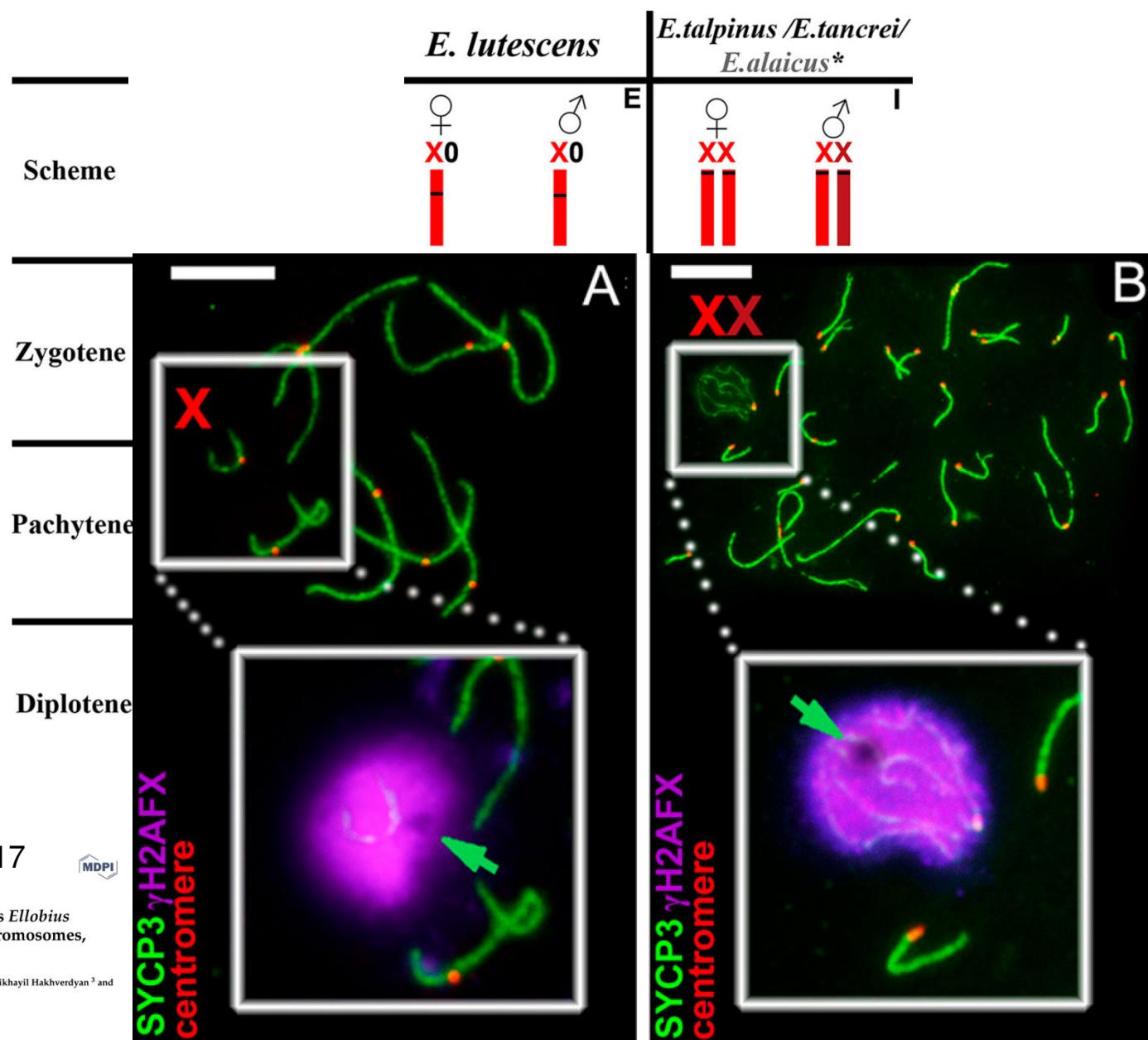


Article

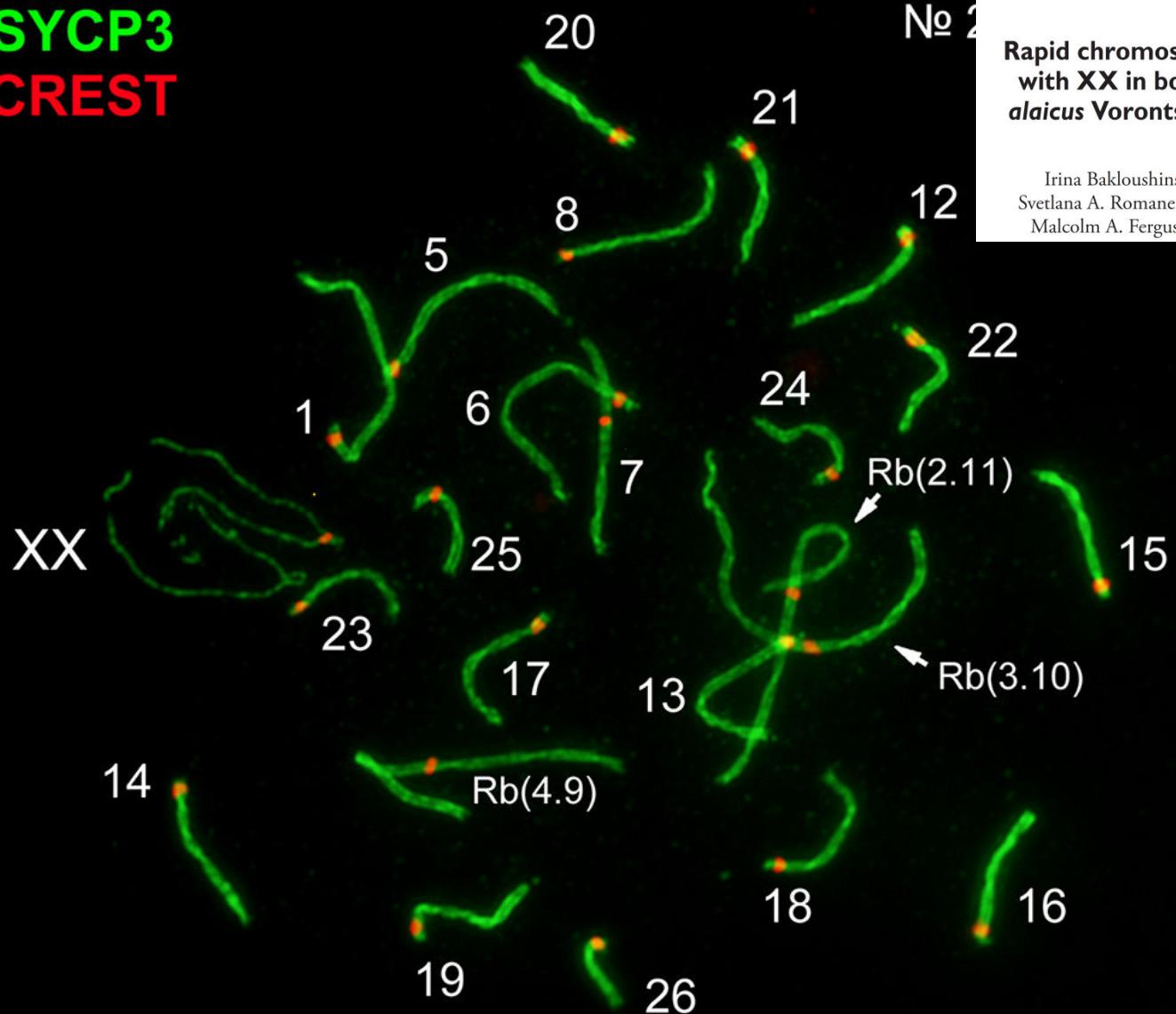
Chromosomal Evolution in Mole Voles *Ellobius* (Cricetidae, Rodentia): Bizarre Sex Chromosomes, Variable Autosomes and Meiosis

Sergey Matveevsky ^{1,*} , Oxana Kolomiets ¹, Alexey Bogdanov ², Mikhayil Hakhverdyan ³ and Irina Bakloushinskaya ²

Ellobius male sex chromosomes behaviour in meiotic prophase I



SYCP3
CREST

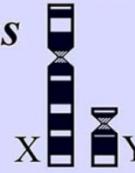
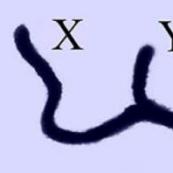
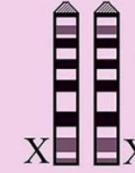
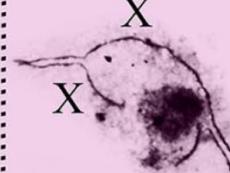
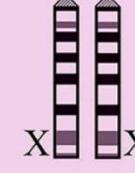
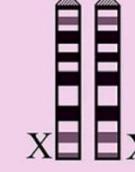


Nº 2

Rapid chromosomal evolution in enigmatic mammal
with XX in both sexes, the Alay mole vole *Ellobius*
alaicus Vorontsov et al., 1969 (Mammalia, Rodentia)

Irina Bakloushinskaya¹, Elena A. Lyapunova¹, Abdusattor S. Saidov²,
Svetlana A. Romanenko^{3,4}, Patricia C.M. O'Brien⁵, Natalia A. Serdyukova³,
Malcolm A. Ferguson-Smith⁵, Sergey Matveevsky⁶, Alexey S. Bogdanov¹

E. alaicus, male

G-band sex chromosomes	Male sex bivalent	Recombination (sex chromosome)	MSCI and transcription	<i>Sry / Eif2s3y</i>
<i>E. lutescens</i> $X0\text{♂♀}$			MLH1 focus was not detected (Mulugeta et al., 2016) The chromatin of the X chromosome undergoes a multi-stage reorganization and is inactivated transcriptionally. Male X chromosomes form a typical sex body	No <i>Sry</i> <i>Eif2s3y</i> is maintained in male and female genomes
<i>E. fuscocapillus</i> $XY\text{♂}/XX\text{♀}$			?	Fragments of the <i>Sry</i> and <i>Eif2s3y</i> are maintained in male and female genomes
<i>E. talpinus</i> $XX\text{♂♀}$			Centromere Synaptic site 1 Asynaptic region Synaptic site 2 frequency Two peaks MLH1 distribution	The chromatin of the sex chromosomes undergoes a multi-stage reorganization and is inactivated transcriptionally. Male XX chromosomes form a typical sex body
<i>E. tancrei</i> $XX\text{♂♀}$			?	No <i>Sry</i> <i>Eif2s3y</i> is maintained in male and female genomes
<i>E. alaicus</i> $XX\text{♂♀}$		?		

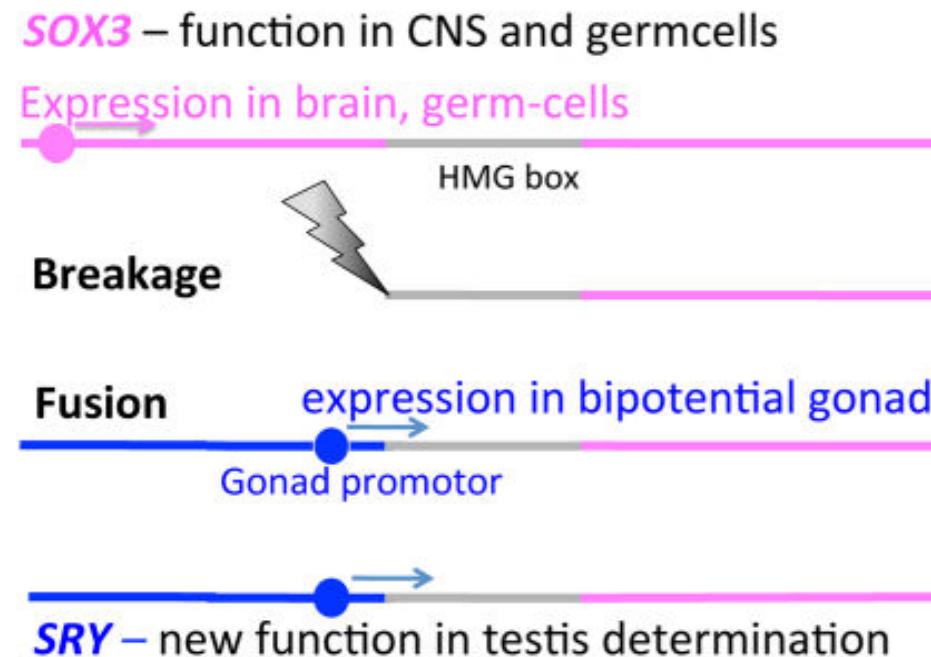


Did sex chromosome turnover promote divergence of the major mammal groups?

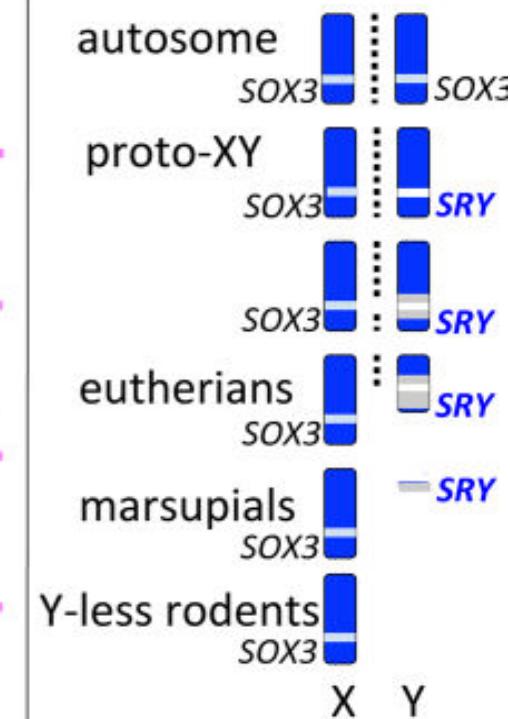
De novo sex chromosomes and drastic rearrangements may have posed reproductive barriers between monotremes, marsupials and placental mammals

Jennifer A. M. Graves^{1,2}

A Evolution of SRY



B Evolution of XY



The Y chromosomes of the great apes

Pille Hallast^{1,2} and Mark A. Jobling³

Human genetics, 2017



Partial synapsis in male XX

Complete synapsis in female XX

Open Access

OBM Genetics

2018

LIDSEN
LIDSEN Publishing Inc.

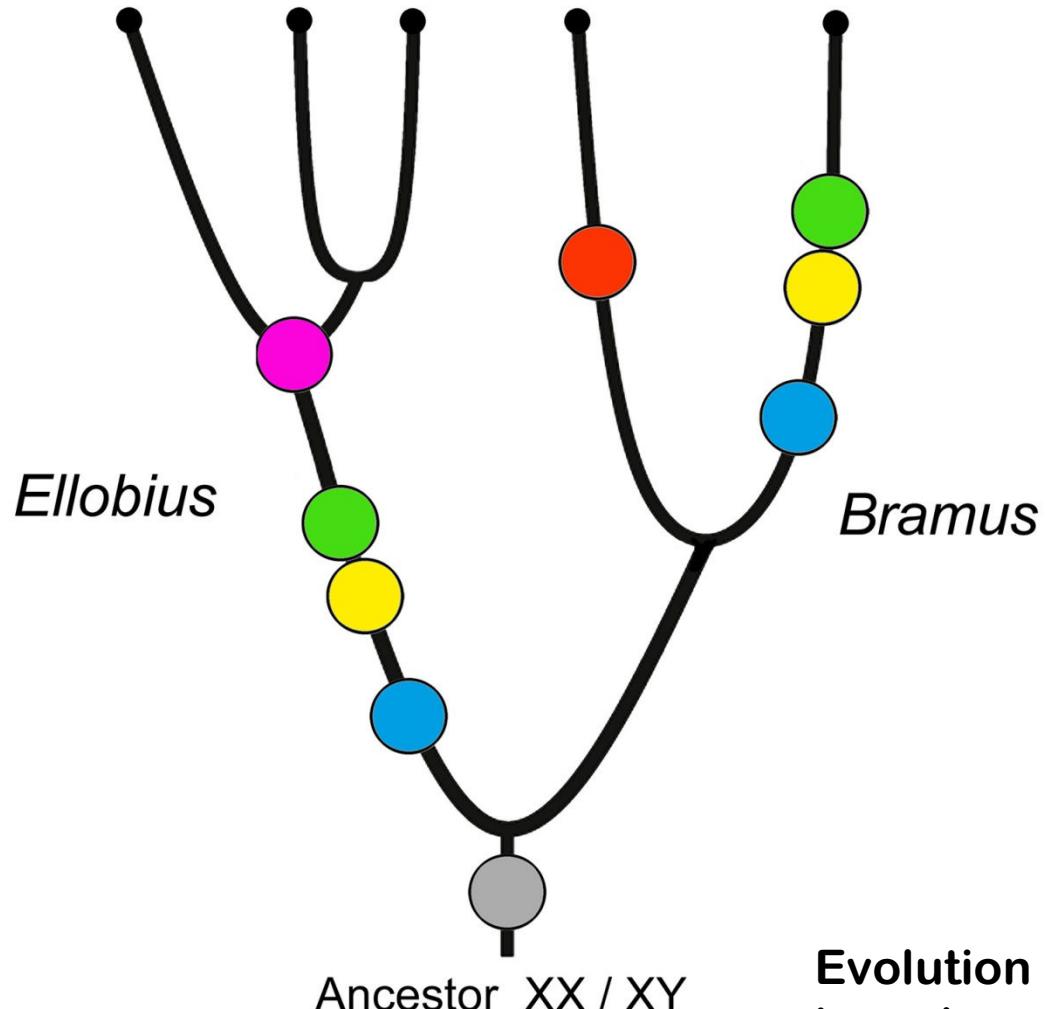
Review

Unusual Ways to Lose a Y Chromosome and Survive with Changed Autosomes: a Story of Mole Voles *Ellobius* (Mammalia, Rodentia)

Irina Bakloushinskaya ^{1,*}, Sergey Matveevsky ²

Male sex bivalent forms typical sex body

E.talpinus *E.alalicus* *E.tancrei* *E.fuscocapillus* *E.lutescens*



- Sry and *Eif2s3Y* fragments maintain in female genome
- X duplication
- Sry loss
- Y chromosome loss
- Eif2s3Y* translocation
- TESCO deletion

Evolution of sex chromosomes
in mole voles *Ellobius*

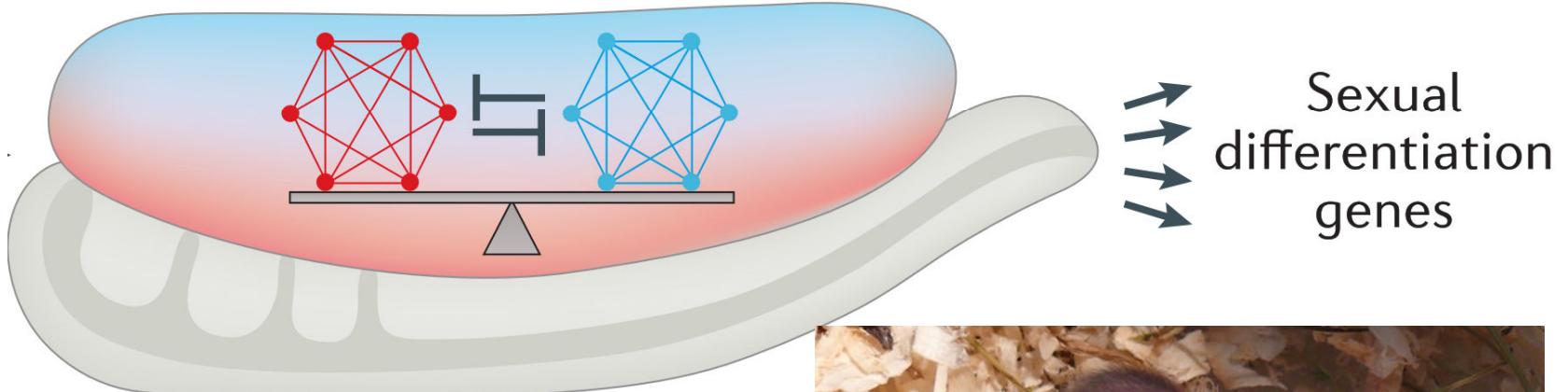
**sex is typically determined by
X and Y chromosomes**

myth

**sex is controlled by one
master-switch gene**

myth

Multi-component, mutually antagonistic pathways



Vertebrate sex determination:
evolutionary plasticity of a
fundamental switch

Blanche Capel

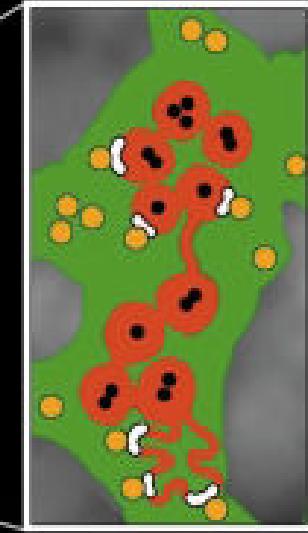
Робертсоновские транслокации, монобрахиальная гомология и виdeoобразование



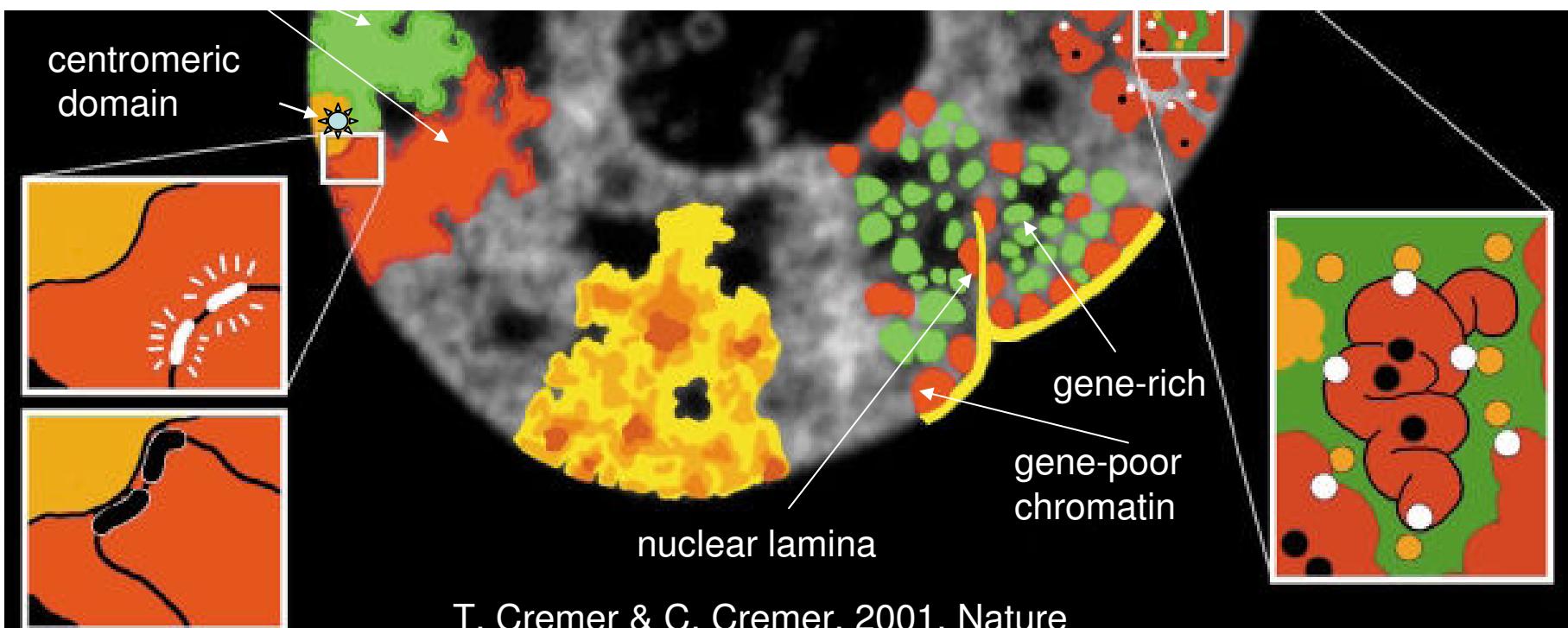
Гибридизация и мейотический драйв
могут вести к образованию новых
форм и видов в случае
монобрахиальной гомологии

CHROMOSOME TERRITORIES

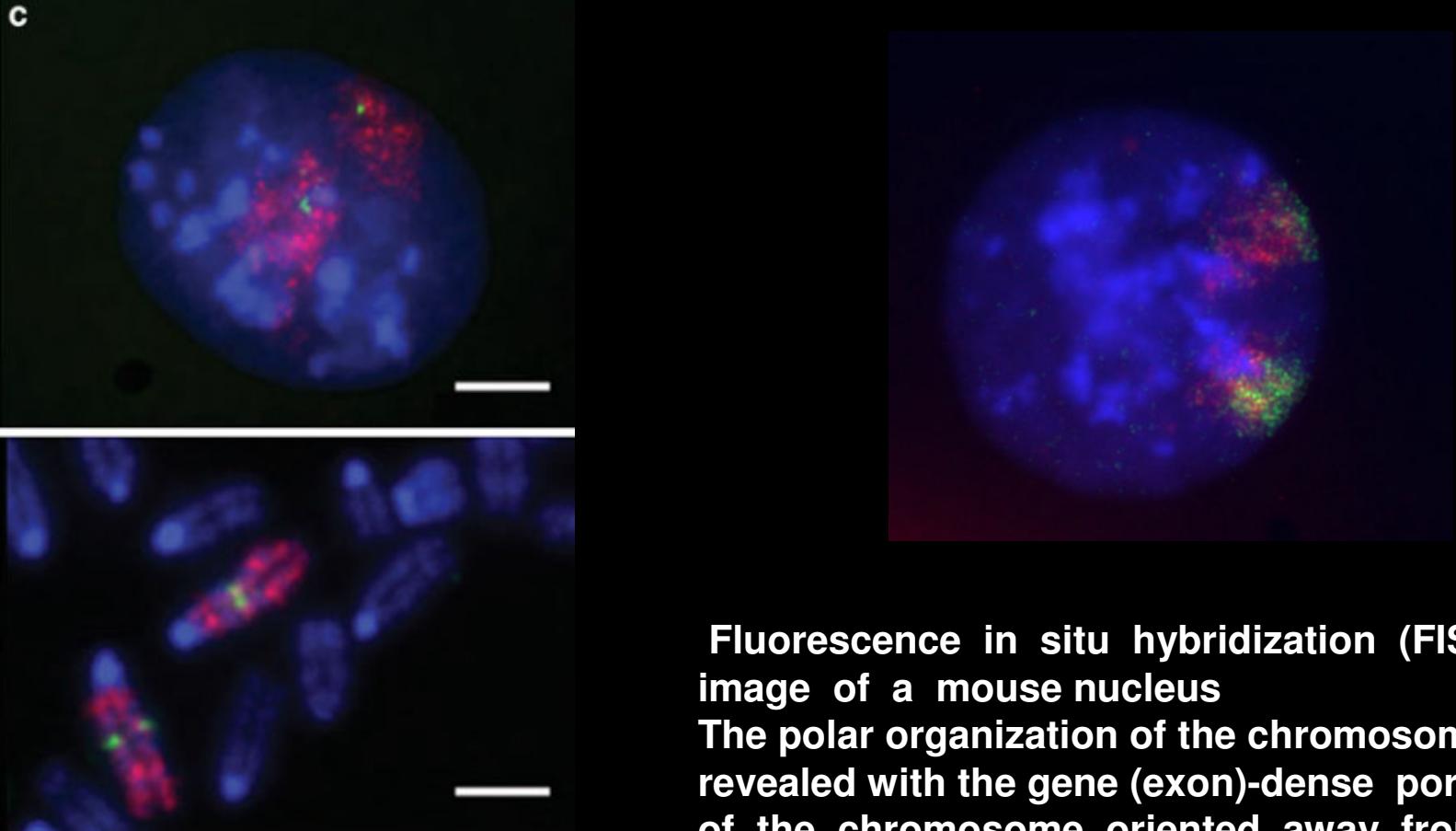
Boveri, 1909



Species specific genome structure is a kind of predisposition to translocations
Changing of nuclear architecture may lead to a new genetic system of species



T. Cremer & C. Cremer, 2001, Nature

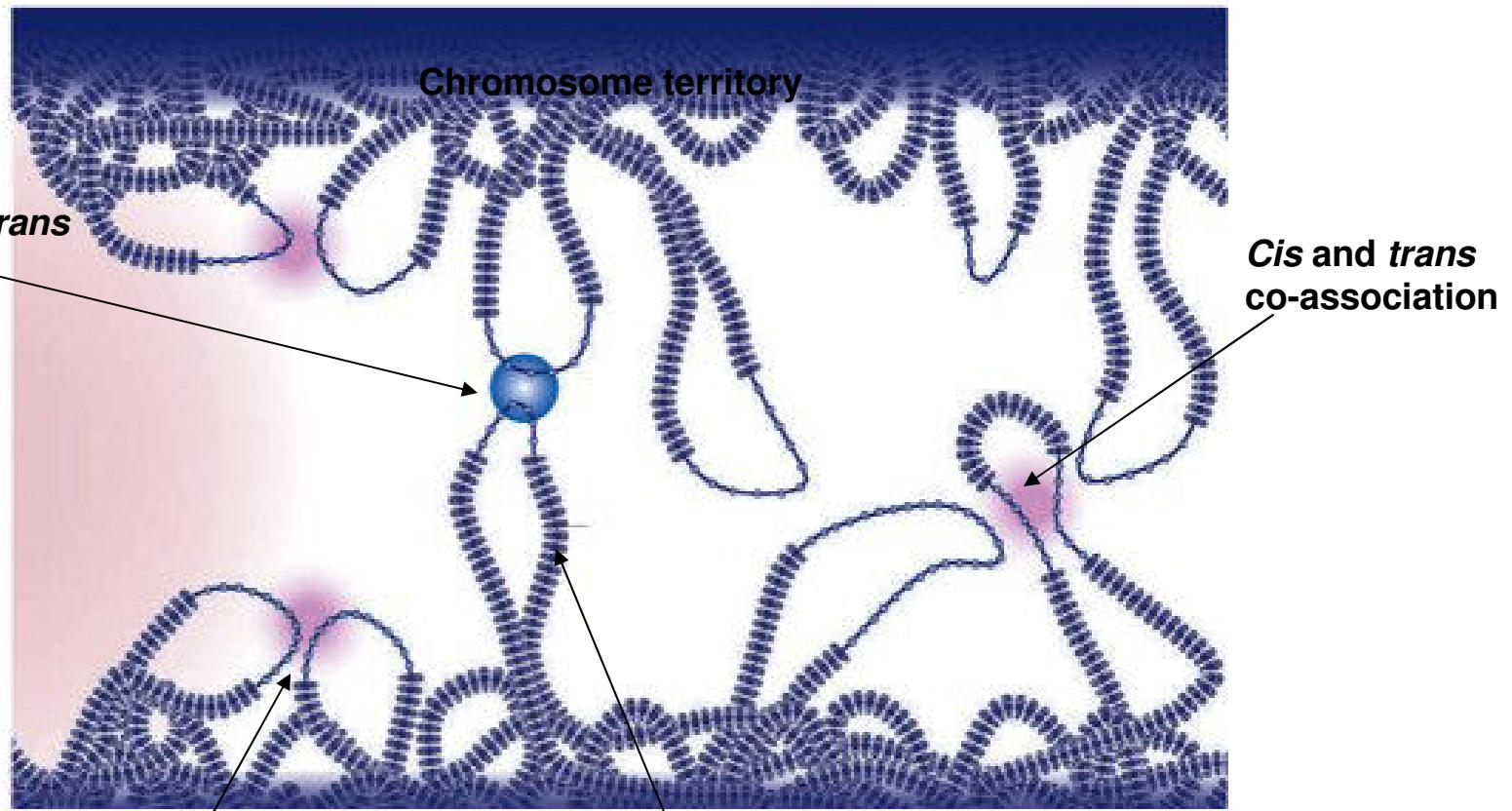


**Fluorescence in situ hybridization (FISH)
image of a mouse nucleus
The polar organization of the chromosome is
revealed with the gene (exon)-dense portion
of the chromosome oriented away from
the nuclear periphery**

Chromosome Res (2011) 19:901–909
DOI 10.1007/s10577-011-9245-0

**Fluorescence in situ hybridization with high-complexity
repeat-free oligonucleotide probes generated by massively
parallel synthesis**

Shelagh Boyle · Matthew J. Rodesch ·
Heather A. Halvensleben · Jeffrey A. Jeddeloh ·
Wendy A. Bickmore



Transcription factory

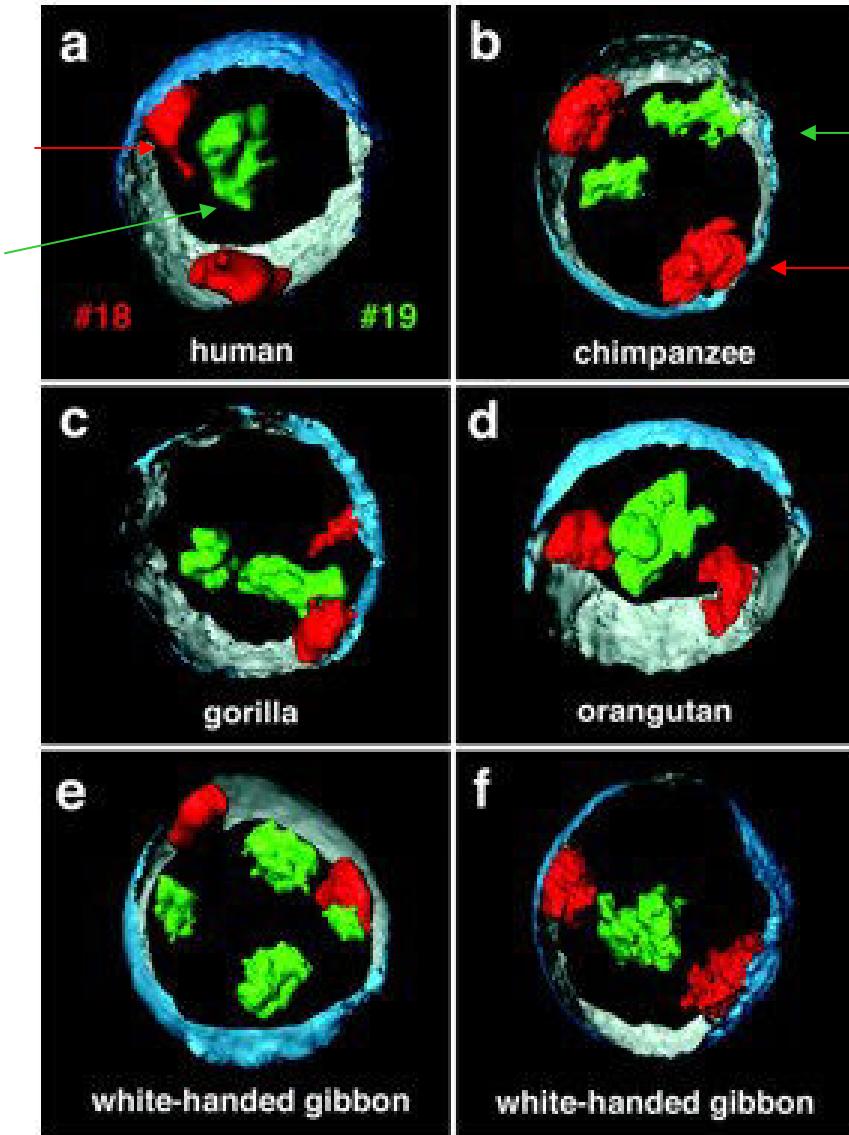
Chromatin loop

(Fraser & Bickmore, 2007)

Р а с п о л о ж е н и е х р о м о с о м и
Э к с п р е с с и я г е н о в

Human Chr 18
(gene poor)

Human Chr 19
(gene dense)

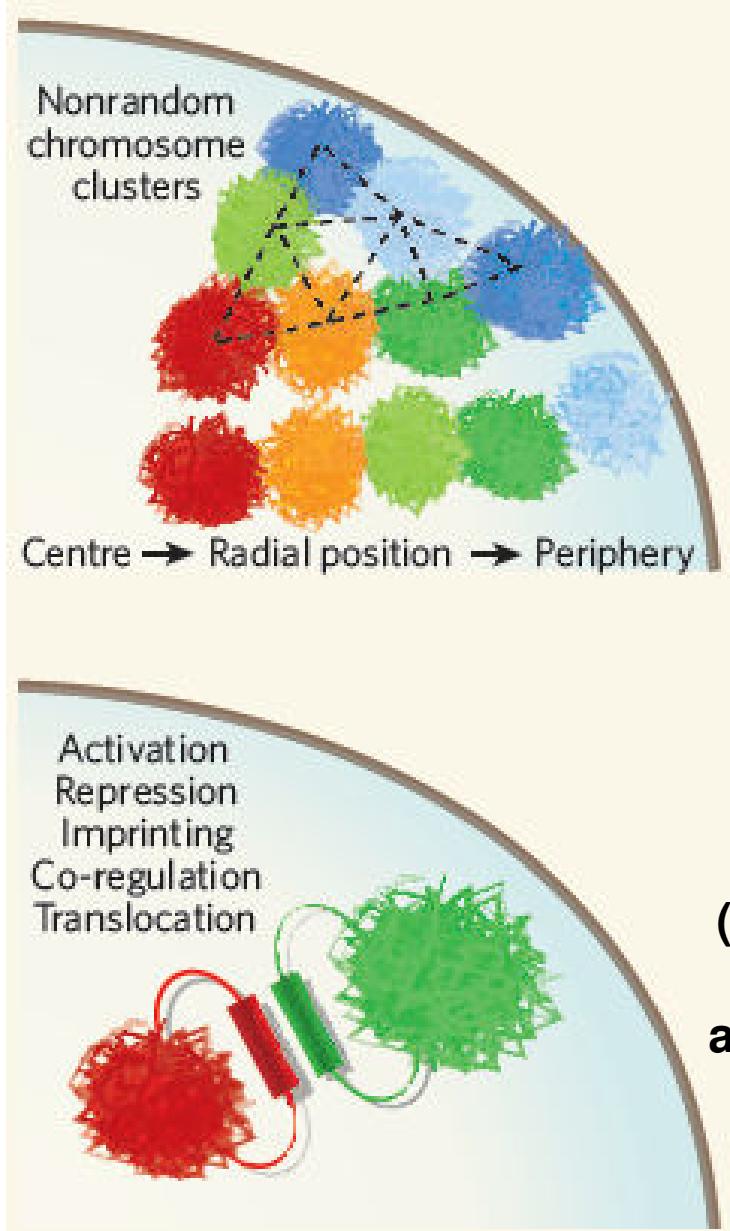


Homologous to
Human Chr 19

Homologous to
Human Chr 18

(Tanabe et al, 2002)

К о н с е р в а т и в н о с т ь х р о м о с о м н ы



**Chromosomes occupy
nonrandom radial positions relative to
the centre of the nucleus**

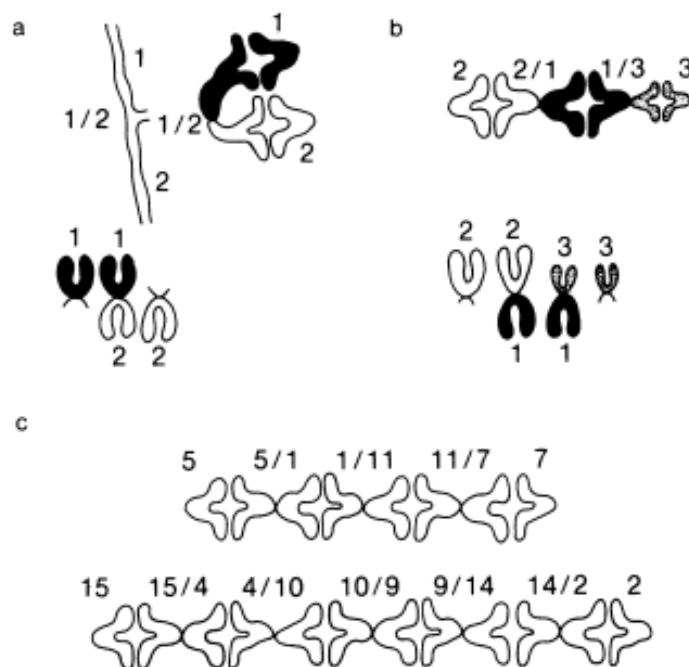
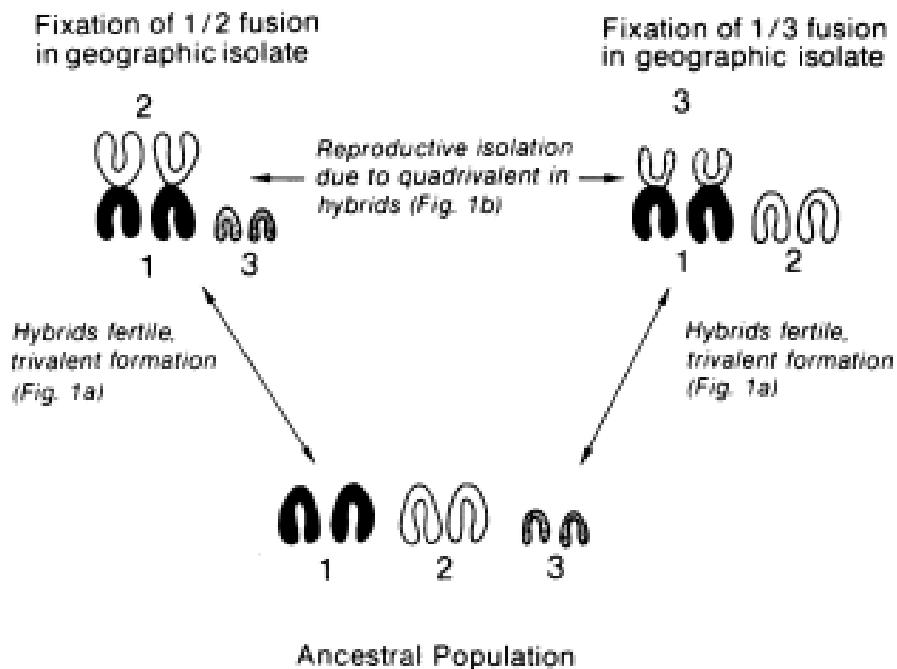
**Changing the
relative arrangement of genome regions
(coloured rectangles) to bring them into close
proximity is functionally relevant for gene
activity, and for the formation of chromosomal
translocations**

**Species-specific genome structure is a kind of predisposition to translocations
Changing of nuclear architecture may lead to a new genetic system of species**

Speciation by monobrachial centric fusions

(chromosomes/reproductive isolation/cryptic species/population genetics)

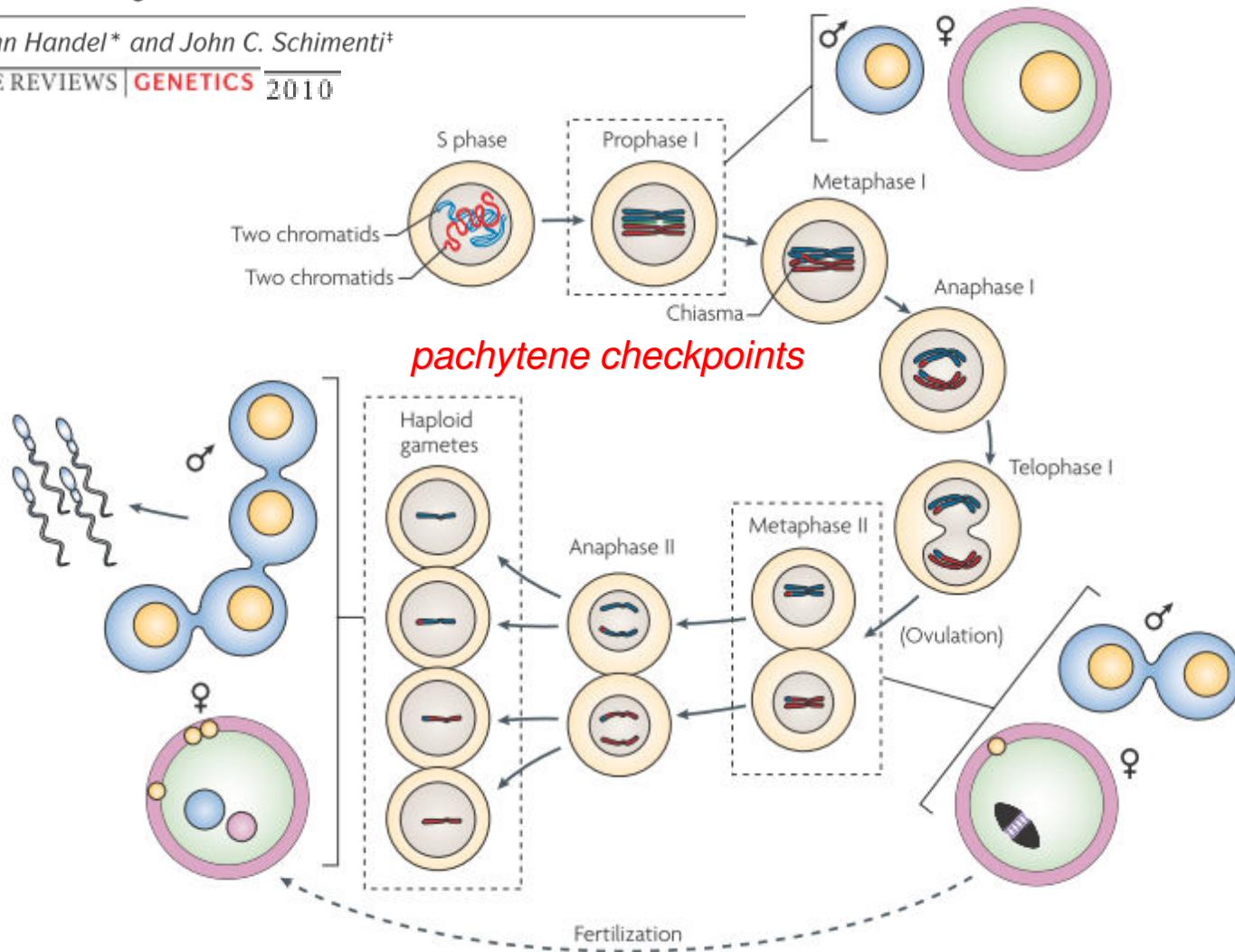
ROBERT J. BAKER* AND JOHN W. BICKHAM†



Genetics of mammalian meiosis: regulation, dynamics and impact on fertility

Mary Ann Handel* and John C. Schimenti†

NATURE REVIEWS | GENETICS 2010



Female Meiosis Drives Karyotypic Evolution in Mammals

Fernando Pardo-Manuel de Villena* and Carmen Sapienza†

1181

Female Meiotic Drive in Evolution

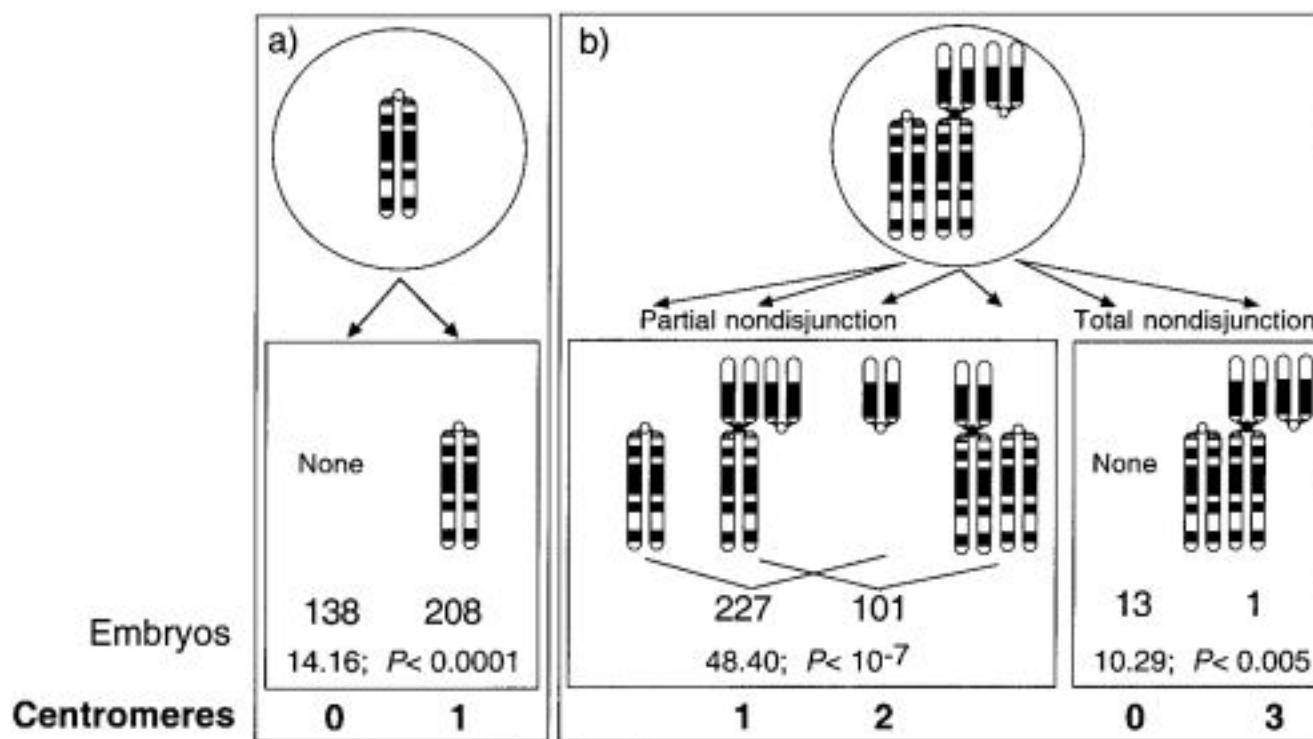
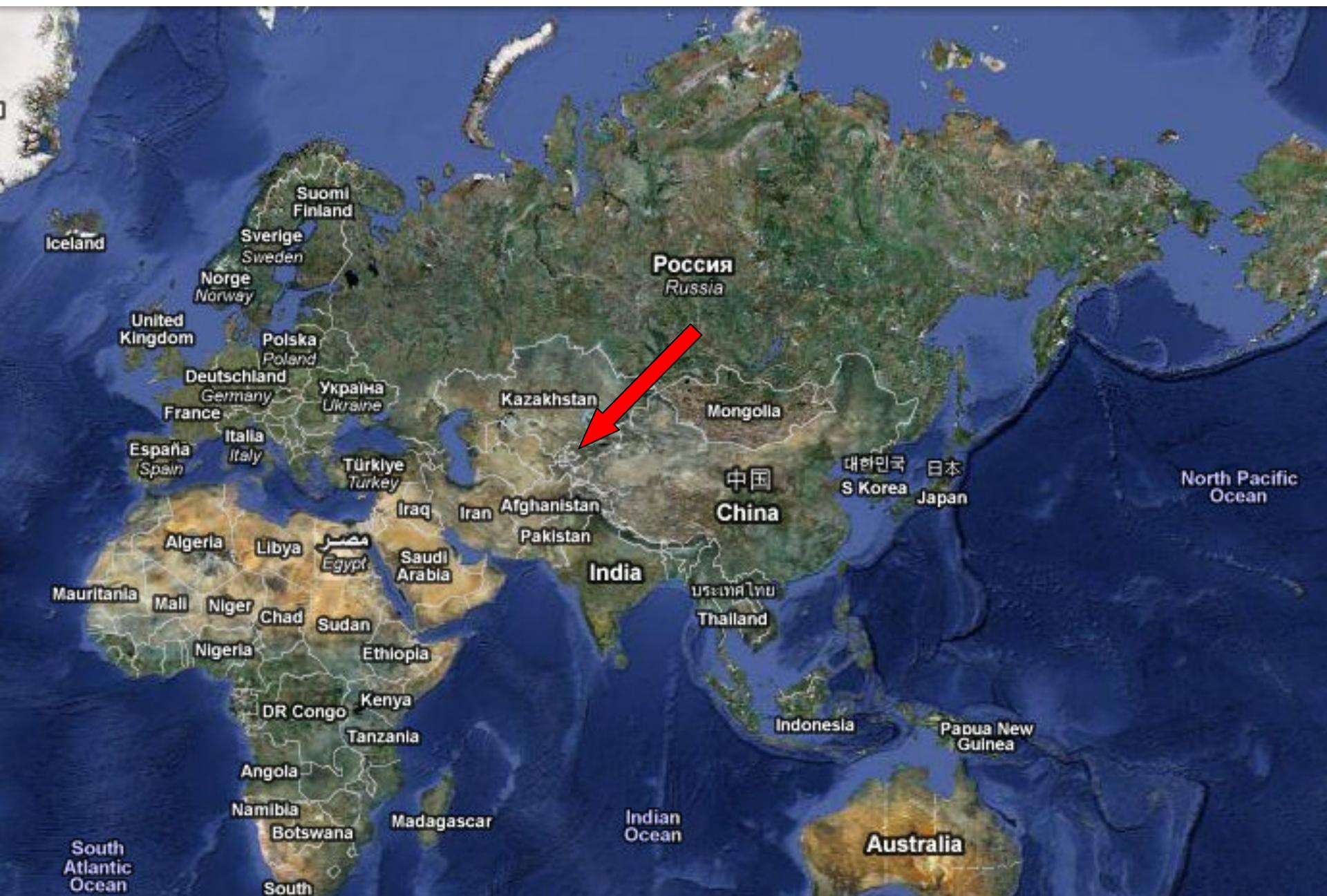
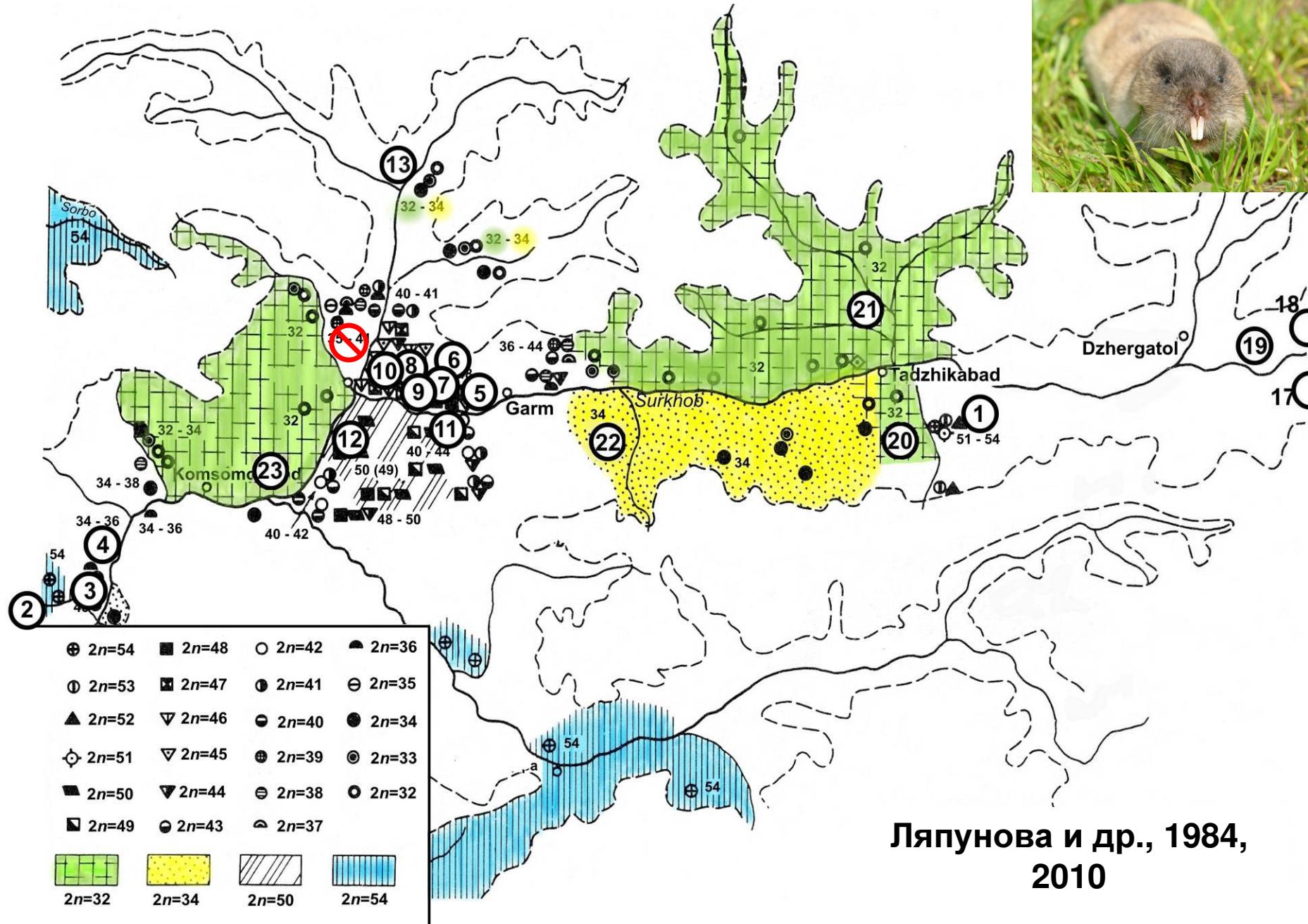
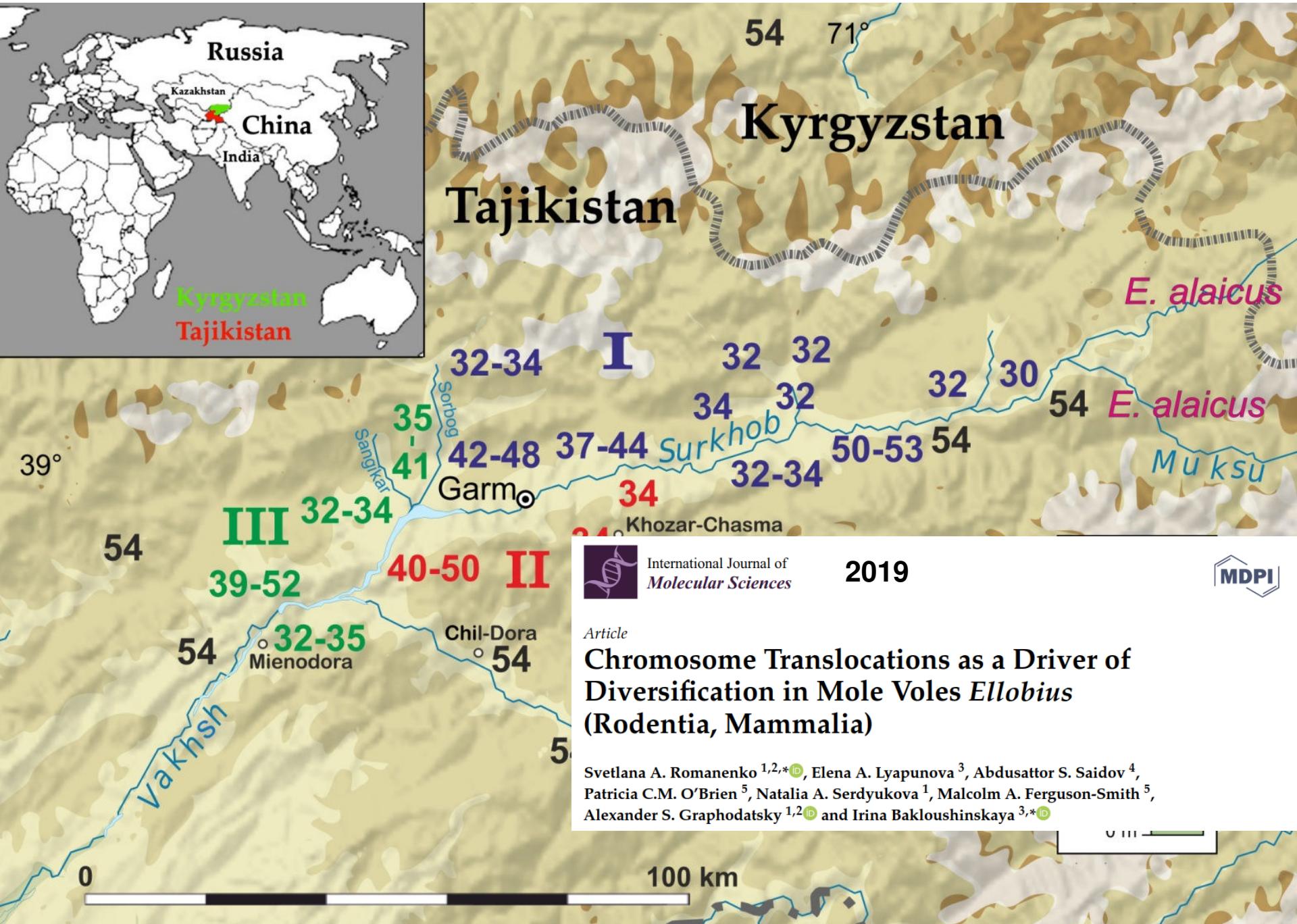
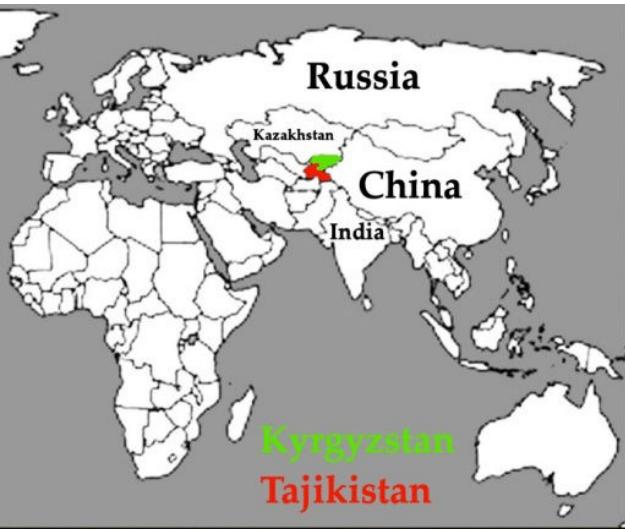


FIGURE 2.—Chromosome segregation in unbalanced products of female meiosis. Segregation in *XO* female mice (a) and segregation in chickens that are balanced carriers of chromosome fissions (b) are depicted. Top row of numbers in each box is the number of meiotic products containing the chromosome depicted above. In b, the top row of numbers represents the sum of all unbalanced products with the indicated number of centromeres. Bottom row of numbers in each box is the χ^2 , followed by the P -value for H_0 : random segregation.







International Journal of
Molecular Sciences

2019

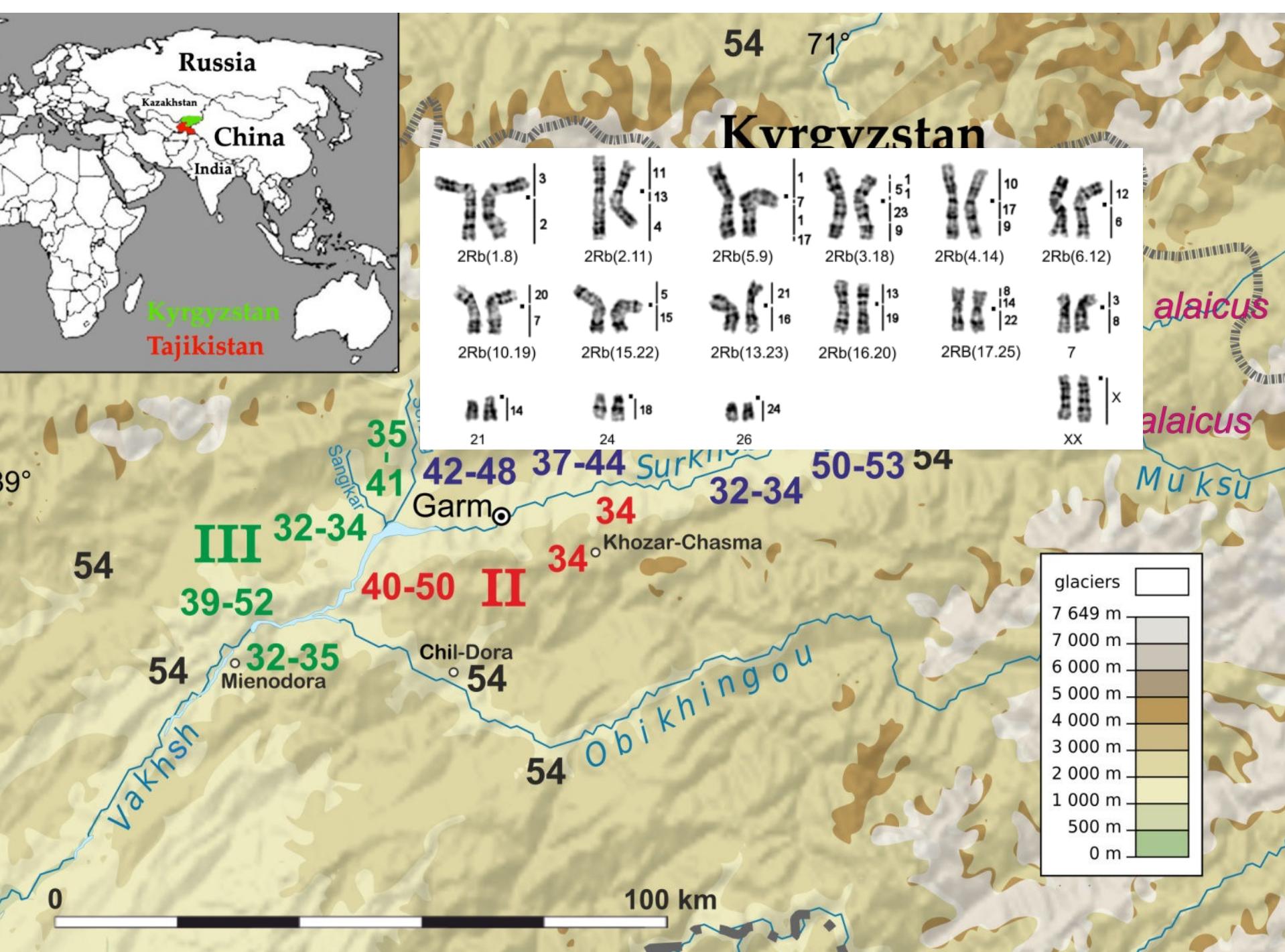


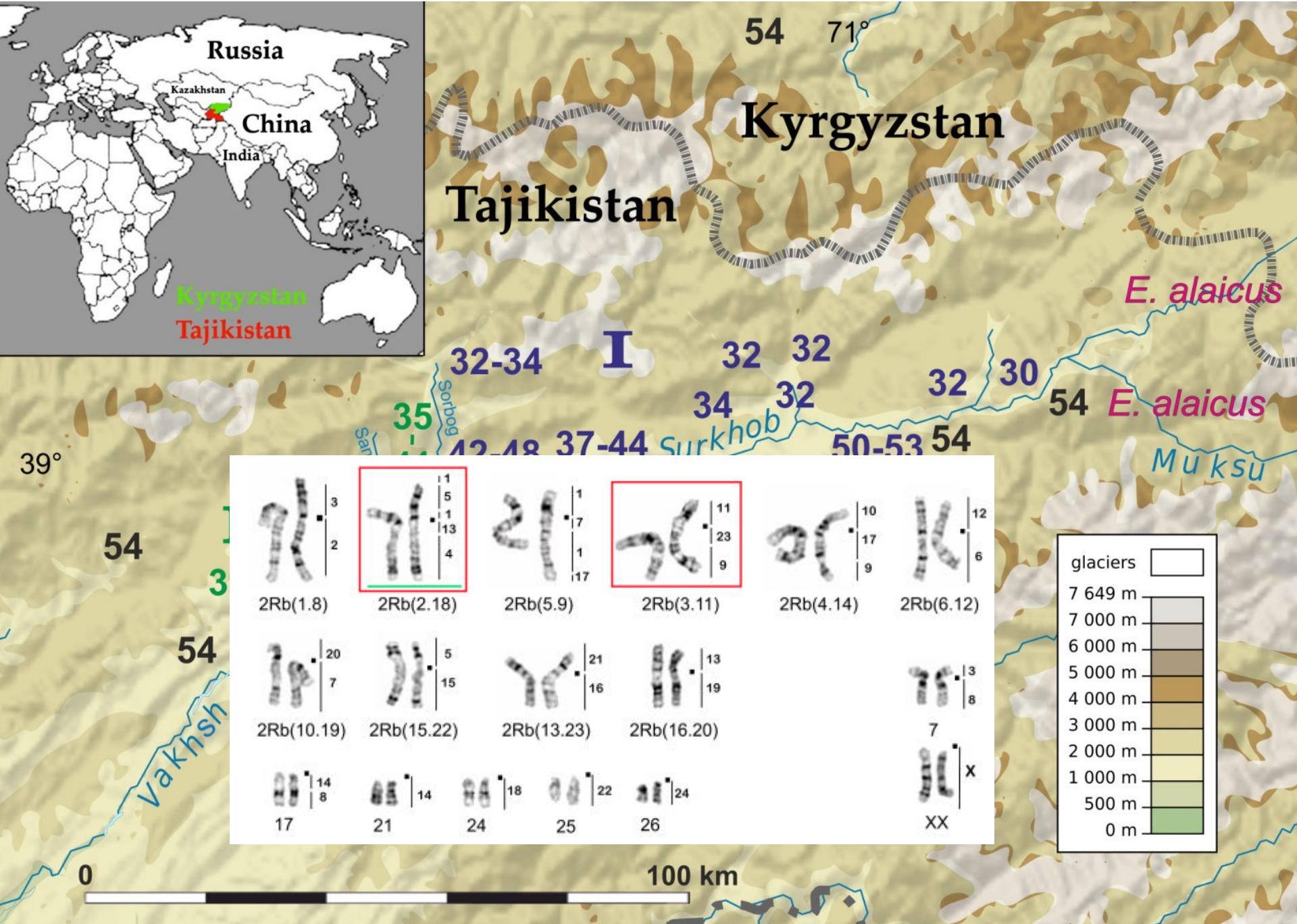
Article

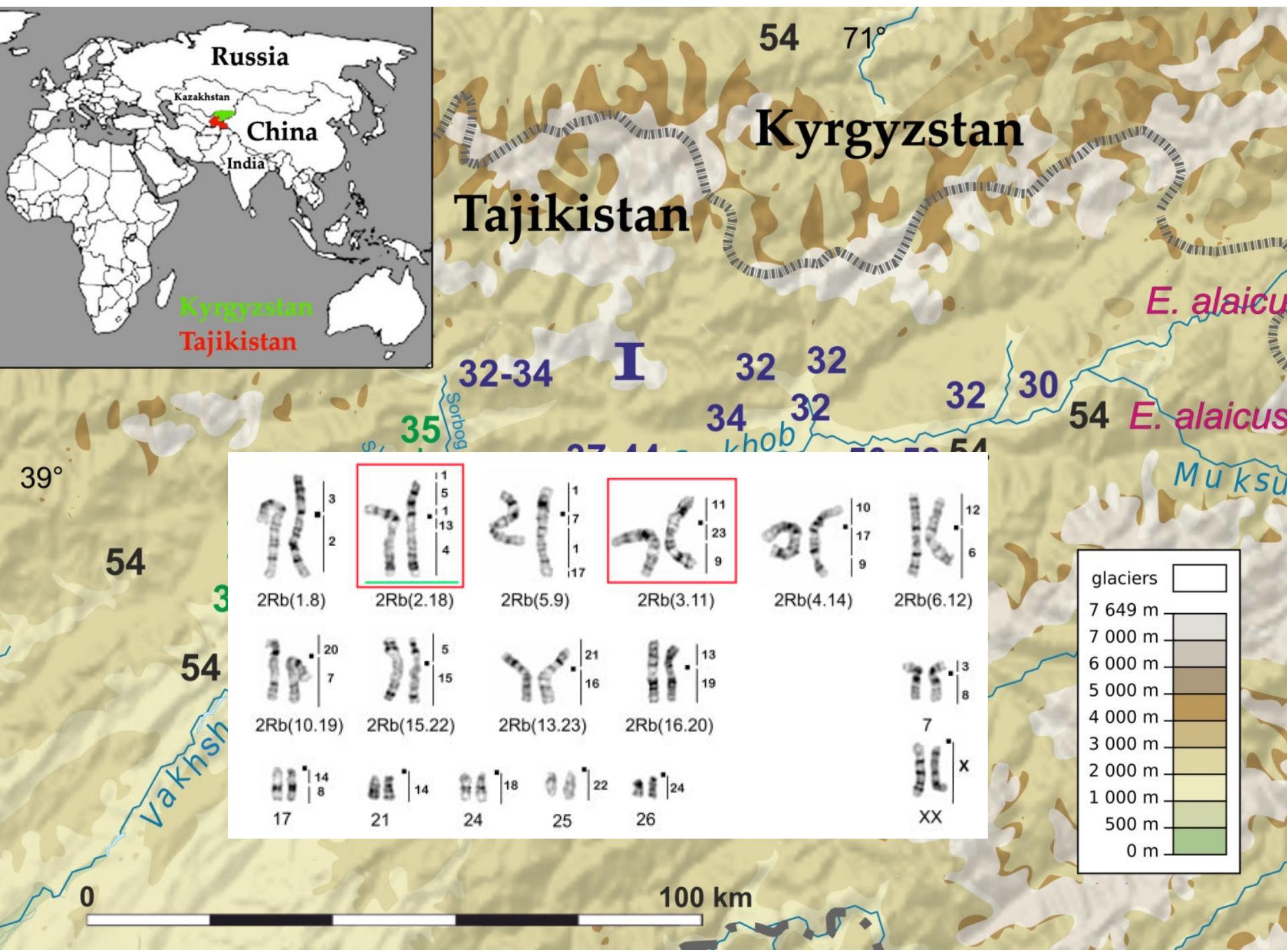
Chromosome Translocations as a Driver of Diversification in Mole Voles *Ellobius* (Rodentia, Mammalia)

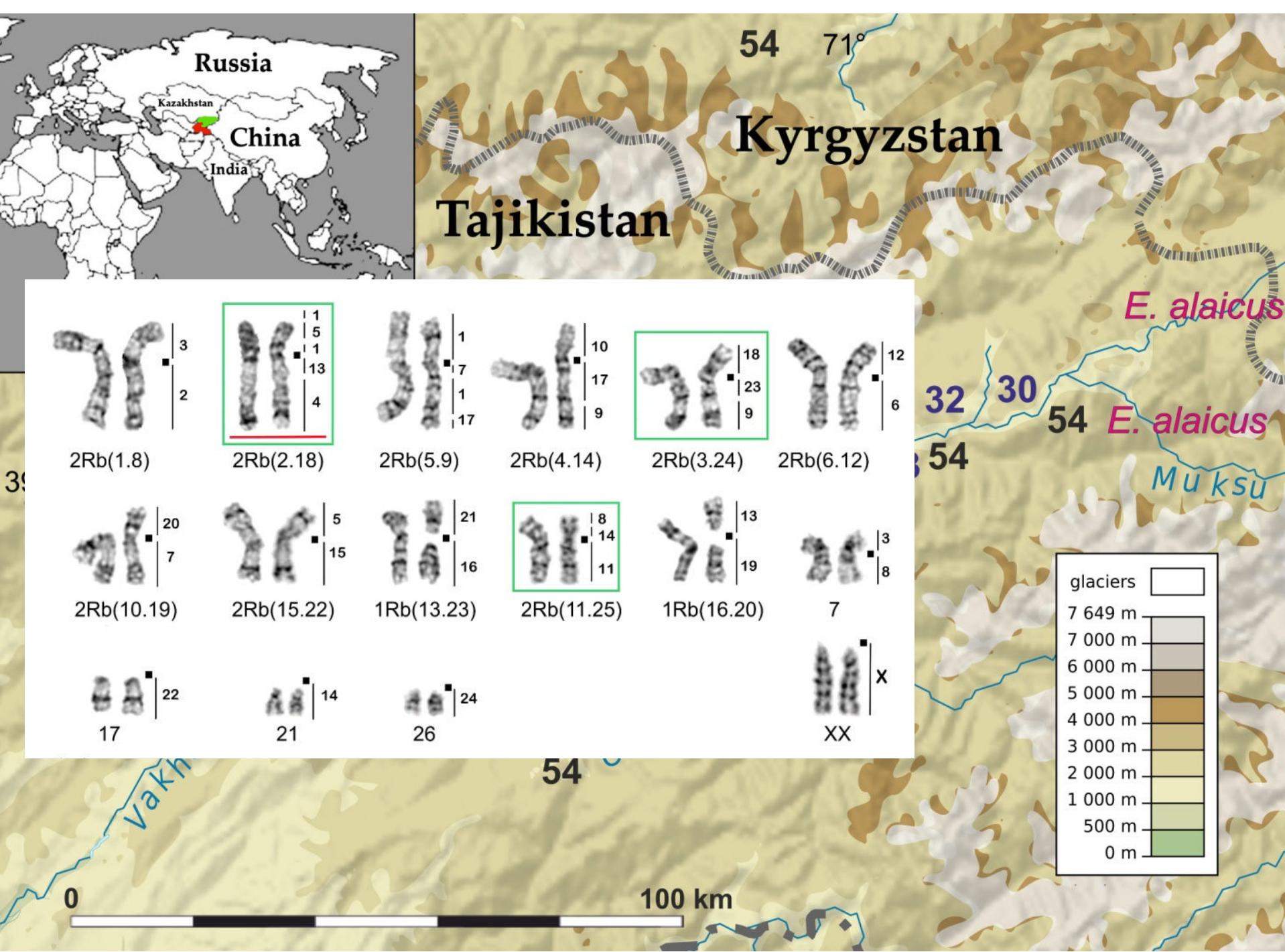
Svetlana A. Romanenko ^{1,2,*} , Elena A. Lyapunova ³, Abdusattor S. Saidov ⁴, Patricia C.M. O'Brien ⁵, Natalia A. Serdyukova ¹, Malcolm A. Ferguson-Smith ⁵, Alexander S. Graphodatsky ^{1,2} and Irina Bakloushinskaya ^{3,*}

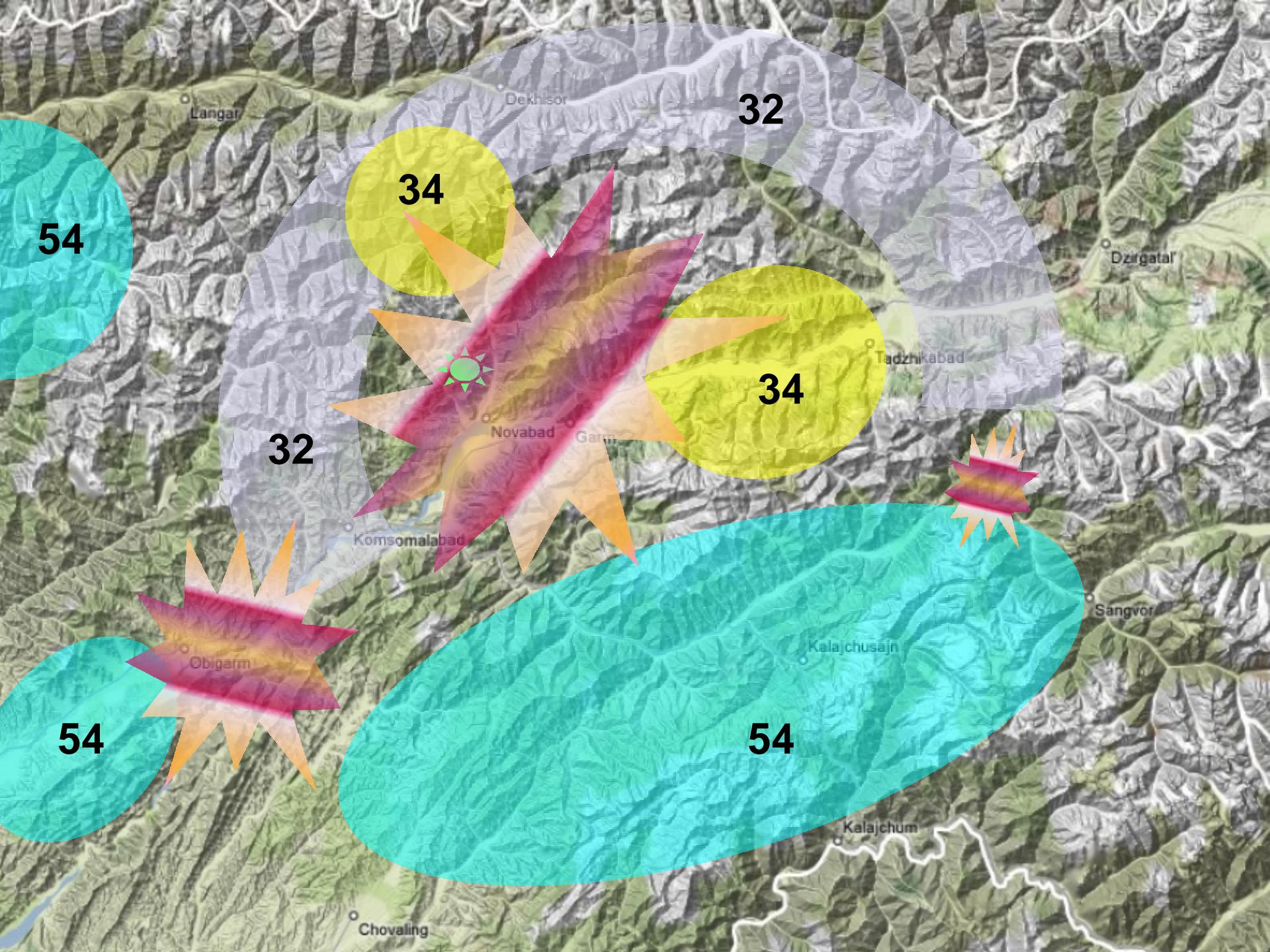
100 km

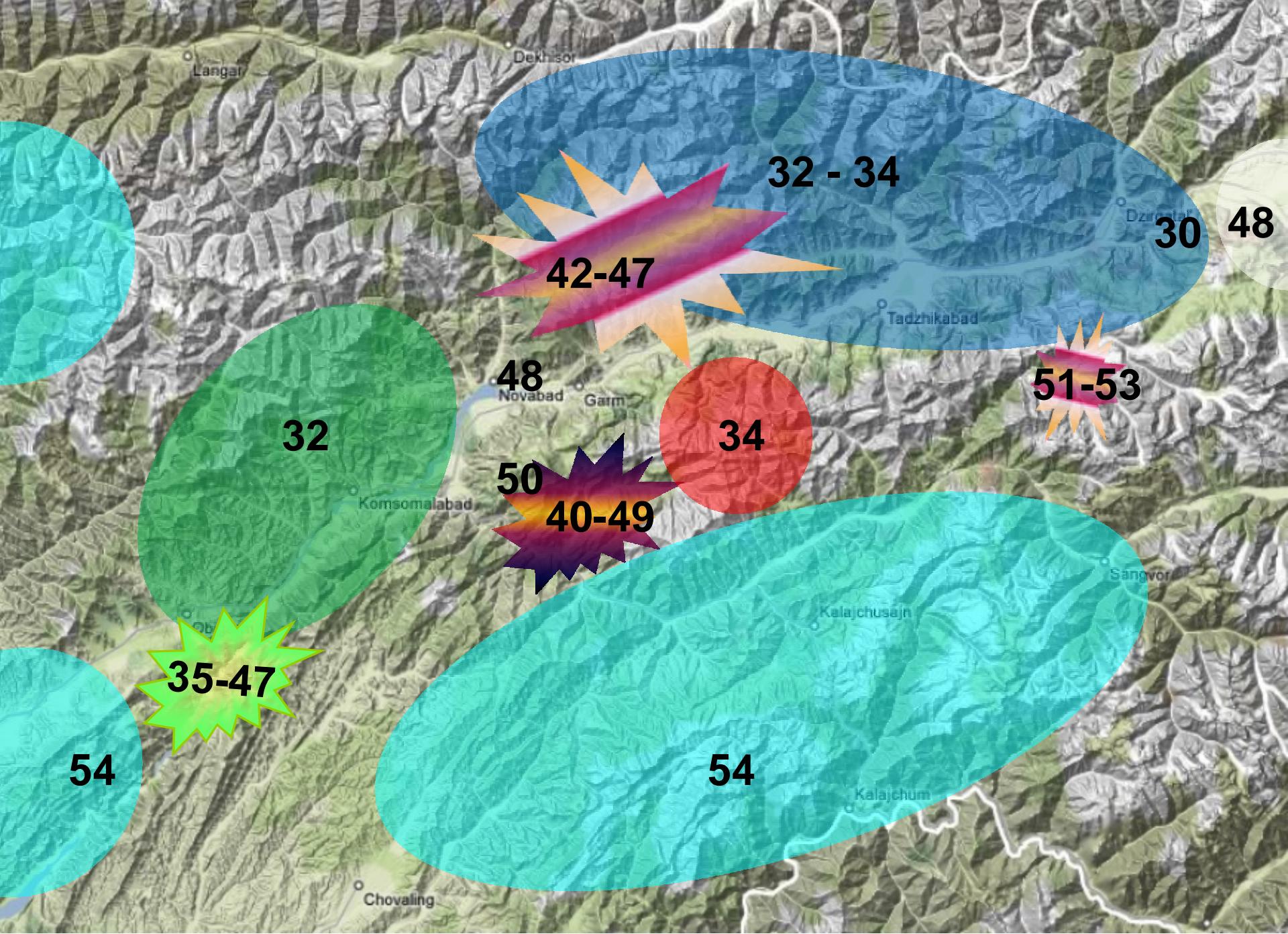


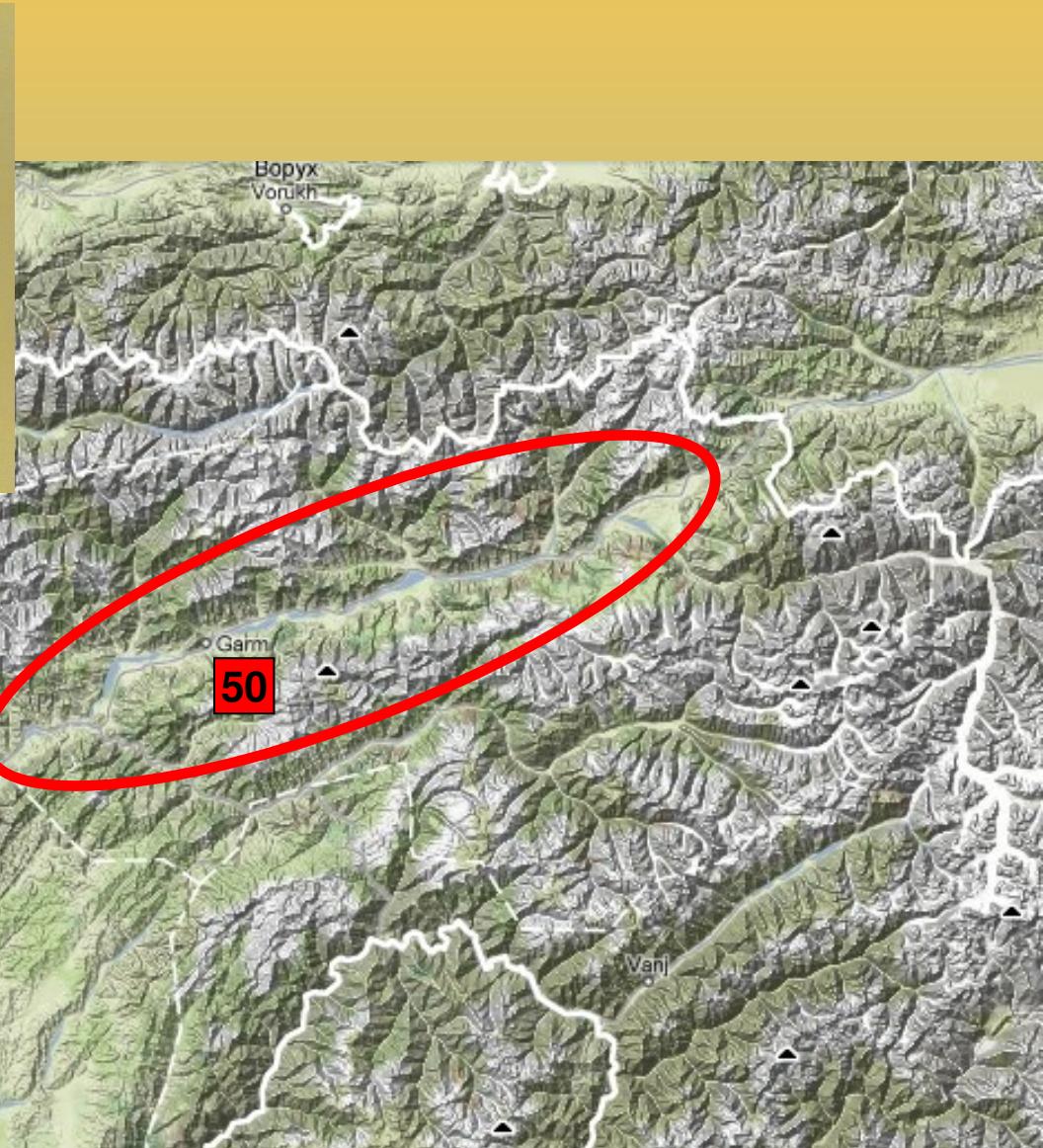
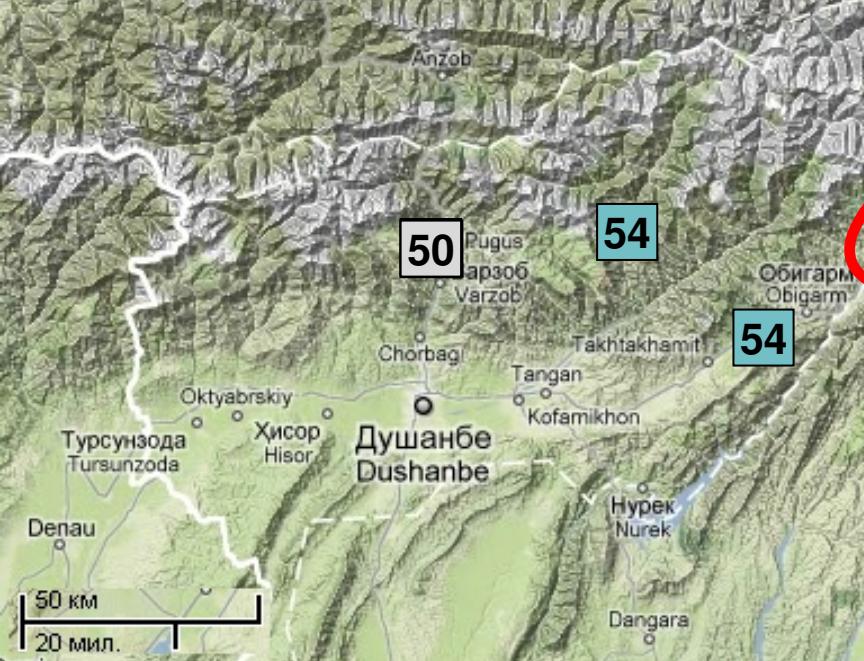




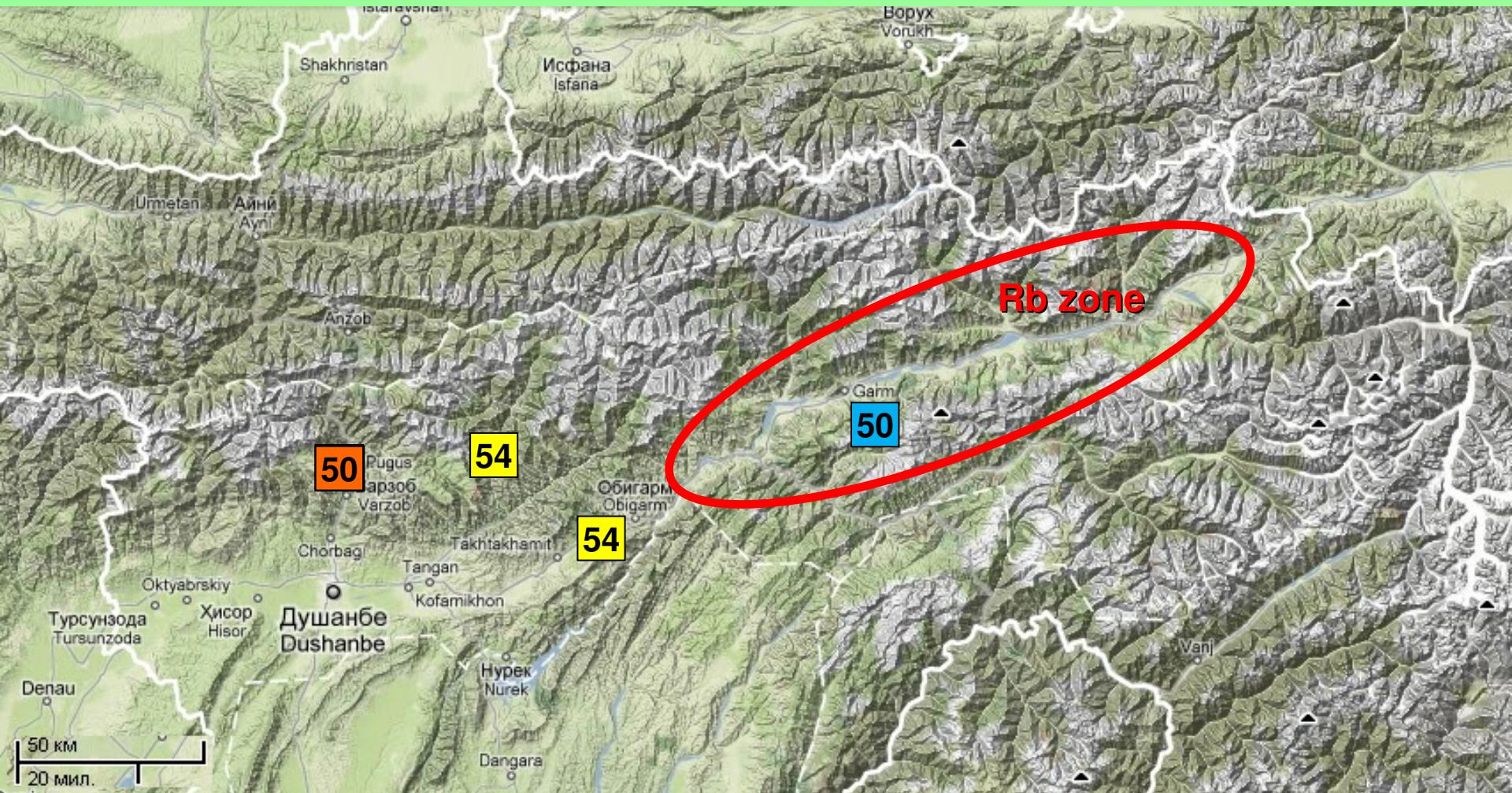








Монобрахиальная гомология – эксперимент по скрещиванию



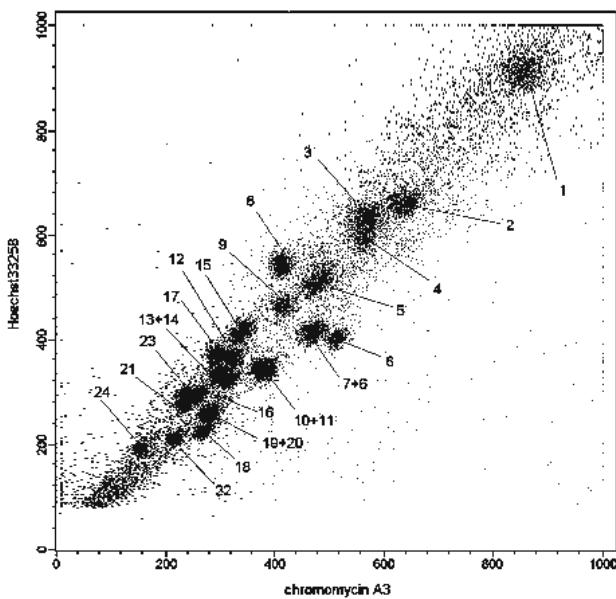
Pamiro-Alay, zone of Robertsonian polymorphism

- 50 Khodzha-Obi-Garm
- 50 Voidara

Rb zone $2n=53-30$

Chromosomal evolution of Arvicolinae (Cricetidae, Rodentia). I. The genome homology of tundra vole, field vole, mouse and golden hamster revealed by comparative chromosome painting

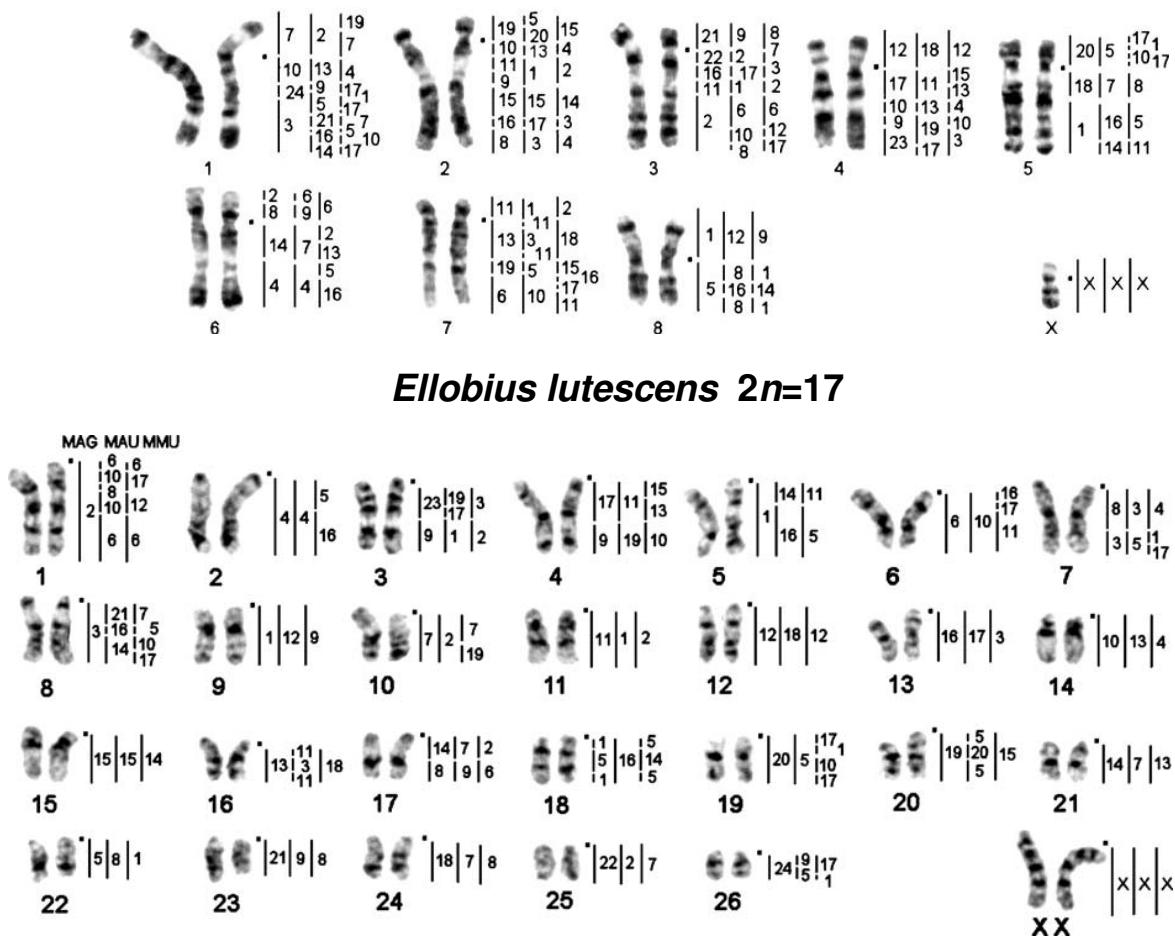
Natalia A. Sitnikova¹, Svetlana A. Romanenko¹, Patricia C. M. O'Brien², Polina L. Perelman¹, Beiyuan Fu², Nadezhda V. Rubtsova¹, Natalya A. Serdukova¹, Feodor N. Golenishchev³, Vladimir A. Trifonov^{1,2}, Malcolm A. Ferguson-Smith², Fengtang Yang⁴ & Alexander S. Graphodatsky^{1*}



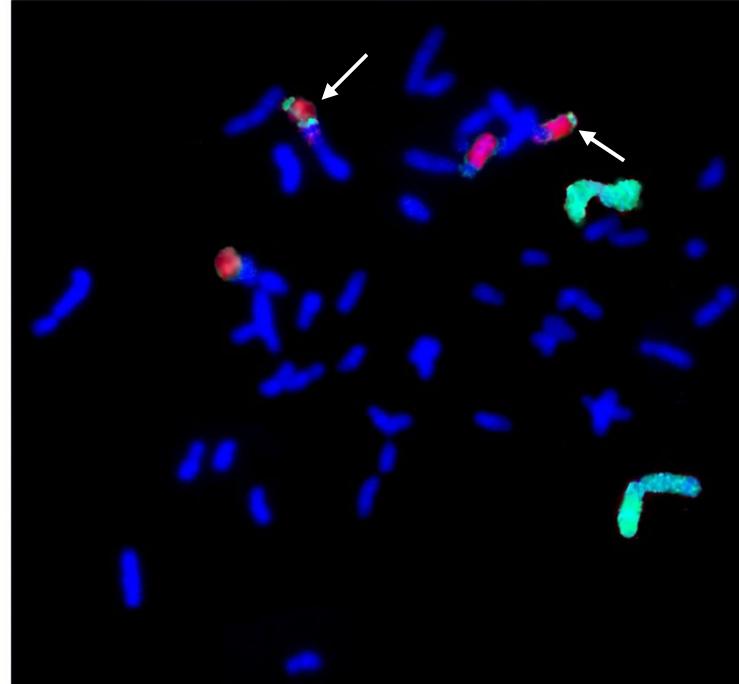
Bivariate flow karyotype of the field vole (*M. agrestis*) cells with autosomal assignments. The giant sex chromosomes are located outside of the illustrated area.

Chromosomal evolution of Arvicolinae (Cricetidae, Rodentia). II. The genome homology of two mole voles (genus *Ellobius*), the field vole and golden hamster revealed by comparative chromosome painting

Svetlana A. Romanenko¹, Natalia A. Sitnikova¹, Natalya A. Serdukova¹, Polina L. Perelman¹, Nadezhda V. Rubtsova¹, Irina Yu. Bakloushinskaya², Elena A. Lyapunova², Walter Just³, Malcolm A. Ferguson-Smith⁴, Fengtang Yang⁵ & Alexander S. Graphodatsky^{1*}

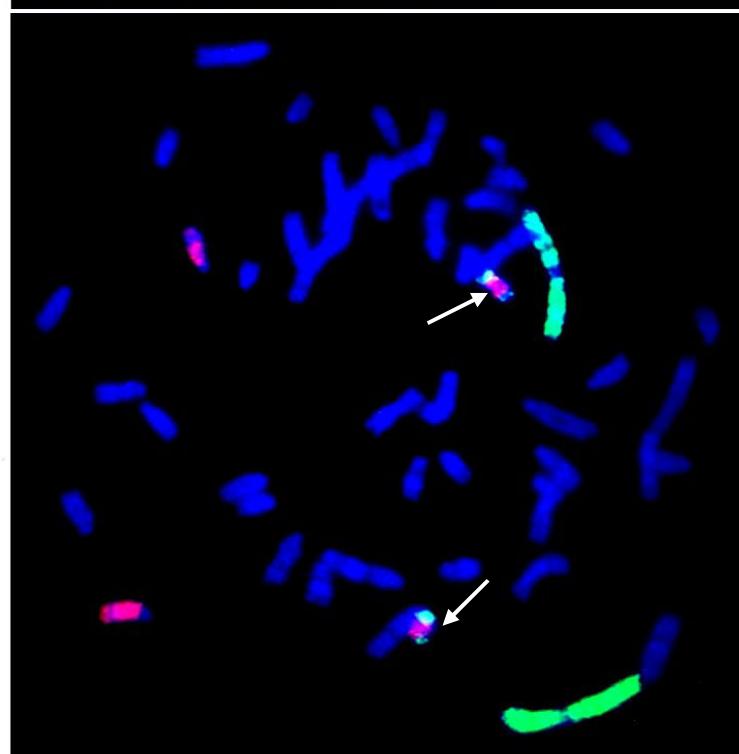


Ellobius talpinus 2n=54



Zoo-FISH

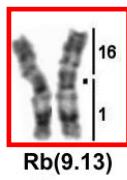
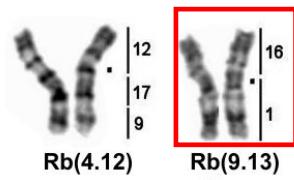
Ellobius tancrei
2n=50
Nº1733 ♂



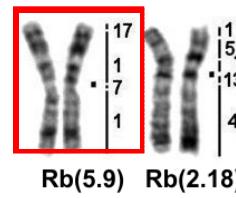
MAG1-5

Ellobius tancrei
2n=48
1736 ♀

Скрещивание форм с $2n=50$

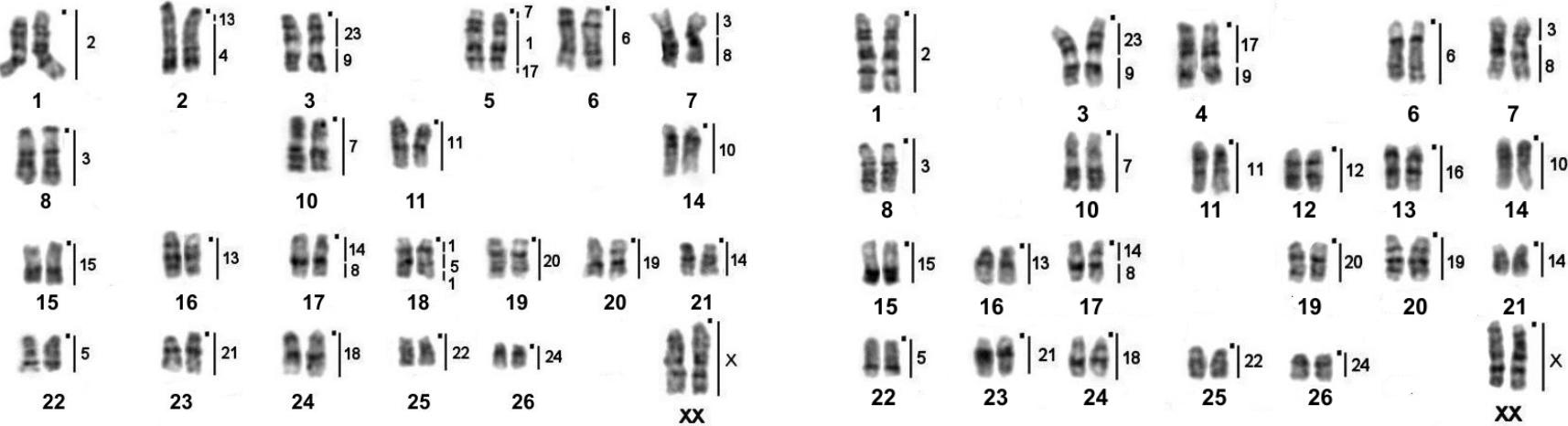


1738 самка
Ходжа-Оби-Гарм



Rb(2.18)

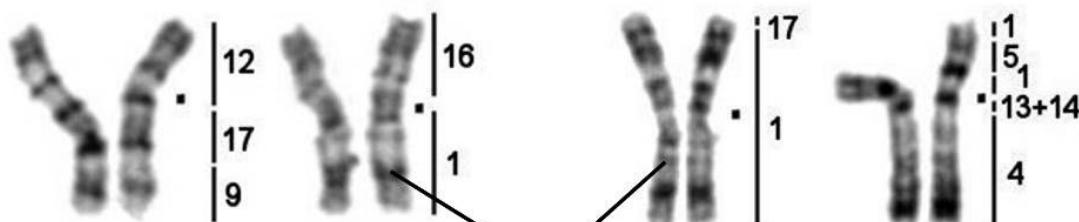
1733 самец
Войдара



R самка
Ходжа-Оби-Гарм

$2n=50$

$2n=50$



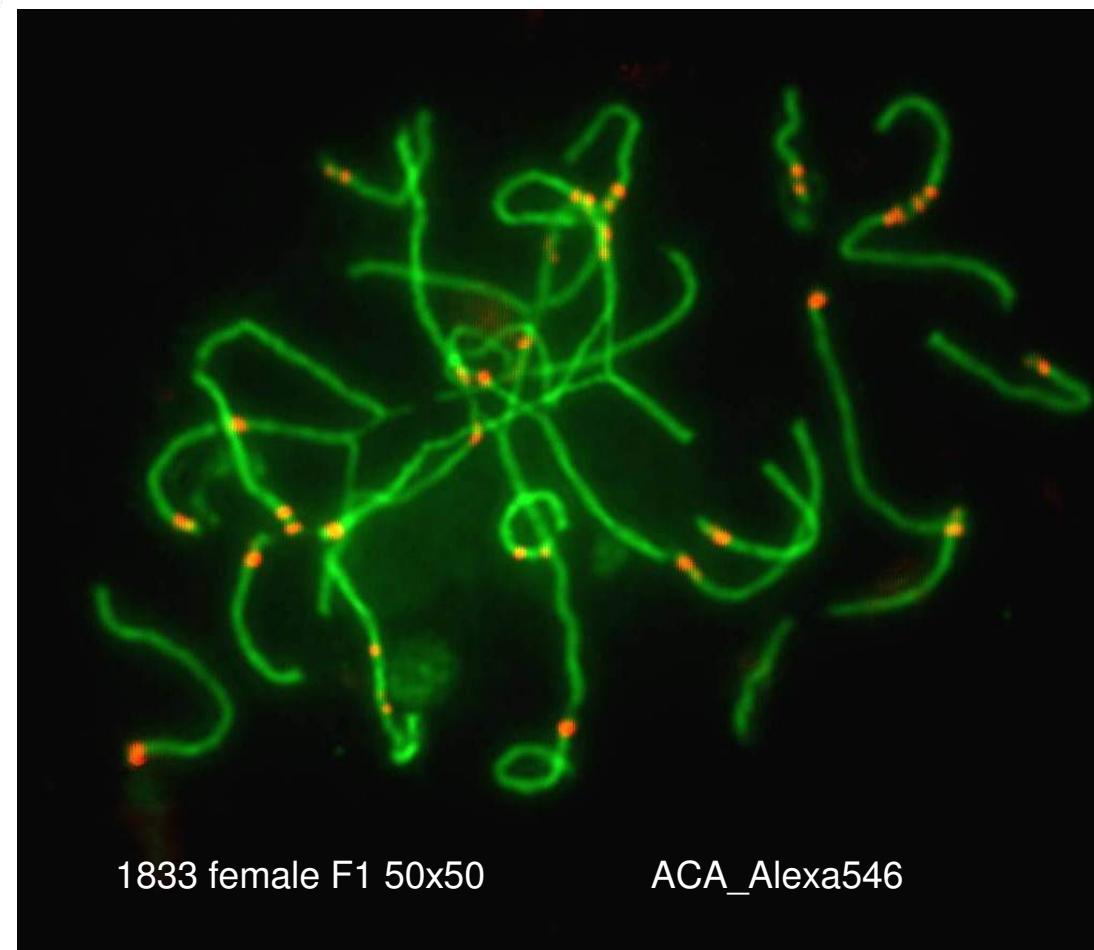
Khodza-Obi-Garm

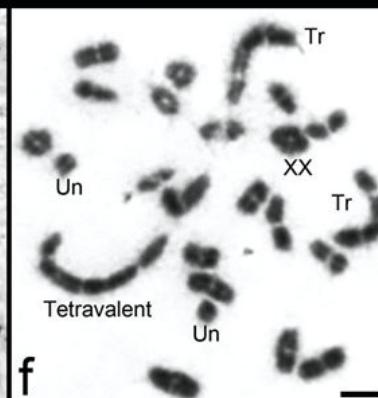
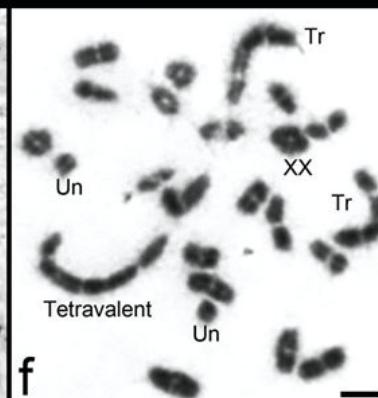
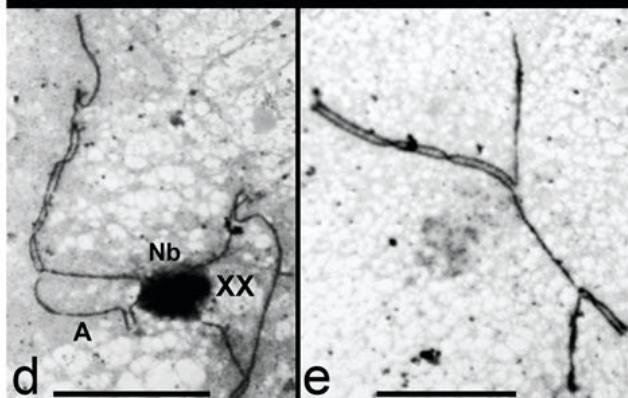
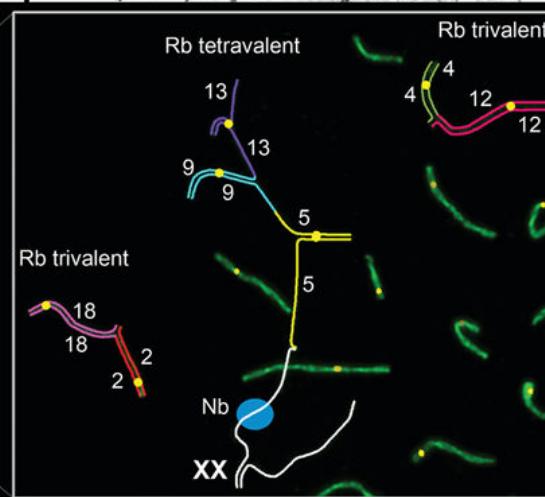
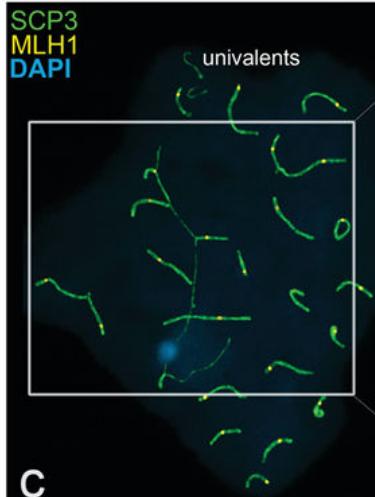
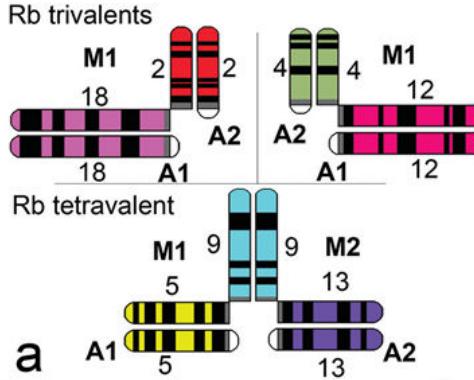
homology

Voidara

Monobrachial Homology

F1

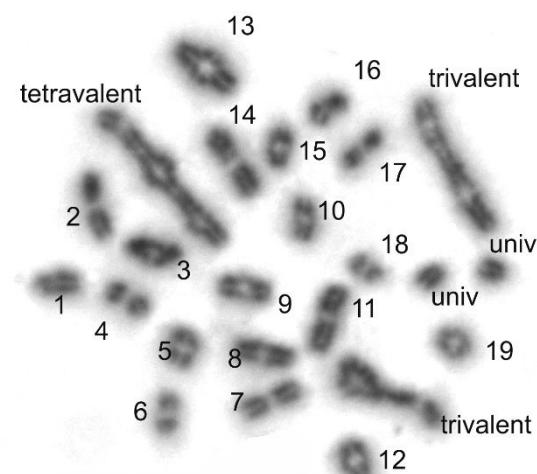




Analysis of meiotic chromosome structure and behavior in Robertsonian heterozygotes of *Ellobius tancrei* (Rodentia, Cricetidae): a case of monobrachial homology

Sergey Matveevsky¹, Irina Bakloushinskaya², Valentina Tambovtseva³,
 Svetlana Romanenko^{4,5}, Oxana Kolomiets¹

**Профаза мейоза I гибридов F1,
скрещивание форм *E. tancrei***
 $2n = 50$, $NF = 56$



50x50

Breeding
strict inbreeding (sibs)

Parental fertility

P1 x P2 30 litters, 86 pups
 $(2,87 \pm 0,57)$

Hybrid fertility

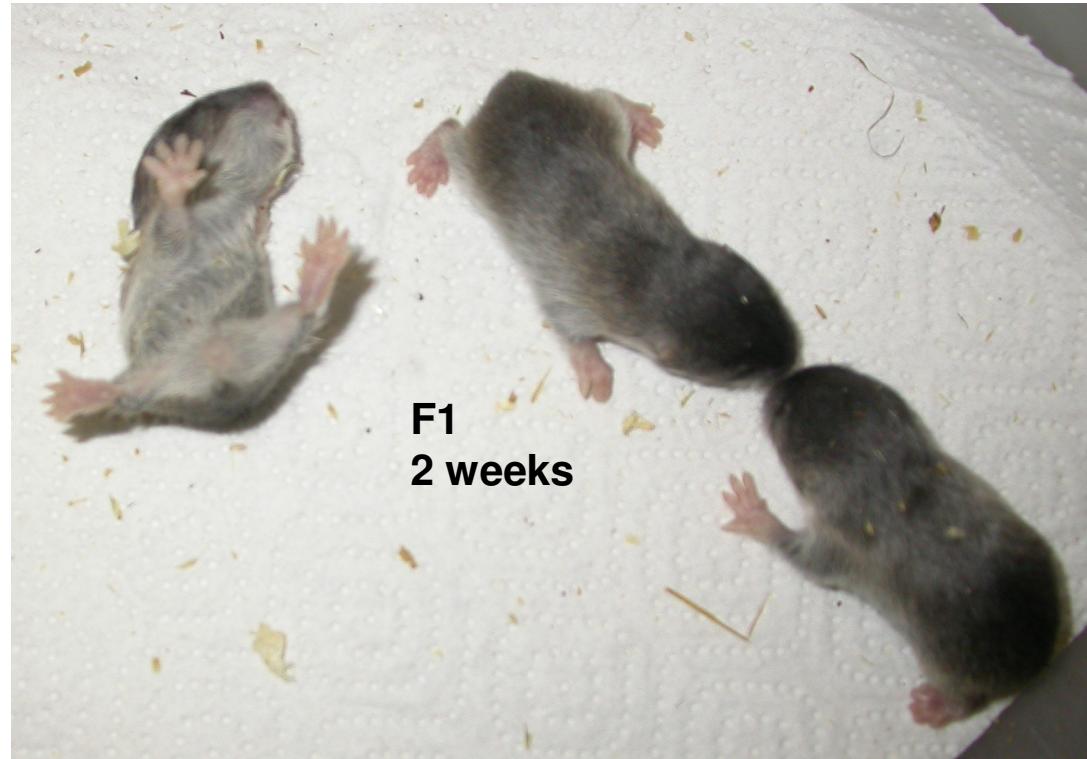
F1 44 litters, 71 pups
 $(1,61 \pm 0,84)$
F2 45 litters, 98 pups
 $(2,18 \pm 0,83)$

...

F11

**277 litters
613 animals**

F6
newborn

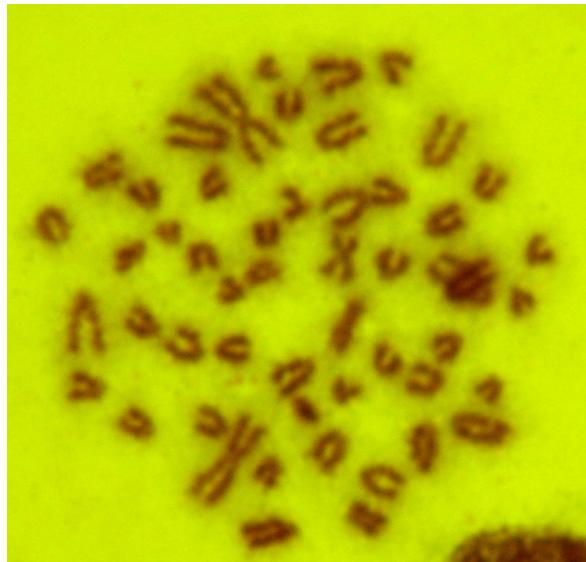


**F1
2 weeks**

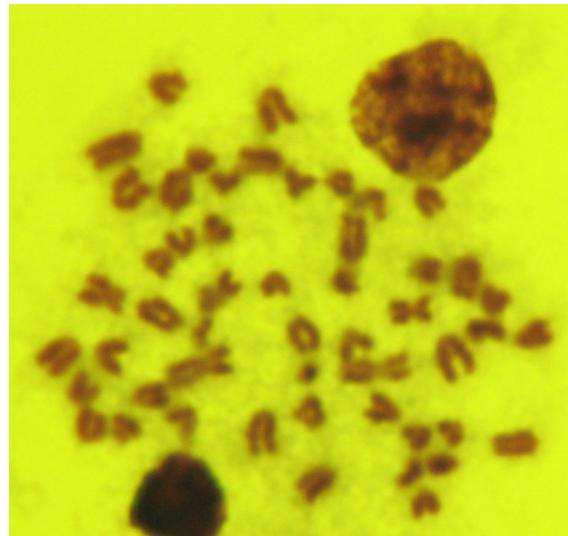


**F4
2 weeks**

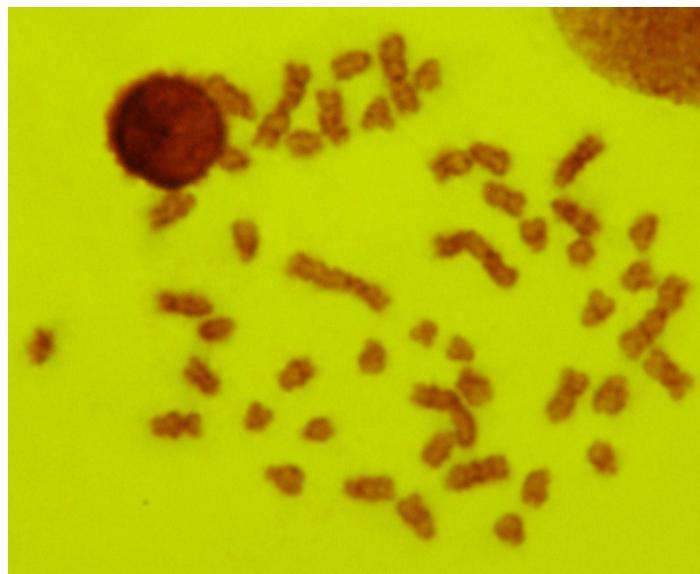
F2 female 26433 2n=52 2Rb(9.13)



F2 male 26334 2n=52 1Rb(4.12) 1Rb(9.13)



F2 male 26432 2n=48 2 Rb(2.18), 2Rb(4.12), 1Rb(9.13), 1(5.9)

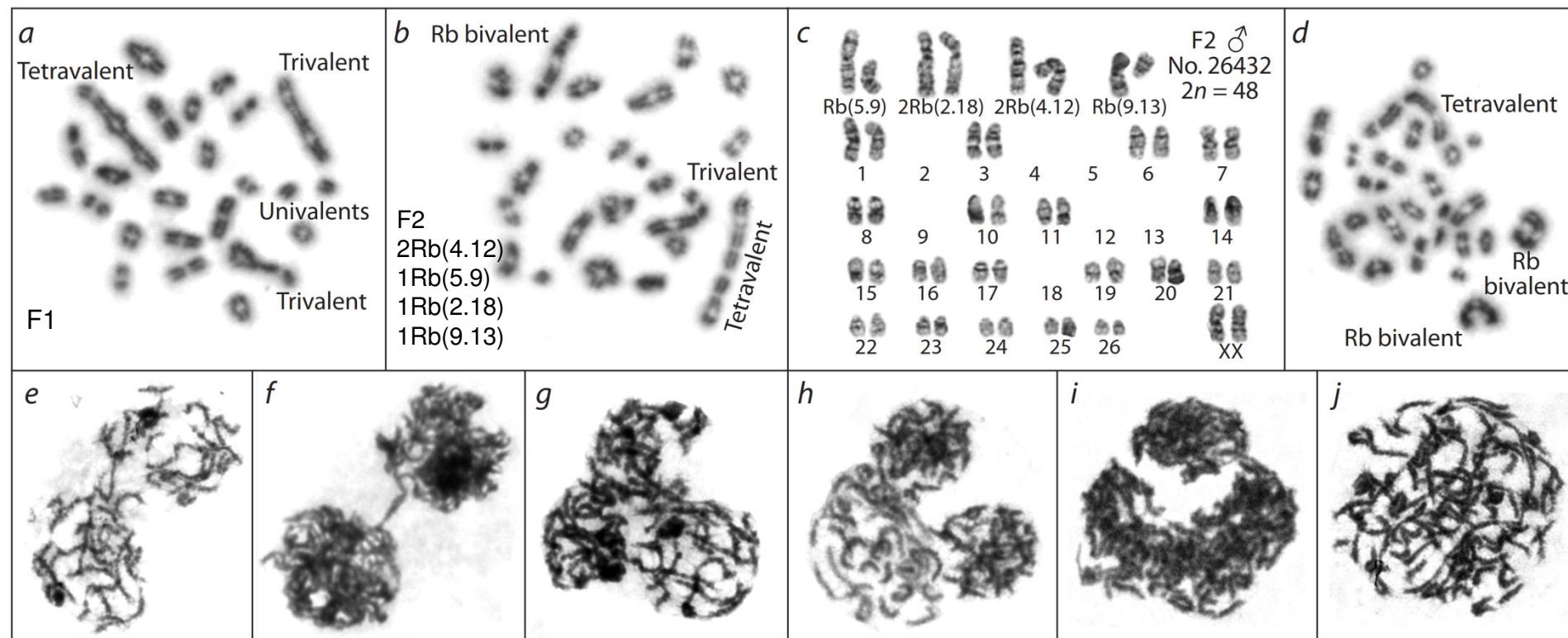


F2



A meiotic mystery in experimental hybrids of the eastern mole vole (*Ellobius tancrei*, Mammalia, Rodentia)

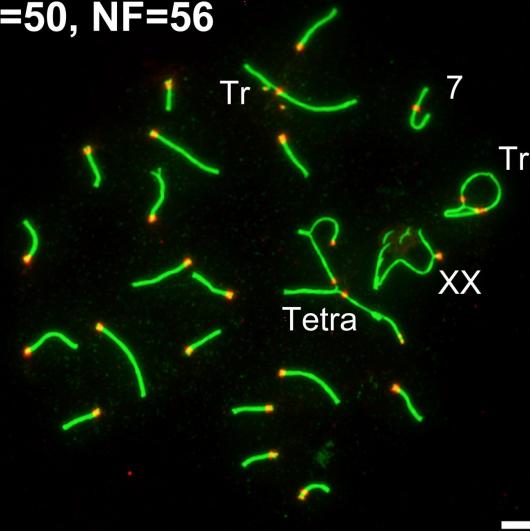
V.G. Tambovtseva¹✉, S.N. Matveevsky², A.A. Kashintsova², A.V. Tretiakov², O.L. Kolomiets², I.Yu. Bakloushinskaya¹✉



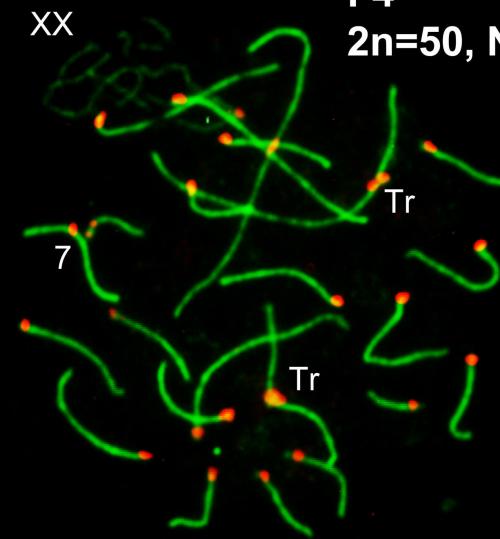
Гибриды F1–F9 *E. tancrei*

Chromosome synapsis in pachytene spermatocytes of *E. tancrei* hybrids of different generations

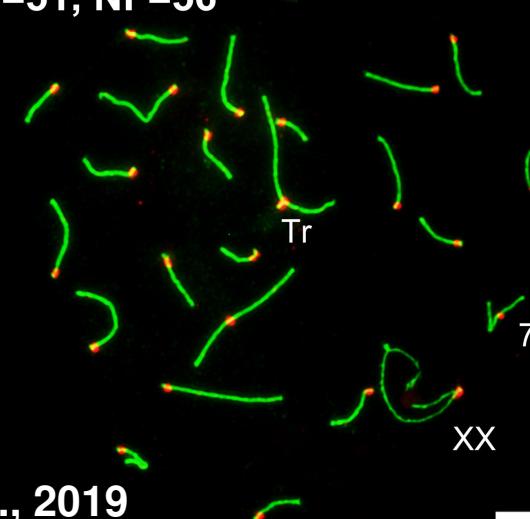
F1
 $2n=50$, NF=56



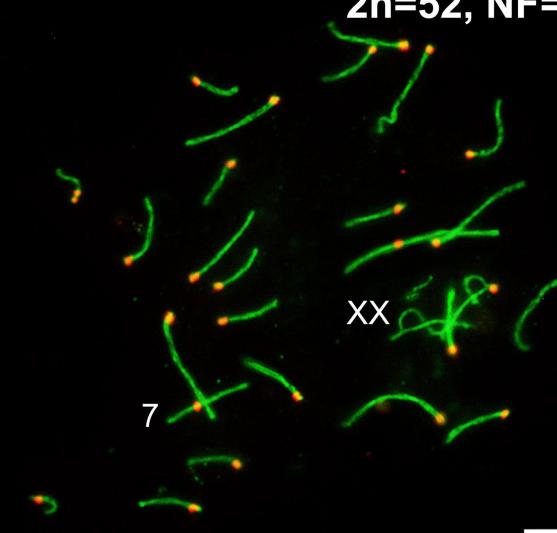
F4
 $2n=50$, NF=56



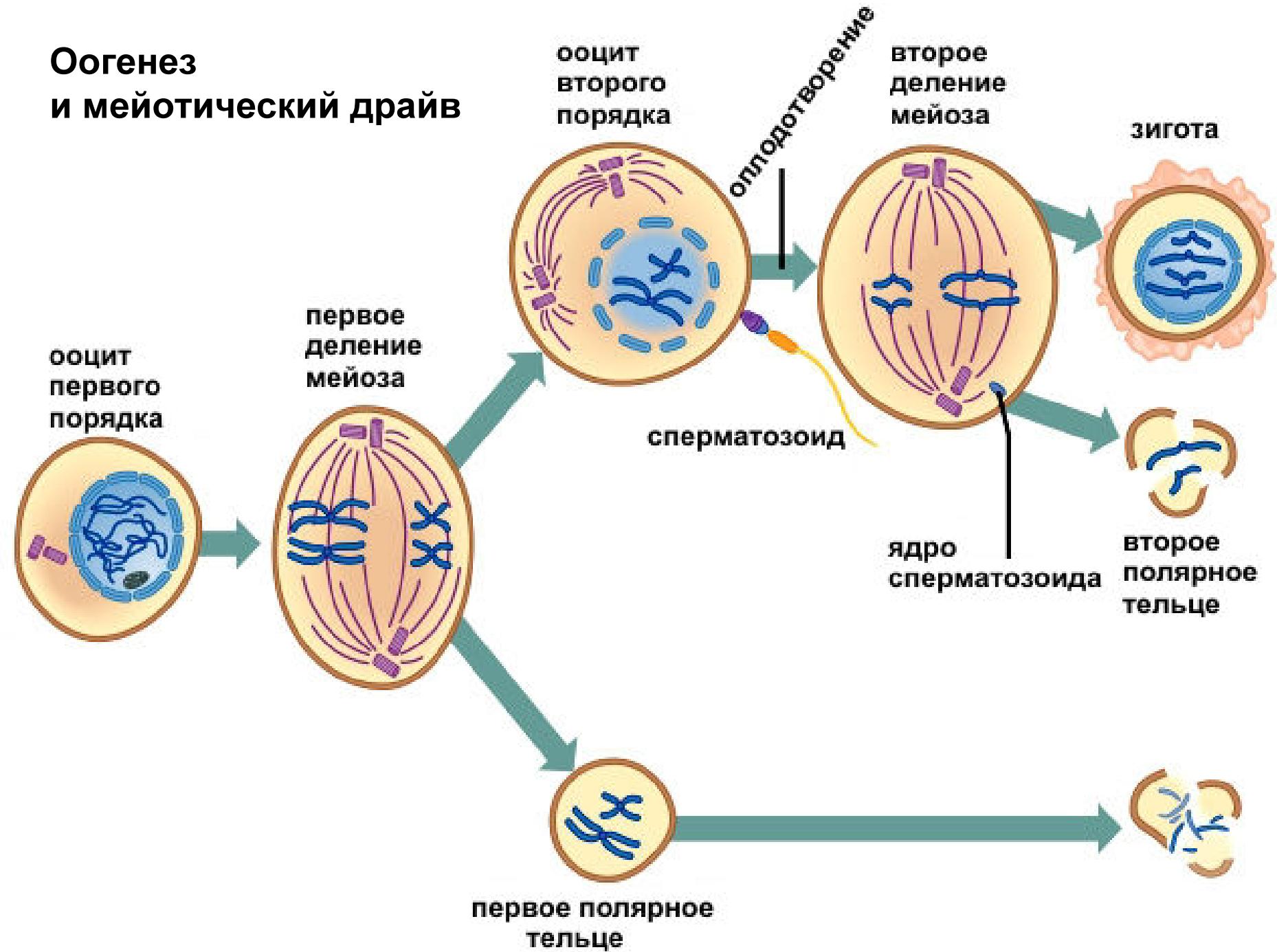
F7
 $2n=51$, NF=56



F9
 $2n=52$, NF=56



Оогенез и мейотический драйв





CompCytogen \$\$: @@ (2019)
doi: 10.3897/CompCytogen.v@i@.34224
<http://compcytogen.penssoft.net>

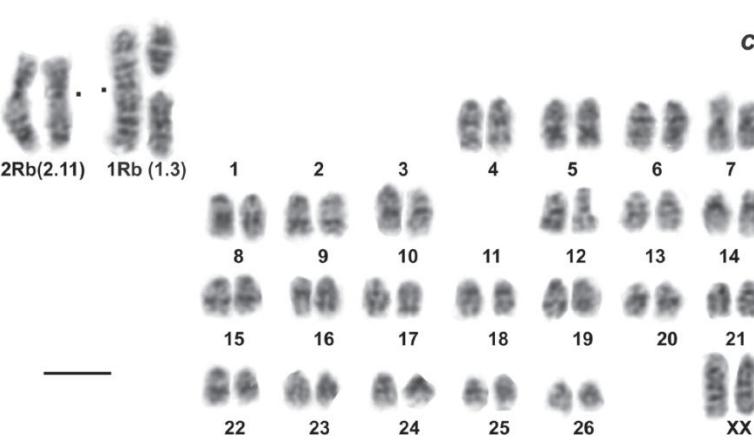
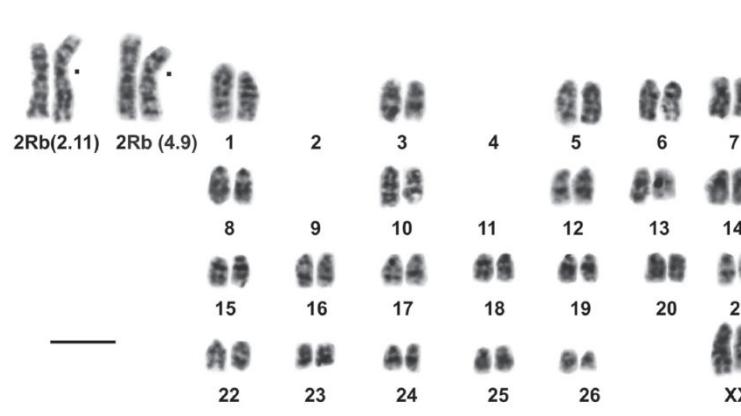
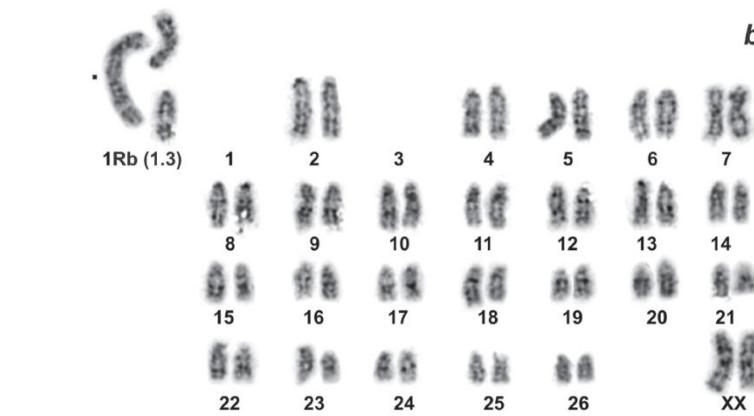
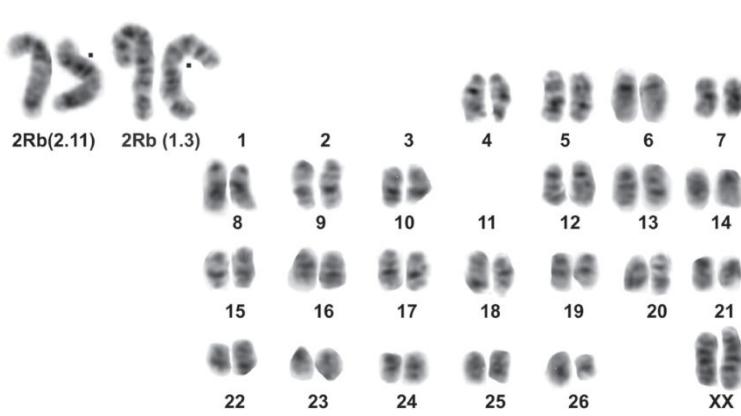
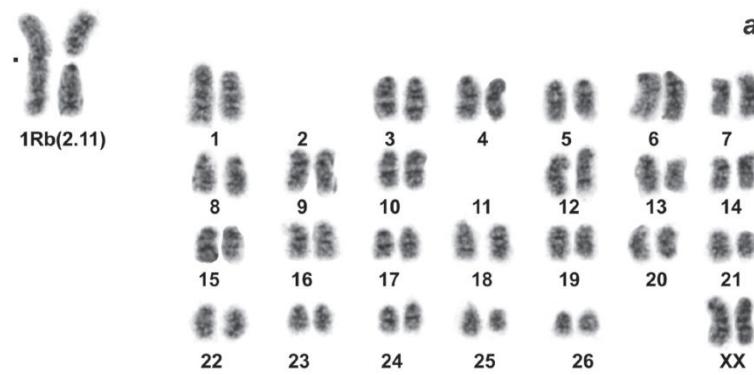
DATA PAPER

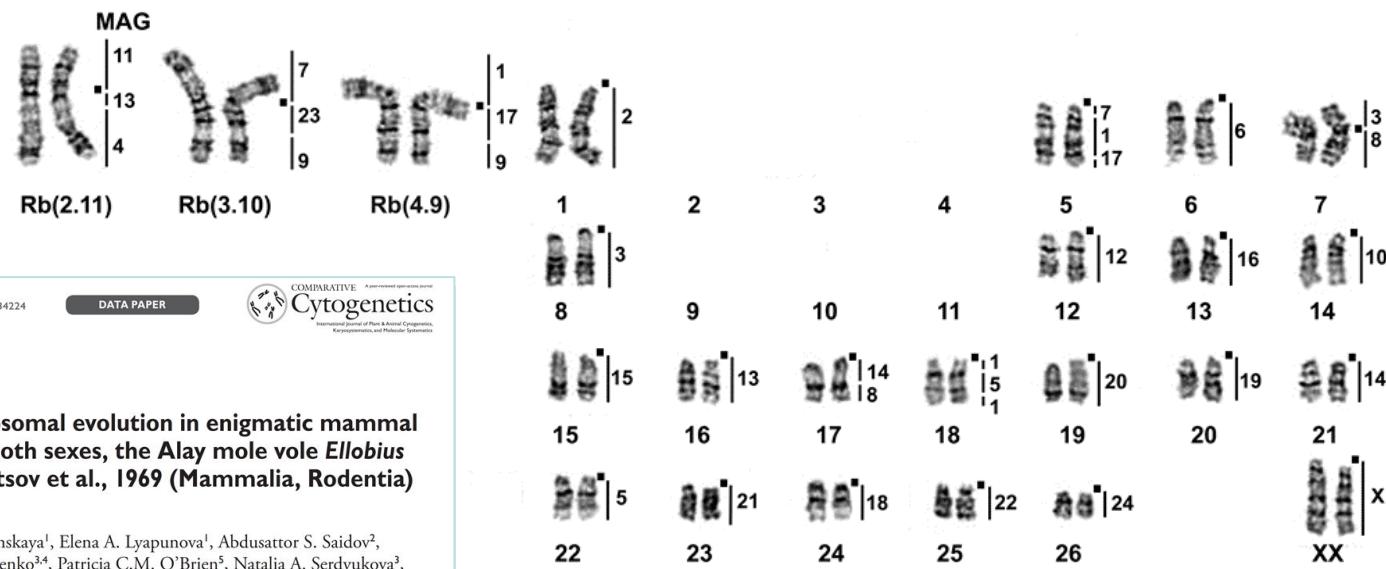
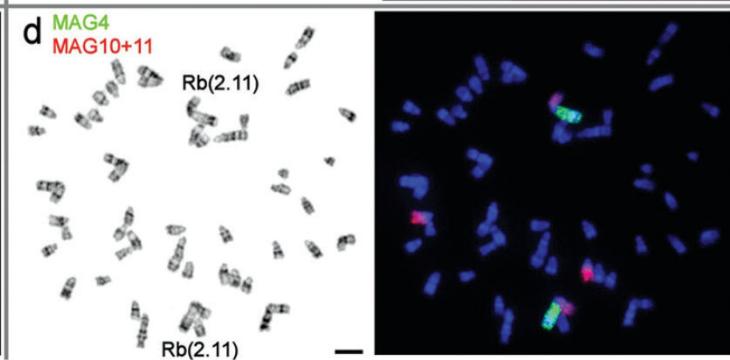
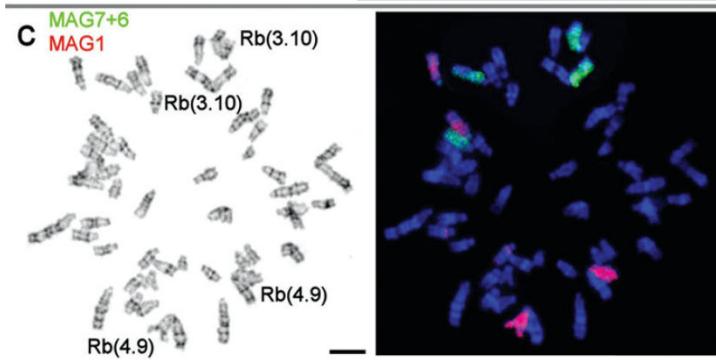
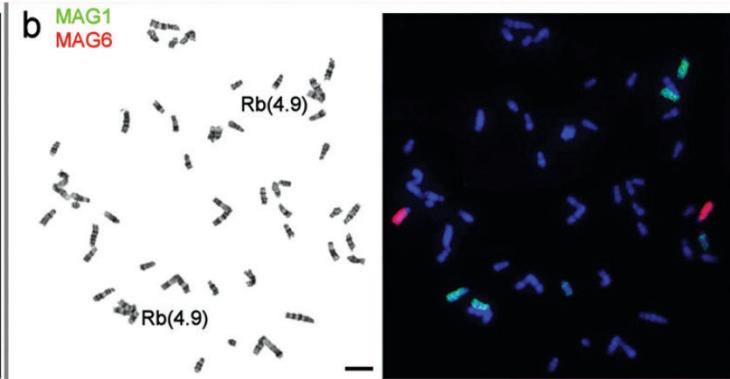
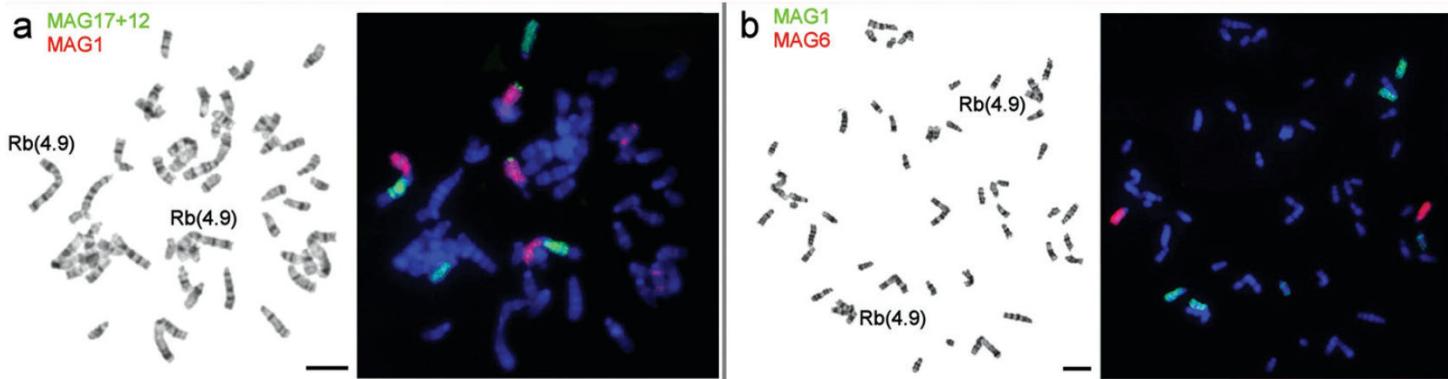
COMPARATIVE
Cytogenetics
International Journal of Plant & Animal Cytogenetics,
Karyosystematics, and Molecular Systematics

Rapid chromosomal evolution in enigmatic mammal with XX in both sexes, the Alay mole vole *Ellobius alaicus* Vorontsov et al., 1969 (Mammalia, Rodentia)

Irina Bakloushinskaya¹, Elena A. Lyapunova¹, Abdusattor S. Saidov²,
Svetlana A. Romanenko^{3,4}, Patricia C.M. O'Brien⁵, Natalia A. Serdyukova³,
Malcolm A. Ferguson-Smith⁵, Sergey Matveevsky⁶, Alexey S. Bogdanov¹

Ellobius alaicus



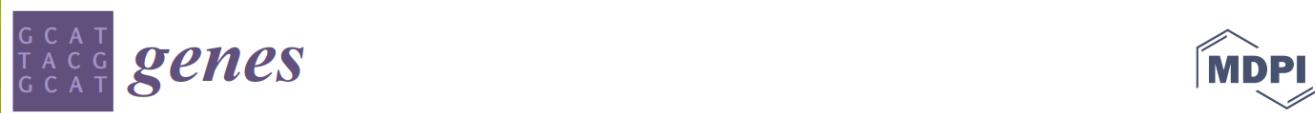


Заключение

Все элементы генома, от хромосом до отдельных пар нуклеотидов, образуют мультикомпонентную систему, а не существуют сами по себе.

Адаптивность на уровне генома – естественный отбор

Гибридизация и мейотический драйв могут быть механизмами, обеспечивающими формирование новых форм и видов



Review

Chromosomics: Bridging the Gap between Genomes and Chromosomes

Janine E. Deakin ^{1,*}, Sally Potter ^{2,3,†}, Rachel O'Neill ^{4,†}, Aurora Ruiz-Herrera ^{5,6,†},
Marcelo B. Cioffi ⁷, Mark D.B. Eldridge ³, Kichi Fukui ⁸, Jennifer A. Marshall Graves ^{1,9},
Darren Griffin ¹⁰, Frank Grutzner ¹¹, Lukáš Kratochvíl ¹², Ikuo Miura ¹³,
Michail Rovatsos ¹¹, Kornsorn Srikulnath ¹⁴, Erik Wapstra ¹⁵ and Tariq Ezaz ^{1,*}

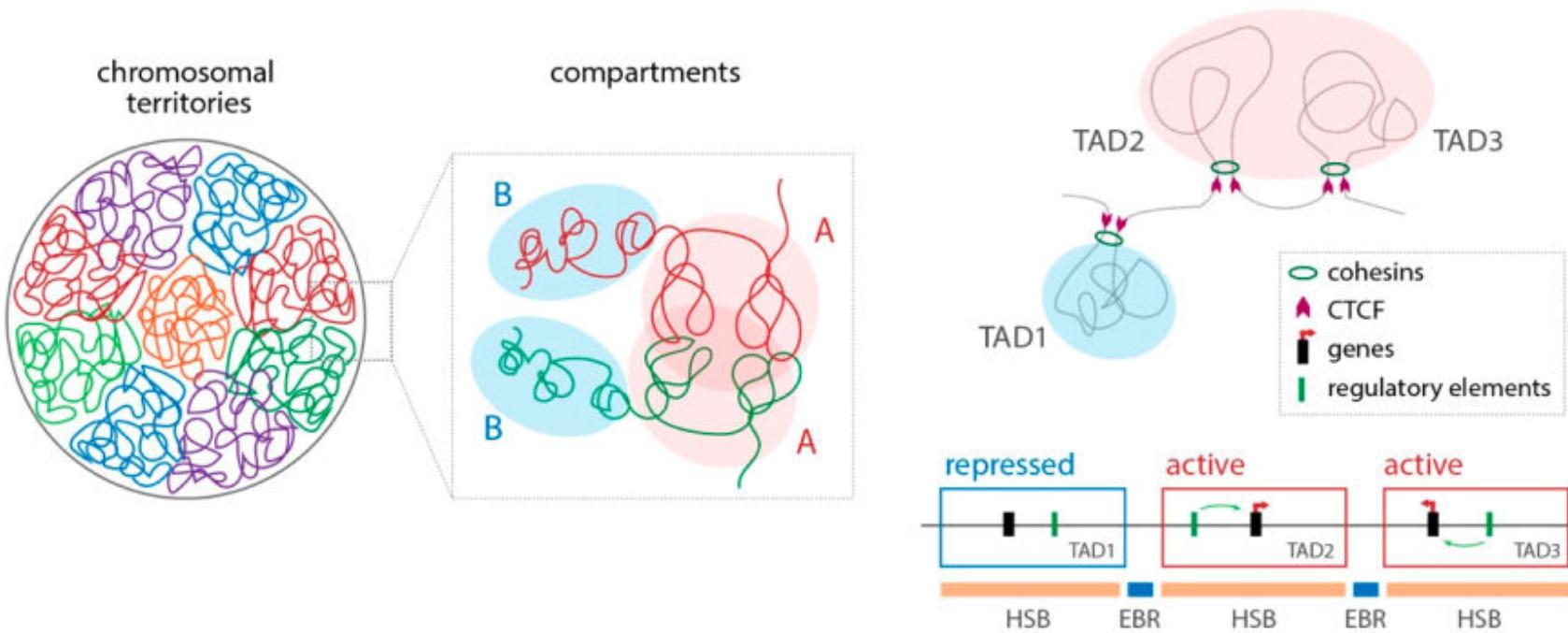
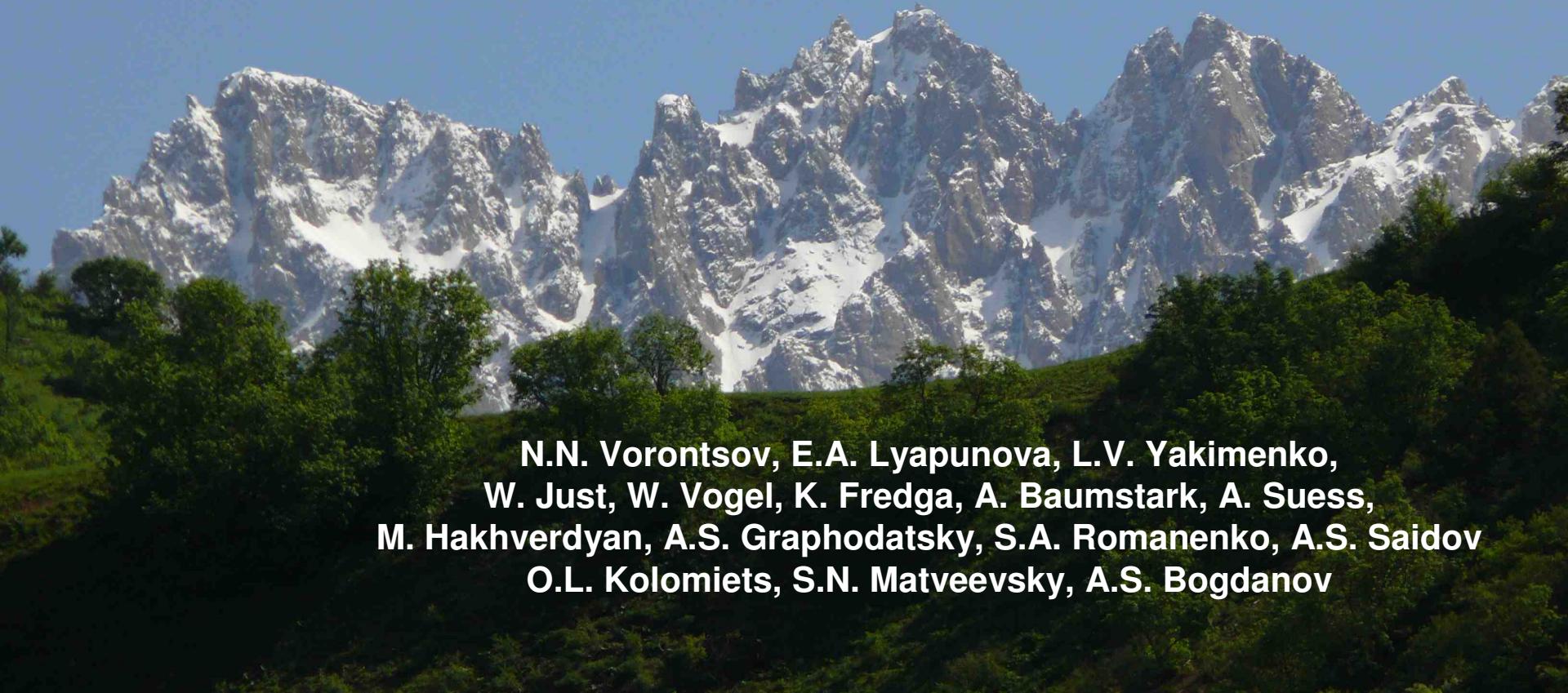


Figure 3. The integrative breakage model, a multilayer framework for the study of genome evolution that takes into account the high-level structural organisation of genomes and the functional constraints that accompany genome reshuffling [64]. Genomes are compartmentalised into different levels of organisation that include: (i) chromosomal territories, (ii) ‘open’ (termed ‘A’)/‘closed’ (termed ‘B’) compartments inside chromosomal territories, (iii) topologically associated domains (TADs) and (iv) looping interactions. TADs, which are delimited by insulating factors such as CTCF and cohesins, harbour looping topologies that permit long-range interactions between target genes and their distal enhancers, thus providing ‘regulatory neighbourhoods’ within homologous syntenic blocks (HSBs). In this context, the integrative breakage model proposes that genomic regions involved in evolutionary reshuffling (evolutionary breakpoint regions, EBRs) which will likely be fixed within populations are (i) those that contain open chromatin DNA configurations and epigenetic features that could promote DNA accessibility and therefore genomic instability, and (ii) that do not disturb essential genes and/or gene expression.

"The more we learn about the world, and the deeper our learning, the more conscience, specific, and articulate will be our knowledge of what we do not know, our knowledge of our ignorance. For this, indeed, is the main source of our ignorance--the fact that our knowledge can be only finite, while our ignorance must necessarily be infinite." Karl Popper



**N.N. Vorontsov, E.A. Lyapunova, L.V. Yakimenko,
W. Just, W. Vogel, K. Fredga, A. Baumstark, A. Suess,
M. Hakhverdyan, A.S. Graphodatsky, S.A. Romanenko, A.S. Saidov
O.L. Kolomiets, S.N. Matveevsky, A.S. Bogdanov**

A Comparative Analysis of the Mole Vole Sibling Species *Ellobius tancrei* and *E. talpinus* (Cricetidae, Rodentia) through Chromosome Painting and Examination of Synaptonemal Complex Structures in Hybrids

I.Yu. Bakloushinskaya^a S.N. Matveevsky^b S.A. Romanenko^c N.A. Serdukova^c

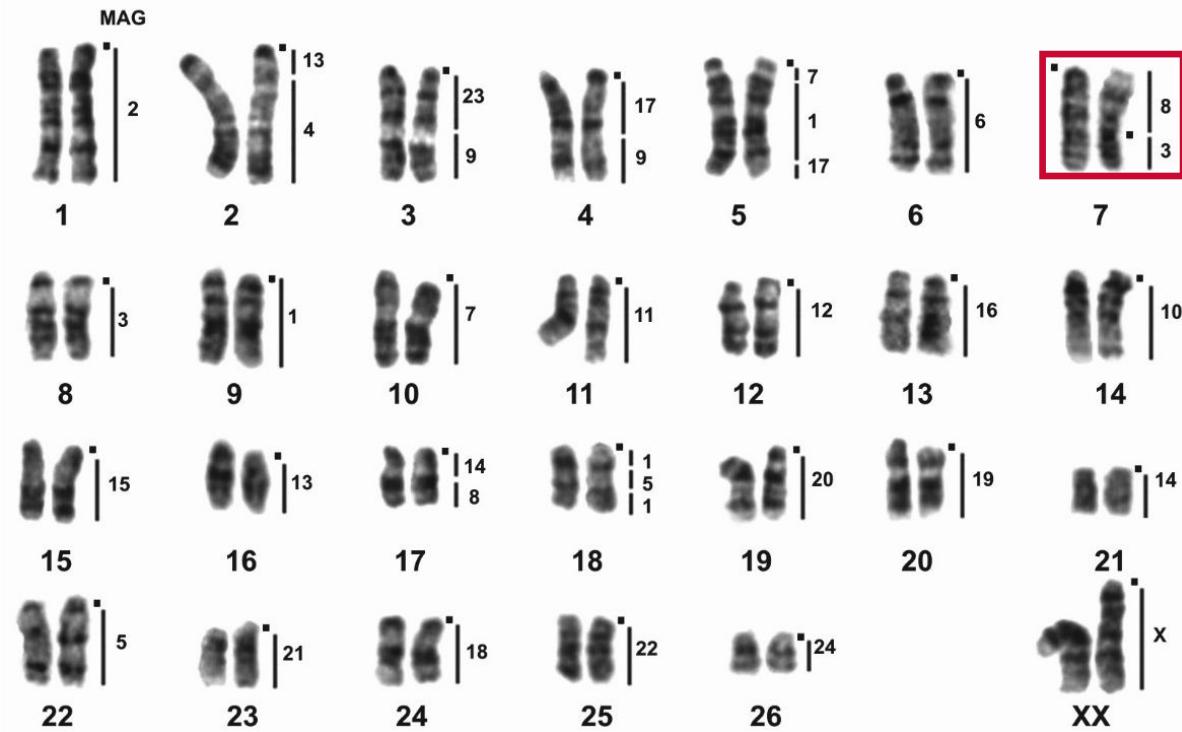
O.L. Kolomiets^b V.E. Spangenberg^b E.A. Lyapunova^a A.S. Graphodatsky^c



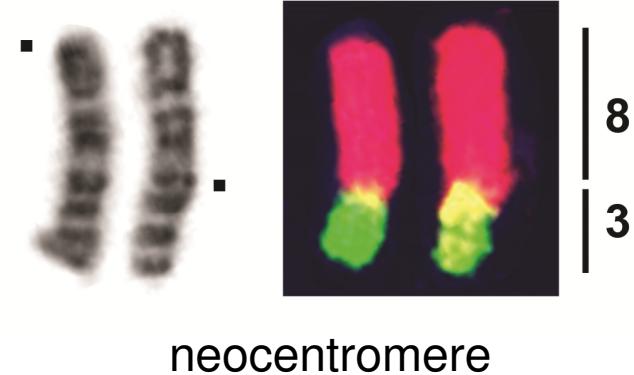
E. tancrei

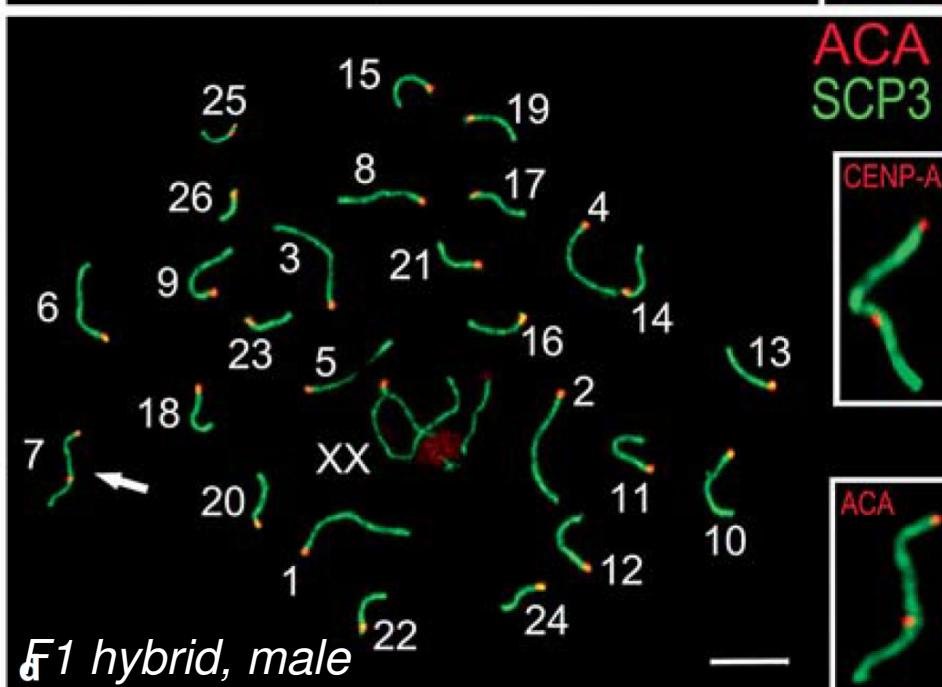
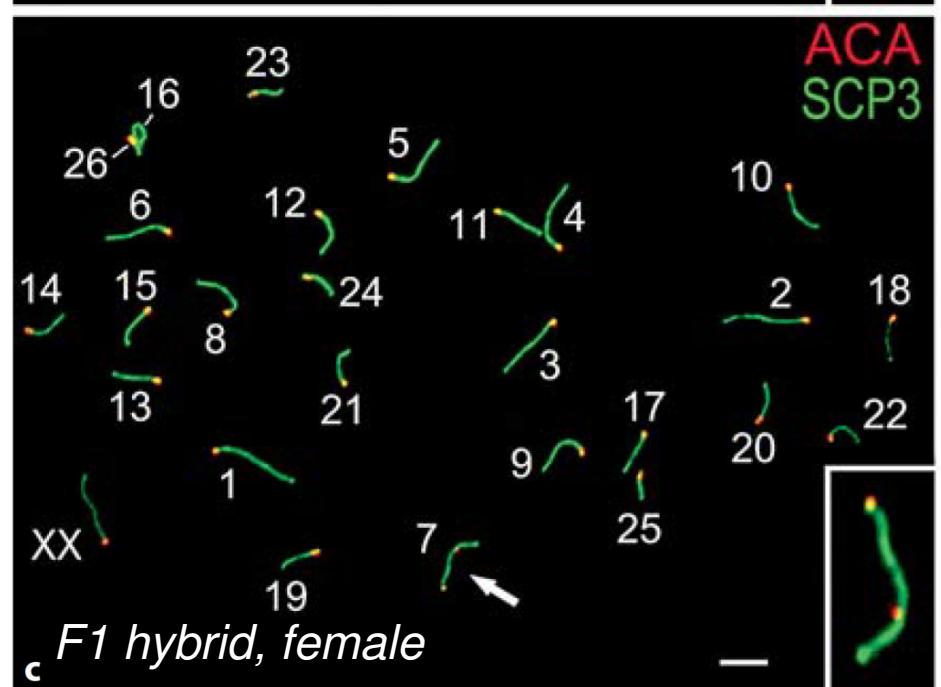
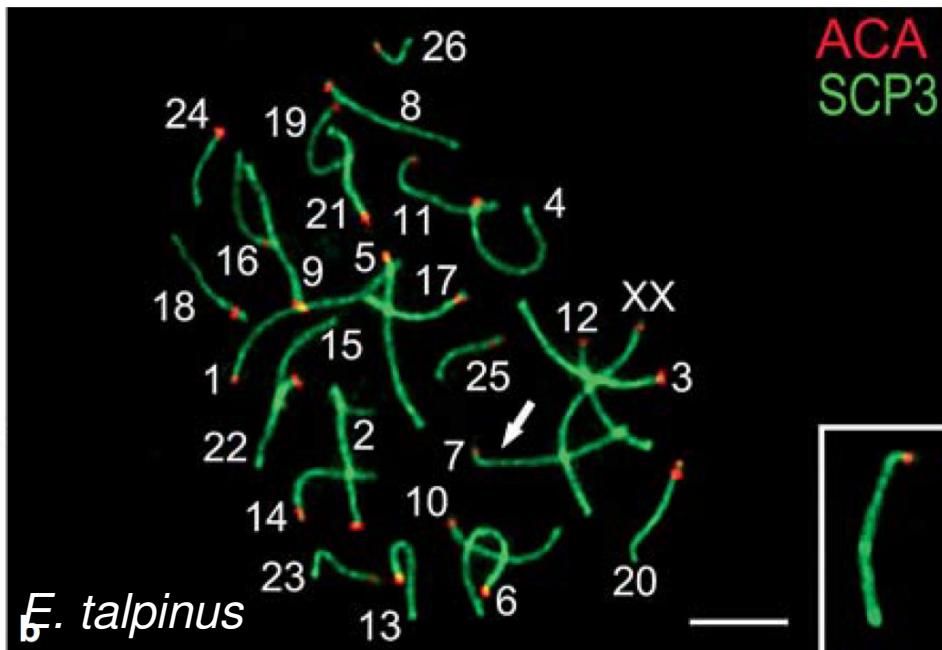
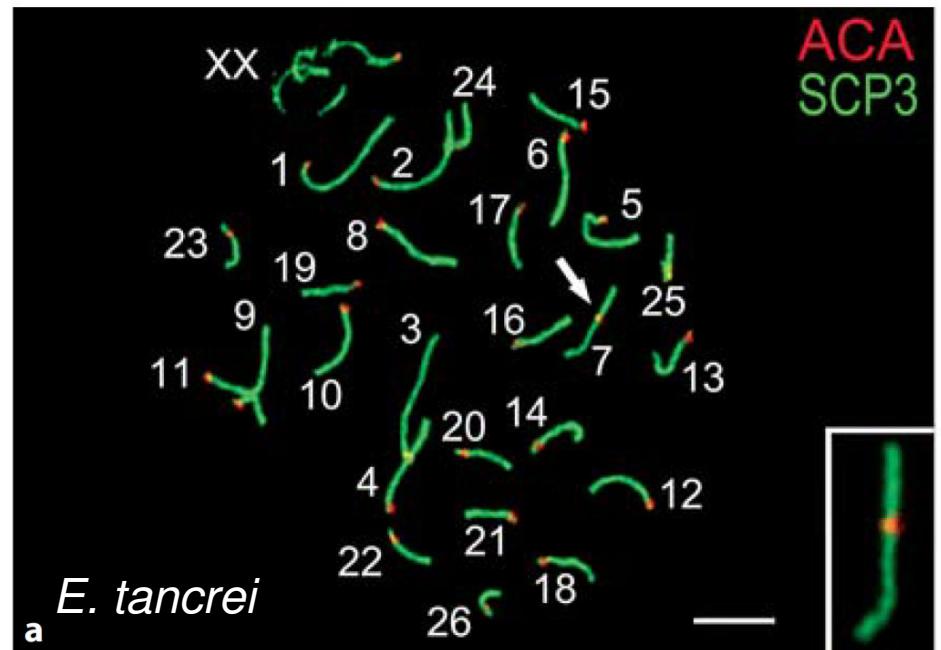


E. talpinus



F1 hybrid *E. tancrei* x *E. talpinus*

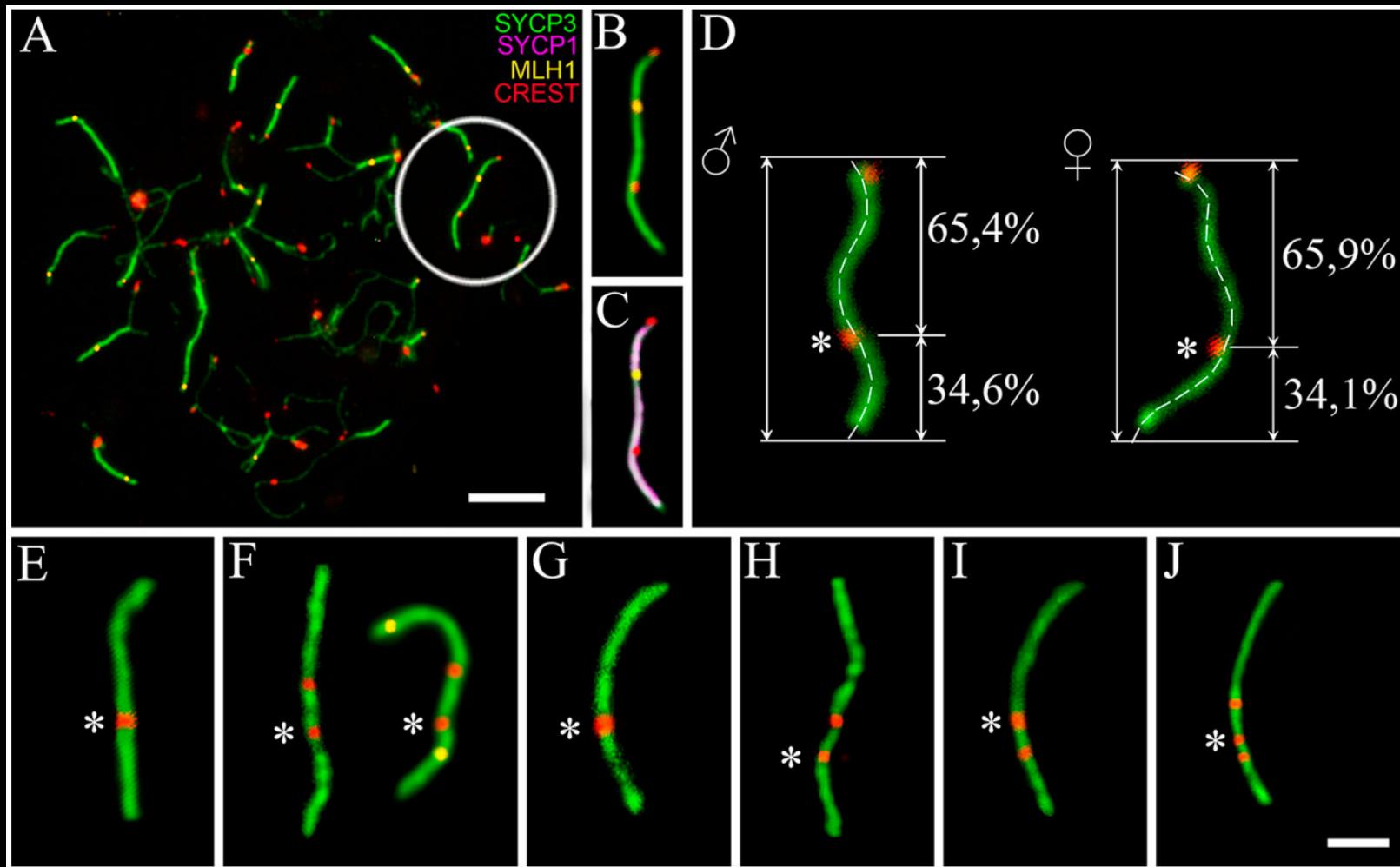




Article

Chromosomal Evolution in Mole Voles *Ellobius* (Cricetidae, Rodentia): Bizarre Sex Chromosomes, Variable Autosomes and MeiosisSergey Matveevsky ^{1,*} , Oxana Kolomiets ¹, Alexey Bogdanov ², Mikhayil Hakhverdyan ³ and Irina Bakloushinskaya ² 

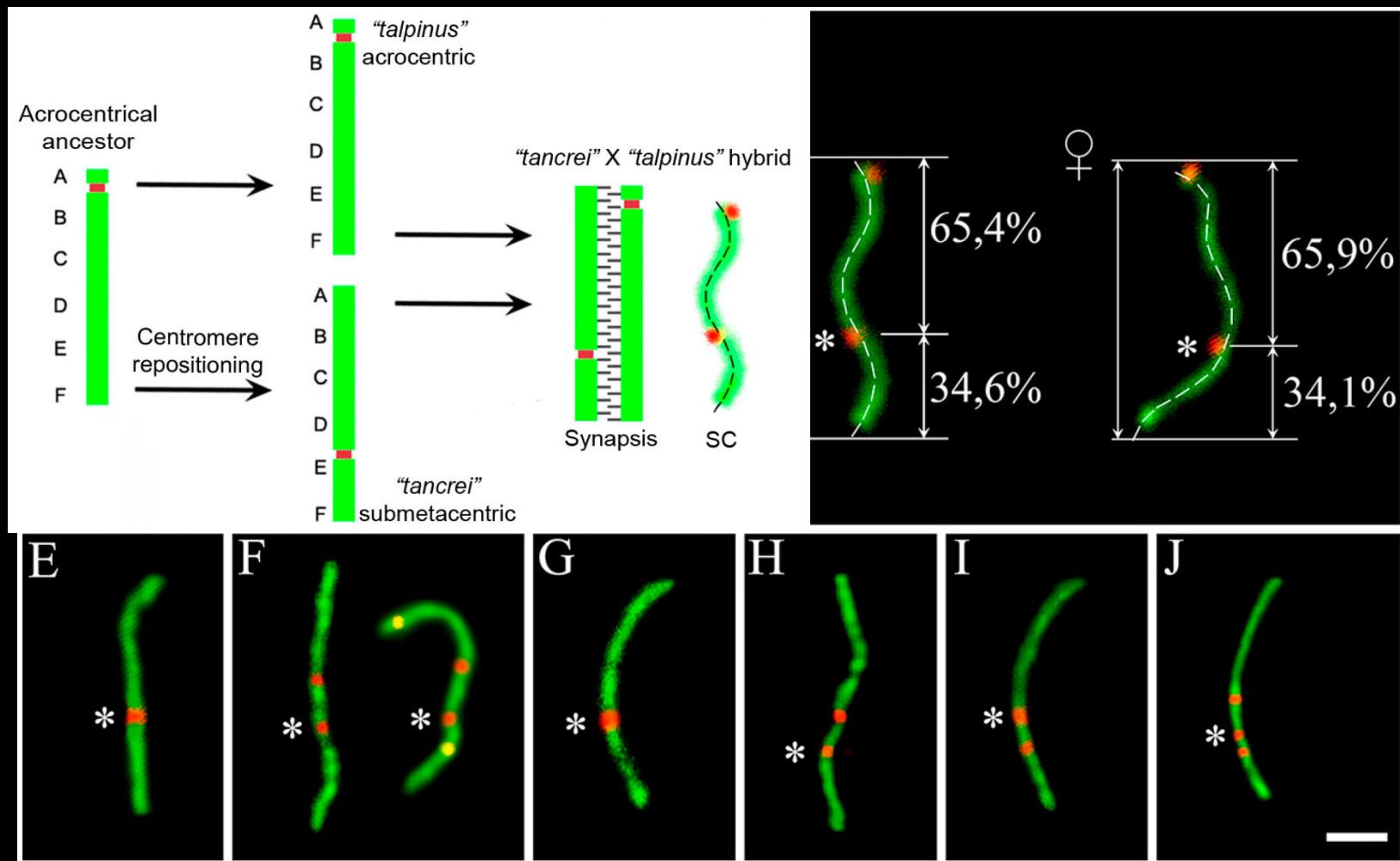
Variations of a centromere position in the submetacentric chromosome in the early meiotic prophase I (interspecific hybrids and *E. tancrei*).



Article

Chromosomal Evolution in Mole Voles *Ellobius* (Cricetidae, Rodentia): Bizarre Sex Chromosomes, Variable Autosomes and MeiosisSergey Matveevsky ^{1,*} , Oxana Kolomiets ¹, Alexey Bogdanov ², Mikhayil Hakhverdyan ³ and Irina Bakloushinskaya ² 

Variations of a centromere position in the submetacentric chromosome in the early meiotic prophase I (interspecific hybrids and *E. tancrei*).





Our special thanks to Dr. Abdusattor Saidov,
Director of Institute of Zoology and Parasitology,
Tajik Academy of Sciences

