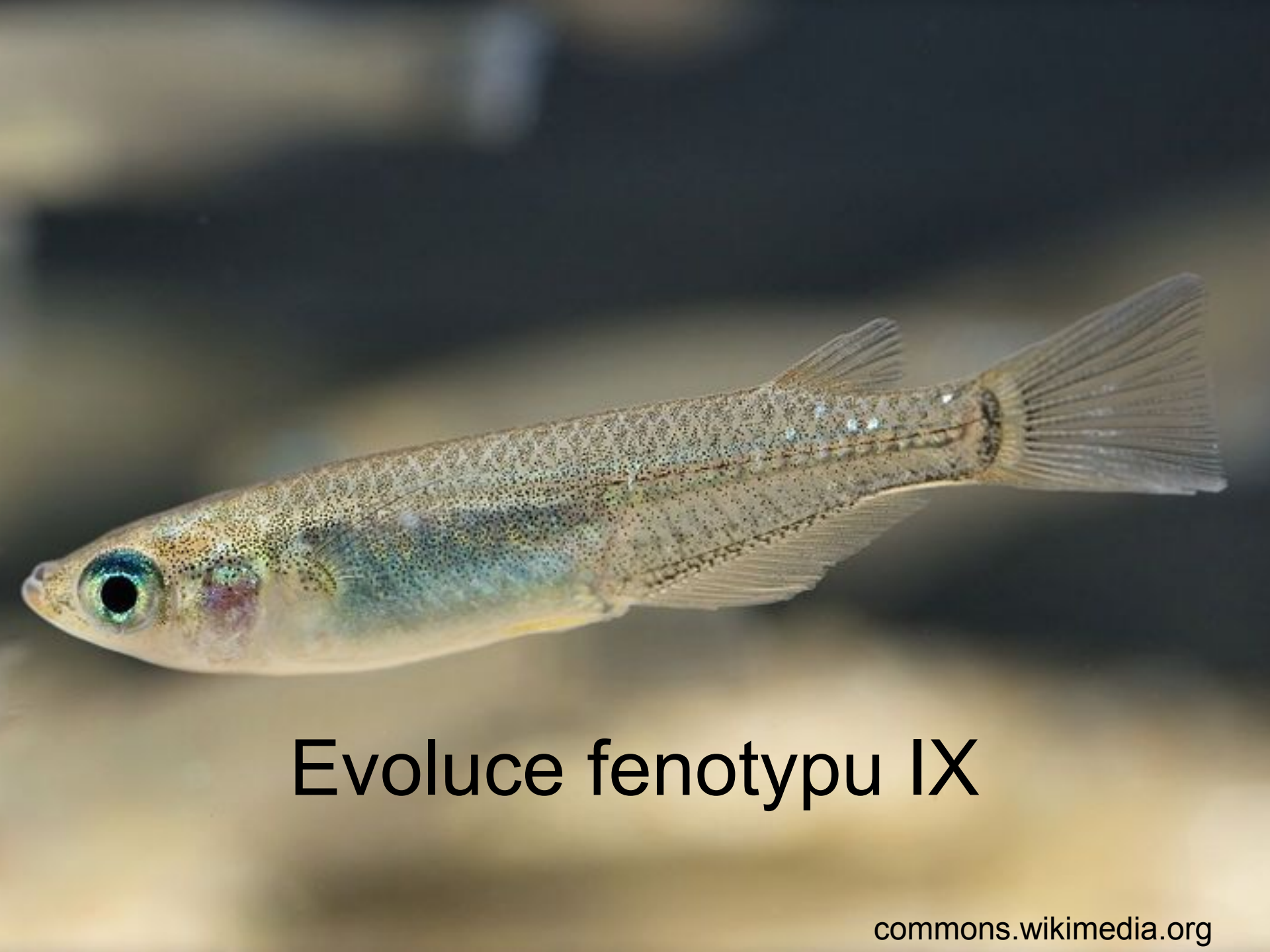
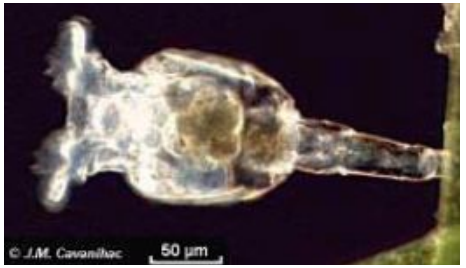


Evoluce fenotypu IX

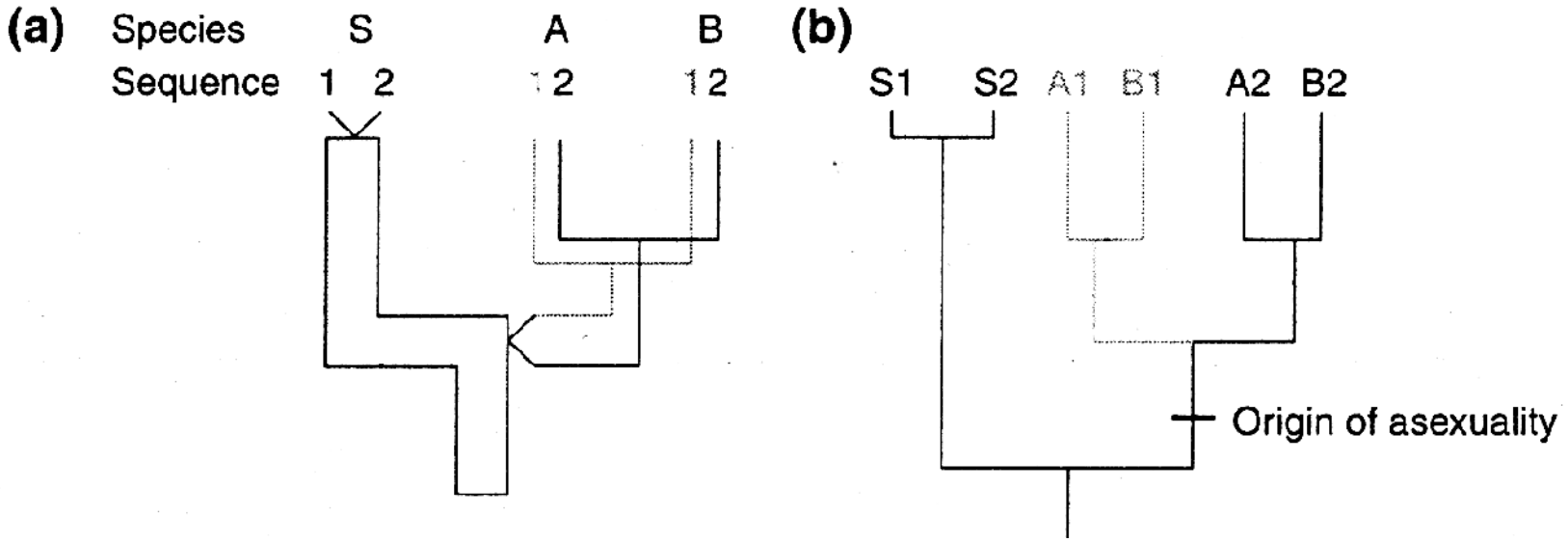
commons.wikimedia.org

Mechanismy určování pohlaví



- <u>asexuální:</u>

-obligatorní: zpravidla mladé linie (některé ryby, obojživelníci
– gynogeneze či hybridogeneze; hadi, gekoni,
ještěrky – thelytokie; vířníci ze skupiny Bdelloidea, pancířníci, Darwinulidae)
- thelytokie apomiktická (mitotická)
- thelytokie automiktická (např. premeiotické zdvojení genomu v primárních oocytech)



Meselson M (2004)

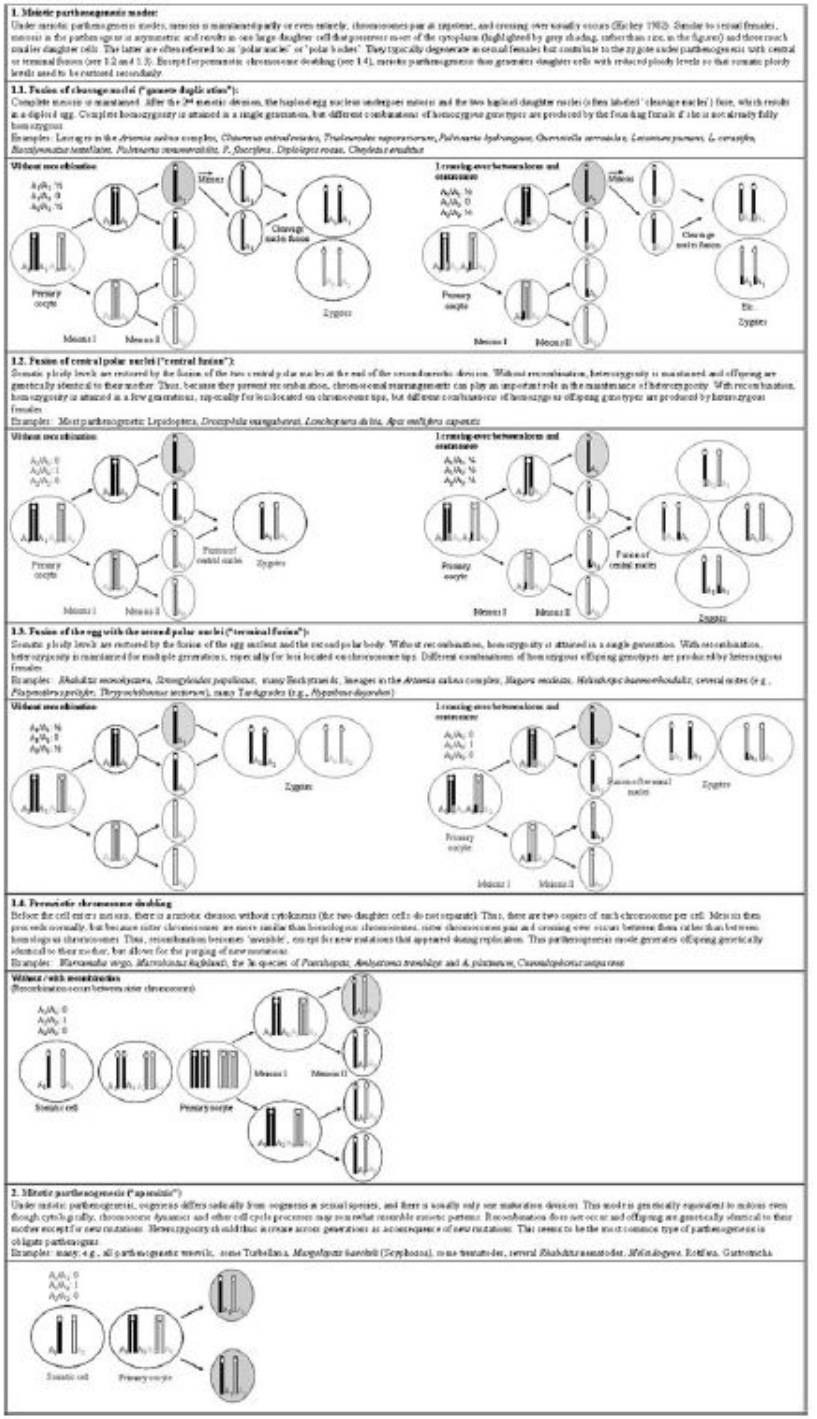
Trends in Ecology & Evolution

Evol Biol
DOI 10.1007/s11692-011-9113-z

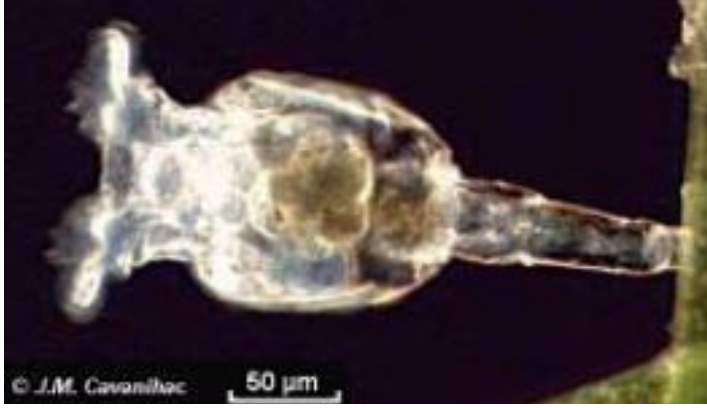
SYNTHESIS PAPER

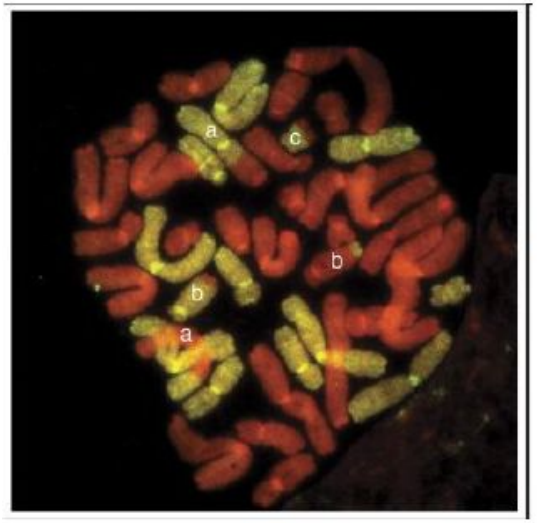
Using Parthenogenetic Lineages to Identify Advantages of Sex

Maurine Neiman · Tanja Schwander



Existují asexuální živočichové?





Triploidní hybrid ($3n = 42$)
2x *A. jeffersonianum* (červená)
1x *A. laterale* (žlutá)

Bogart et al.

Massive Horizontal Gene Transfer in Bdelloid Rotifers

Eugene A. Gladyshev,[1] Matthew Meselson,[1,2]* Irina R. Arkhipova[1,2]*

30 MAY 2008 VOL 320 SCIENCE

Gene ID, name	Contig ID	Introns	AI	% Identity to best hit	Best hit, E-value	Best hit, metazoan	Best hit, taxonomy	Definition
AV10027_*XynB*	Av212A	0	460	63	0.00E+00	No hits	Bacteria; Bacteroidetes	Xylosidase/arabinosidase
AV10001_*NRPS*	Av110A	10	460	32	0.00E+00	No hits	Bacteria; (Proteobacteria/ Cyanobacteria)	Nonribosomal peptide synthetase
AV10134_*PheA*	161F07	0	400	61	1.00E-174	No hits	(Fungi; Bacteria)	Monooxygenase, FAD dependent
AV10002_*TrkA*	Av110A	0	379	54	1.00E-175	4.00E-11	Bacteria; Proteobacteria	Monooxygenase, NAD dependent
PR10002_*MviM*	182F10	0	327	67	1.00E-149	2.00E-07	Bacteria; (Acidobacteria/ Chloroflexi)	Oxidoreductase
PR10010_*DAP2*	182F10	0	310	27	1.00E-140	1.00E-05	Bacteria; (Acidobacteria/ Proteobacteria)	Prolyl oligopeptidase*
AV10104_*Dur3*	AvTelL.B	1	243	44	1.00E-132	4.00E-27	Eukaryota; Fungi	Urea active transporter*
PR10012_*RamA*	182J17	0	246	31	1.00E-107	No hits	(Bacteria; Fungi)	α-L-Rhamnosidase
AV10121_*NRPS*	99O7	4	237	30	1.00E-103	No hits	Bacteria; Cyanobacteria	Nonribosomal peptide synthetase
AV10153_*XghA*	210B3	0	212	50	1.00E-108	2.00E-16	Eukaryota; Fungi	Endo-xylogalacturonan hydrolase
AV10042_*HemK*	Av240B	1	199	56	2.00E-91	1.00E-04	Bacteria; Proteobacteria	HemK-like methyltransferase
AV10092_*β-Gal*	AvTelL.A	0	153	33	1.00E-105	4.00E-39	Eukaryota; Viridiplantae	β-D-Galactosidase
AV10044_*Alr*	Av240B	1	152	38	1.00E-67	No hits	Bacteria; Bacteroidetes	Alanine racemase
AV10025_*AMH*	Av212A	1	150	52	8.00E-77	2.00E-11	Eukaryota; Fungi	Amidohydrolase
AV10045_*Ddl*	Av240B	1	138	40	1.00E-60	No hits	Bacteria; Bacteroidetes	D-Alanine-D-alanine ligase
AV10140_*PLDc*	193E18	2	126	31	1.00E-55	No hits	Eukaryota; Fungi	Phospholipase-D active site motif protein*
AV10016_*FabG*	Av212A	0	98	58	1.00E-74	8.00E-32	Bacteria	Short-chain dehydrogenase/reductase
AV10109_*FabG*	AvTelL.B	0	92	57	4.00E-73	5.00E-33	Bacteria	Short-chain dehydrogenase/reductase*
AV10011_*FabG*	Av212A	0	88	54	6.00E-67	2.00E-28	Bacteria	Short-chain dehydrogenase/reductase
AV10071_*HAL*	AvTelK.A	0	77	48	2.00E-61	1.00E-27	Bacteria	Histidine ammonia-lyase
AV10095_*GCN5*	AvTelL.A	0	59	35	2.00E-27	No hits	Bacteria; Proteobacteria	GCN5-related *N*-acetyltransferase*/*
AV10158_*FabG*	210B3	2	46	41	2.00E-39	2.00E-19	Bacteria	Short-chain dehydrogenase/reductase

Mechanismy určování pohlaví

- <u>asexuální:</u>

- obligatorní

- cyklická partenogeneze: mšice, někteří korýši (*Daphnia*)

- fakultativní partenogeneze (*Thamnophis, Crotalus, Acrochordus, Varanus* – potomci jsou homozygotní samci: terminální fúze (splývá jádro sekundárního oocytu + 2. polárního tělíska); vs. *Python* – potomci jsou samice geneticky identičtí s matkou, mechanismus neznámý: *Heredity* 2003)

Parthenogenesis in Komodo dragons

Nature **444**, 1021-1022 (21 December 2006)

Mechanismy určování pohlaví

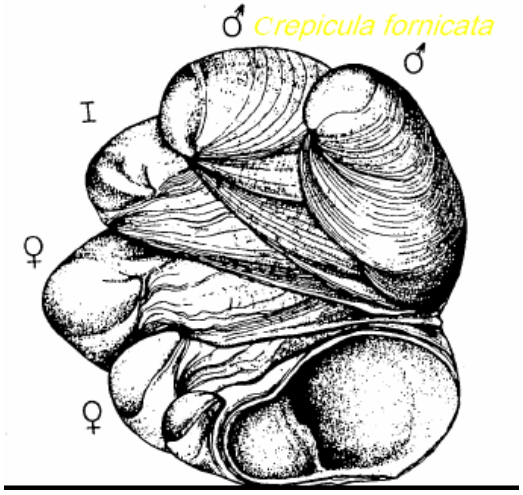
Hermafroditismus:

- simultánní hermafroditi
  - samooplození – z obratlovců jen jeden halančík

- androdioecie *Caenorhabditis elegans*

- gynodioecie – sasanka *Epiactis prolifera* (malé samice, velké hermafroditi)

- sekvenční hermafroditi:
protogynie, protandrie (Gobiidae,Muraenidae)



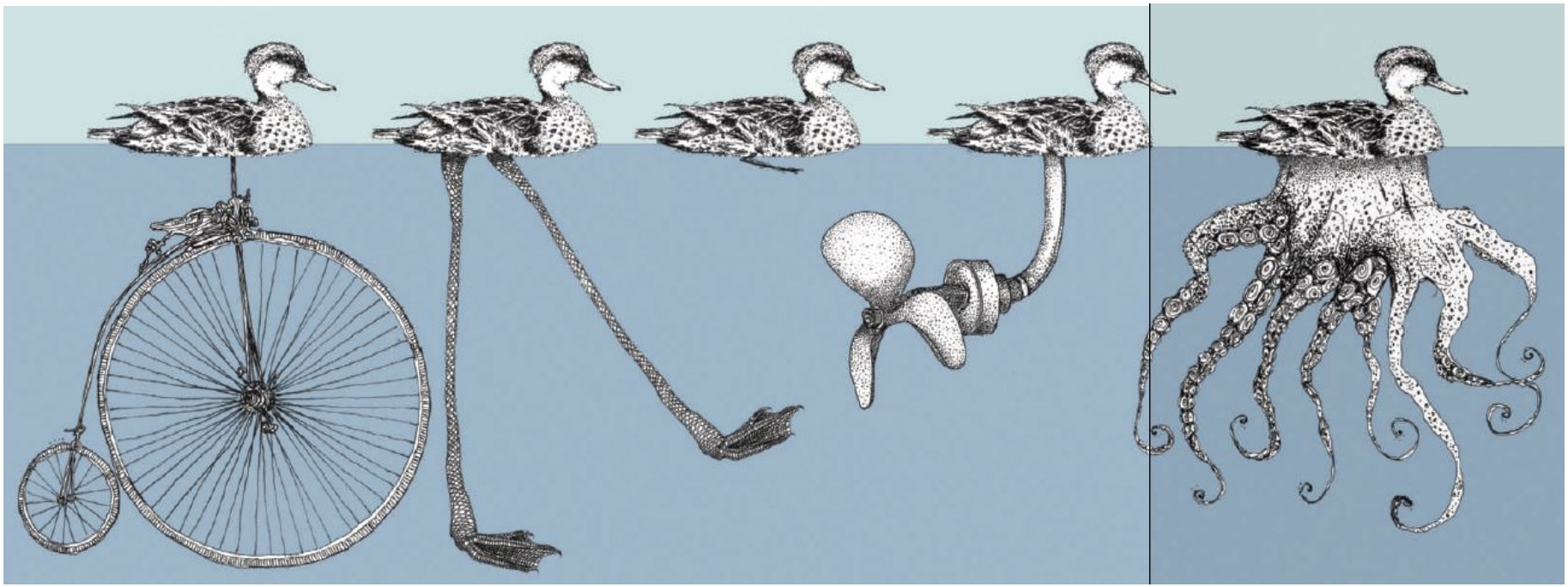
Size and growth modification in clownfish

Sex change is not the only way these fish achieve dominance — they grow into the role.

NATURE | VOL 424 | 10 JULY 2003

Mechanismy určování pohlaví

Gonochoristi



Beneath the surface

You might think that once evolution has found one way to get something done, it will stick with it. But similar physical forms can hide radically different wiring, finds **Tanguy Chouard**.

30 APRIL 2010 VOL 328 SCIENCE

NATURE|Vol 456|20 November 2008

Mechanismy určování pohlaví

Gonochoristi

Haplodiploidie: (Hymenoptera, Thysanoptera, Homoptera, roztoči, vířníci)

- arrhenotokie:

  - samci z neoplozených a samice z oplozených vajíček

    - mechanismem:

      a) komplementární determinace pohlaví (CSD)
      - diploidní heterozygoti samice, homozygoti samci

      - jeden lokus (*csd* u *Apis mellifera*)
      - multilokusová CSD

      b) epigenetické určení pohlaví (maternální imprinting u *Nasonia*)

- eliminace paternálního genomu

Maternal Control of Haplodiploid Sex Determination in the Wasp *Nasonia*

Eveline C. Verhulst, Leo W. Beukeboom, Louis van de Zande*

30 APRIL 2010 VOL 328 SCIENCE

Mechanismy určování pohlaví:

Gonochoristi:

- environmentálně určené pohlaví
  - sociálně určené pohlaví (*Bonellia*)
  - pohlaví určené množstvím potravy (hlísti, ryby?)
  - teplotně určené pohlaví (někteří plazi, ryby?)

- genotypicky určené pohlaví

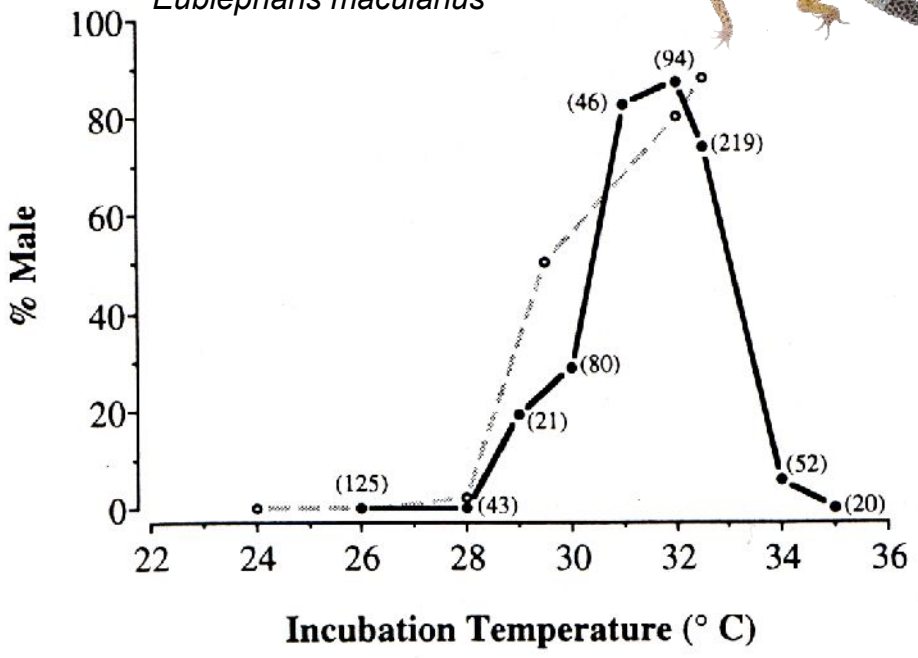
Jak odlišit?

Rapid growth and out-crossing promote female development in zebrafish (*Danio rerio*)

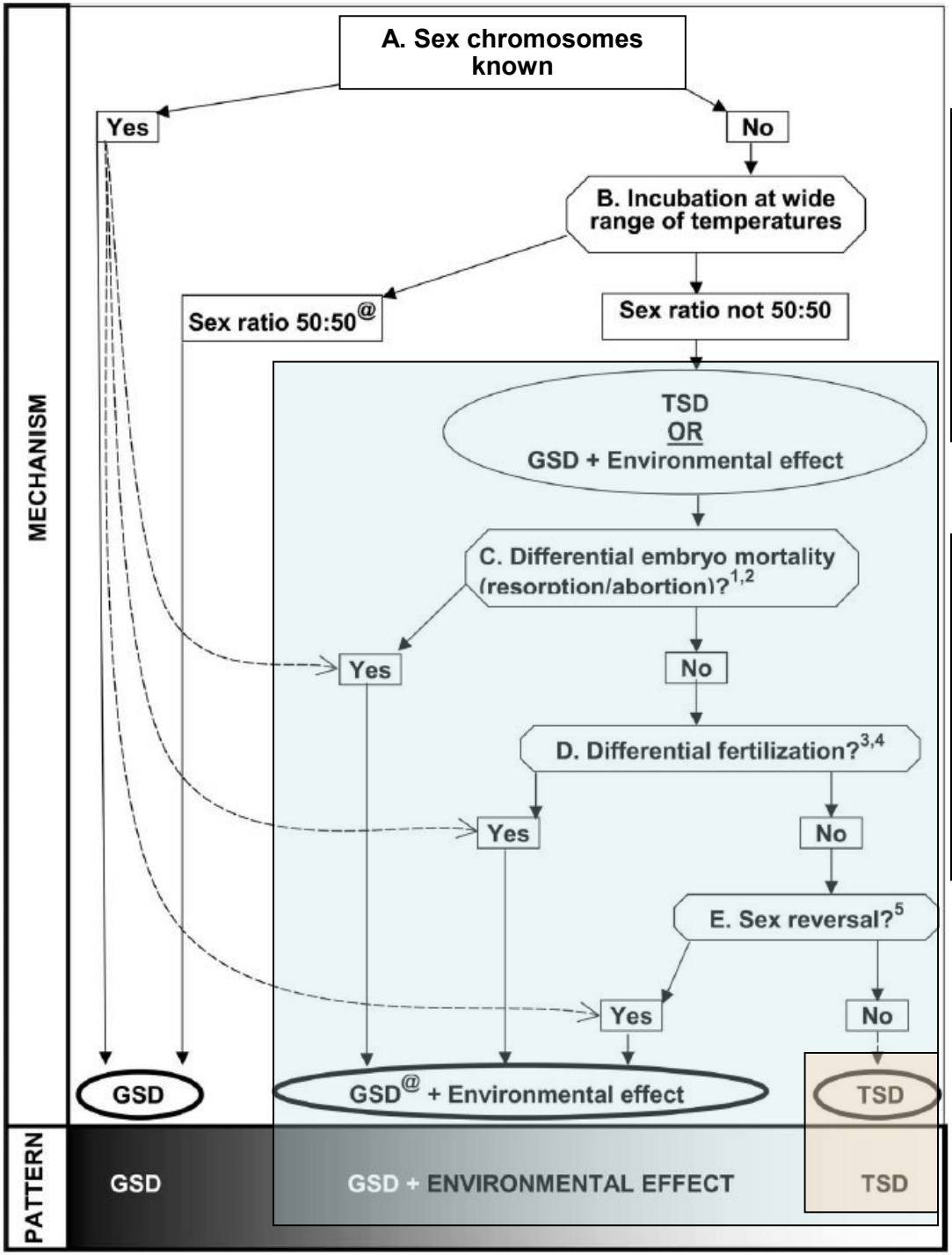
Christian Lawrence · John P. Ebersole · Richard V. Kesseli

Environ Biol Fish (2008) 81:239–246

Eublepharis macularius



Viets et al. *J.Exp.Zool.* 1993



Definice

Environmental sex-determination

= absence of sex-specific genotypes

→ dichotomy GSD vs. ESD

Valenzuela, Adams, Janzen *Am. Nat.* 2003

Environmental sex-determination

= environmentally-dependent sex ratio

→ continuum GSD ↔ ESD

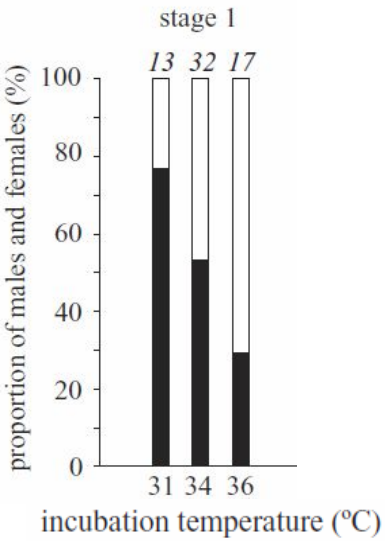
…recent reports have expanded TSD to viviparous and oviparous species with both XX/XY and ZZ/ZW sex-determining systems (2009)

David Crews

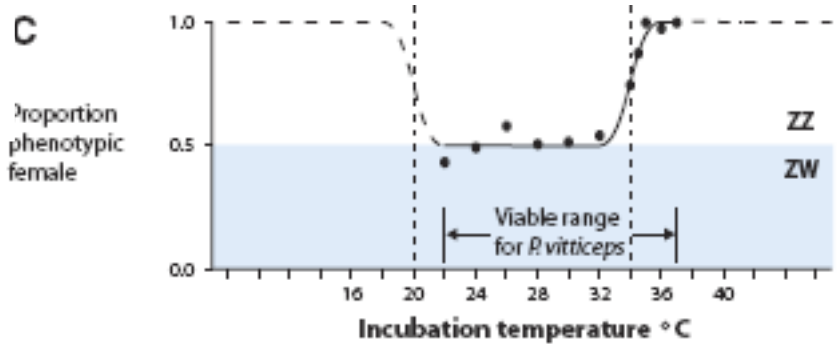
Co není pohlaví určené prostředím podle def. 1:

Temperature-dependent sex ratio in a bird

Ann Göth[1,2*] and David T. Booth[3]



Quinn et al. *Science* 2007



Pogona vitticeps ZZ/ZW

Genotypicky určené pohlaví:

- polygenní vzácné

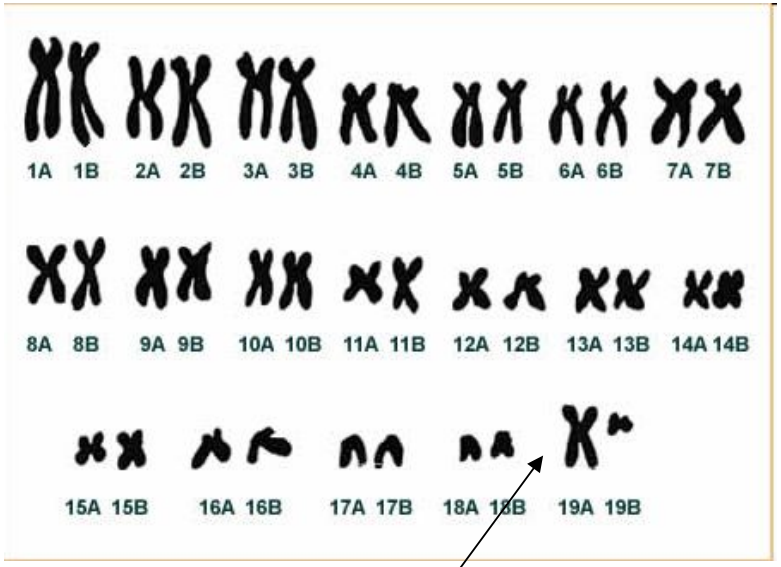
DOI: 10.1534/genetics.107.072140

A Polygenic Hypothesis for Sex Determination in the European Sea Bass *Dicentrarchus labrax*

Marc Vandeputte,*,†,1 Mathilde Dupont-Nivet,* Hervé Chavanne‡ and Béatrice Chatain†

- heterogametičtí samci nebo samice

  - geny určující pohlaví na W a Y, či na X a Z

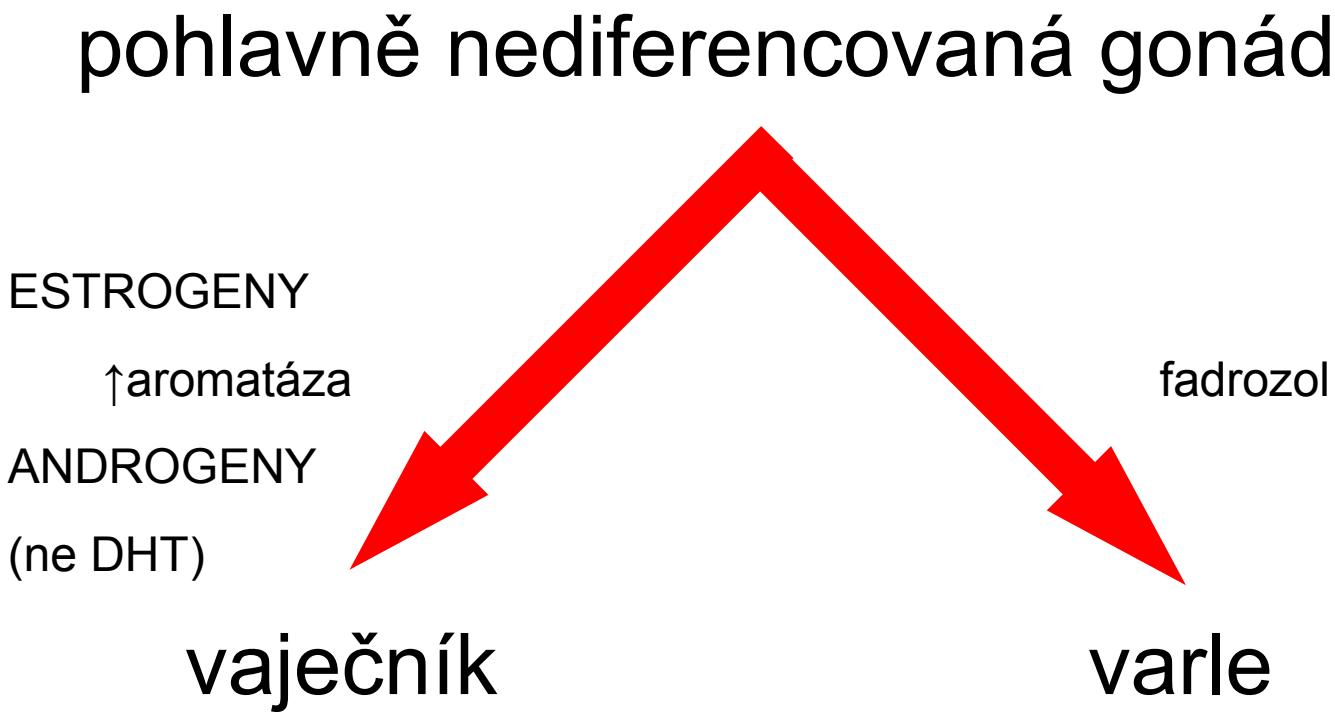


- dva typy spermií (X, Y)

- dva typy vajíček (Z, W)

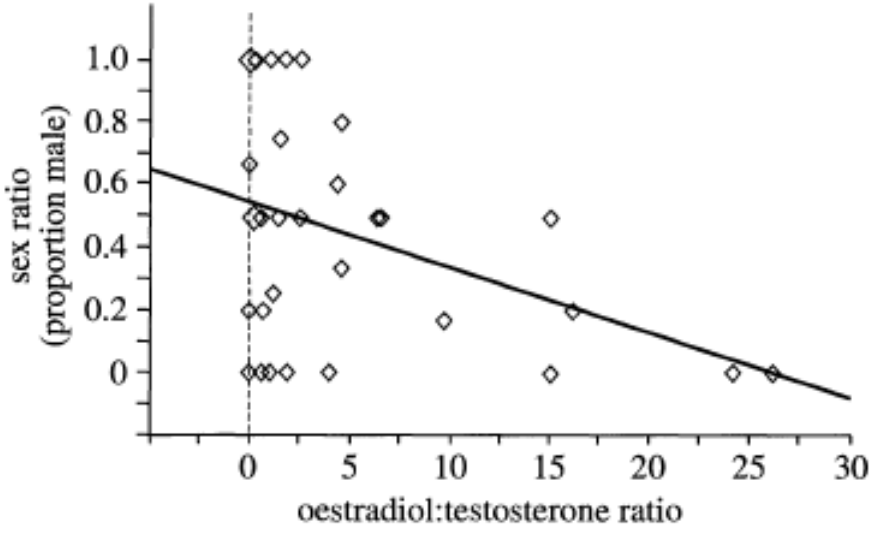
pohlavní chromozomy

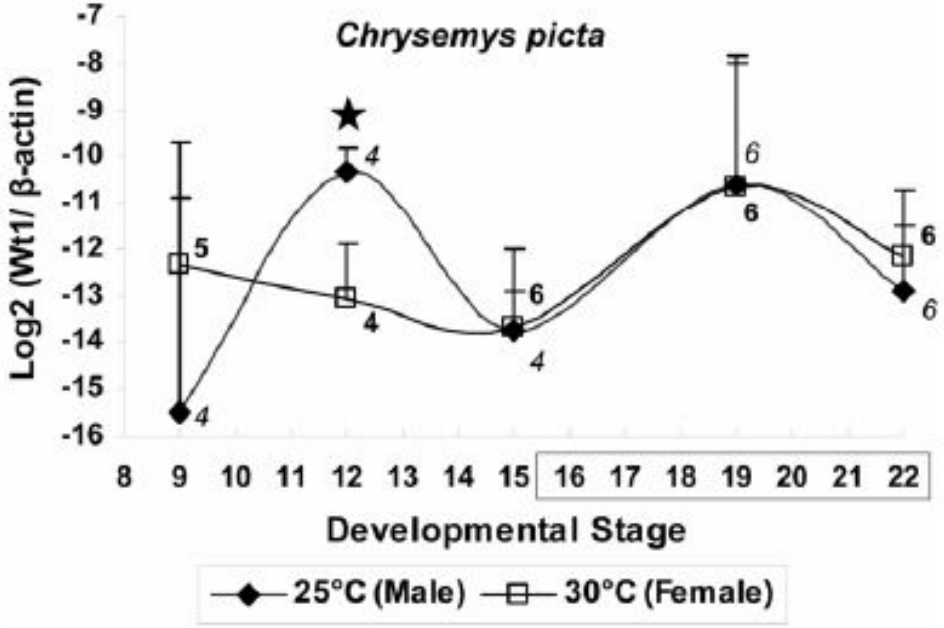
TSD: úloha pohlavních hormonů při determinaci pohlaví nebo diferenciaci?



Pieau & Dorizzi, *J. Endocrinol.* 2004

Determinují pohlaví u TSD druhů primárně maternální pohlavní hormony nebo teplotně-závislá exprese nějakého genu či teplotně-závislá aktivita enzymu?





Bowden et al. *Proc. R. Soc. Lond. B* 2000

- qRT-PCR:

Sox9, aromatáza, Wt1, Dmrt1…

Valenzuela *Evolution* 2007

Fylogeneze určování pohlaví u amniot

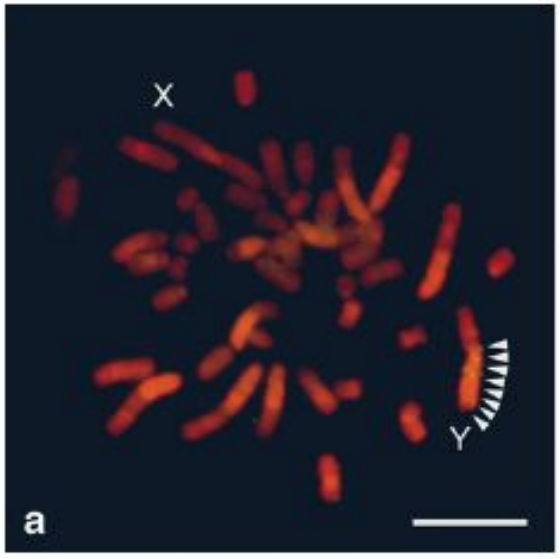
Savci

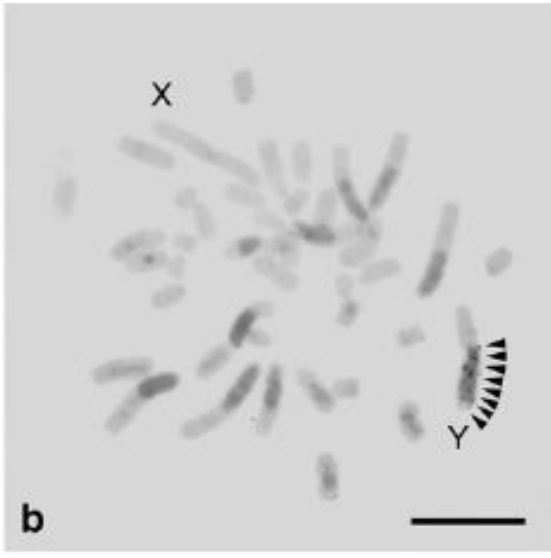
- většina XX/XY
- pohlaví determinující gen *Sry*

Multiple copies of *SRY* on the large Y chromosome of the Okinawa spiny rat, *Tokudaia muenninki*

Chie Murata · Fumio Yamada · Norihiro Kawauchi · Yoichi Matsuda · Asato Kuroiwa

Chromosome Research (2010) 18:623–634





GENES IN CONFLICT

Table 3.2 Taxonomic distribution of rodents with unusual sex chromosome and sex-determining systems

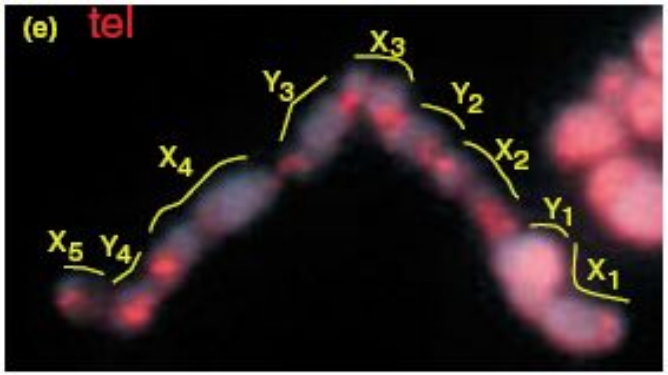
	Female Soma (germ)	Male Soma (germ)
Order Rodentia		
Family Muridae		
Subfamily Arvicolinae (Microtinae)		
Dicrostonyx torquatus	XX, XX*, X*Y	XY
Myopus schisticolor	XX, XX*, X*Y(X*X*)	XY
Microtus oregoni	XO(XX)	XY(YO)
Ellobius lutescens	XO	XO
E. tancrei, E. talpinus, E. alaicus	XX	XX
Subfamily Hesperomyinae		
Akodon azarae, A. molis, A. varius	XX, XY*	XY
Subfamily Murinae		
Tokudaia osimensis	XO	XO

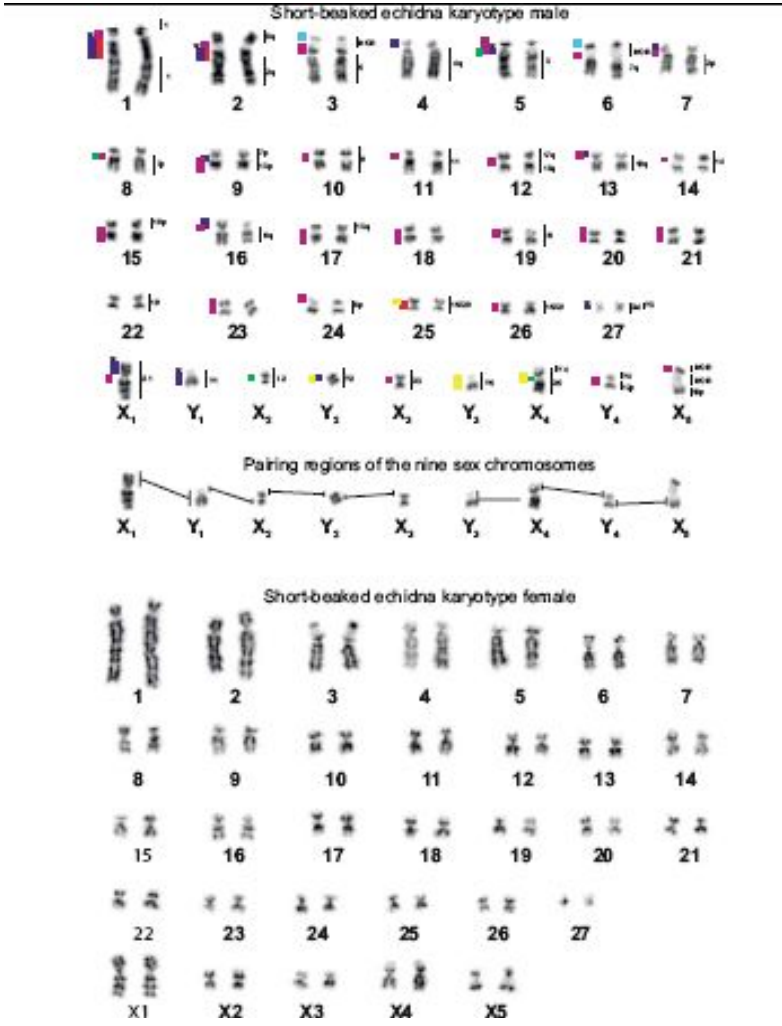
If the premeiotic genotype differs from the somatic genotype, it is given in parentheses afterwards. From Fredga (1994).

- *T. muenninki* hodně Sry kopií na Y
- *T. osimensis* X0/X0 – ztráta Y, nemá Sry, ale ostatní geny z Y na autozomech (XX+Sry myš samec, ale neplodný)

Savci

- většina XX/XY
- pohlaví determinující gen *Sry*
- *Sry* chybí u ptakořitných





The multiple sex chromosomes of platypus and echidna are not completely identical and several share homology with the avian Z

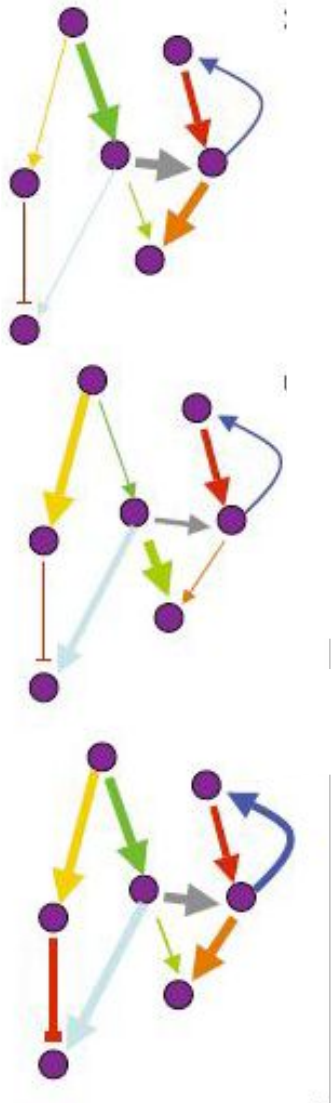
Willem Rens*, Patricia CM O'Brien*, Frank Grützner†, Oliver Clarke*, Daria Graphodatskaya*, Enkhjargal Tsend-Ayush†, Vladimir A Trifonov*‡, Helen Skelton*, Mary C Wallis*, Steve Johnston§, Frederic Veyrunes*, Jennifer AM Graves¶ and Malcolm A Ferguson-Smith*

Genome Biology 2007, Volume 8, Issue 11, Article R243

Sex determination and SRY: down to a wink and a nudge?

Ryohei Sekido and Robin Lovell-Badge

Division of Developmental Genetics, Medical Research Council National Institute for Medical Research, The Ridgeway, Mill Hill, London NW7 1AA, UK



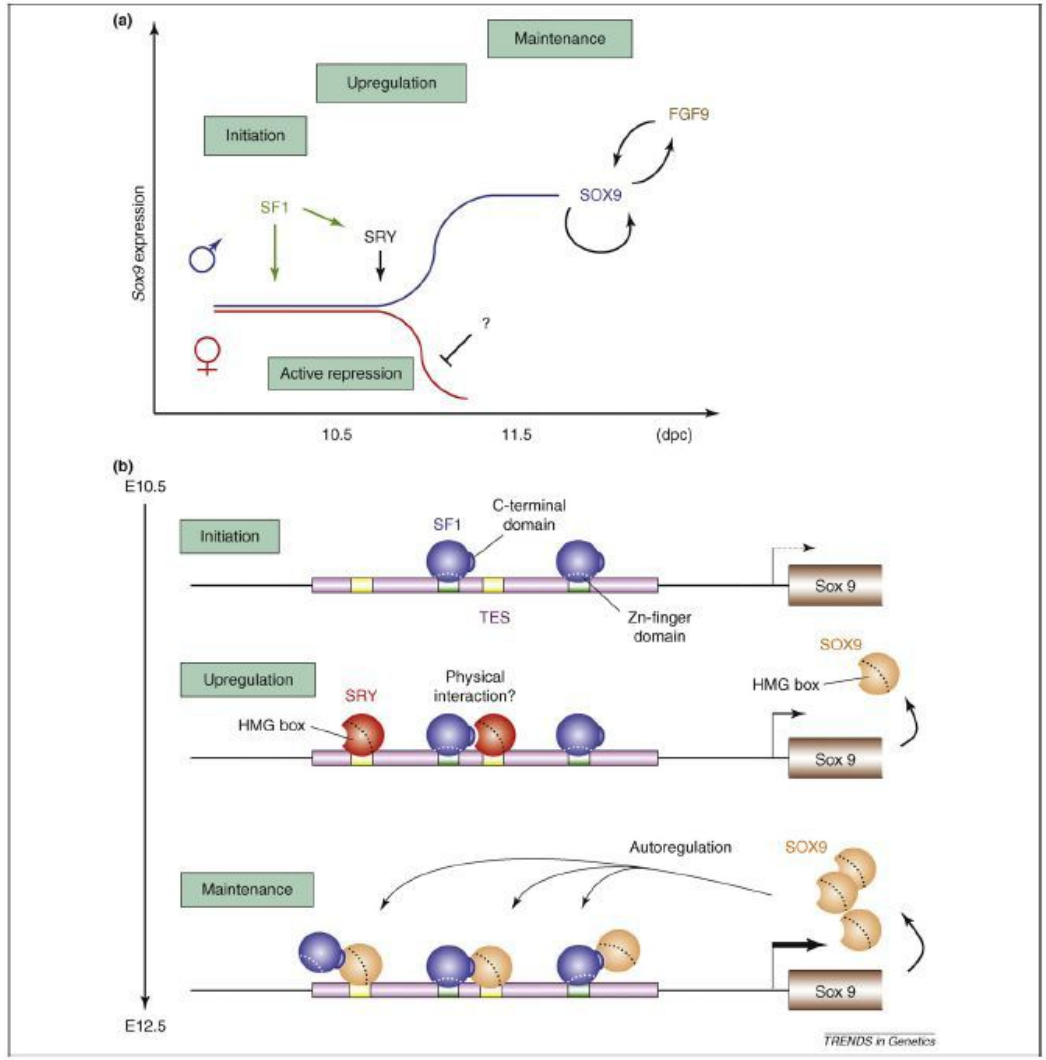
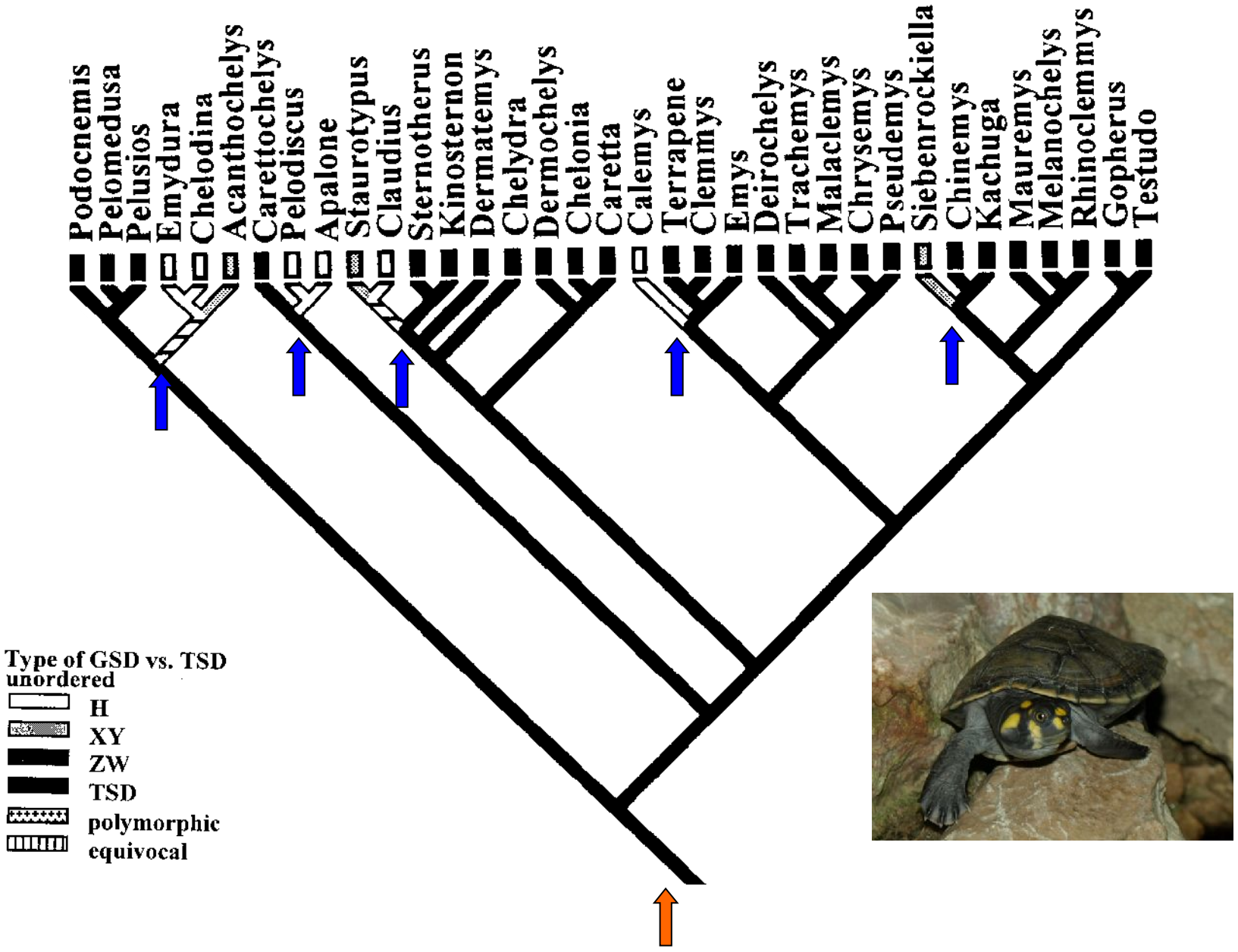


Figure 2. A model for *Sox9* transcriptional regulation in the gonad. Gonadal *Sox9* transcriptional regulation consists of three phases: initiation, upregulation and maintenance. **(a)** SF1 sensitizes *Sox9*, initiating a low level of expression in the genital ridge of both sexes at 10.5 dpc. In the male, SF1 (probably with other factors such as $WT1^{-KTS}$) also activates *Sry* expression. *Sox9* expression is upregulated by the action of SRY together with SF1, whereas it is downregulated in the female. This downregulation is unlikely to be passive, implying the presence of one or more currently unknown repressors. After the transient expression of *Sry* has ceased, high levels of SOX9 are maintained by its direct autoregulation and via FGF9 signaling. **(b)** SF1 binds to SF1-BSs (green) in TES via its Zn-finger domain (white dotted line) at 10.5 dpc. When SRY is expressed, it binds to SRY-BSs (yellow) via its HMG-box (black dotted line) and cooperates with SF1 to upregulate *Sox9* expression. In turn, SOX9, also together with SF1, maintains its own expression. SOX9 binds directly to the enhancer, replacing SRY at some sites, but because the SOX9 HMG box can physically interact with the SF1 C-terminal domain, the two proteins also recruit each other to additional binding sites.

Želvy – původně poměr určené teplotou, nejméně 6x vznik pohlavních chromozomů



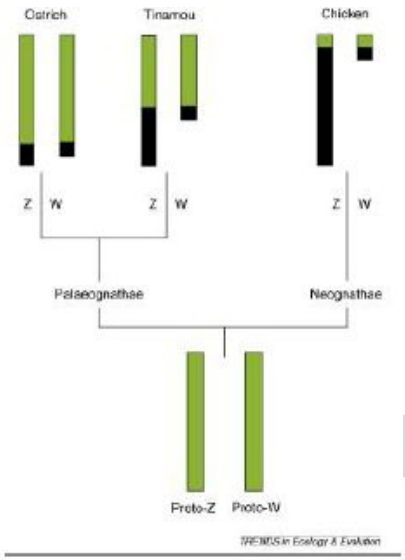
Janzen & Pauksis *Temperature-dependent sex determination in vertebrates* 2004

Archosauři (ptáci a krokodýli)

- krokodýli: u 12 druhů pohlaví určené teplotou

- ptáci:
  - konzervativně ZZ/ZW:
  - *Dmrt1* - u ptáků na Z, podezřelý z determinace pohlaví

  - ZZZ sterilní samci
  - ZZW intersex
  - Z0 neznámí (letální?)

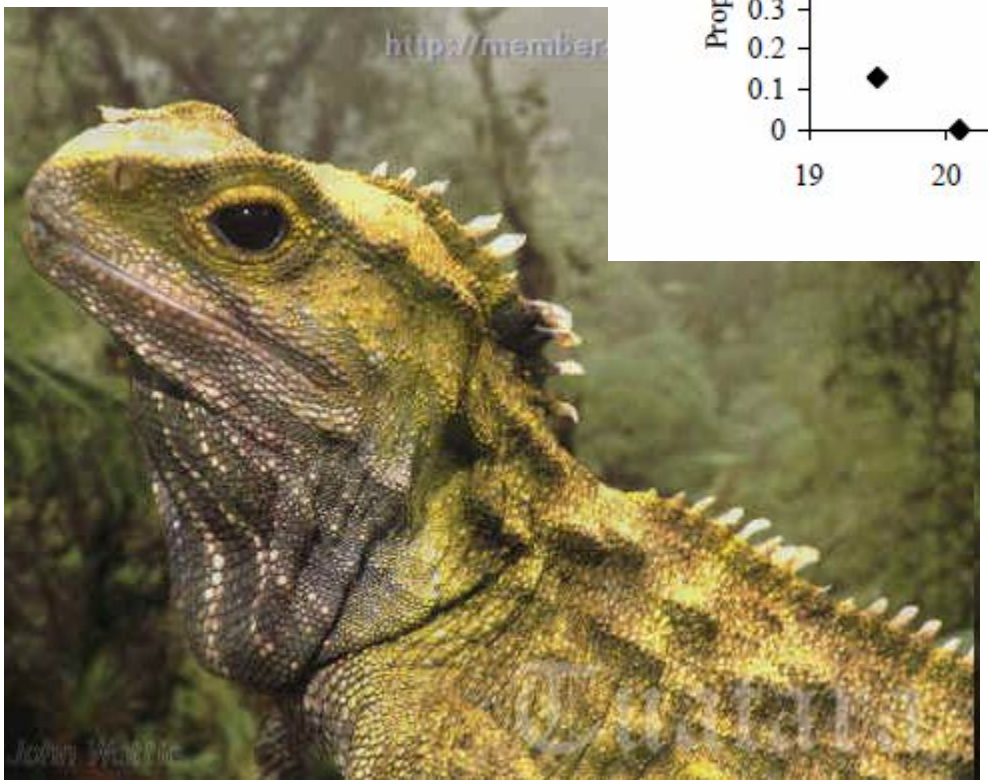


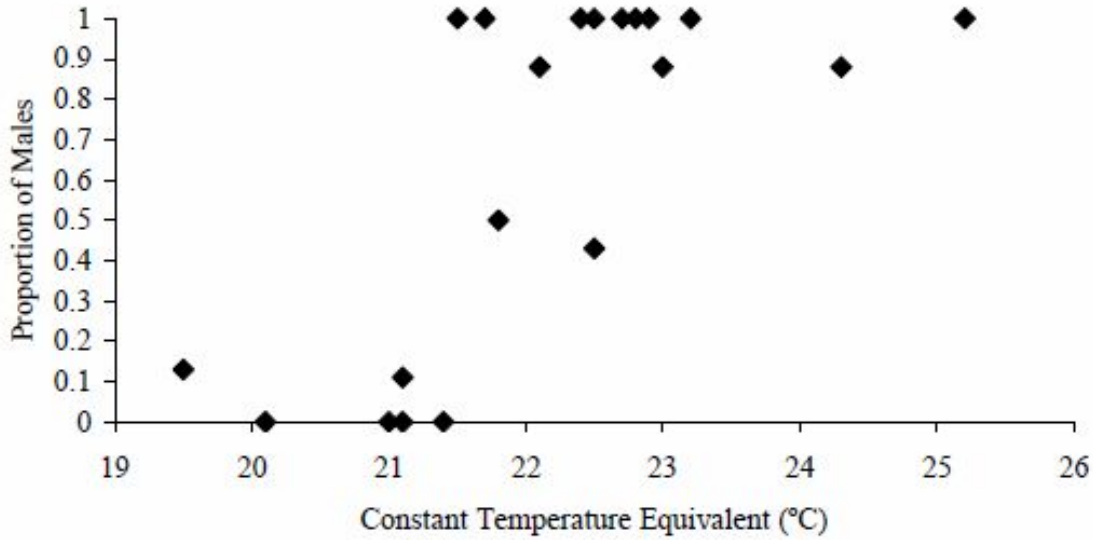
The avian Z-linked gene *DMRT1* is required for male sex determination in the chicken

Craig A. Smith[1], Kelly N. Roeszler[1], Thomas Ohnesorg[1], David M. Cummins[2], Peter G. Farlie[1], Timothy J. Doran[2] & Andrew H. Sinclair[1]

Vol 461|10 September 2009|doi:10.1038/nature08298

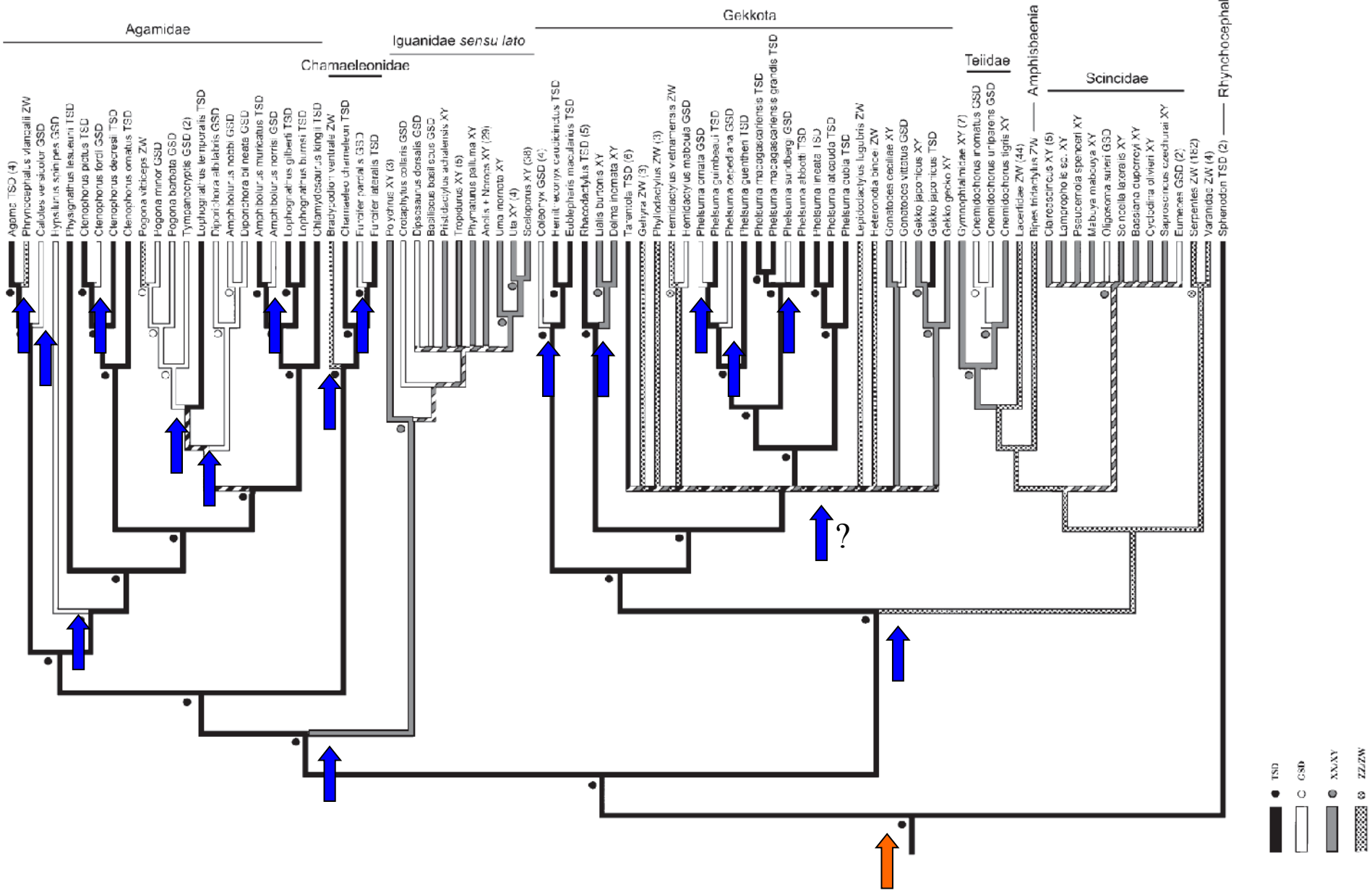
Hlaveně – oba druhy poměrně úzce teplotou





Nicola J. Nelson

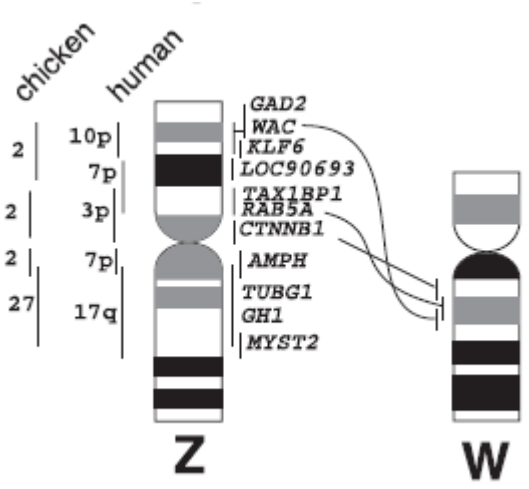
Šupinatí plazi

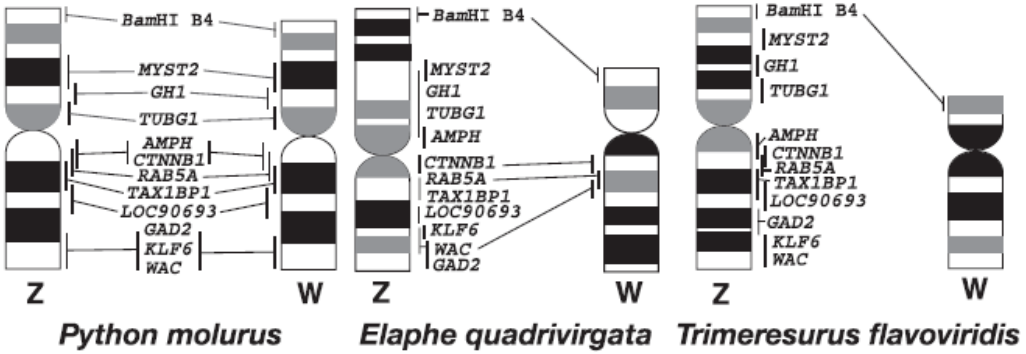


Pokorná a Kratochvíl, *Zool. J. Linn. Soc.* 2009

Hadi

- někteří ZZ/ZW
- nesyntenní s ptáky
- nesyntenní se savci
- někteří homomorfní pohlavní chromosomy





(Matsubara et al., *PNAS* 2006)

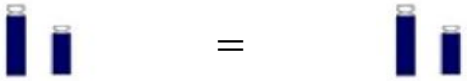
Gekko hokouensis

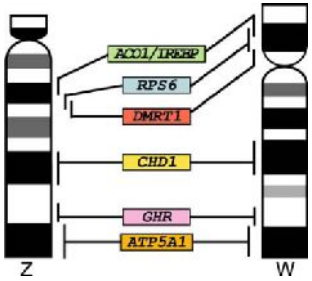
The ZW sex chromosomes of *Gekko hokouensis* (Gekkonidae, Squamata) represent highly conserved homology with those of avian species

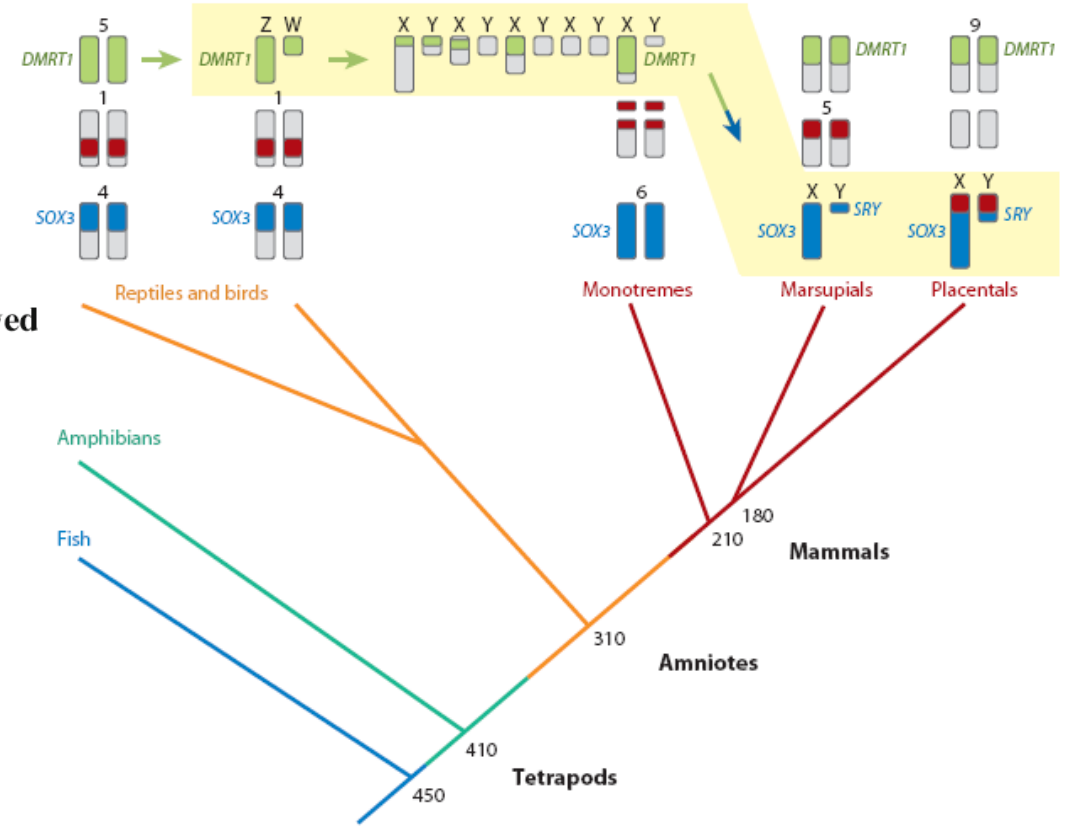
Aya Kawai · Junko Ishijima · Chizuko Nishida · Ayumi Kosaka · Hidetoshi Ota · Sei-ichi Kohno · Yoichi Matsuda

Chromosoma

- gene mapping



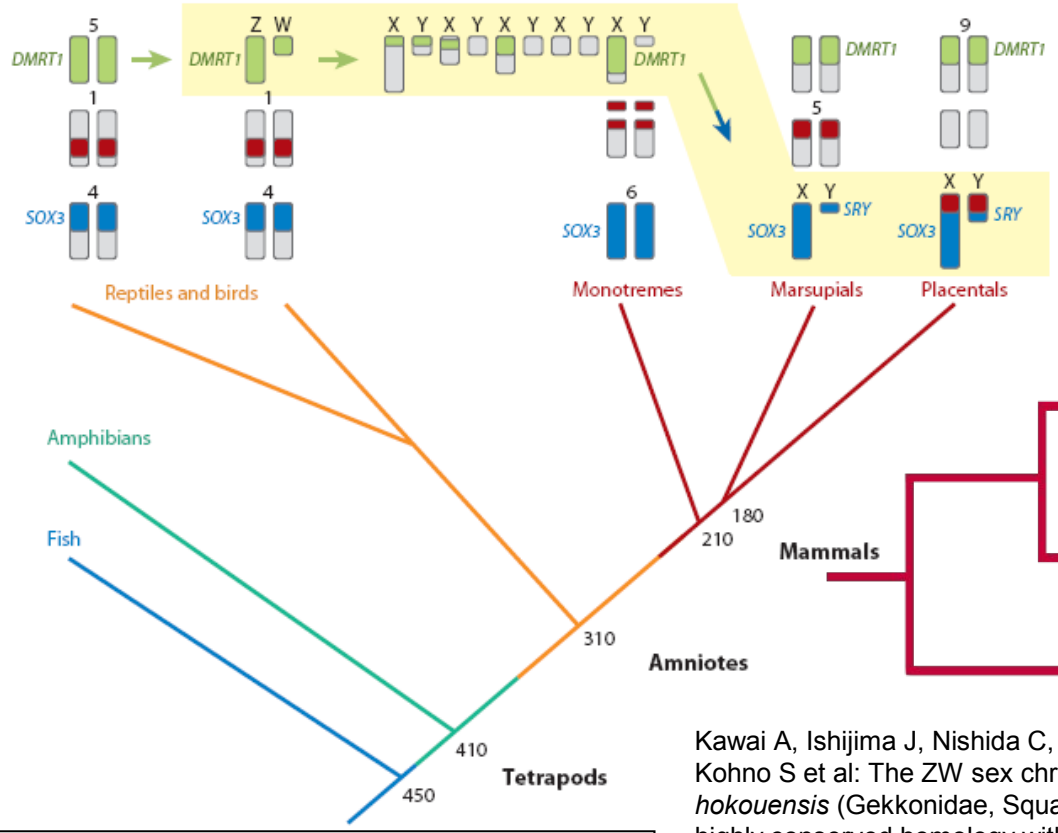




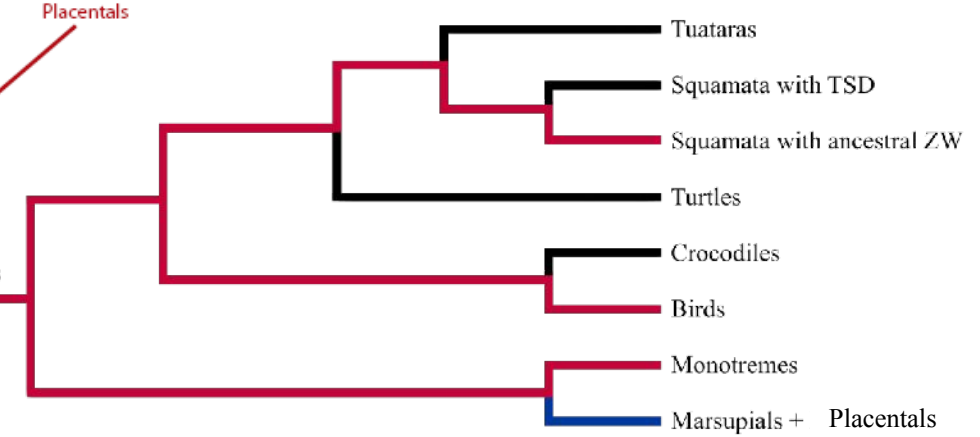
Graves, *Annu Rev Genet* 2008

„Homology between platypus and bird sex chromosomes suggests that a common amniote ancestor had an ancient ZW sex-determining system, perhaps sharing the same conserved master switch gene.“

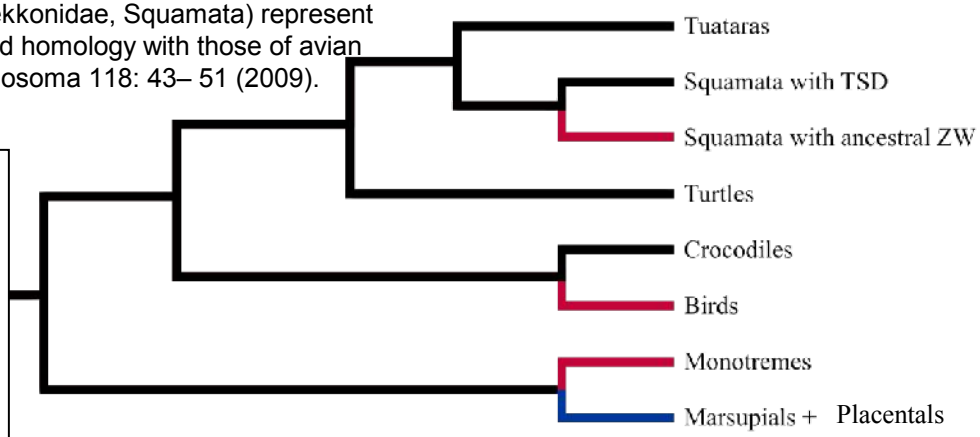
Sex-determination in amniots



Graves 2008 *Annu Rev Genet*

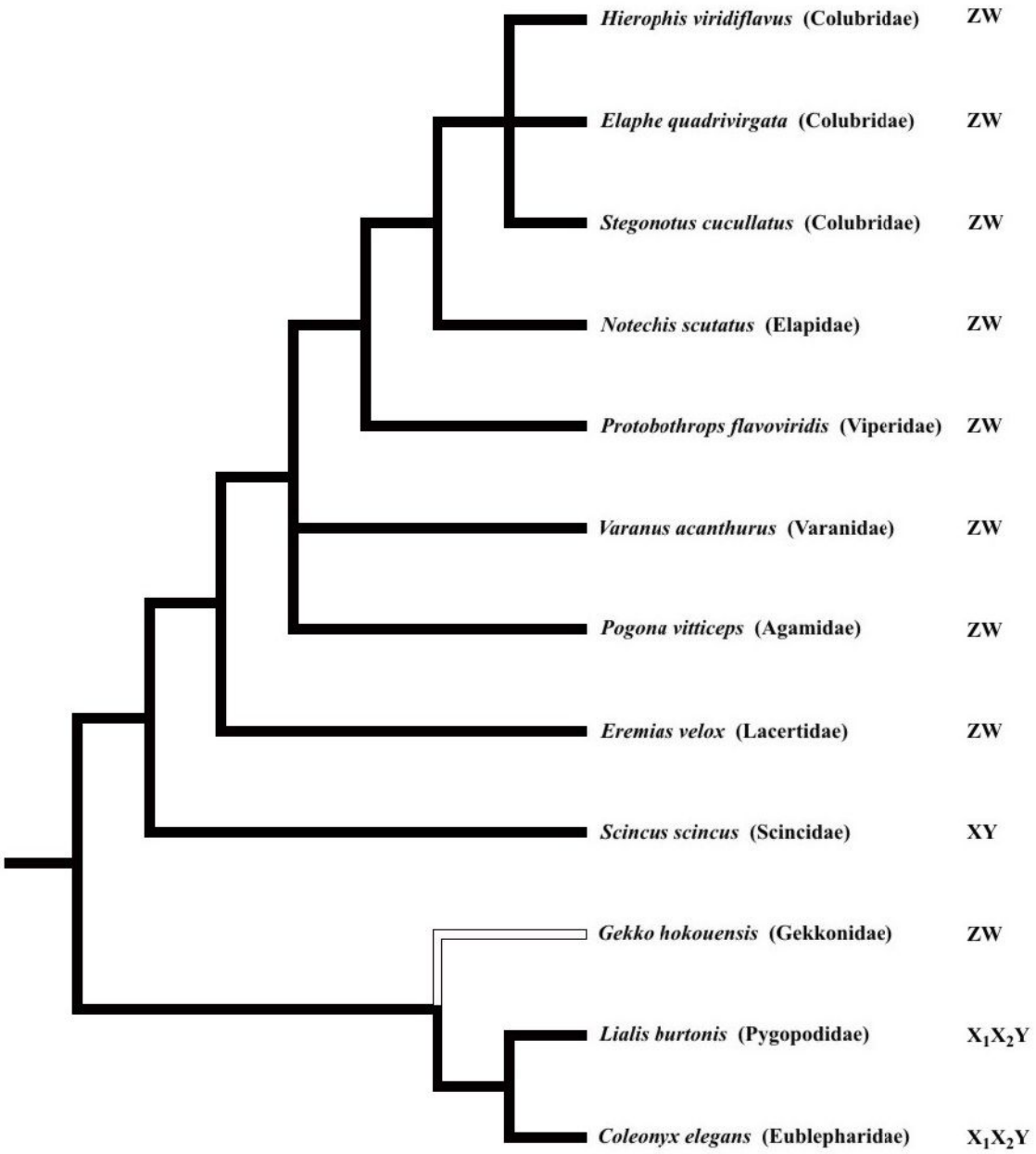


Kawai A, Ishijima J, Nishida C, Kosaka A, Ota H, Kohno S et al: The ZW sex chromosomes of *Gekko hokouensis* (Gekkonidae, Squamata) represent highly conserved homology with those of avian species. Chromosoma 118: 43– 51 (2009).



Homology between platypus and bird sex chromosomes suggests that a common amniote ancestor had an ancient ZW sex-determining system, perhaps sharing the same conserved master switch gene.

syntenie není totéž co homologie!



- pohlavní chromosomy jednotlivých linií (mimo *G. hokouensis*) nejsou homologické s ptačím Z

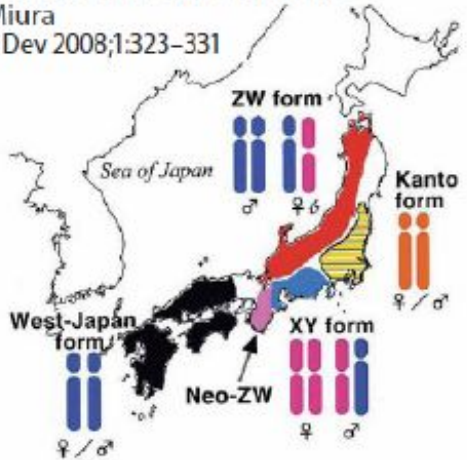
- ancestrálně pohlavní chromosomy nehomologické s ptačími pohlavními chromosomy

Obojživelníci:

- GSD

An Evolutionary Witness: the Frog *Rana rugosa* Underwent Change of Heterogametic Sex from XY Male to ZW Female

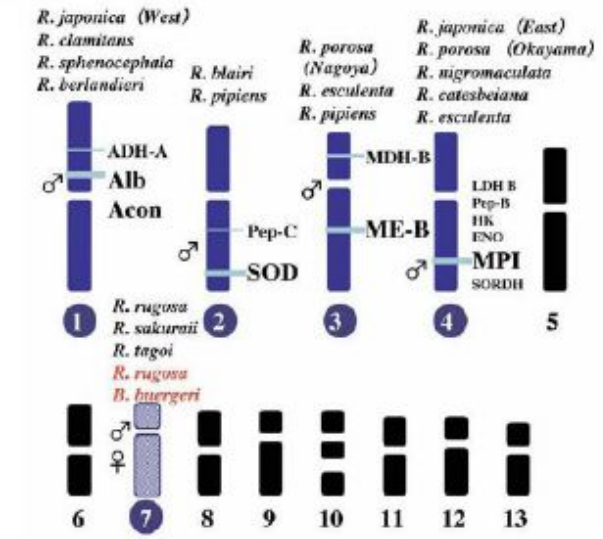
I. Miura
Sex Dev 2008;1:323–331



A W-linked DM-domain gene, DM-W, participates in primary ovary development in *Xenopus laevis*

Shin Yoshimoto*, Ema Okada*, Hirohito Umemoto*, Kei Tamura*, Yoshinobu Uno†, Chizuko Nishida-Umehara†, Yoichi Matsuda†, Nobuhiko Takamatsu*, Tadayoshi Shiba*, and Michihiko Ito*‡

PNAS | February 19, 2008 | vol. 105 | no. 7

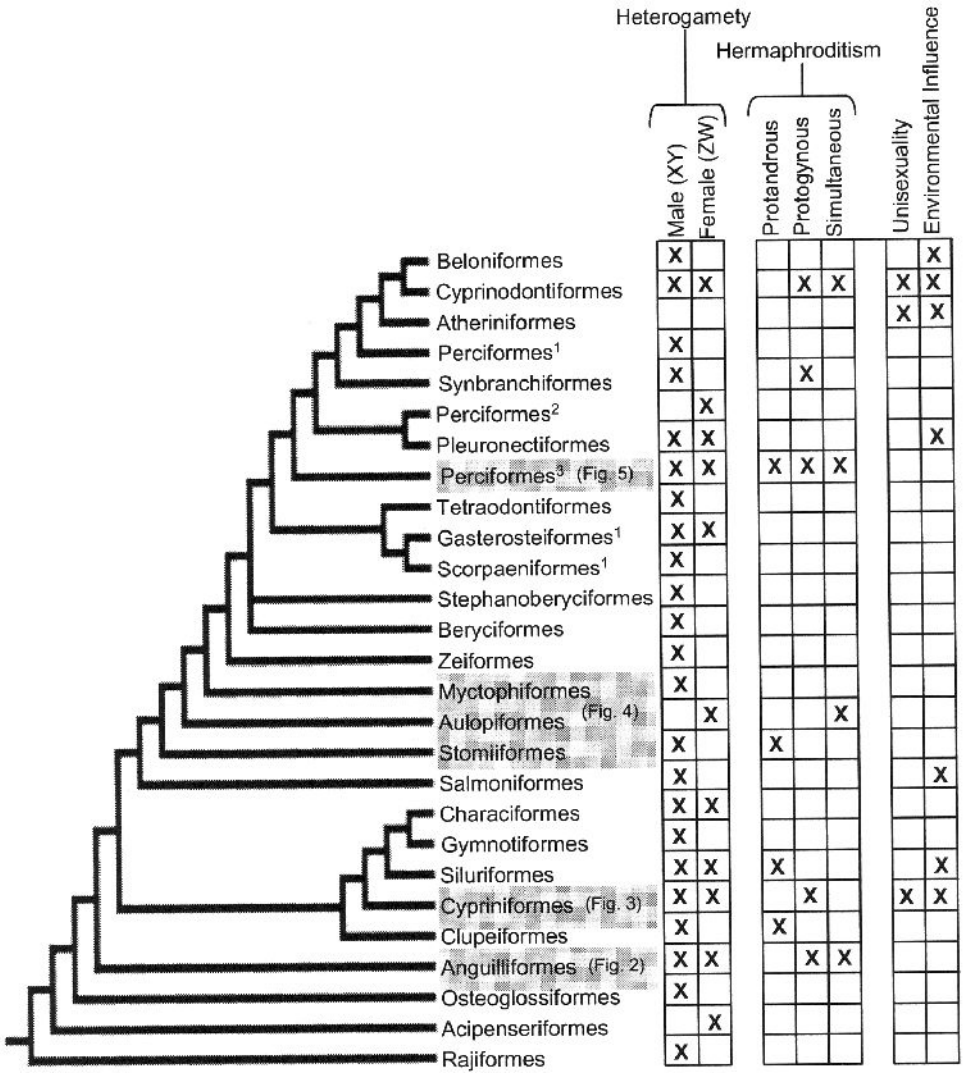


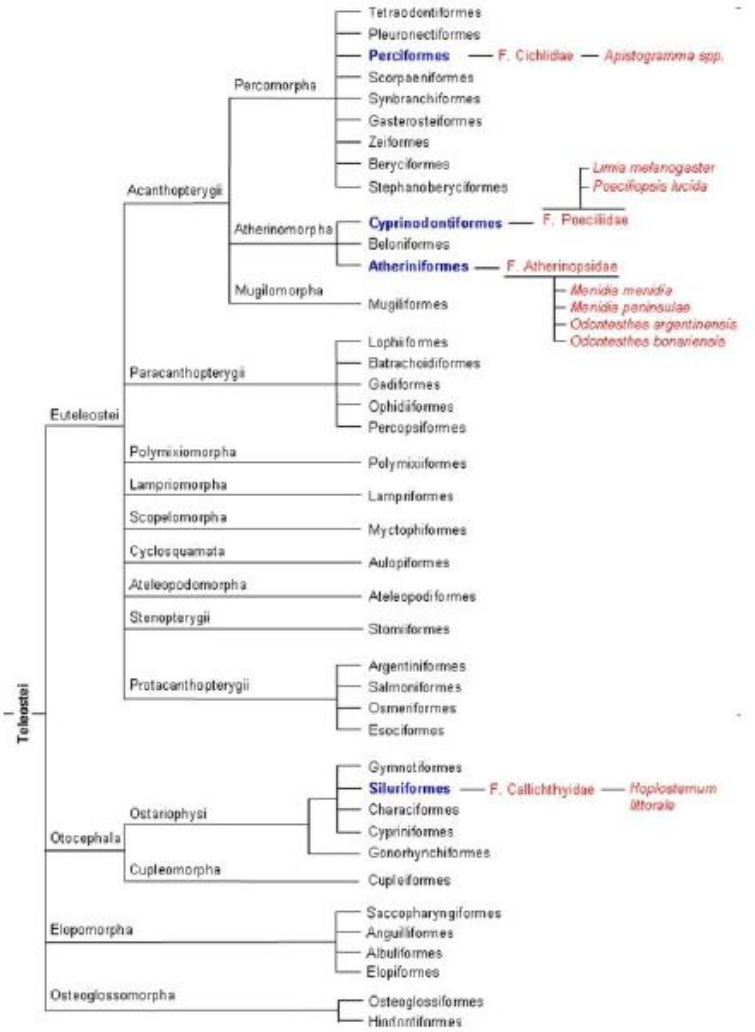
Ryby:

Biological Journal of the Linnean Society, 2006, **87**, 83–93. With 5 figures

Evolution of alternative sex-determining in teleost fishes

JUDITH E. MANK*, DANIEL E. L. PROMISLOW and JOHN C. A





Temperature-Dependent Sex Determination in Fish Revisited: Prevalence, a Single Sex Ratio Response Pattern, and Possible Effects of Climate Change

Natalia Ospina-Álvarez[¤], Francesc Piferrer*

PLoS one July 2008

Oryzias:

- pohlavní revertanti (hormony, teplota) plodní
- YY životaschopní a fertilní

Oryzias latipes

Dmy (= *Dmrt1bY*)

- paralog Dmrt1 (ten na autozomech u *O. latipes*)

- jediný funkční gen v Y-specifické oblasti

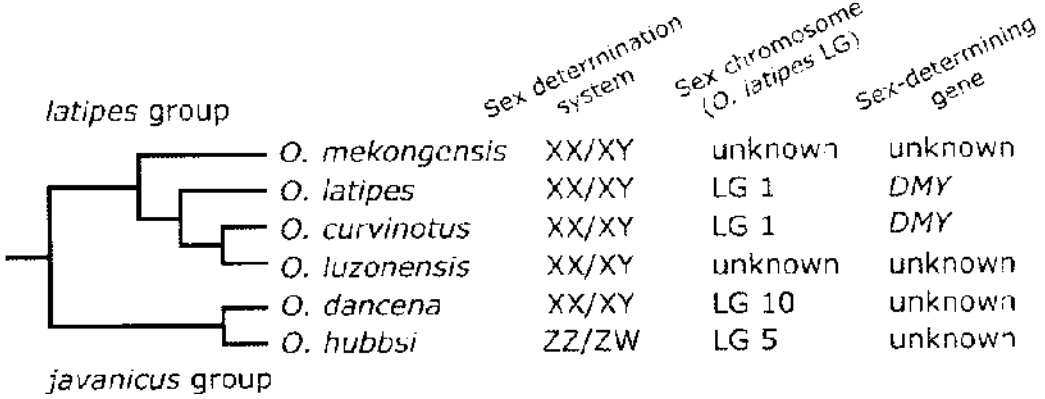
- mutace -> samice

- transgenní XX jedinci s *Dmy* samci

- XY embrya revertovaná estrogenem exprimují *Dmy* jako samci, ale jsou to samice -> *Dmy* nahoře kaskády diferenciace pohlaví

- *Dmy* novou funkci nebo jen zvyšuje dávku DMRT1?

Matsuda et al. *Proc. Nat. Acad. Sci USA* 2007

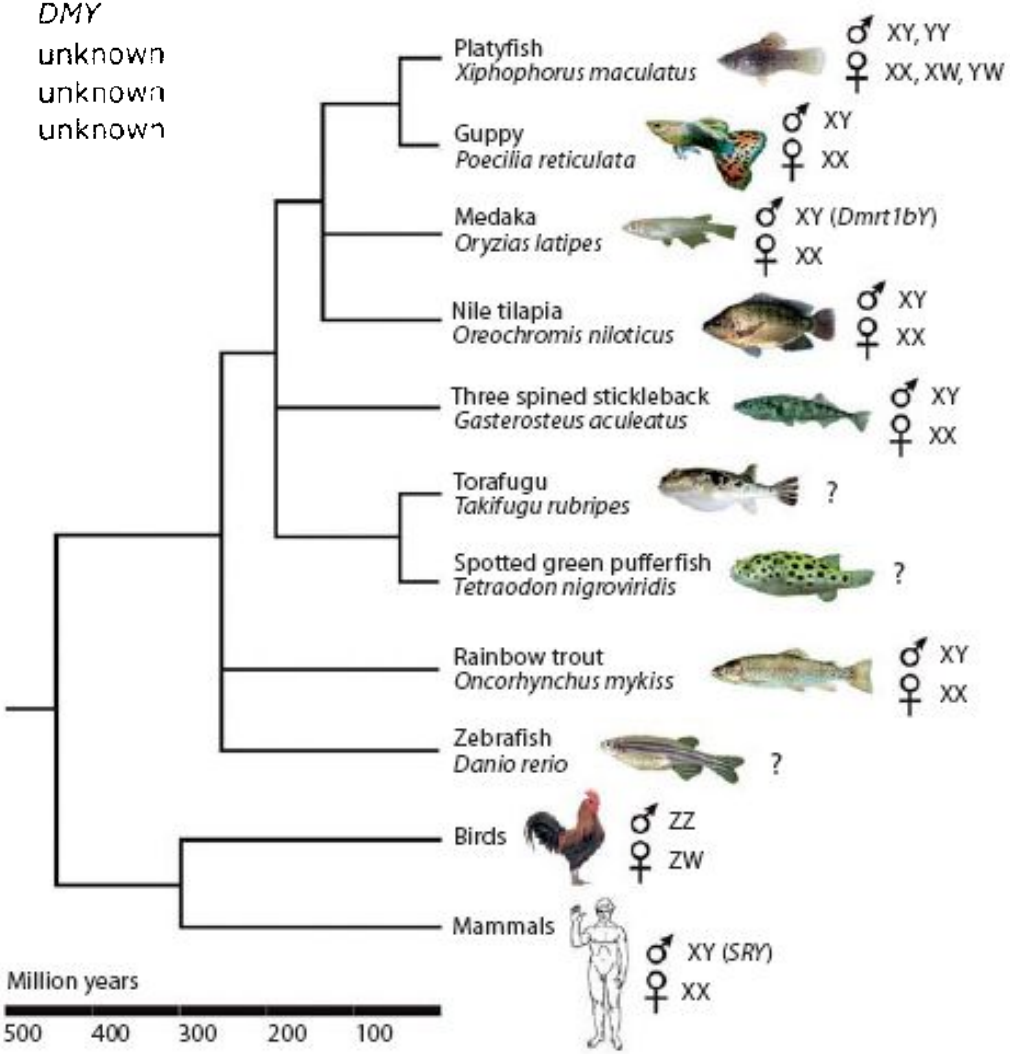


Chromosoma (2007) 116:463–470

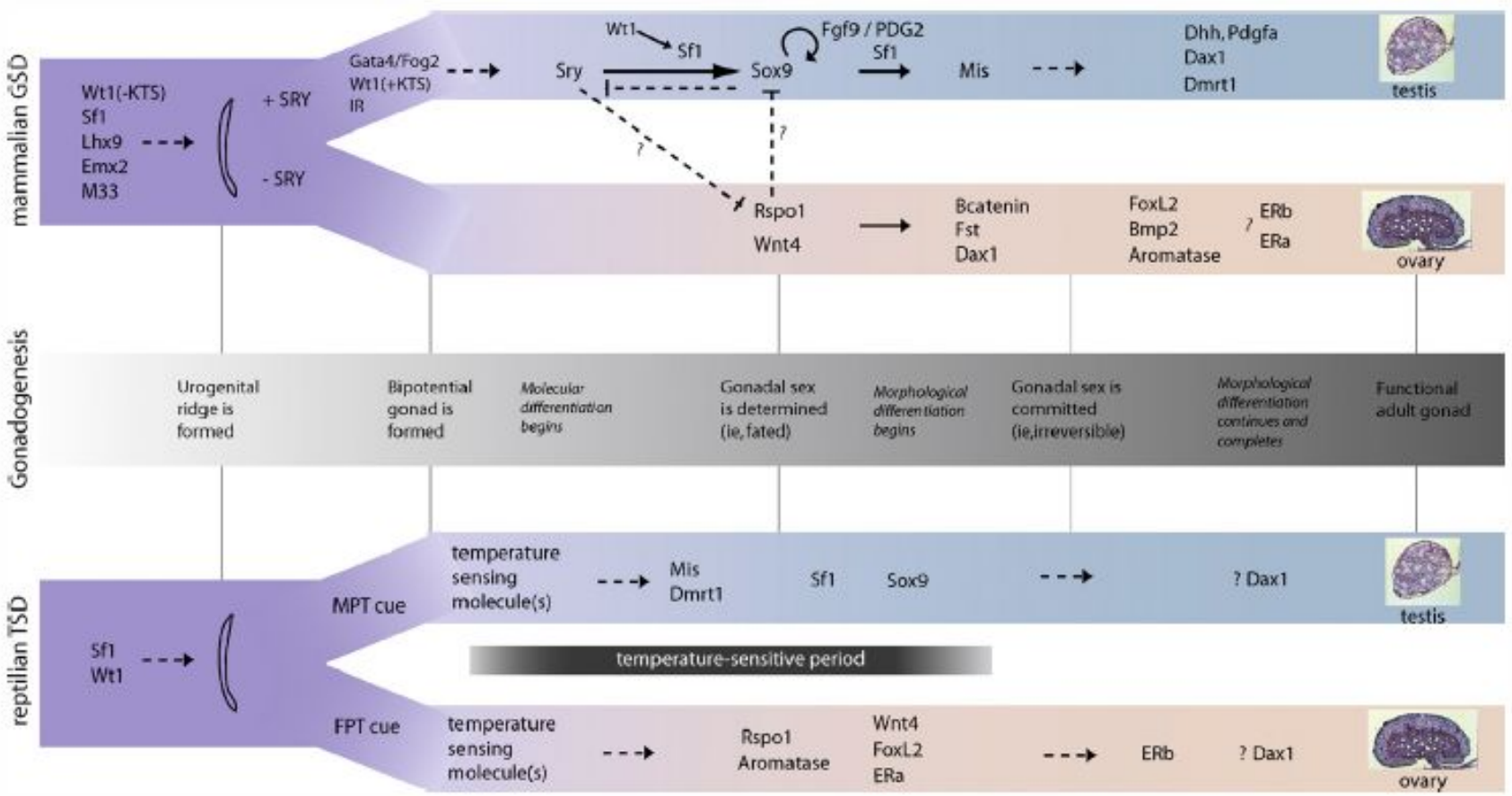
Governing Sex Determination in Fish: Regulatory Putsches and Ephemeral Dictators

J.-N. Volff[a, c] I. Nanda[b] M. Schmid[b] M. Schartl[a]

Sex Dev 2007;1:85–99



Molekulární mechanismus určení pohlaví obratlovců



Review

Analyzing the coordinated gene network underlying temperature-dependent sex determination in reptiles☆

Christina M. Shoemaker, David Crews*

Seminars in Cell & Developmental Biology 20 (2009) 293–303

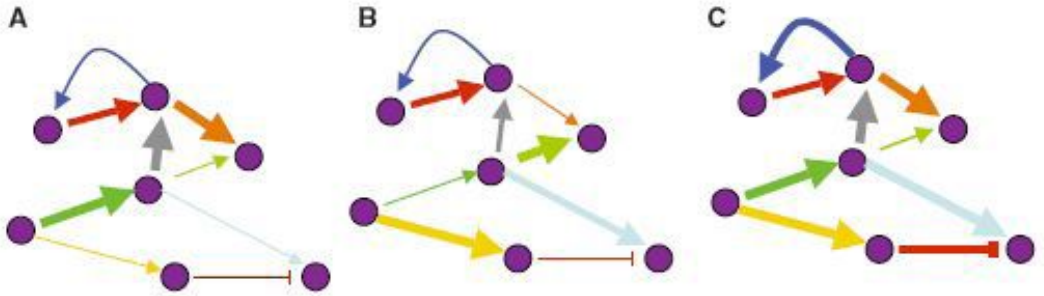
Změna způsobů určování pohlaví

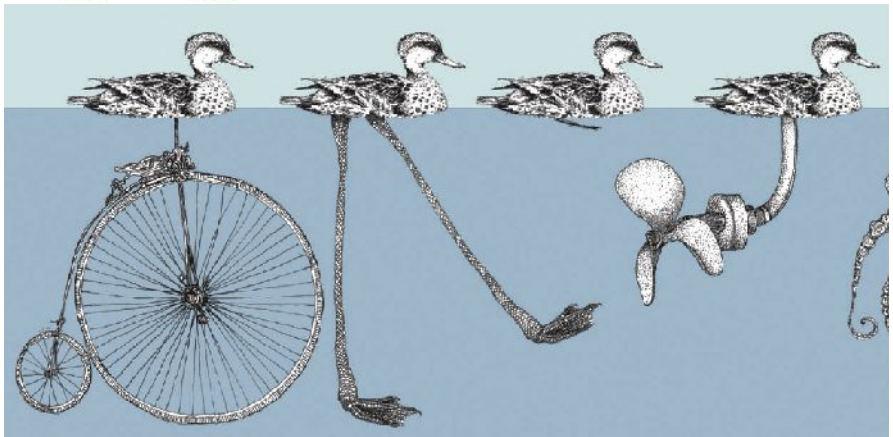
- vznik nových genů určujících pohlaví, které přebijí starší geny?

- vznik změnou *DMRT1*:



- vznik změnou *Sox3*:





Shrnutí

- definice jednotlivých způsobů určování pohlaví se liší, zde zdůrazněna definice, kde environmentálně určené pohlaví odpovídá polyfénii
- způsoby určování pohlaví jsou v některých liniích velmi variabilní, jinde velmi fylogeneticky konzervativní
- dokonce i u obratlovců (amniot) se ví málo o homologii způsobů určování pohlaví
- geny určující pohlaví vznikají pravděpodobně změnou funkce nebo změnou genové dávky genů pohlavně-diferenciační kaskády