



Evoluce fenotypu X



# Proximální mechanismy pohlavního dimorfismu

## Sexual Dimorphism

[Fig. 7]



Draenei



Taurens



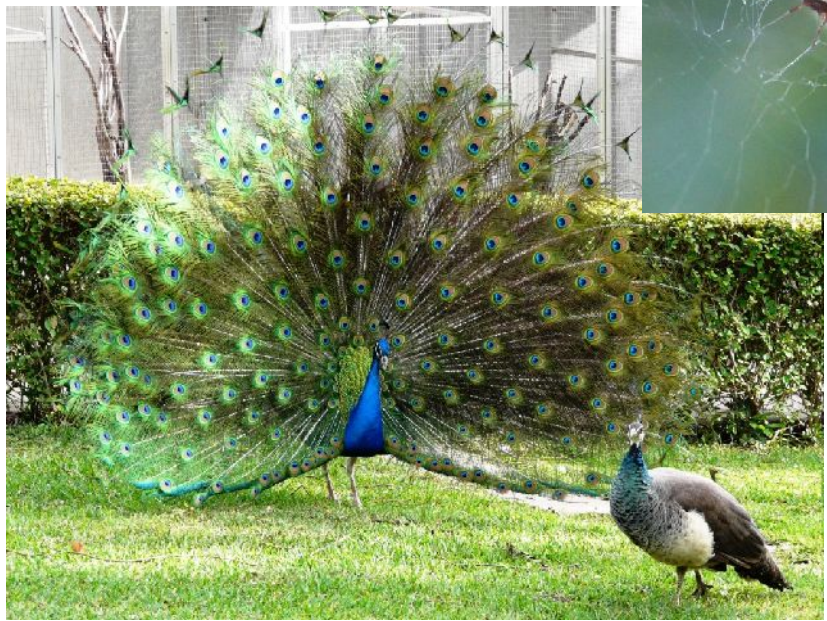
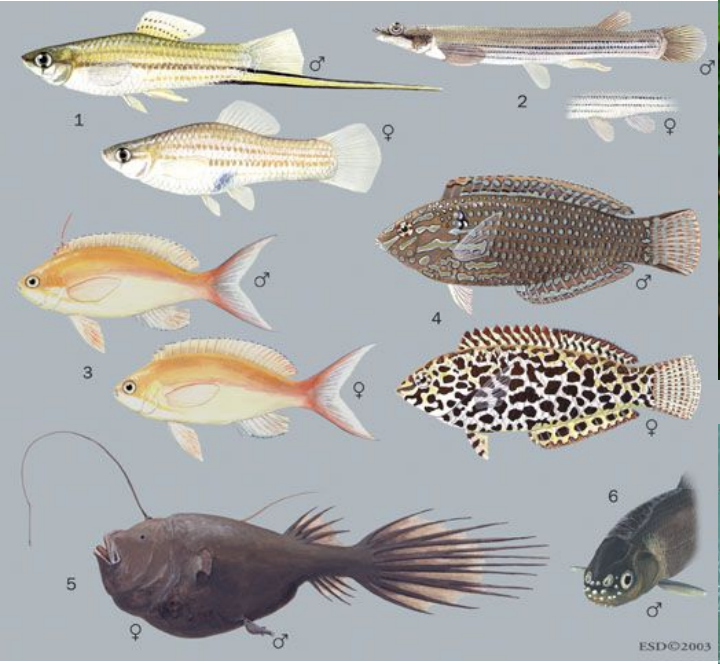
Orcs



Trolls



# Pohlavní dimorfismus





# Ultimální příčiny pohlavního dimorfismu



kolibřík *Eulampis jugularis* a *Heliconia*

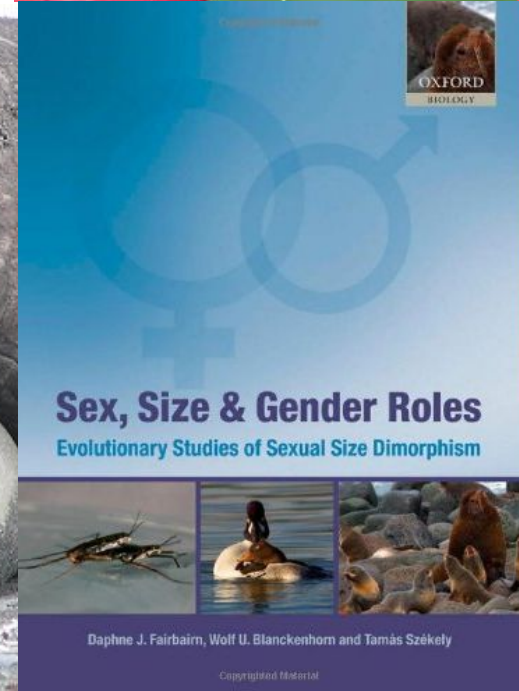


- divergence nik

- rozdílné reprodukční role samců a samic

- důsledek anizogamie

- intenzita a forma vnitropohlavního a mezipohlavního pohlavního výběru a rozdílné životní strategie

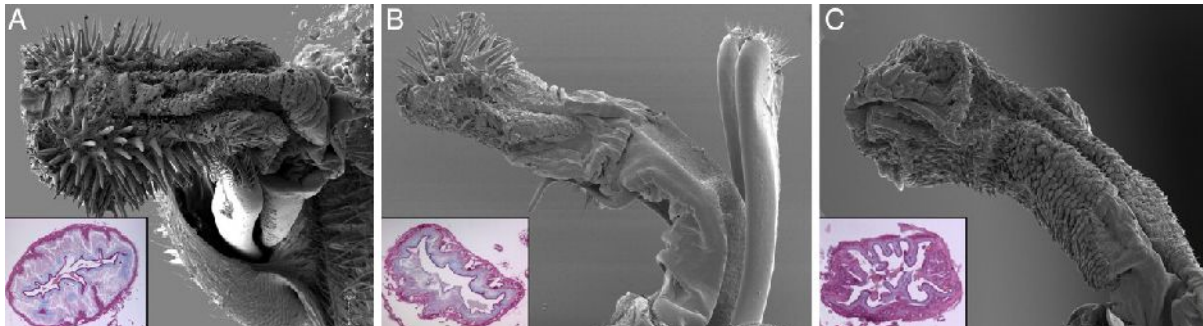
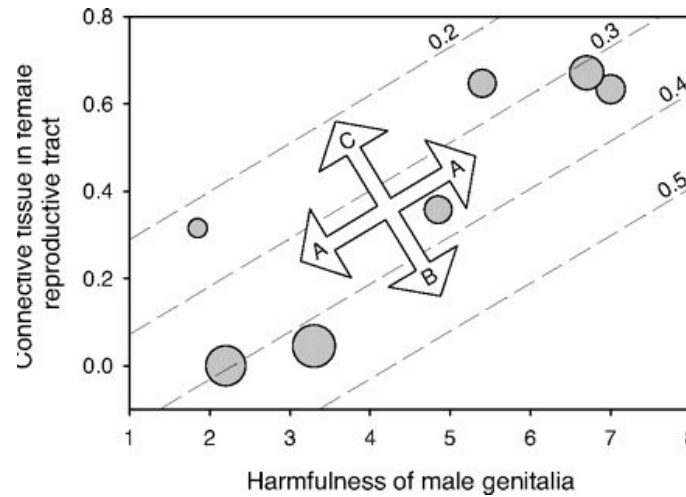


# Ultimální příčiny pohlavního dimorfismu

- interlokusový sexuální konflikt
- vede ke koevoluci (závody ve zbrojení mezi samci a samicemi)

## Coevolution between harmful male genitalia and female resistance in seed beetles

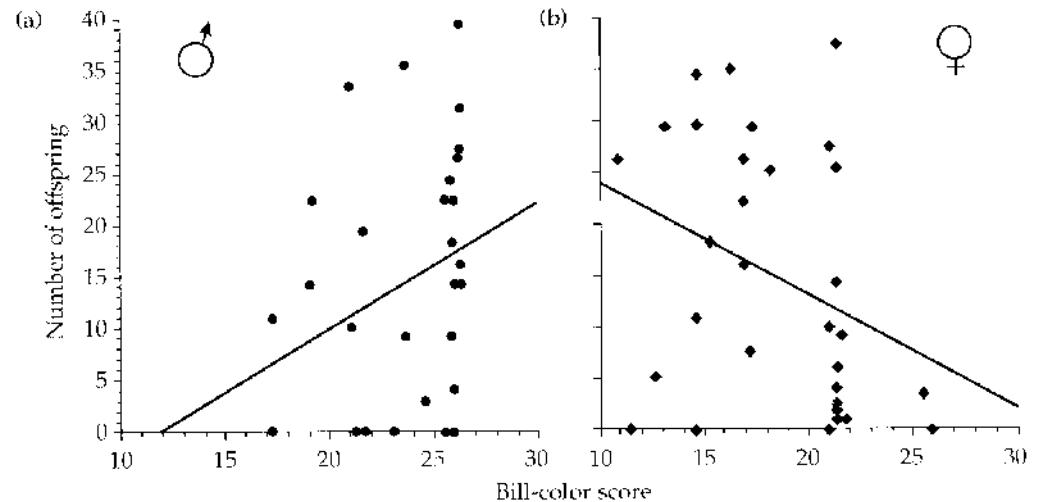
Johanna Rönk, Marí Kabrala, and Göran Arnqvist\*  
PNAS | June 16, 2007 | vol. 104





## Proximální příčiny pohlavního dimorfismu

- vznik pohlavního dimorfismu omezuje genetická korelace mezi pohlavími
- pohlavně antagonistická selekce o míru exprese daného znaku vede ke vzniku intralokusového sexuálního konfliktu



**Figure 18.2** Number of offspring reaching independence (2 weeks after fledging) produced by male (a) and female (b) zebra finches (*Taenopygia guttata*) as a function of bill-color score. The lines represent the best least-squares regression. The selection differential for males is 0.74 ( $P=0.036$ ) and for females is  $-0.35$  ( $P=0.015$ ), clearly showing diverging selection pressures on bill color in males and females. Redrawn from Price and Burley 1994 (with permission)

# Sexuální konflikt

- intralokusový sexuální konflikt

## Negative genetic correlation for adult fitness between sexes reveals ontogenetic conflict in *Drosophila*

Adam K. Chippindale\*, Jonathan R. Gibson, and William R. Rice

PNAS | February 13, 2001 | vol. 98 | no. 4 | 1671-1675

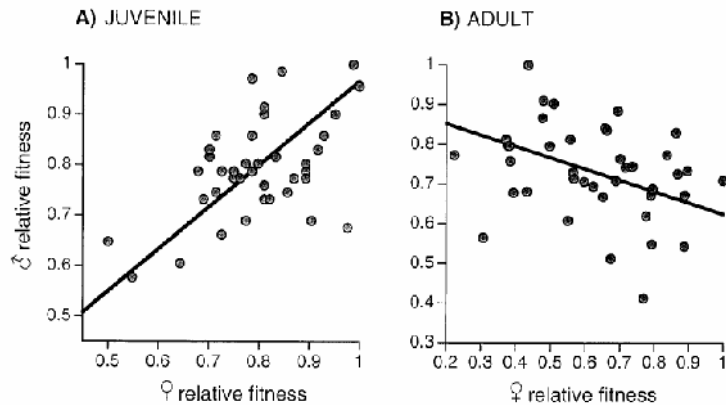


Fig. 2. Interspecific regression for juvenile and adult fitness components: (A) egg-to-eclosion viability and (B) adult reproductive success (male fertilization success or female fecundity), calculated as the principal axis regression. Data are expressed as relative fitness values by dividing, in each sex separately, by the value of the fittest genotype. The null expectation is that each genome will have identical effects on fitness in both sexes, therefore creating a strong positive association. The interspecific genetic correlations were  $+0.49$  and  $-0.30$ , for juvenile and adult fitness, respectively.

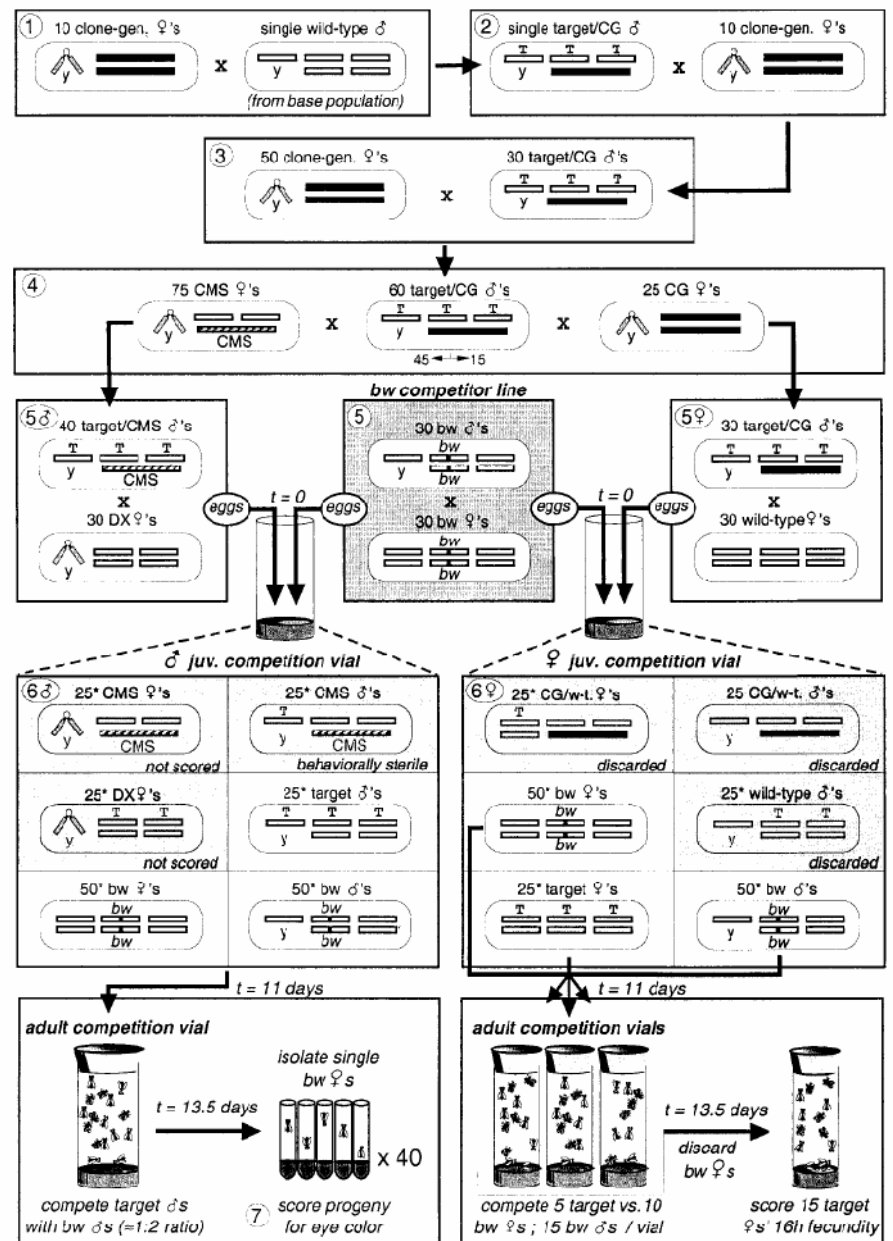
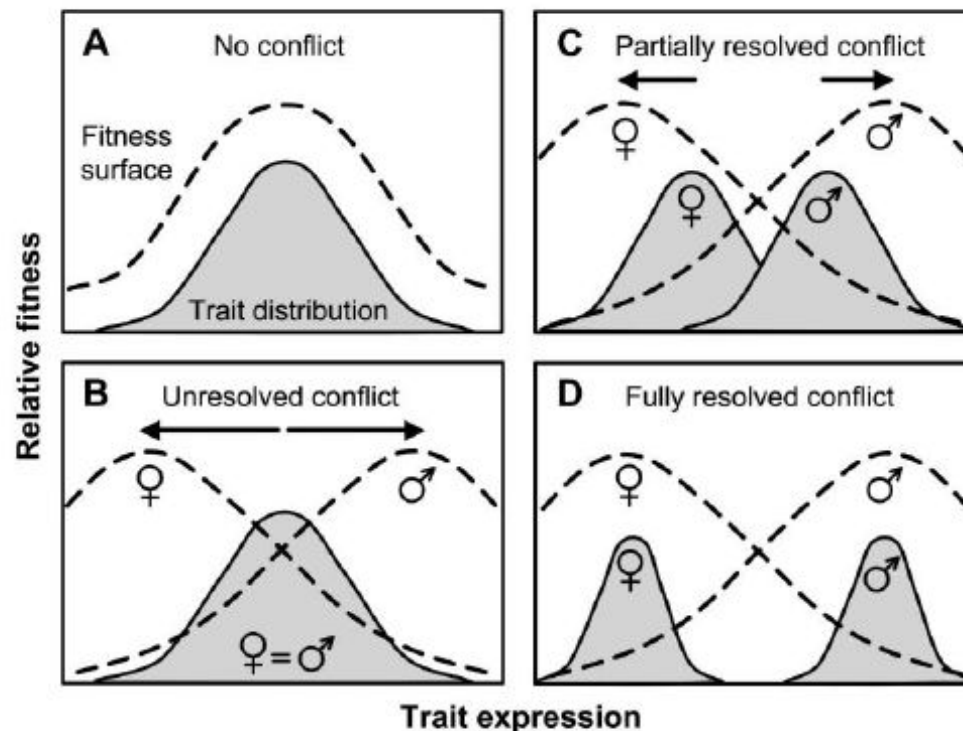


Fig. 1. Protocol for sampling and cloning a single haploid genome (denoted T for "target"; steps 1-4), returning it to its original (wild-type) genetic background (step 5), and then measuring its fitness in males and females over a full generation (steps 5-7). Numbered steps indicate generations. Chromosomes I (X), II, and III are depicted as rectangles arranged Left to Right, respectively. Excepting the compound X (depicted as a chevron symbol) and autosomal translocations (shown as elongated rectangles spanning chromosomal positions 2 and 3), all chromosomes were derived from the base population; wild-type chromosomes are shown as open rectangles and marked ones with fill or crosshatching. For clarity, only offspring that were viable and used in a subsequent cross are shown in steps 1-5. By using this protocol, 40 haploid genomes were cloned and measured for juvenile, adult, and total fitness. Steps 4-7 were independently repeated three times for each genome. Asterisks indicate average numbers of viable eggs used to begin the fitness assay. See *Materials and Methods* for additional details.

## Sexually Antagonistic Selection, Sexual Dimorphism, and the Resolution of Intralocus Sexual Conflict

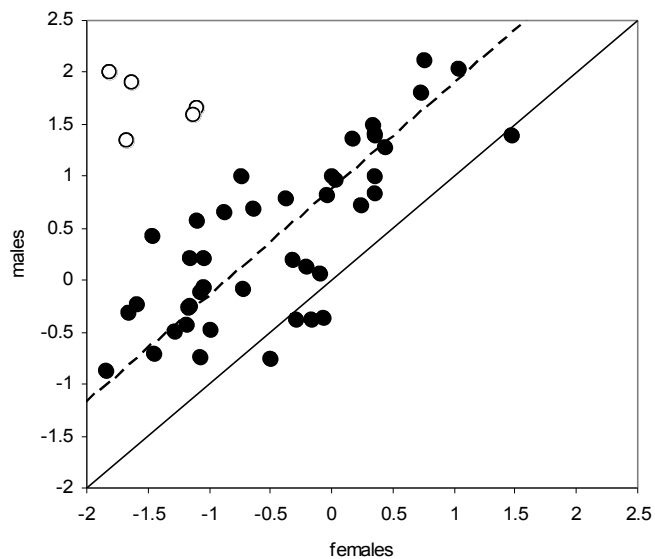
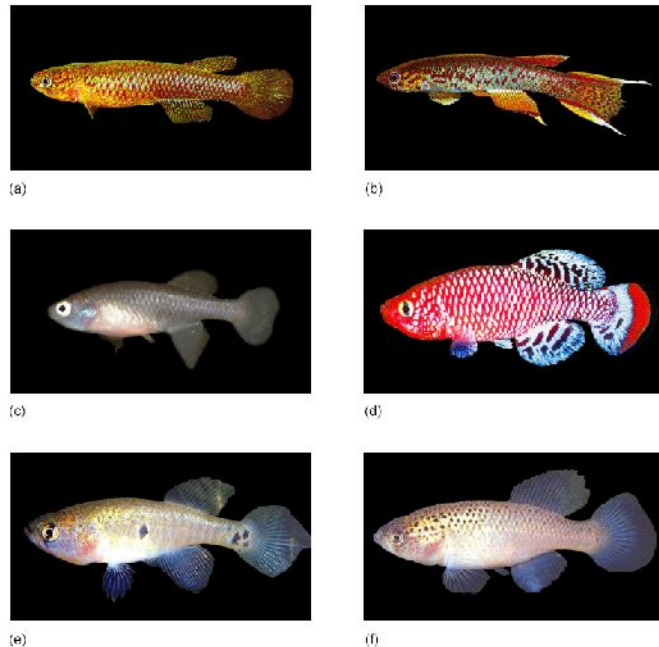
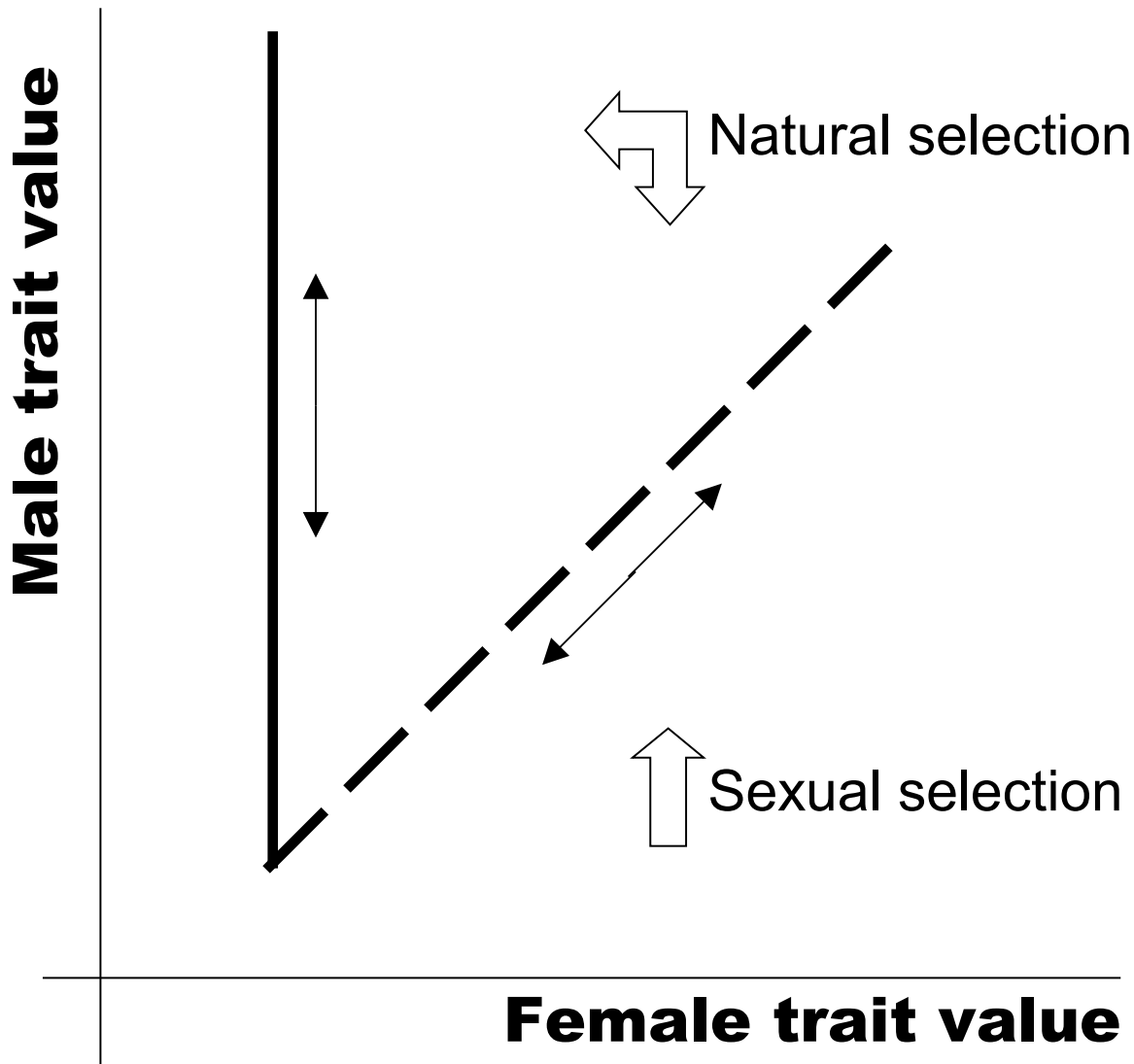
Robert M. Cox\* and Ryan Calsbeek



**Figure 1:** Potential relationships between sexual dimorphism and intralocus sexual conflict. Shaded areas indicate phenotypic distributions for a hypothetical quantitative trait, and dashed lines signify fitness functions for that trait. Arrows indicate the discrepancy between the fitness optimum and the phenotypic mean in each sex. The magnitude of this discrepancy corresponds to the strength of directional selection, and the magnitude of sexually antagonistic directional selection defines the magnitude of unresolved sexual conflict. Adapted from figures in Rice and Chippindale (2001), Day and Bonduriansky (2004), and Bedhomme and Chippindale (2007).

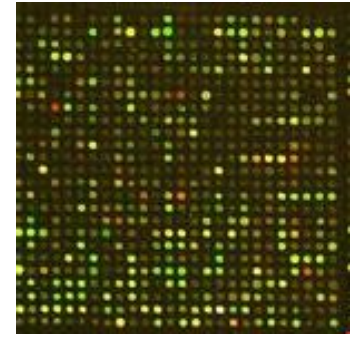


# Vznik sexuálního dimorfismu – prolomení korelace mezi pohlavími



## Jak častý je intralokusový sexuální konflikt?

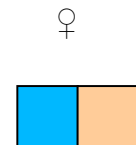
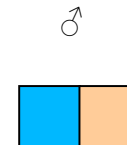
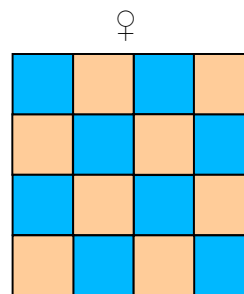
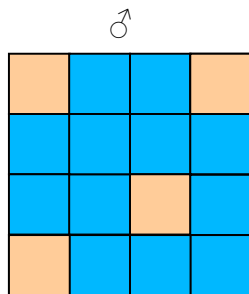
- cca. 20% ze sledovaných 14 142 lokusů u *Drosophila melanogaster* vykazuje pohlavně-specifickou transkripci – intralokusový sexuální konflikt je většinou vyřešen



X

- ale jen 3% v tělech po odstranění gonád – nevyřešený intralokusový sexuální konflikt je velmi častý

(Parisi et al. 2003, 2004)





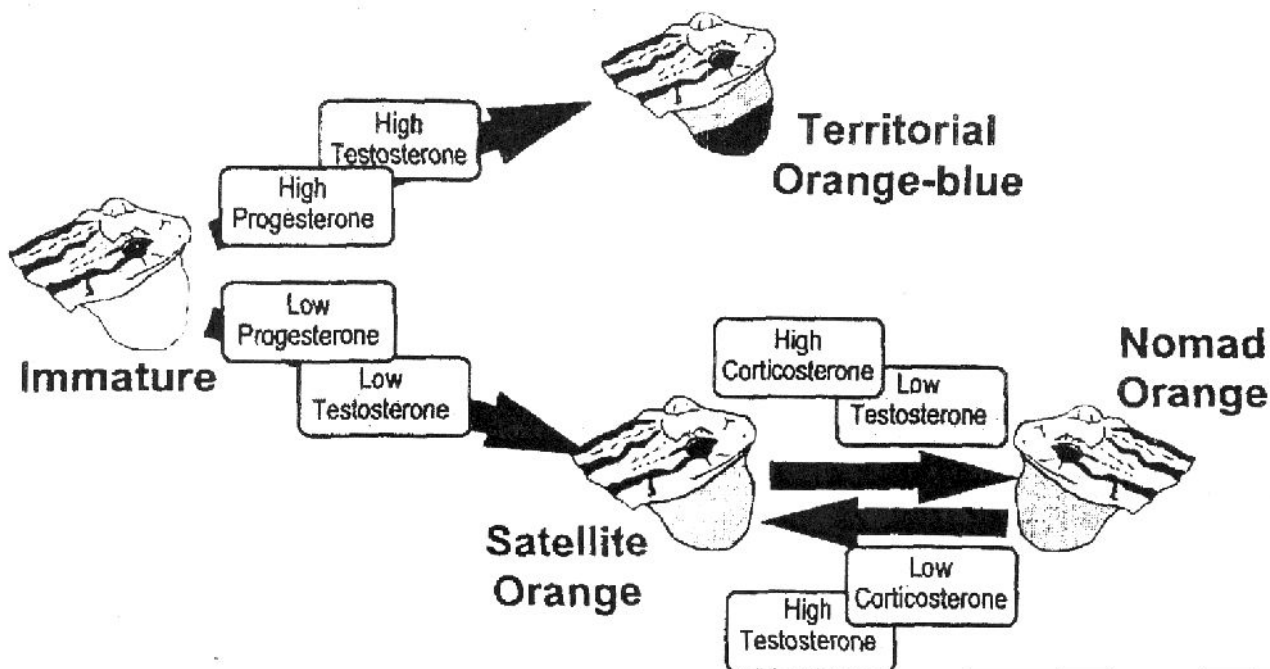
## Vznik sexuálního dimorfismu – prolomení korelace mezi pohlavími

A) Pohlavně specifická exprese genů na autozomech:



- řízená pohlavními hormony (organizační vs. aktivační účinky a jejich kombinace)

### Tree Lizard Dewlap Polymorphism



## Prolomení korelace mezi pohlavími

### A) Pohlavně specifická exprese genů na autozomech:

řízená pohlavními hormony (organizační vs. aktivační účinky a jejich kombinace)

odhad Carrol et al. (2006) a Horie-Inoue et al. (2004):  
u člověka v genomu:

3665 míst vážících receptor pro estrogen  
563 pro androgenní receptory

X

20000-25000 strukturních genů





## Vznik sexuálního dimorfismu – prolomení korelace mezi pohlavími

B) Pohlavně specifická exprese genů na autozomech řízená geny na pohlavních chromozomech

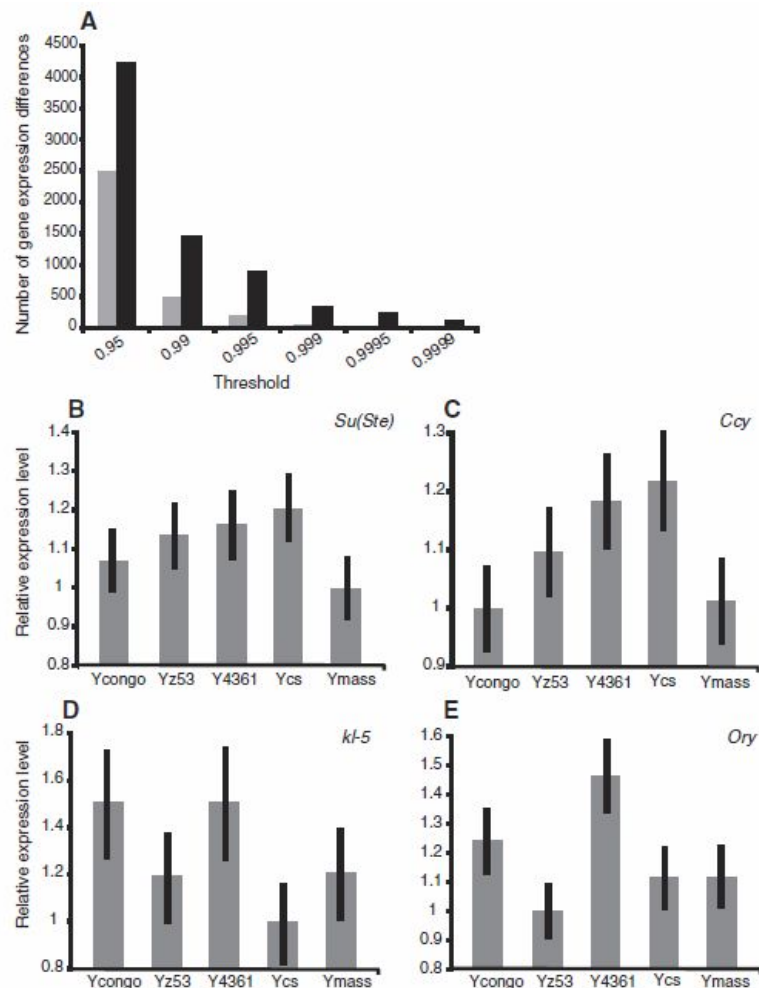
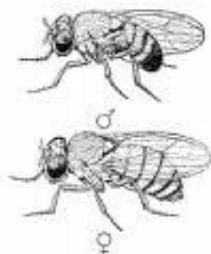
- epistatické interakce mezi lokusy na pohlavních chromozomech a na autozomech

### Polymorphic Y Chromosomes Harbor Cryptic Variation with Manifold Functional Consequences

Bernardo Lemos,\* Luciana O. Araripe, Daniel L. Hartl

SCIENCE VOL 319 4 JANUARY 2008

Y chromozomem ovlivněna stabilita mikrotubulů, metabolismus lipidů a mitochondriální metabolismus, teplotní sensitivita spermatogeneze



**Fig. 1.** (A) Number of genes differentially expressed among Y-chromosome substitution lines (black bars) as a function of the Bayesian posterior probability of differential expression. Gray bars indicate the estimated number of genes expected by chance. (B to E) Four Y-linked genes [*Su(Ste)*, *kt-5*, *Ccy*, and *Occludin-related Y (Ory)*] with significant expression variation among Y-chromosome substitution lines. Estimated relative differences in expression are shown. Black bars denote 95% credible interval for estimated relative difference.

## Vznik sexuálního dimorfismu – prolomení korelace mezi pohlavími

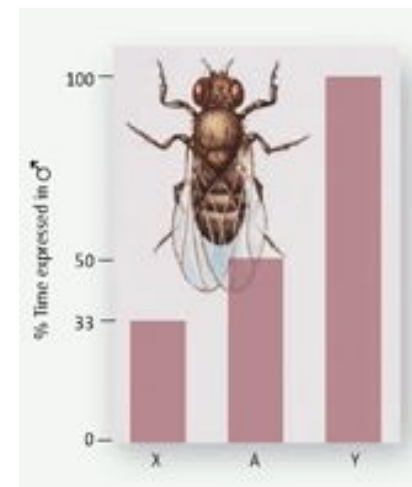
### C) Rozdíly v genotypu mezi pohlavími – vazba na pohlavní chromozomy

- u některých zvířat neexistují rozdíly mezi pohlavími v genotypu

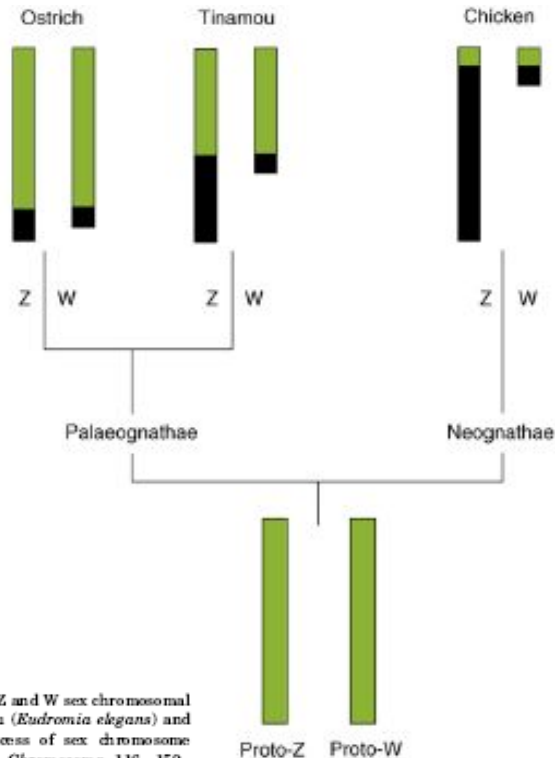
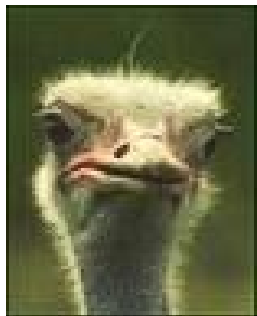
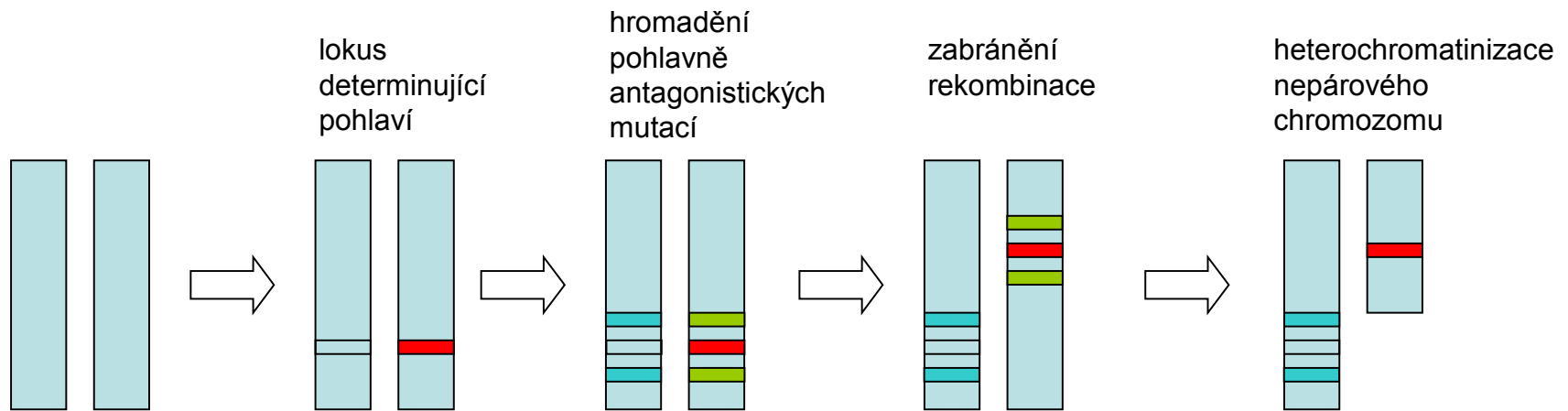
- vazba na pohlavní chromozomy:

<i>Drosophila melanogaster</i>	16 % na X 0,06% na Y	2303 z 14449 genů 9
<i>Homo sapiens</i>	5.6% na X 0.19% na Y	1344 z 24000 genů 45
<i>Gallus domesticus</i>	1.4 % na Z 0.2% na W	328 z 23000 genů 47

(data z Rhen 2007)



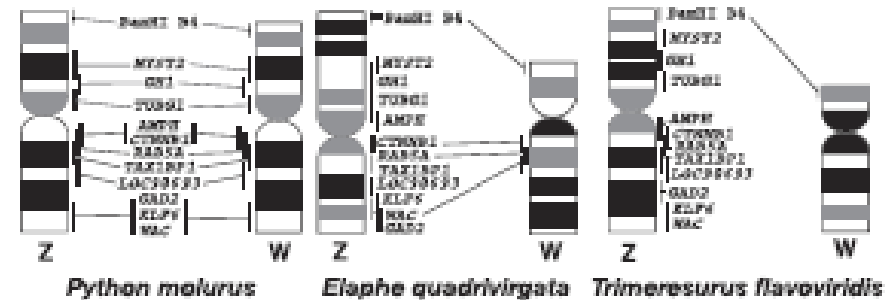




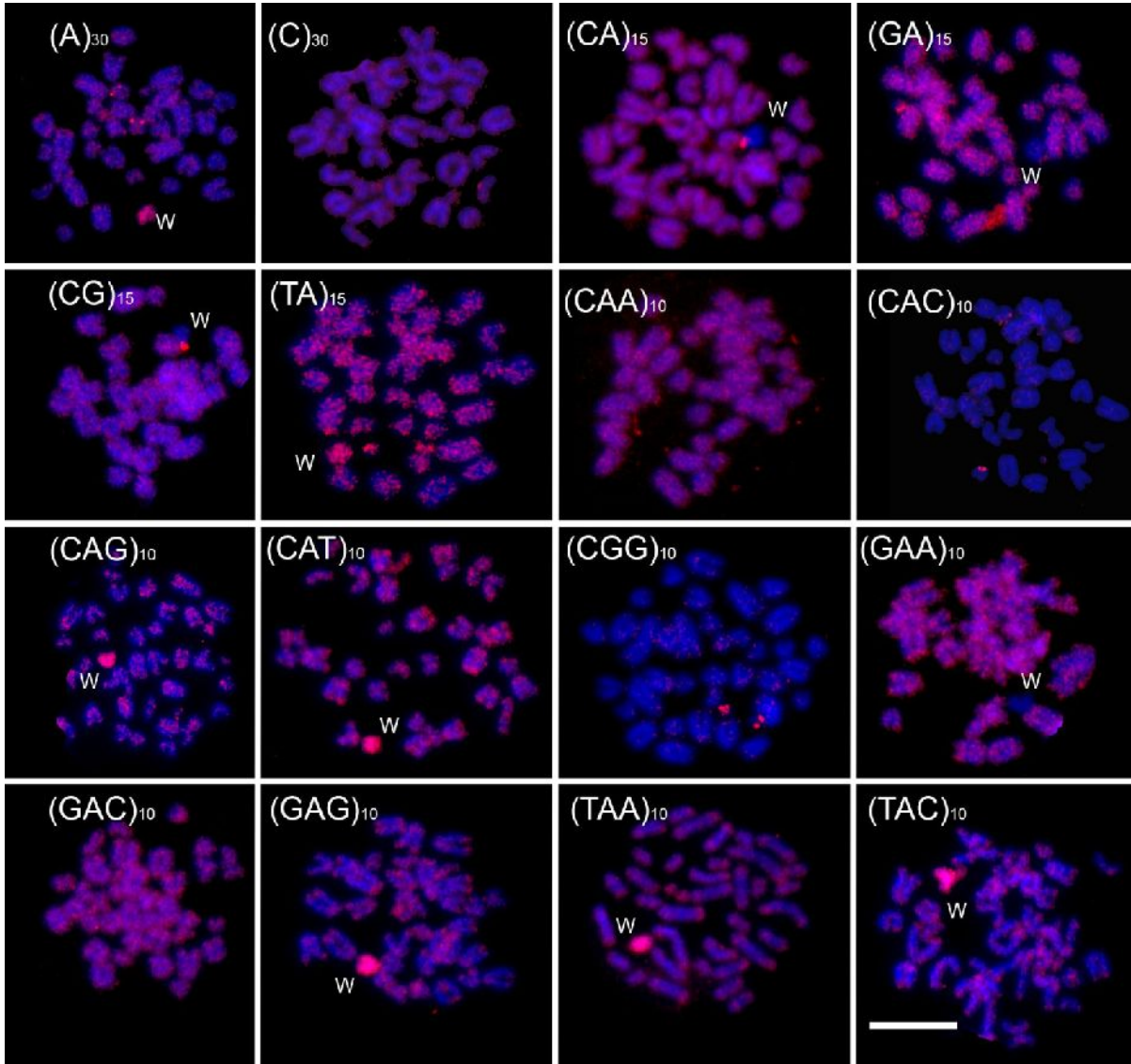
## Evidence for different origin of sex chromosomes in snakes, birds, and mammals and step-wise differentiation of snake sex chromosomes

Kazumi Matsubara\*, Hiroshi Tarui†, Michihisa Toriba‡, Kazuhiko Yamada\*, Kazuhiko Yamada\*, Chizuko Nishida-Umehara\*§, Kiyokazu Agata\*, and Yoichi Matsuda\*¶

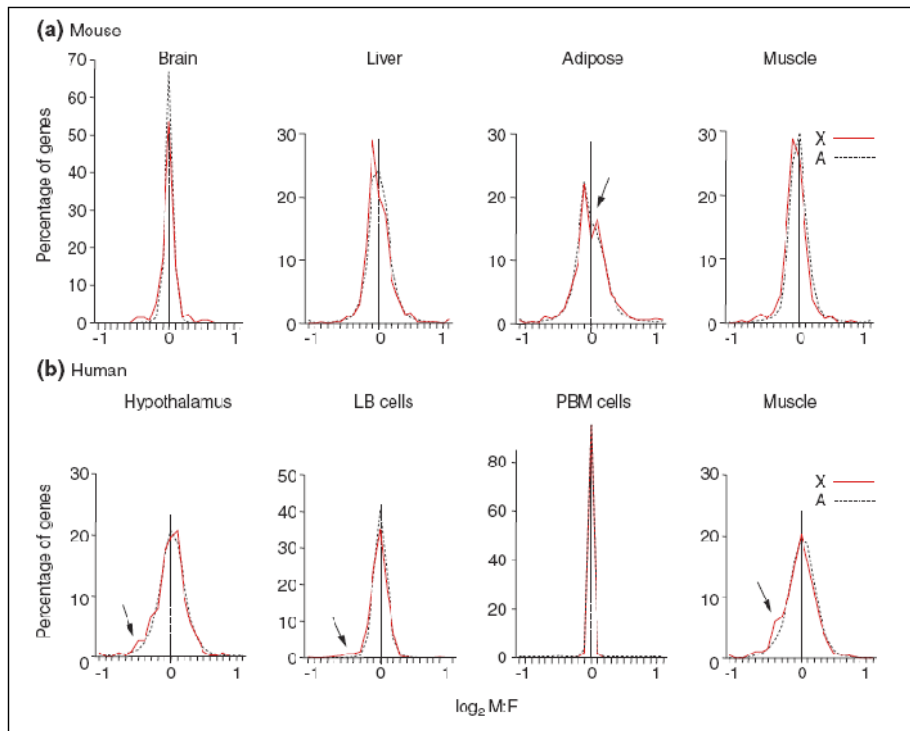
PNAS | November 26, 2006 | vol. 103 | no. 48



Tsuda, Y. *et al.* (2007) Comparison of the Z and W sex chromosomal architectures in elegant crested tinamou (*Eudromia elegans*) and ostrich (*Struthio camelus*) and the process of sex chromosome differentiation in palaeognathous birds. *Chromosoma* 116, 159–173



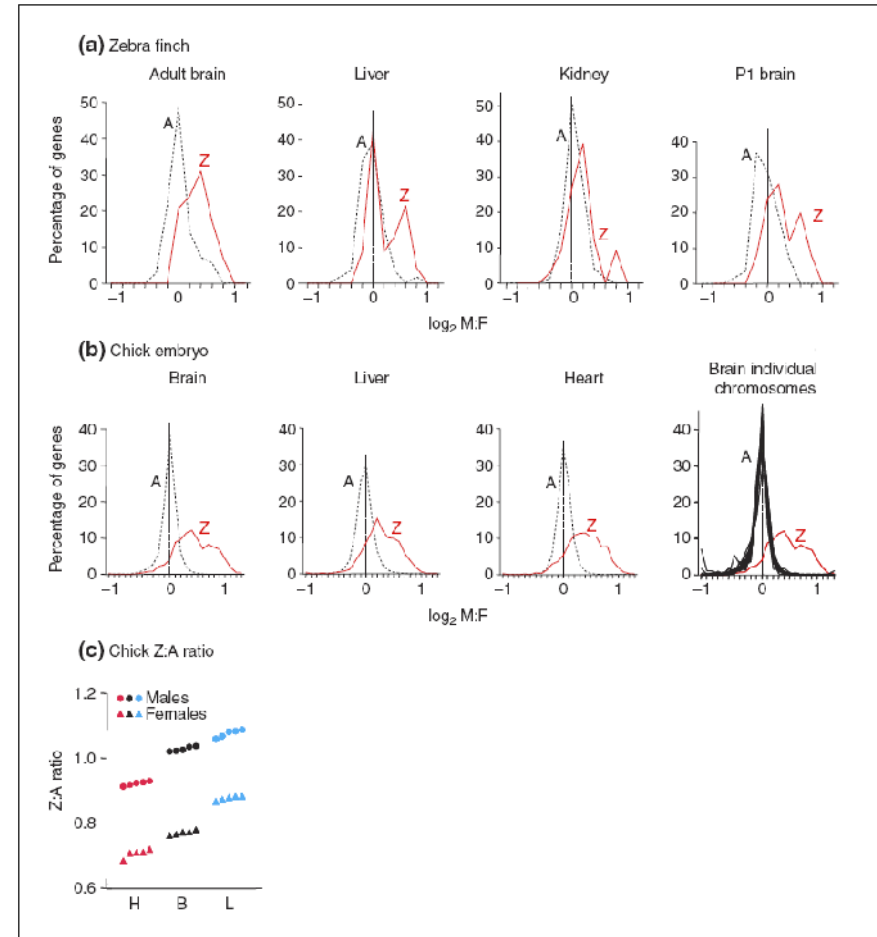




**Figure 3**  
Comparison of male and female gene expression in mammals. In mouse (a) and humans (b), each tissue has a distinct distribution of M:F ratios, but in each case the distribution for X genes (red line) fits closely to the distribution for A genes (dotted black line). LB, lymphoblastoid cell lines. PBM cells, peripheral blood mononuclear cells. Arrows point to regions where the X and A curves diverge, or to the inflection point in the mouse adipose tissue curve.

## Dosage compensation is less effective in birds than in mammals

Yuichiro Itoh<sup>\*□</sup>, Esther Melamed<sup>\*□</sup>, Xia Yang<sup>†</sup>, Kathy Kampf<sup>\*</sup>,  
Susanna Wang<sup>†</sup>, Nadir Yehya<sup>†</sup>, Atila Van Nas<sup>†</sup>, Kirstin Replogle<sup>‡</sup>,  
Mark R Band<sup>§</sup>, David F Clayton<sup>‡</sup>, Eric E Schadt<sup>¶</sup>, Aldons J Lusis<sup>†</sup>  
and Arthur P Arnold<sup>\*</sup>



**Figure 4**  
Distributions of male-to-female (M:F) ratios of gene expression based on microarray studies of birds. (a) M:F ratios in zebra finches, in adult brain, liver, and kidney, and brain of post-hatch day 1 (P1). Autosomal genes (A) are represented by the black dotted line, Z genes (Z) by the red line. The vertical dashed line is centered at a M:F ratio of 1 (log<sub>2</sub> ratio of 0). (b) M:F ratios of embryonic chick brain, liver, and heart. In each case Z genes are expressed at higher M:F ratios than A genes. In (b) the panel on the far right shows distributions for brain of individual chromosomes containing more than 50 genes. In all panels in (a) and (b) the rightmost bin (at the rightmost mark on the abscissa) includes all genes with M:F ratios at that value or greater, and the leftmost bin includes all genes with M:F ratios at that value or smaller. (c) Z:A ratios of five male and five female chicken samples for heart (H), brain (B) and liver (L).

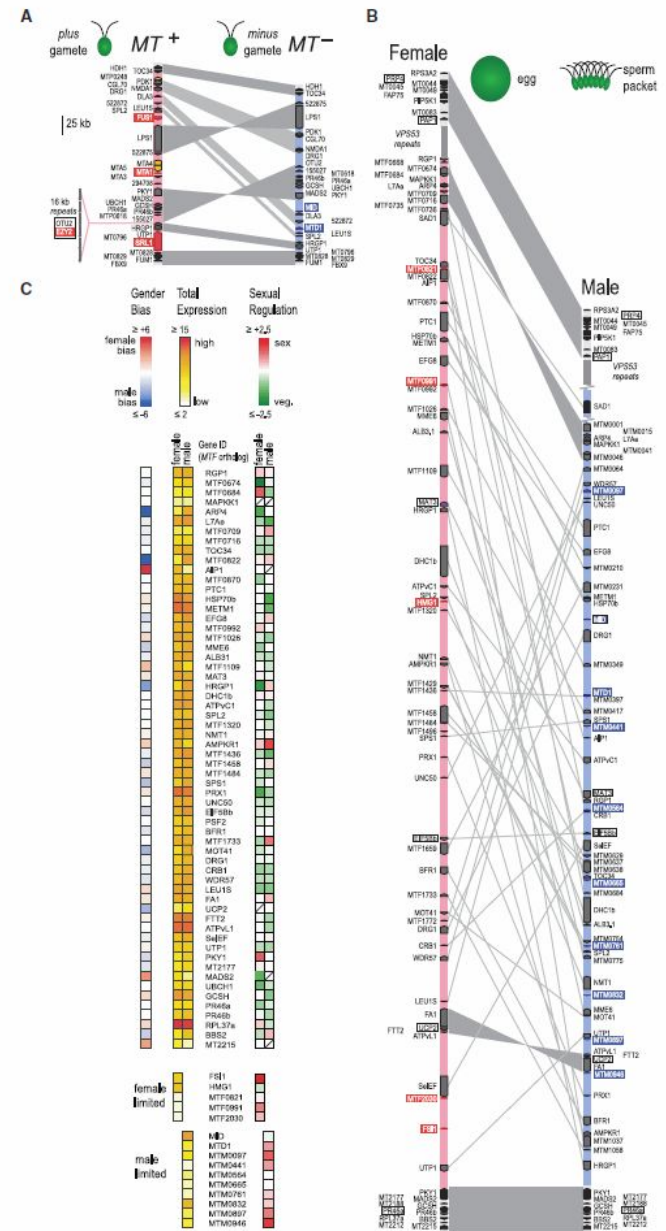
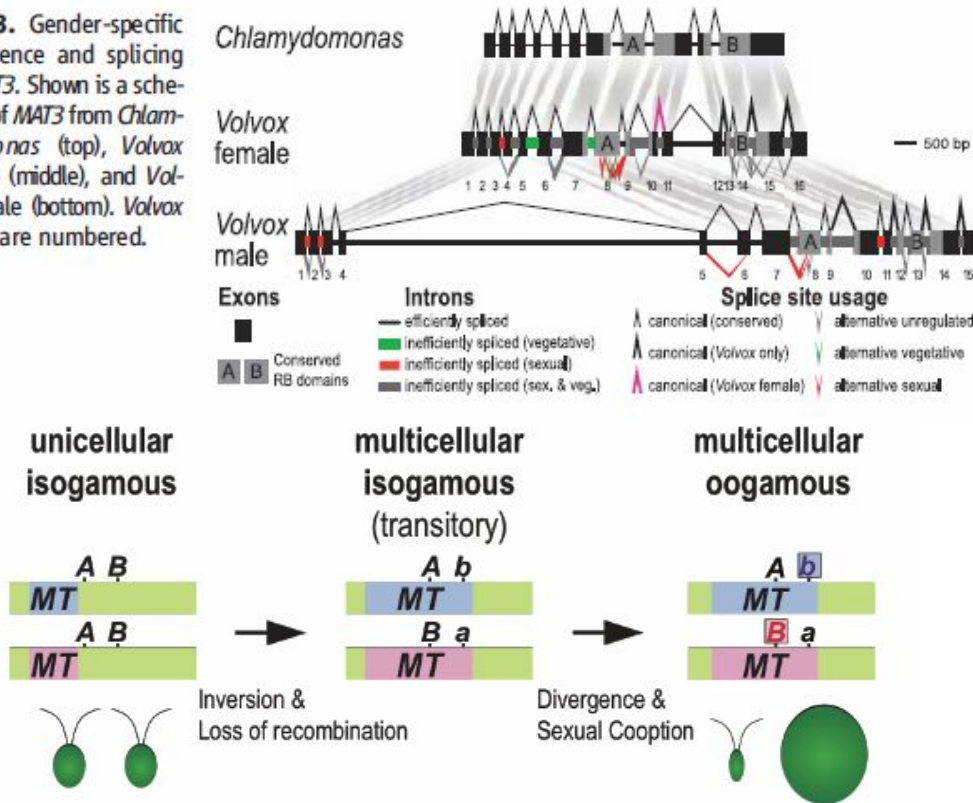
# Evolution of an Expanded Sex-Determining Locus in *Volvox*

Patrick Ferris,<sup>1\*</sup> Bradley J. S. C. Olson,<sup>1\*</sup> Peter L. De Hoff,<sup>1</sup> Stephen Douglass,<sup>2</sup> David Casero,<sup>2</sup> Simon Prochnik,<sup>3</sup> Sa Geng,<sup>1</sup> Rhitu Rai,<sup>1,4</sup> Jane Grimwood,<sup>5</sup> Jeremy Schmutz,<sup>5</sup> Ichiro Nishii,<sup>6</sup> Takashi Hamaji,<sup>7</sup> Hisayoshi Nozaki,<sup>7</sup> Matteo Pellegrini,<sup>2</sup> James G. Umen<sup>1†</sup>

SCIENCE VOL 328 16 APRIL 2010

MAT3 – homolog retinoblastoma tumor suppressor

**Fig. 3.** Gender-specific divergence and splicing of *MAT3*. Shown is a schematic of *MAT3* from *Chlamydomonas* (top), *Volvox* female (middle), and *Volvox* male (bottom). *Volvox* exons are numbered.



**Fig. 1.** Expansion of *Volvox* *MT* and sex-regulated gene expression. **(A)** Schematic of *Chlamydomonas* mating locus with rearranged domains in light blue or pink. *MT*<sup>+</sup>-limited genes are shaded red if unique or orange if they have an autosomal copy. *MT*<sup>-</sup>-limited genes are shaded blue. Flanking and shared genes are shaded black and gray, respectively. Synteny is indicated by gray shading. **(B)** Schematic of *Volvox* *MT* scaled as in **(A)**. Boxed genes were used for mapping. The bottom segment represents a transposon repeat region containing copies of *VP553*. **(C)** Expression heat maps of *Volvox* *MT* genes. (Left) Female/male expression ratio. (Middle) Total expression. (Right) Sexual induction (Sex) or repression (Veg). Diagonal hatch indicates insufficient data.

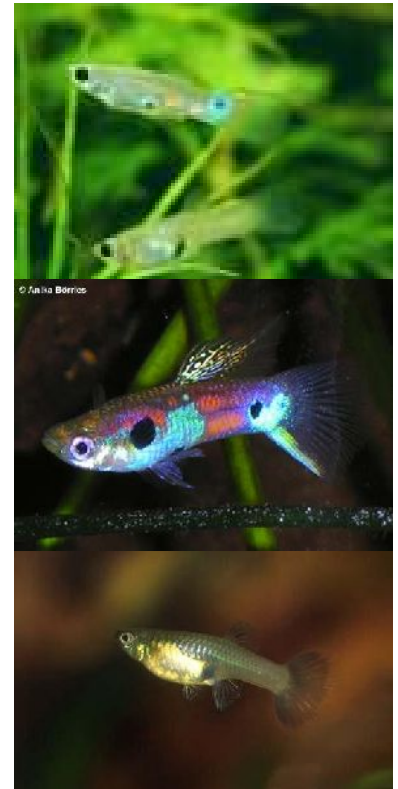


## Sex Chromosomes and Sexual Selection in Poeciliid Fishes

Anna Lindholm<sup>1,\*</sup> and Felix Breden<sup>2,†</sup>S216 *The American Naturalist*

Table 2: Phenotypic traits unrelated to sexual differentiation that are linked to the Y or W (heterogametic) chromosome

Family and species	Trait	Heterogametic sex	Reference
<b>Chrysomelidae:</b>			
<i>Gonioctena variabilis</i>	Pigmentation	Male	de Zulueta 1925; Galán 1931
<i>Phyllotreta nemorum</i>	Survival on host plant	Male	Segarra and Petitpierre 1990; Nielsen 1997
<b>Cichlidae:</b>			
<i>Neochromis omnicaruleus</i>	Pigmentation	Male or female <sup>a</sup>	Seehausen et al. 1999
<b>Cyprinodontidae:</b>			
<i>Oryzias latipes</i>	Pigmentation	Male	Matsuda et al. 1998; Wada et al. 1998
<b>Hominidae:</b>			
Human	Height, tooth growth	Male	Alvesalo 1997; Kirsch et al. 2000
<b>Muridae:</b>			
<i>Mus musculus</i>	Aggression	Male	Selmanoff et al. 1975; Sluyter et al. 1994
<b>Papilionidae:</b>			
<i>Papilio glaucus</i>	Pigmentation	Female	Scriber et al. 1996
<b>Poeciliidae:</b>			
<i>Gambusia holbrooki</i>	Pigmentation	Male	Black and Howell 1979; Angus 1989
<i>Limia perugiae</i>	Size	Male	Erbelding-Denk et al. 1994
<i>Poecilia latipinna</i>	Size	Male	Travis 1994
<i>Poecilia parae</i>	Pigmentation	Male	A. Lindholm and F. Breden, unpublished data
<i>Poecilia reticulata</i>	Pigmentation, fin shape and size, courtship, attractiveness	Male	Winge 1927; Farr 1983; Brooks 2000; Brooks and Endler 2001
<i>Xiphophorus andersi</i>	Size	Male	Kallman 1989
<i>Xiphophorus maculatus</i>	Pigmentation, size	Male or female <sup>a</sup>	Kallman 1970; Kallman and Borkoski 1978
<i>Xiphophorus milleri</i>	Pigmentation, size	Male	Kallman and Borowsky 1972
<i>Xiphophorus montezumae</i>	Pigmentation, size	Male	Kallman 1983
<i>Xiphophorus multilineatus</i> <sup>b</sup>	Pigmentation, bar suppressor, size, courtship	Male	Zimmerer and Kallman 1988, 1989; Kallman 1989
<i>Xiphophorus nigrensis</i> <sup>b</sup>	Pigmentation, size	Male	Zander 1968; Kallman 1989
<i>Xiphophorus pygmaeus</i>	Pigmentation, size	Male	Kallman 1989
<i>Xiphophorus variatus</i>	Pigmentation, size	Male	Borowsky 1984, 1987

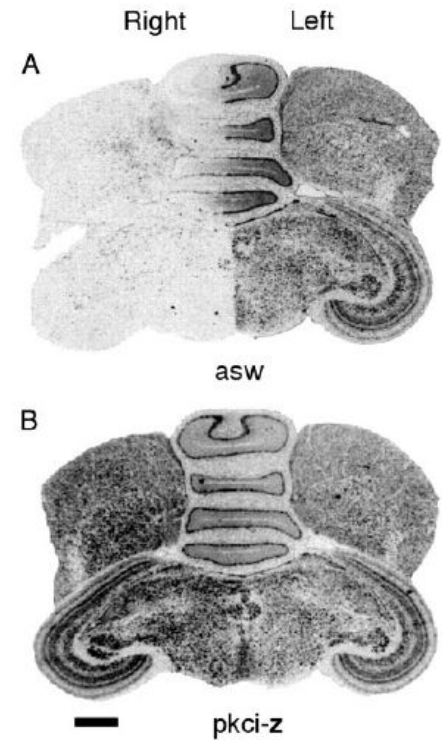
<sup>a</sup> Multiallelic system.<sup>b</sup> Sensu Rauchenberger et al. 1990.



## Neural, not gonadal, origin of brain sex differences in a gynandromorphic finch

Robert J. Agate\*, William Grisham\*, Juli Wade<sup>1</sup>, Suzanne Mann\*\*, John Wingfield<sup>3</sup>, Carolyn Schanen\*\*, Aarno Palotie\*, and Arthur D. Arnold\*<sup>1</sup>

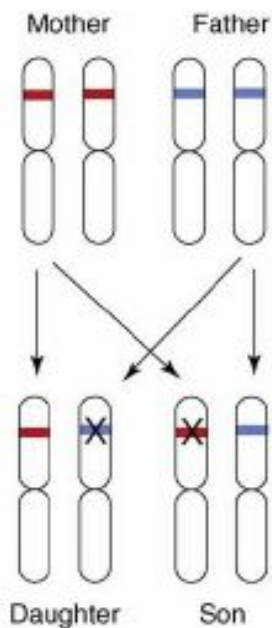
PNAS | April 15, 2003 | vol. 100 | no. 8 | 4873–4878



## Vznik sexuálního dimorfismu

### D) Transgenerační epigenetické vlivy:

- genomový imprinting



# Intralocus sexual conflict

Russell Bonduriansky<sup>1</sup> and Stephen F. Chenoweth<sup>2</sup>

*Trends in Ecology and Evolution* Vol.24 No.5

21 March 2009

## AN EXAMPLE OF IMPRINTING



1 In mammals, the growth factor Igf2 interacts with the Igf2 receptor.



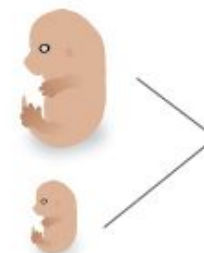
Genes from mom:  
Igf2 receptor - ON  
Igf2 - OFF

Genes from dad:  
Igf2 receptor - OFF  
Igf2 - ON

2 In mice, the genes for Igf2 and the Igf2 receptor are both imprinted.

Deleting the mother's Igf2 receptor gene produces overly large offspring.

Deleting the father's Igf2 gene produces dwarf offspring.



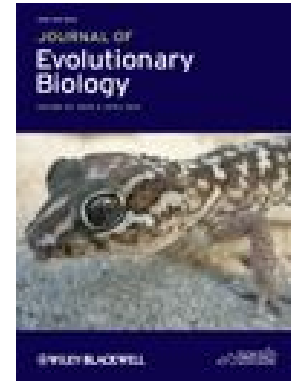
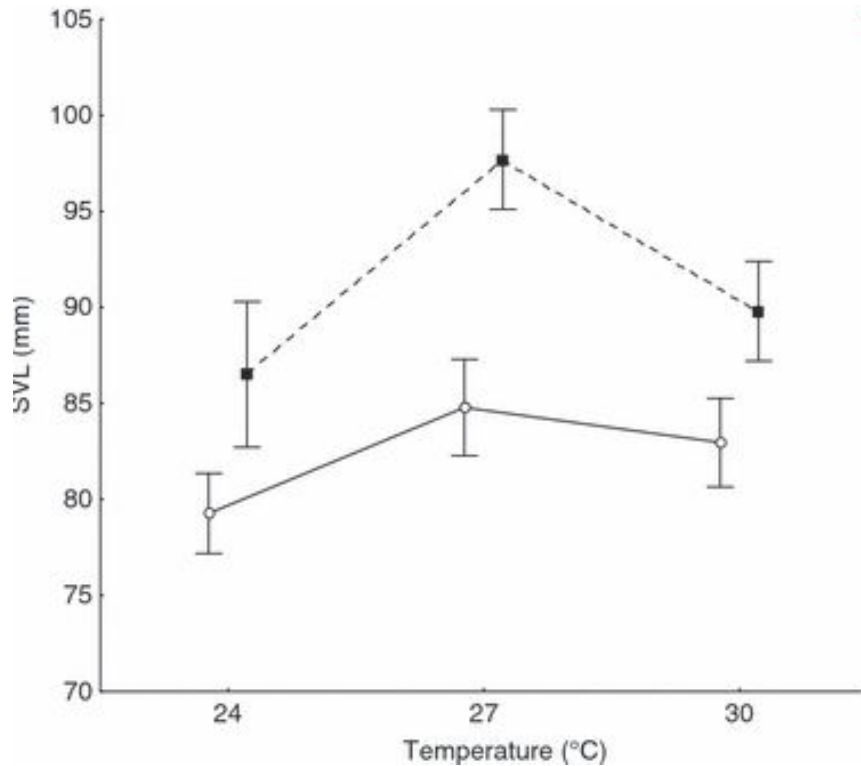
Deleting the mother's Igf2 receptor gene AND the father's Igf2 gene produces normally sized offspring.

3 The imprints on the Igf2 and Igf2 receptor genes normally cancel each other out. Changing the imprint on one copy of the gene has a dramatic effect on the size of the offspring. This result supports the genetic conflict hypothesis



## Vznik sexuálního dimorfismu – prolomení korelace mezi pohlavími

E) Rozdíly v prostředí (např. pohlavně specifická rodičovská alokace, hormonální prostředí v uteru či substrátu apod.), fenotypově plastické normy reakce



## Shrnutí

- Selekcční tlak na vznik pohlavního dimorfismu je velmi častý
- Evoluci pohlavního dimorfismu brání genetická korelace mezi pohlavími vedoucí k intralokusovému sexuálnímu konfliktu
- K prolomení této korelace dochází různými mechanismy, nejdůležitějším je patrně pohlavně-specifická exprese genů na autozomech a vazba na pohlavní chromozomy

