Evoluce fenotypu VII

Evoluci fenotypu ovlivňují omezení (constraints)

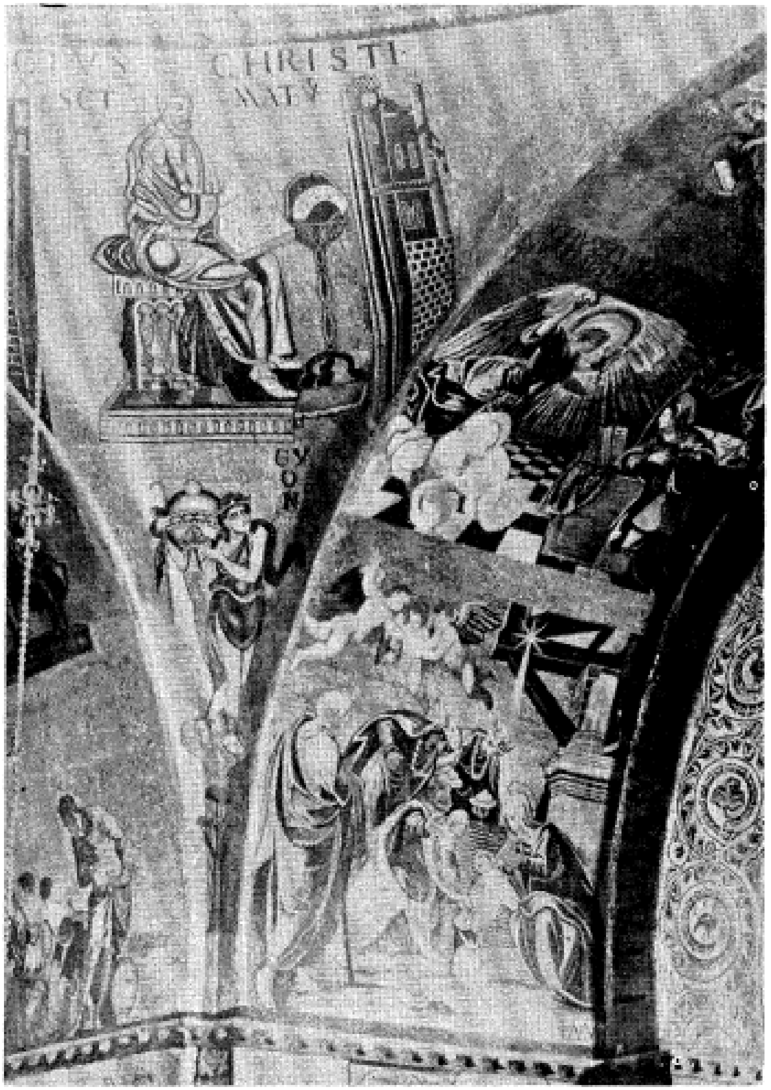
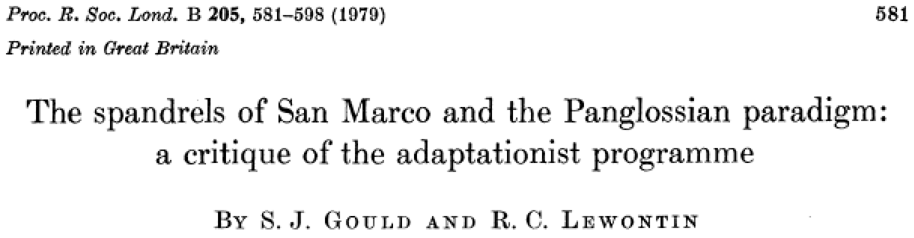


Figure 1. One of the four spandrels of St Mark's; seated evangelist above, personification of river below.



Proc. R. Soc. Lond. B **205**, 581–598 (1979) 581
Printed in Great Britain

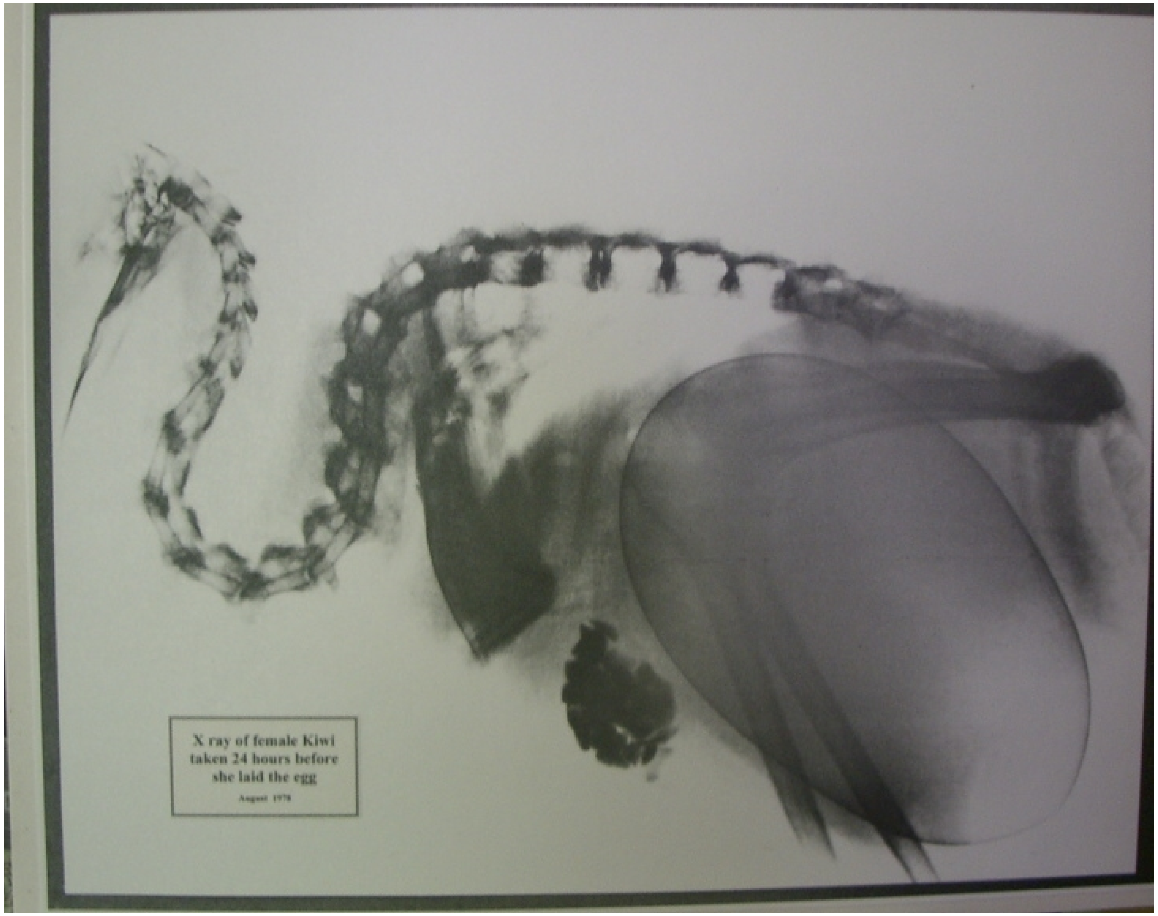
The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme

By S. J. Gould and R. C. Lewontin

Constraints

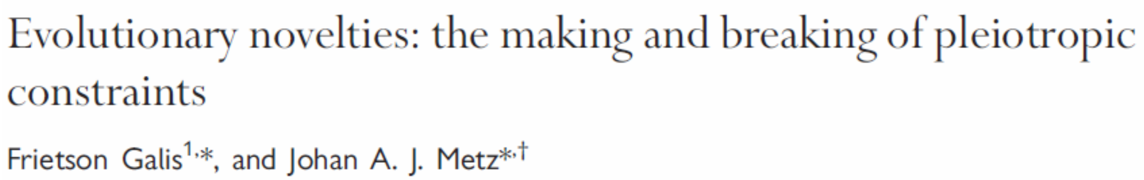
= „mechanisms or processes that limit the ability of the phenotype to evolve or bias it along certain paths“ (Schwenk a Wagner)

- někdy triviální, např. mechanické principy



Constraints

- počty obratlů různě evolučně konzervativní u různých skupin (počet krčních obratlů savců vs. ptáků)



Evolutionary novelties: the making and breaking of pleiotropic constraints

Frietson Galis[1,*], and Johan A. J. Metz[*,†]

Integrative and Comparative Biology, volume 47, number 3, pp. 409–419

Fig. 1 A large number of vertebrae contribute to make a long and flexible neck in flamingoes. Reproduced from Evans (1900) and Owen (1866), respectively left and right.

The number of thoracic vertebrae varies considerably amongst mammals (from nine in the Sowerby's beaked whale, Mesoplodon bidens to 23 in Linnaeus' two-toed sloth, Choloepus didactylis), much more than does the number of cervical vertebrae, which varies from six in manatees (Trichechus) and twotoed sloths (Choloepus) to nine in three-toed sloths (Bradypus, Galis 1999; Narita and Kuratani 2005), and seven in all other mammals.

Evolution of the Vertebral Formulae in Mammals: A Perspective on Developmental Constraints

YUICHI NARITA AND SHIGERU KURATANI*
Laboratory for Evolutionary Morphology, Center for Developmental Biology, RIKEN. Kobe 650-0047. Japan

JOURNAL OF EXPERIMENTAL ZOOLOGY (MOL DEV EVOL) 304B:91–106 (2005)

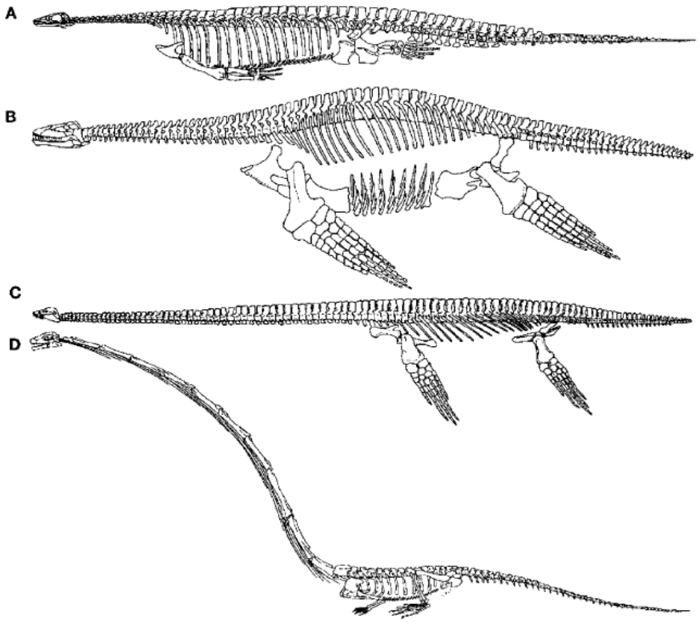


Fig. 4. Skeletons of Mesozoic aquatic reptiles. (**A**) Skeleton of nothosaur, *Pachypleurosaurus*. Redrawn from Carroll and Gaskill ('85). (**B**) Skeleton of the plesiosauroid *Cryptoclidus*. Redrawn from Andrews ('10). (**C**) Skeleton of elasmosaurid *Hydrothecrosaurus*. Redrawn from de Saint-Seine ('55). (**D**) Skeleton of *Tanystropheus*. Redrawn from Wild ('73). Note that the number of cervical vertebrae increased with neck elongation in the first three species. In *Tanystropheus*, however, the length of each cervical vertebra increased.

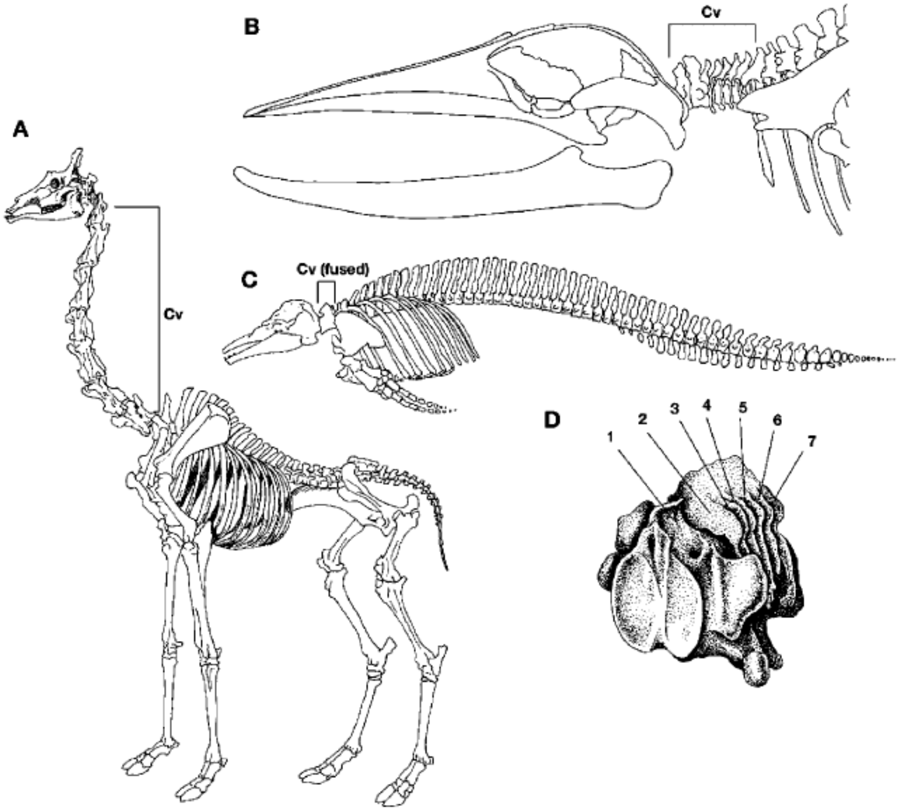


Fig. 1. Skeletons of giraffe and whales. (**A**) Skeleton of giraffe (*Giraffa camelopardalis*). Long neck of the giraffe consists of seven cervical vertebrae (Cv). Redrawn from Owen (1866). (**B**) Skeleton of a balaenopterid whale. Seven separate cervical vertebrae (Cv) are seen. Redrawn from Matthews ('68). (**C**) Skeleton of grampus (*Grampus griseus*). Cervical vertebrae are secondarily fused with each other to form a single bone. Redrawn from Howell ('30). (**D**) Magnification of the fused cervical vertebrae in the bowhead whale, *Balaena mystricetus*. Redrawn from Owen (1866). (1–7) Numbers of cervical vertebrae.

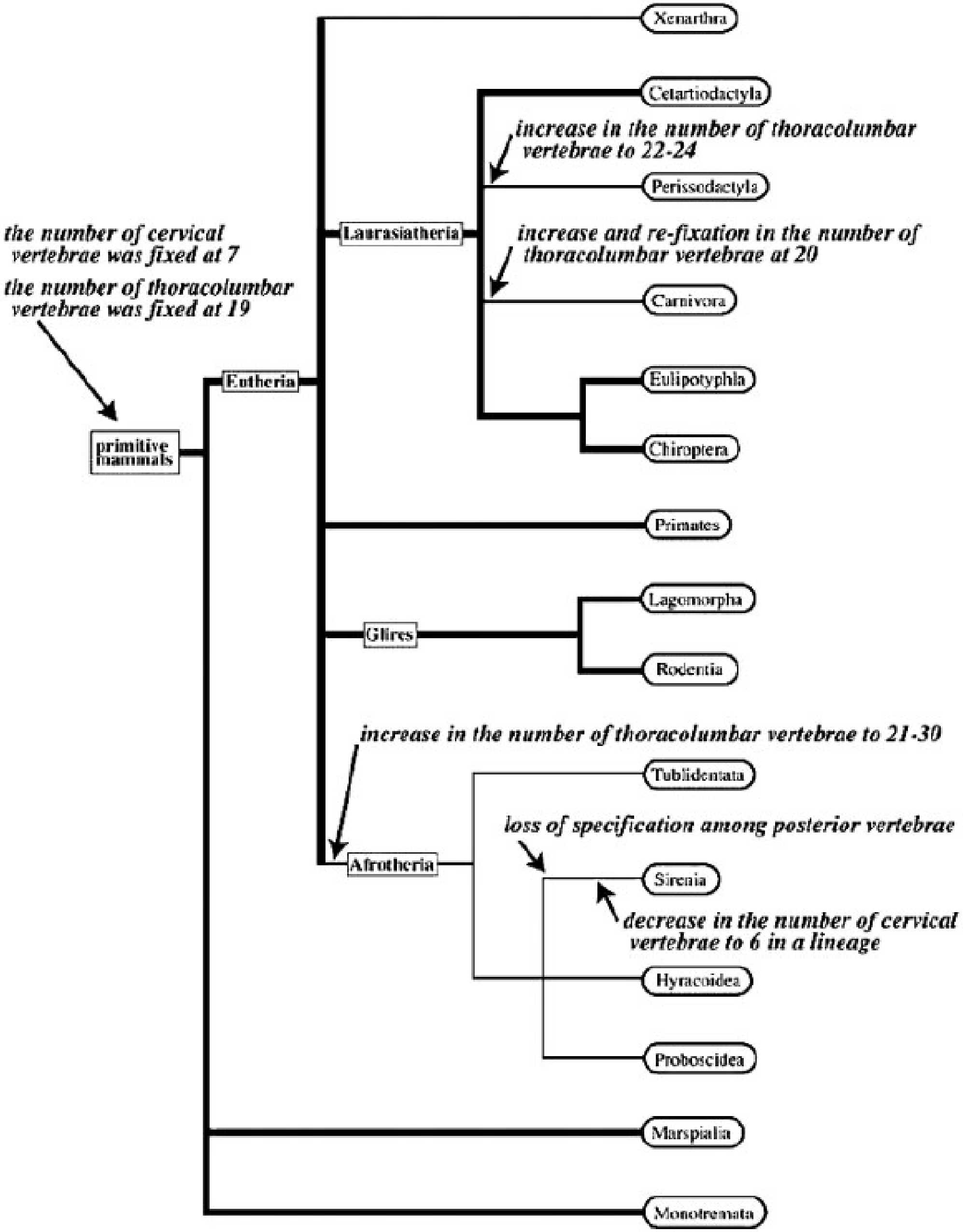
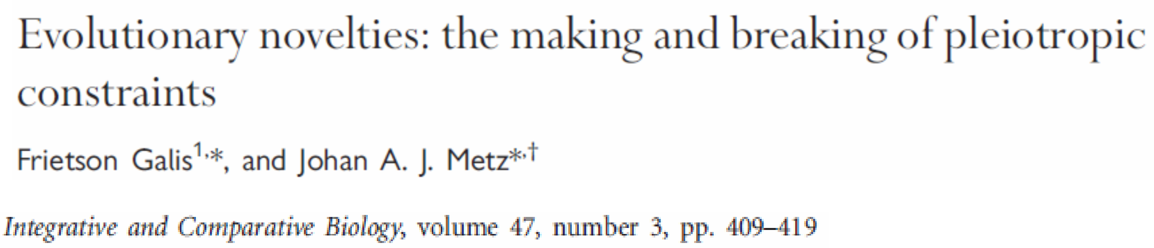


Fig. 2. Distribution of mammalian vertebral formulae along the phylogeny. The vertebral formula of each animal was plotted onto a mammalian phylogenetic tree based mainly on recent molecular analyses (Janke et al., '96, '97; Cao et al., 2000; Murphy et al., 2001; Killian et al., 2001; Lin et al., 2002). The branches with bold lines represent the lineages that retain the primitive vertebral formula, and those with thin lines represent deviation from the primitive state.

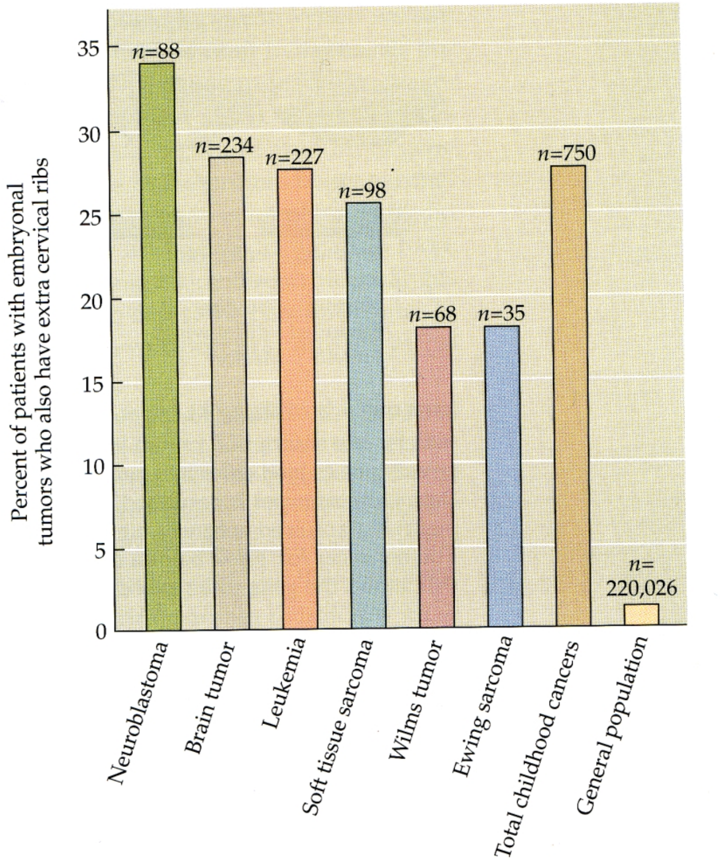
- změny často duplikací modulů a homeotické změny, mutace pro ně časté, ale mají pleiotropní negativní účinky (malformace, rakovina) – „internal selection“



Evolutionary novelties: the making and breaking of pleiotropic constraints

Frietson Galis[1]*, and Johan A. J. Metz*†

Integrative and Comparative Biology, volume 47, number 3, pp. 409–419



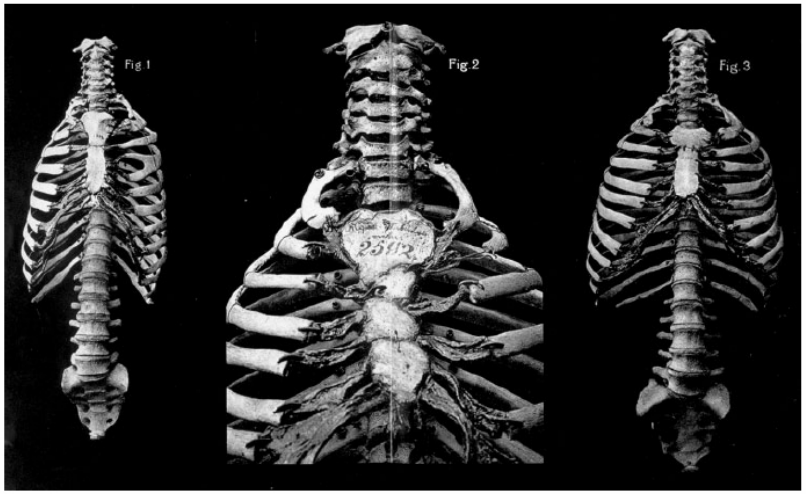
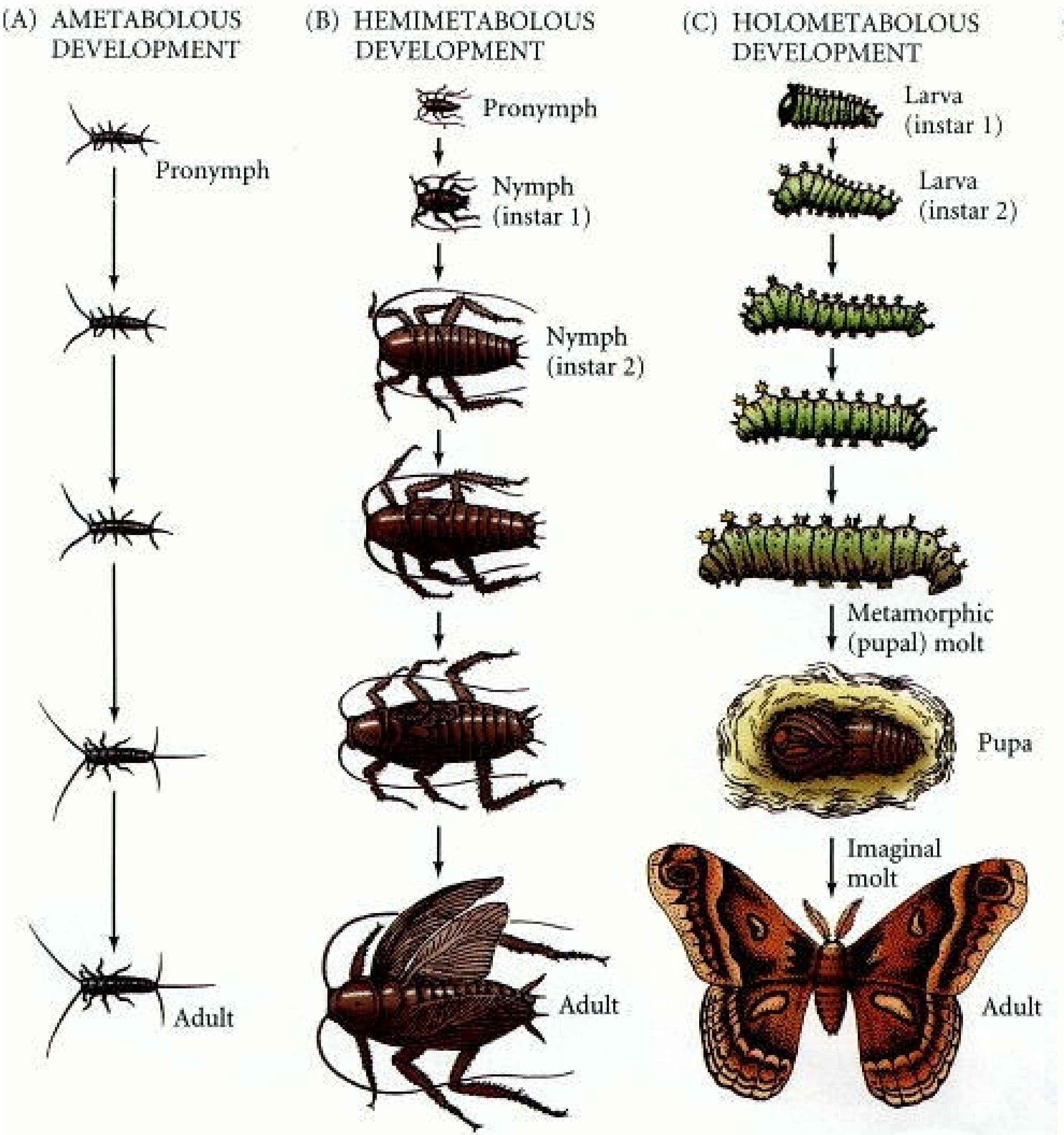


Fig. 3 Skeleton of three humans with a complete cervical rib, i.e., a rib on the seventh cervical vertebra. This change represents both the duplication of a structure, i.e., a rib, and a homeotic change, the change of identity of the seventh vertebra into that of a thoracic vertebra. Reproduced from Fishel (1906).

Constraints

- vývojová omezení
  - ontogenetický konflikt



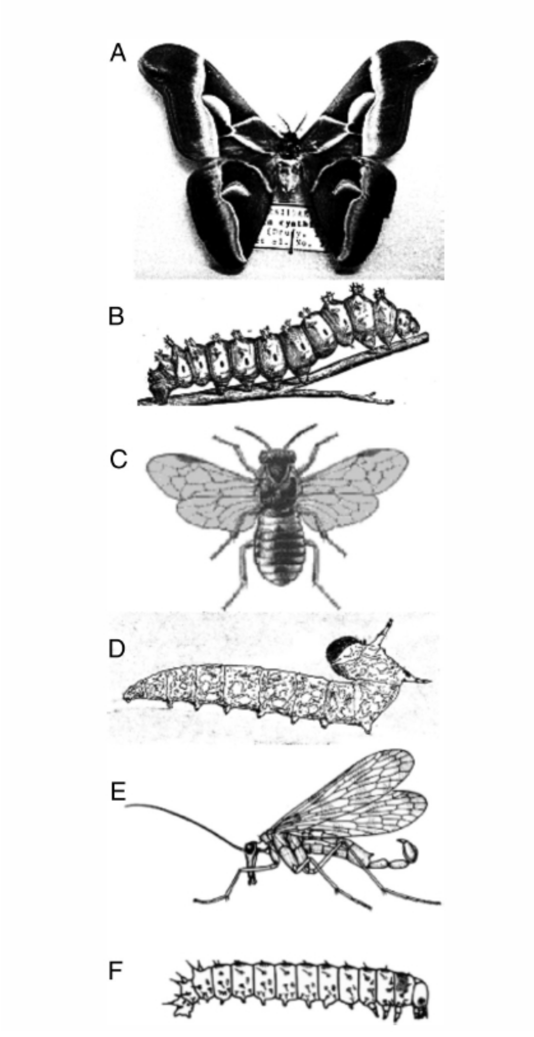
Constraints

- vývojová omezení:
radikální jevy vedou k radikálním hypotézám

Caterpillars evolved from onychophorans by hybridogenesis

Donald I. Williamson[1]

www.pnas.org/cgi/doi/10.1073/pnas.0908357106



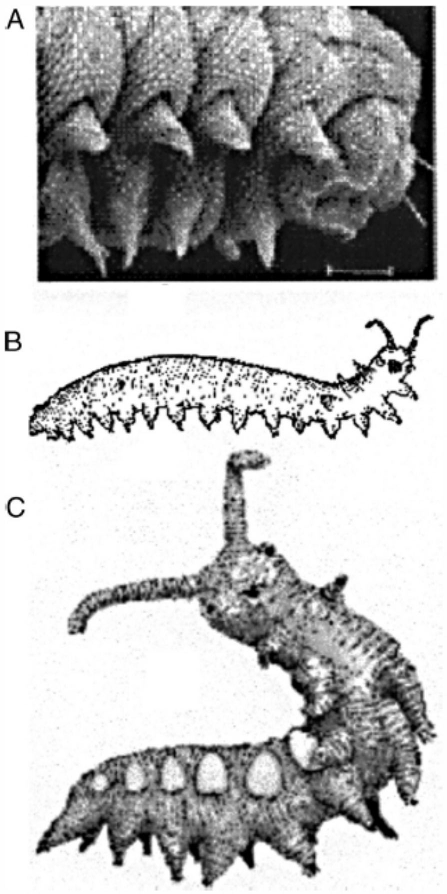


Fig. 3. A caterpillar, an onychophoran, and a lobopod. (*A*) Caterpillar of moth *Micropterix* sp (Lepidoptera): anterior end, ventrolateral view. (*B*) Tasmanian onychophoran, *Ooperipatellus* sp. (*C*) Cambrian lobopod, *Microdictyon* sp. *A* from SEM by Donald R. Davis, National Museum of Natural History, Smithsonian Institution, Washington, DC, with permission; *B* from Tasmanian Multipedes website, http://www.qvmag.tas.gov.au/zoology/multipedes/mulintro.html, with permission; *C* from Brasier (11), with permission.

Constraints

The origins of insect metamorphosis

James W. Truman & Lynn M. Riddiford

NATURE | VOL 401 | 30 SEPTEMBER 1999

- vývojová omezení

Berlese, A. Intorno alle metamorfosi degli insetti. Redia 9, 121-136 (1913).

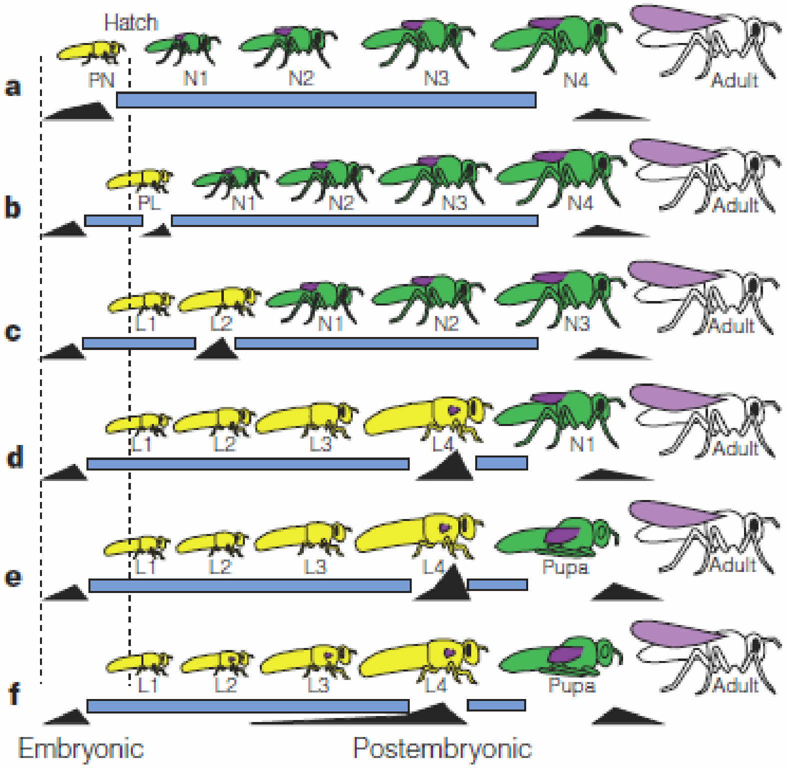


Figure 5 Possible steps in the transition from a hemimetabolous to a holometabolous life history and their relationship to timing of JH production (blue bar) and to growth directed towards the imaginal form (black triangles). The pronymphal (PN), protolarval (PL) and larval (L) instars are in yellow, and the nymphal (N) and pupal stages are in green; wing buds, wing imaginal discs, and wings are in purple. See text for explanation.

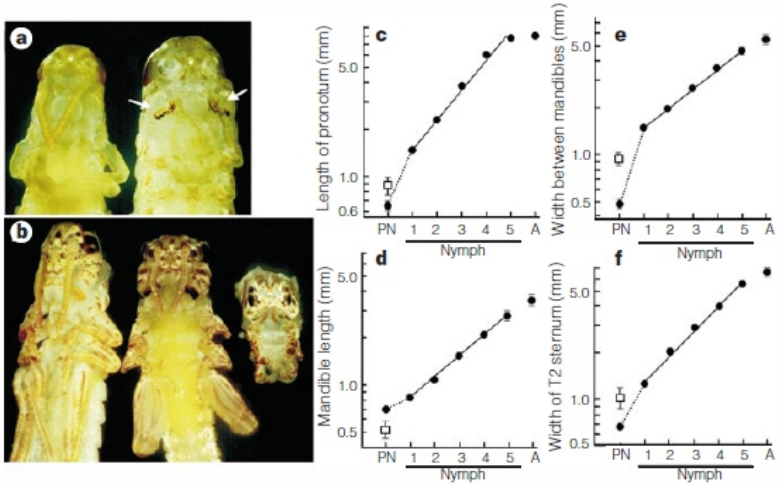
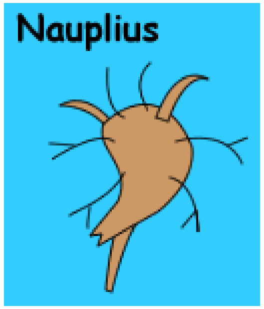


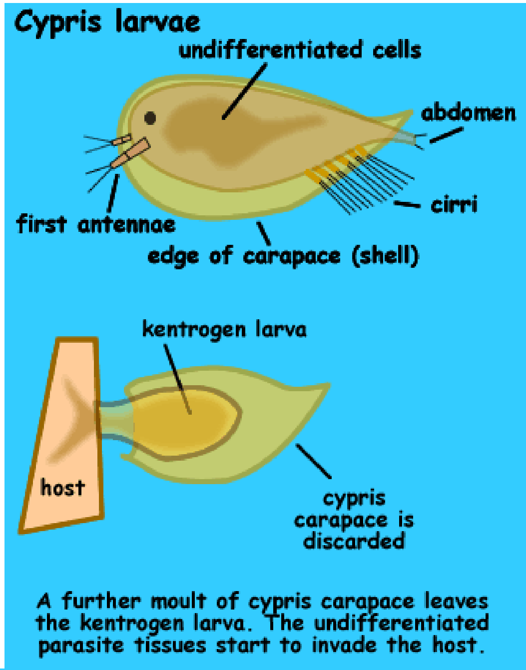
Figure 3 The effects of the JH mimic pyriproxifen on *Locusta* embryos. **a**, A ventral view of the anterior end of embryos three days after treatment with acetone (left) or pyriproxifen (right) at about 47%E. The acetone-treated embryo is a newly ecdysed pronymph (~68%E). Its clutchmate, treated with the JH mimic, shows sclerotized mandibles (arrows) and the dimensions of a head and thorax predicted for a '0'-instar nymph. **b**, Ventral views of (left) control embryo about 1 day before hatching, (middle) a '0'-instar nymph of comparable age produced by JH mimic treatment before dorsal closure, and (right) a '–1'-instar nymph formed after JH mimic treatment before blastokinesis. **c–f**, Quantification of the result of treating embryos with the JH mimic at 45%E. The normal progression of the size of various structures between the pronymph (PN) and nymphal instars is represented as in Fig. 1. Points are the means ± s.e.m. for 10 individuals; s.e.ms smaller than the data points are not shown. The treatment with the JH mimic (squares, ±s.e.m. for $n = 14$) redirected the pronymphal moult to produce animals with proportions that were shifted towards those predicted for a hypothetical '0'-instar nymph. Similar results are seen after treatment with physiological dosages of JHIII.

Constraints

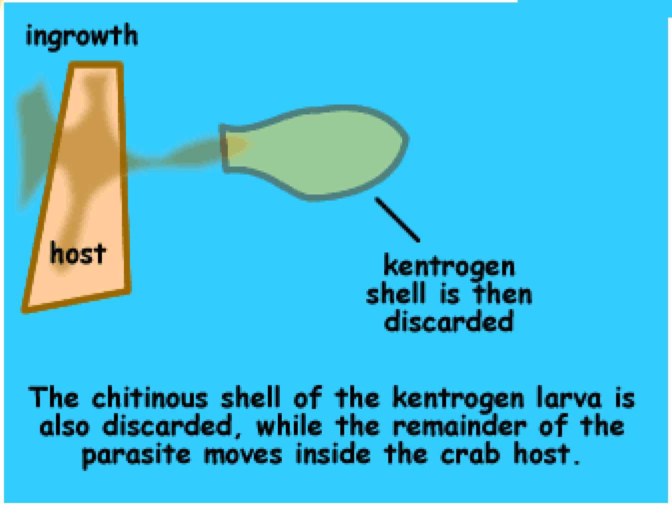
- vývojová omezení

E. Ray Lankester's figure of the "degenerate" adult Sac-culina, *showing the externa (sac) and interna (roots).*





A further moult of cypris carapace leaves the kentrogen larva. The undifferentiated parasite tissues start to invade the host.



The chitinous shell of the kentrogen larva is also discarded, while the remainder of the parasite moves inside the crab host.

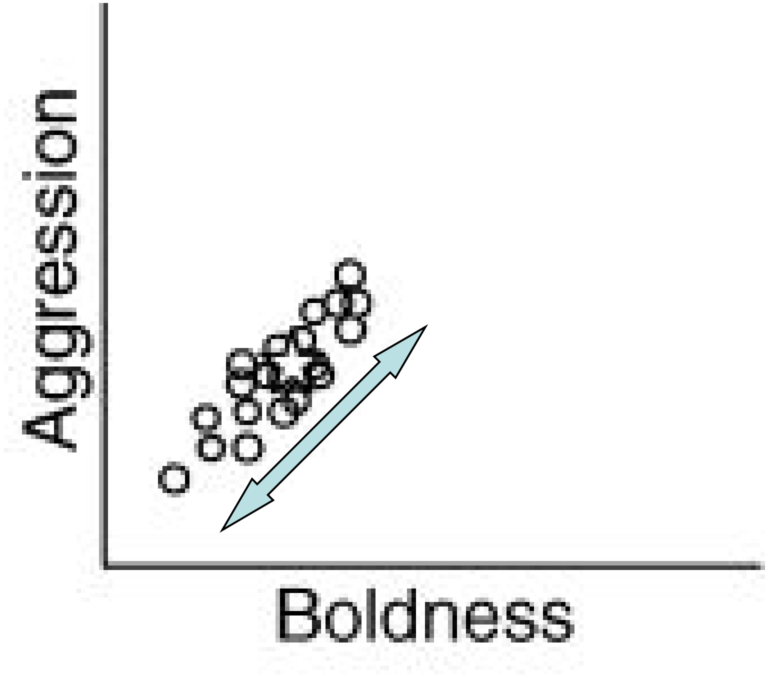
http://www.mesa.edu.au/friends/seashores/crab_parasitism.html

Je korelace mezi znaky důsledkem adaptace nebo omezení?

- korelace mezi znaky – „evolution along the path of the least resistence“

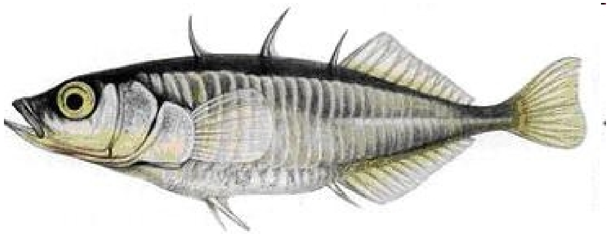
Zvířata (a lidé) mají různé behaviorální typy (též personalitní typy, temperament nebo personalitu), když se liší v kombinaci chování korelovaných přes několik situací nebo kontextů.

Populace nebo druh pak vykazují behaviorální syndrom.



shy-bold syndrom

(nejčastěji korelace agresivity, chování vůči kořisti a predátorům, neofobie)

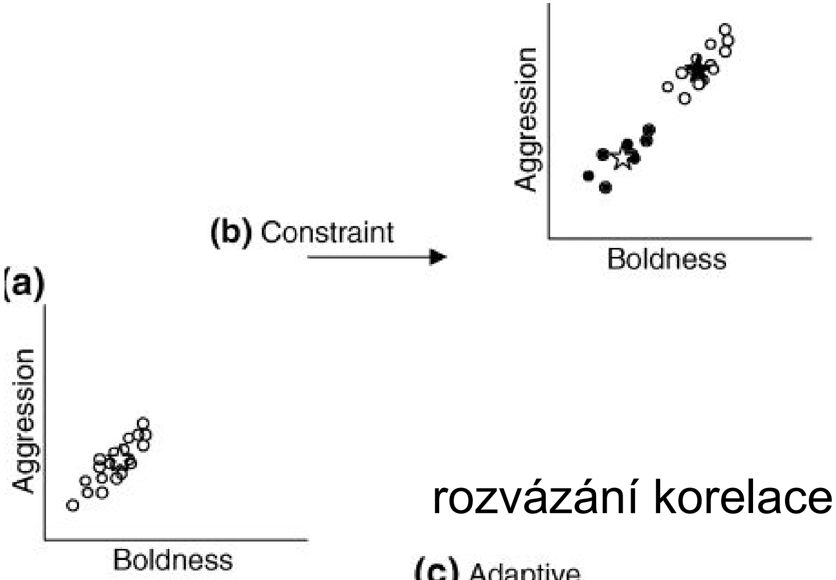


Je behaviorální syndrom důsledkem adaptace nebo evolučního omezení?

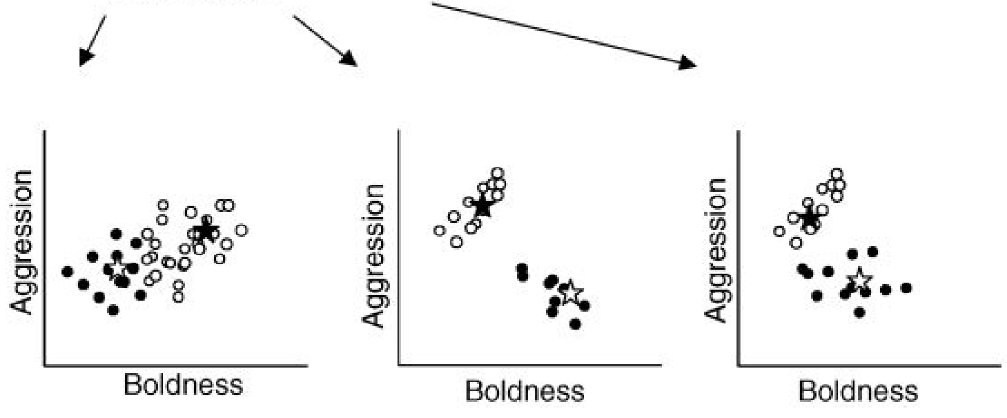
pleiotropie

Strong Personalities Can Pose Problems in the Mating Game

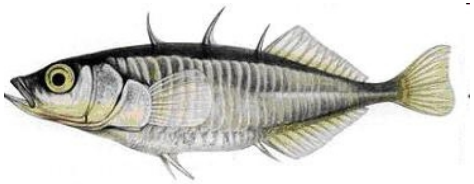
Science 29 July 2005



rozvázání korelace - adaptace



● Population 1
○ Population 2



Constraints

- korelace mezi znaky – „evolution along the path of the least resistence“

- pleiotropní efekt může být někdy důsledkem adaptace, ale může být omezením během další evoluce

- např. aktivační vliv testosteronu u ještěrů: samčí zbarvení (DeNardo & Sinervo, 1994; Cox et al., 2005a), aktivita pachových žlaz (Cole, 1966; Chiu et al., 1970; Alberts et al., 1992), velikost hemipenisů (Rhen et al., 1999), velikost žvýkacích svalů (Crews, 1998), agresivní chování, epigamní chování (Crews et al., 1997).

Constraints

Review TRENDS in Ecology and Evolution Vol.21 No.7 July 2006 Full text provided by www.sciencedirect.com

Evo-devo and constraints on selection

Paul M. Brakefield

Institute of Biology, Leiden University, PO Box 9516, 2300 RA Leiden, the Netherlands

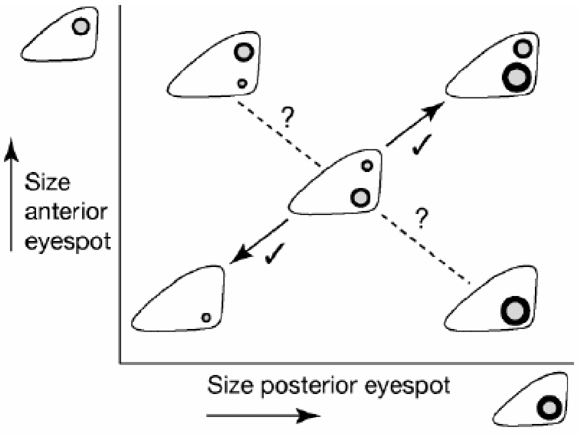
- korelace mezi znaky – „evolution along the path of the least resistence“
- ale znaky se mohou vyvázat (prolomit omezení)

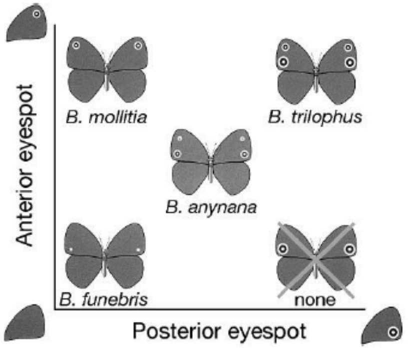
The power of evo-devo to explore evolutionary constraints: experiments with butterfly eyespots**

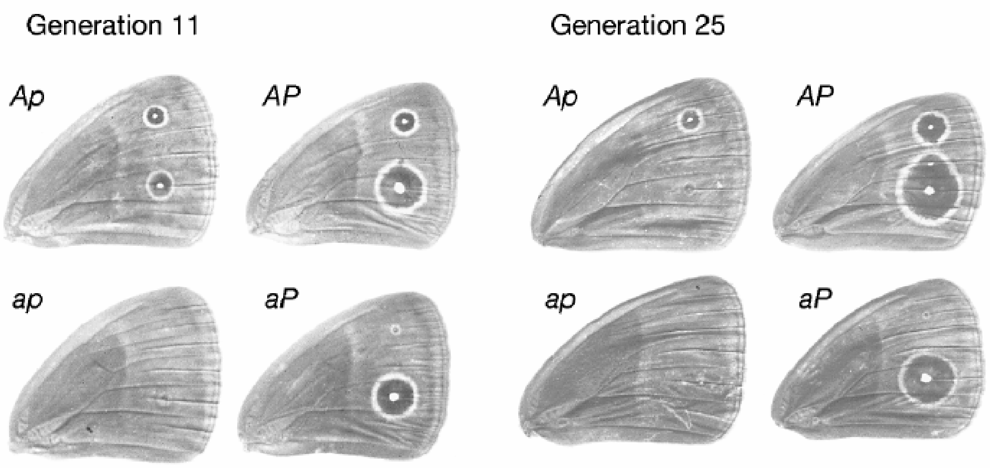
Paul M. Brakefield*

Zoology **106** (2003): 283–290

Fig. 2. Design of the artificial selection experiment using *Bicyclus anynana* to explore the rate of response to selection in different directions of morphological space regarding the forewing pattern of eyespot size (from Brakefield, 1998). The centrally positioned forewing shows the wild-type pattern of this species with a small anterior eyespot and a large posterior eyespot. Selection attempted to change this pattern of eyespot sizes along both an axis of coupled change (i.e., both smaller or both larger) and of uncoupled change (one smaller and the other larger). Selection experiments targetted at the larger, posterior eyespot had already demonstrated positive genetic correlations and thus we predicted that movement along the 'coupled' axis (solid lines) with concerted changes in both eyespots would be rapid and unconstrained (√). In contrast, selection along the 'uncoupled' axis (dotted lines) was expected to be more limited (?).







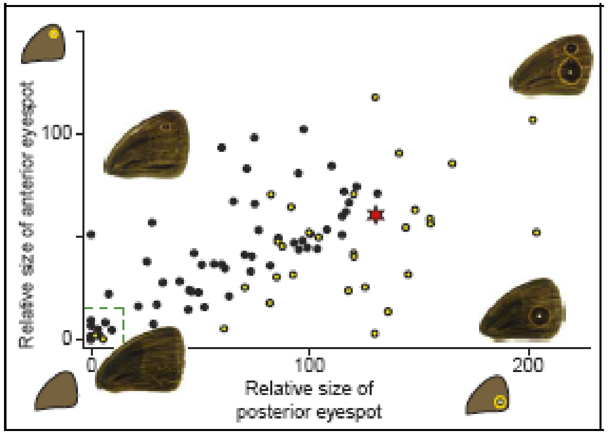
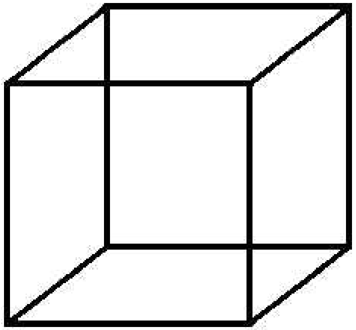


Figure 2. The occupancy of morphological space for the relative size of the two dorsal forewing eyespots of the butterfly *Bicyclus anynana* compared with the variation among species of this African genus and of the closely related Asian genus *Mycalesis*. The four images of the wing in each corner of the morphospace are representative examples of the wing pattern after 25 generations of artificial selection in *B. anynana* [76] towards each of these corners of morphospace, starting from the wild-type for this species as depicted by the star. The four wings are placed in roughly the correct position in the depicted trait space. Circles show the position of the mean patterns of the size of the same eyespots for different species of *Bicyclus* (closed symbols) and of *Mycalesis* (open symbols). The dotted square encloses species for which both eyespots are very small or absent, and frequently difficult to measure. Reproduced with permission from [19].

Constraints



- mnohá omezení jen lokální (z evolučního pohledu), není možno odlišit od adaptace

Hamiltonovo pravidlo:
rb – c > 0
c snížení fitness aktora
b výhoda příjemce
r genetická příbuznost

Altruism, Spite, and Greenbeards

Stuart A. West* and Andy Gardner*

SCIENCE VOL 327 12 MARCH 2010

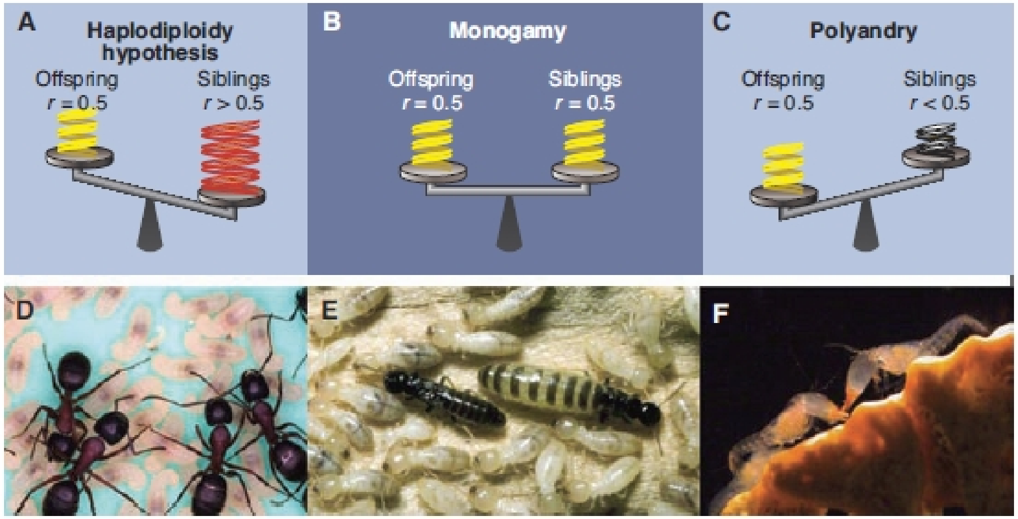


Fig. 3. Monogamy paves the way to eusociality. (**A**) The haplodiploidy hypothesis relies on individuals being more related to siblings than offspring, making siblings worth more than offspring. As originally envisioned, this appears to have been a red herring. (**B**) The monogamy hypothesis emphasizes that if an individual is equally related to its siblings and its offspring, even a very slight efficiency benefit for raising siblings translates into a selective advantage for helping. (**C**) Without strict monogamy, individuals are more related to their offspring than they are to their siblings so that a large efficiency benefit is required in order for sibling-rearing to be favored. (**D**) Sterile workers caring for brood in the ant *Camponotus herculeanus*. (**E**) A lifetime monogamous pair from the termite *Reticulitermes flavipes*. (**F**) Nonbreeding workers in the shrimp *Synalpheus regalis*. [Photos provided by David Nash, Barbara Thorne, and Emmett Duffy]

Alometrie

- proporční změna rozměru jednoho znaku vzhledem k rozměru znaku jiného nebo k celkové velikosti těla

$$y = a*x^b$$

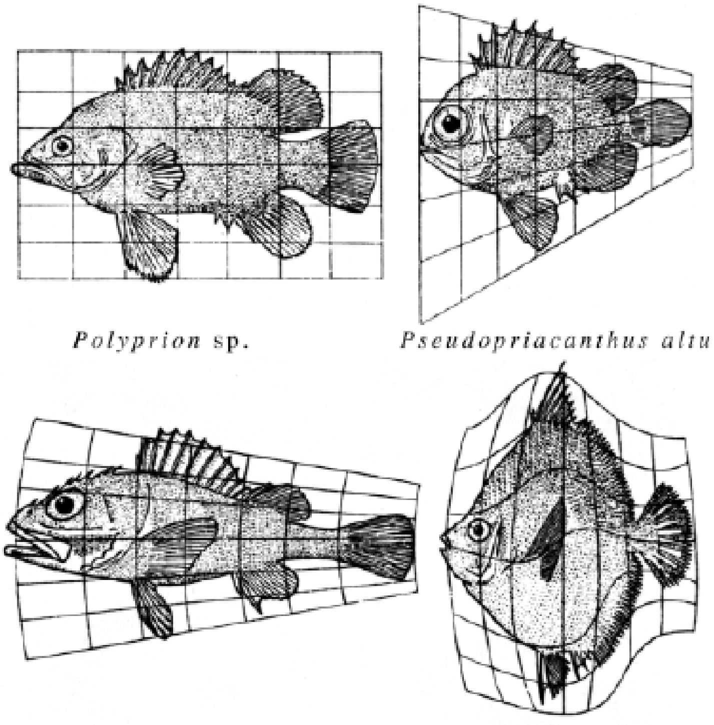


Fig. 1. Acanthopterygian fish with superimposed transformed Cartesian coordinates, reproduced from Thompson (1917) figures 150-153. The regular grid was placed over *Polyprion* sp. and then transformed with angular or radial transformations to 'best fit' the other three fish.

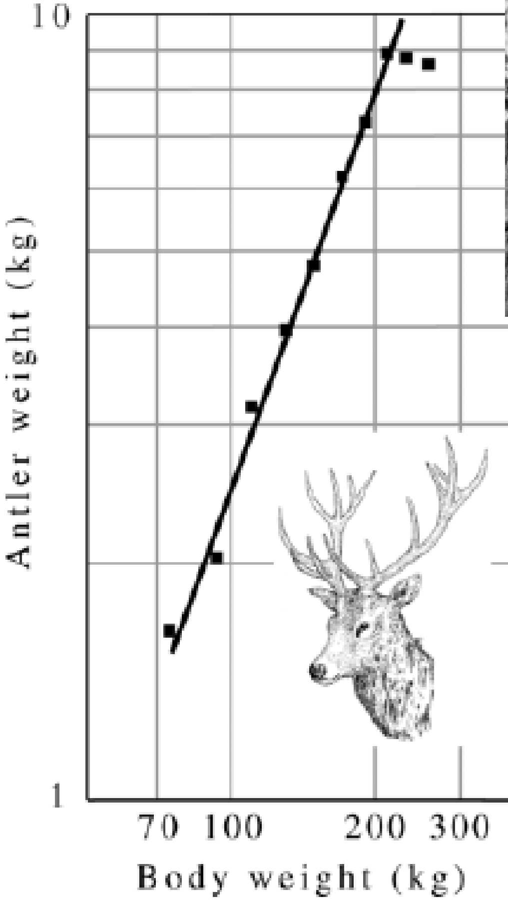
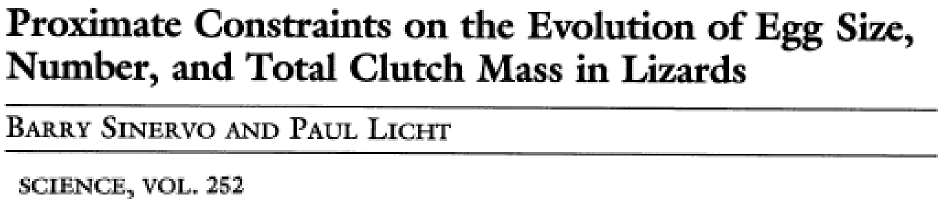


Fig. 9. Antler allometry in red deer. Log-log plot of antler versus body weight. Redrawn from Huxley (1932).

Alometrie

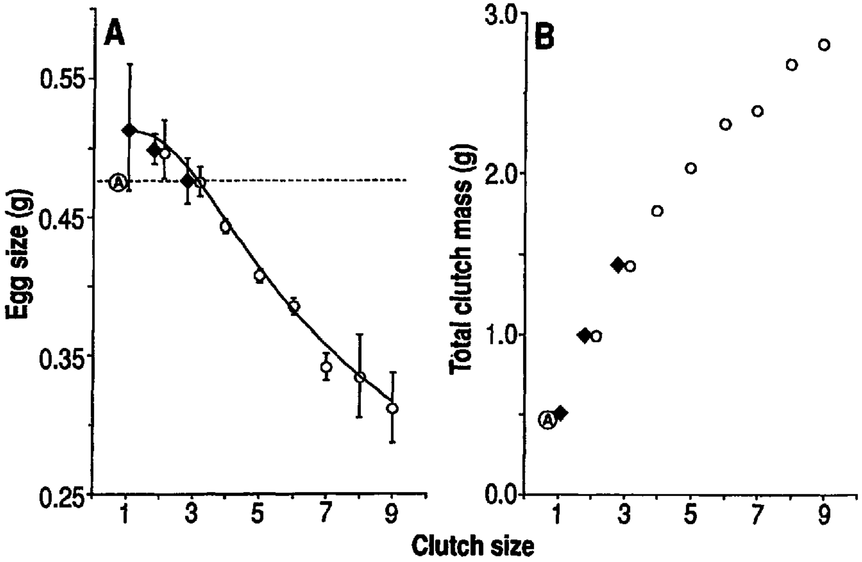
- někdy důsledkem mechanického omezení



Proximate Constraints on the Evolution of Egg Size, Number, and Total Clutch Mass in Lizards

Barry Sinervo and Paul Licht

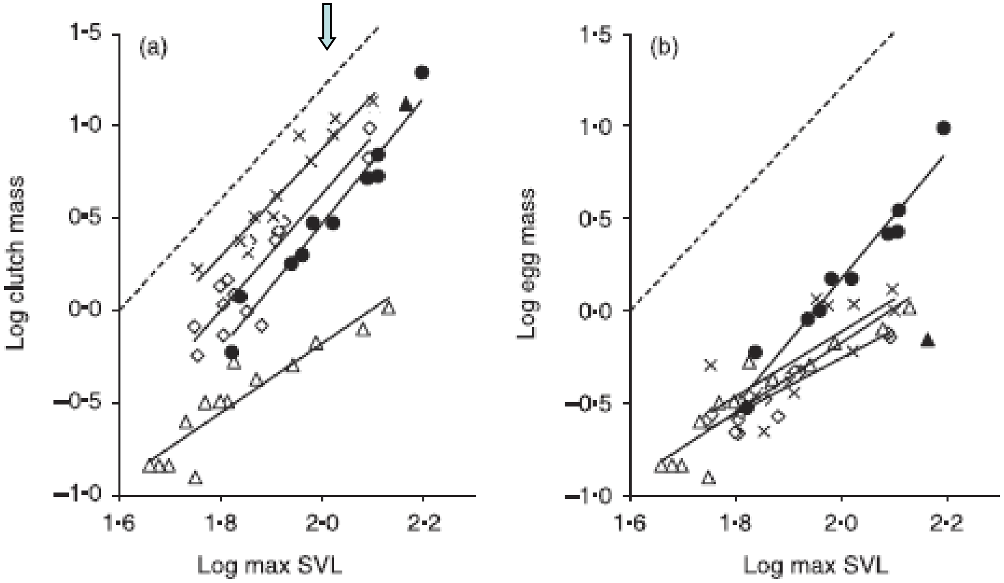
SCIENCE, VOL. 252



Why reduce clutch size to one or two eggs? Reproductive allometries reveal different evolutionary causes of invariant clutch size in lizards

Functional Ecology 2007
21, 171–177

LUKÁŠ KRATOCHVÍL† and LUKÁŠ KUBIČKA



předpokládaný sklon při geometrickém omezení

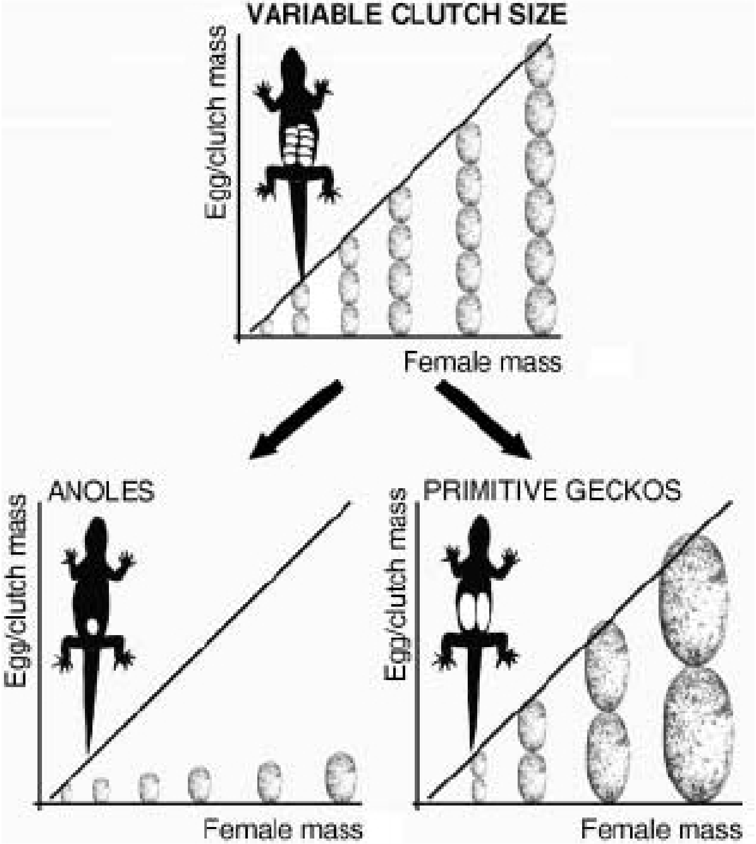


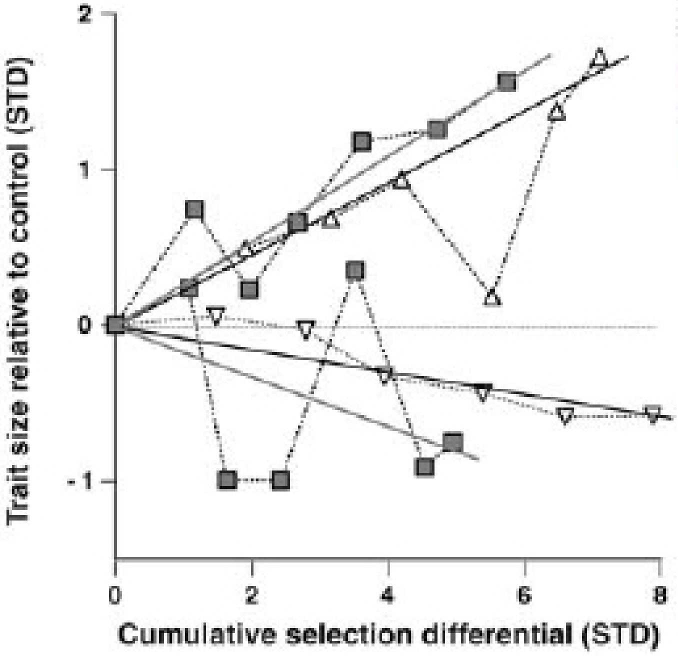
Fig. 1. Allometries of (a) clutch mass and (b) egg mass in four lizard lineages. Dashed line indicates isometry (slope = 3). Solid lines represent the ordinary least square regression for a given clade. Legend: empty triangles – anoles; filed triangles – *Polychrus acutirostris*; circles – eublepharid geckos; squares – lacertids; crosses – sceloporines.

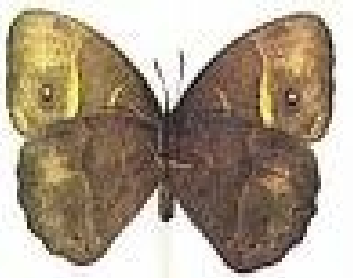
Alometrie může být udržovaná selekcí

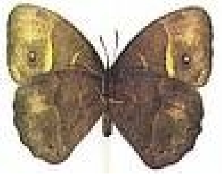
Natural Selection and Developmental Constraints in the Evolution of Allometries

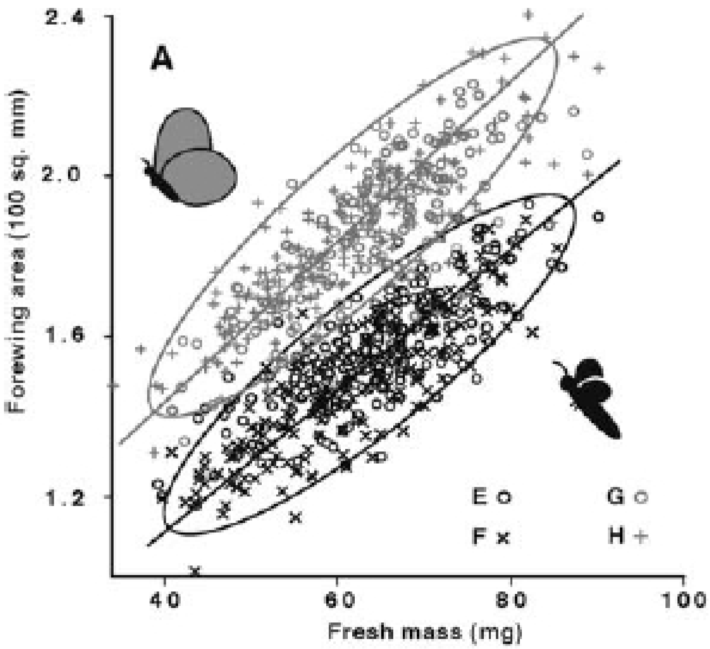
W. Anthony Frankino,[1*†] Bas J. Zwaan,[1] David L. Stern,[2] Paul M. Brakefield[1]

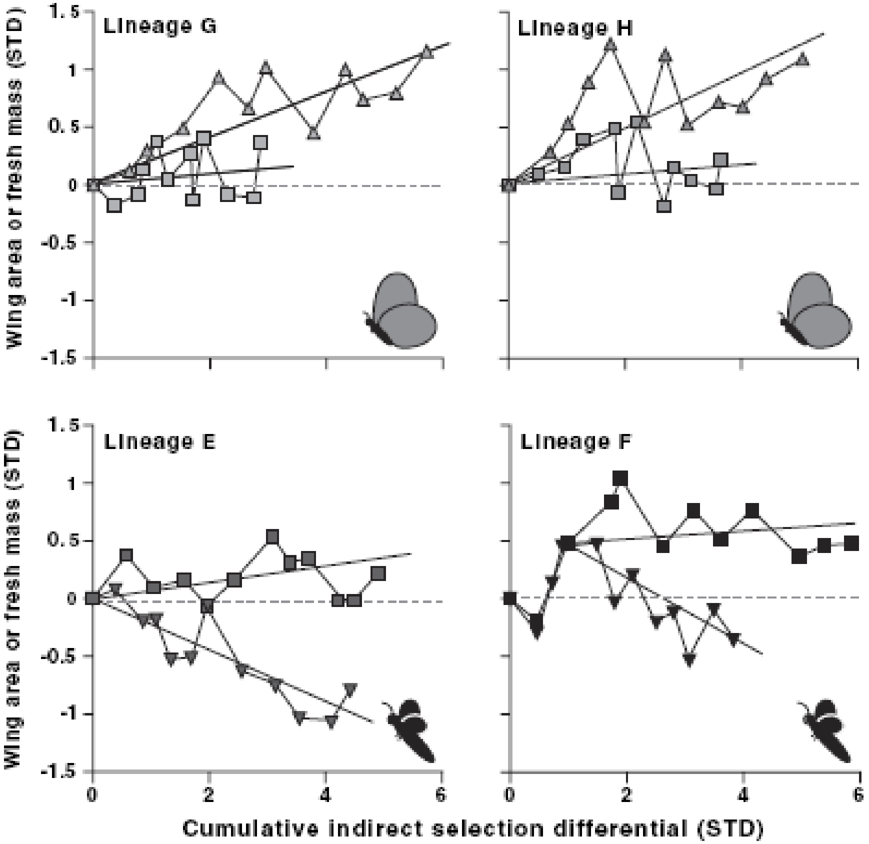
4 FEBRUARY 2005 VOL 307 SCIENCE

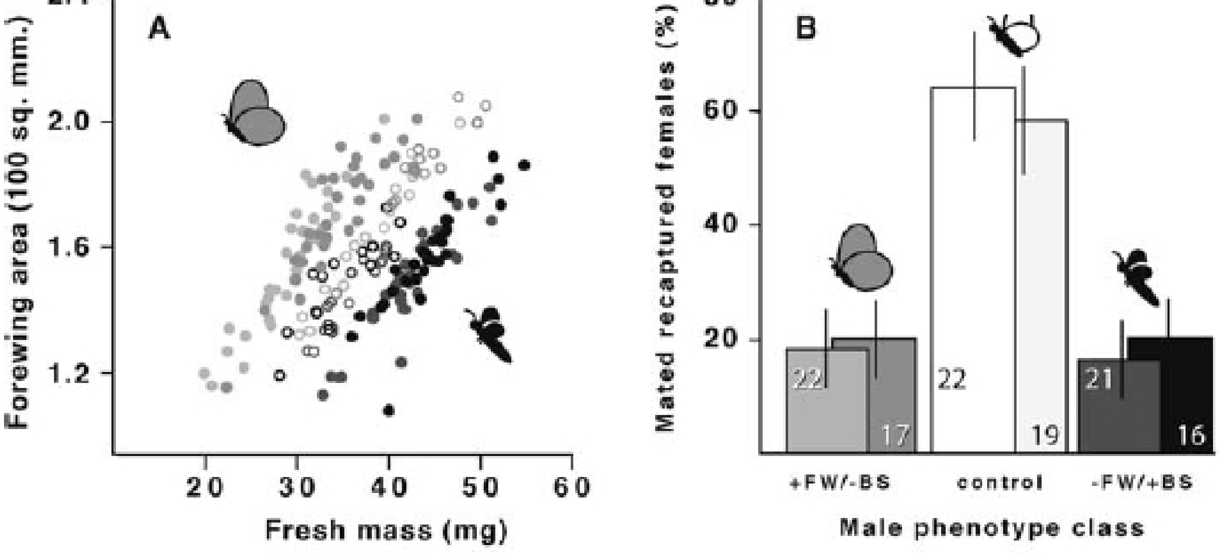







A
Forewing area (100 sq. mm)
2.4
2.0
1.6
1.2
Fresh mass (mg)
40
60
80
100
E ○
F ×
G ○
H +


Lineage G
Lineage H
Lineage E
Lineage F
Wing area or fresh mass (STD)
1.5
1
0.5
0
-0.5
-1
-1.5
Cumulative indirect selection differential (STD)
0
2
4
6


A
Forewing area (100 sq. mm.)
2.4
2.0
1.6
1.2
Fresh mass (mg)
20
30
40
50
60
B
Mated recaptured females (%)
80
60
40
20
22
17
22
19
21
16
+FW/-BS
control
-FW/+BS
Male phenotype class

Alometrická křivka na vyšších škálách ukazuje spíš omezení

Changing sex at the same relative body size

Similar forces may select for gender switching across taxa in all animals with this facility.

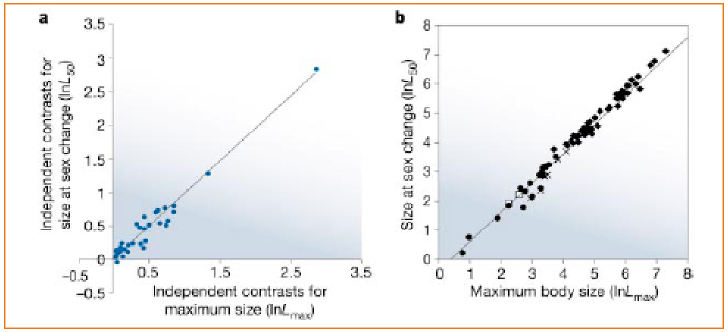


Figure 2 Animals change sex at the same relative body size. **a**, Log–log plot of independent contrasts for L_{50} against L_{max}, where these are the average size and the maximal body size, respectively, at sex change. The slope is fixed at unity and is driven through the origin, as required for the analysis of independent contrasts[9] ($r^2 = 0.908$, $n = 38$ independent contrasts). The ordinary least-squares (OLS) slope is 0.97 ± 0.05 (95% CI; $r^2 = 0.955$). **b**, Log–log plot of L_{50} against L_{max} for a wide range of sex-changing species, each shown as an independent data point. Data are split by taxa: asterisks, Echinodermata; circles, Crustacea; diamonds, Chordata; crosses, Mollusca. The regression has a slope fixed at unity, giving an intercept of -0.32 ± 0.05 (95% CI; $r^2 = 0.97$, $n = 77$ species). The OLS slope is 1.05 (95% CI) 0.03, with an intercept of −0.55 (95% CI) 0.07 (r^2=0.98). The mean relative size at sex change (L_{50}/L_{max}) is 0.72 (95% CI: 0.67–0.77), indicating that individuals change sex when they reach 72% of their maximum size. Size (L_{50} and L_{max}) was measured in millimetres before logarithmic transformation.

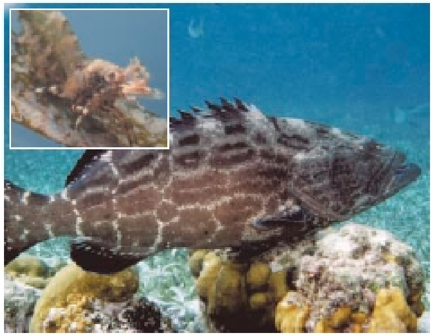


Figure 1 Little and large: the black grouper (1.5 m) and the shrimp *Thor manningi* (2 mm, inset) switch sex at the same relative size.

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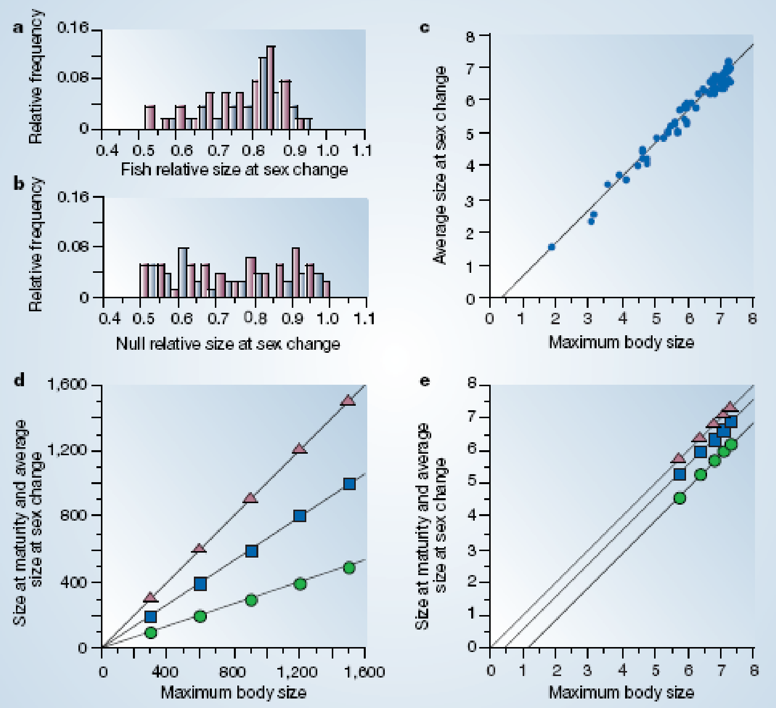
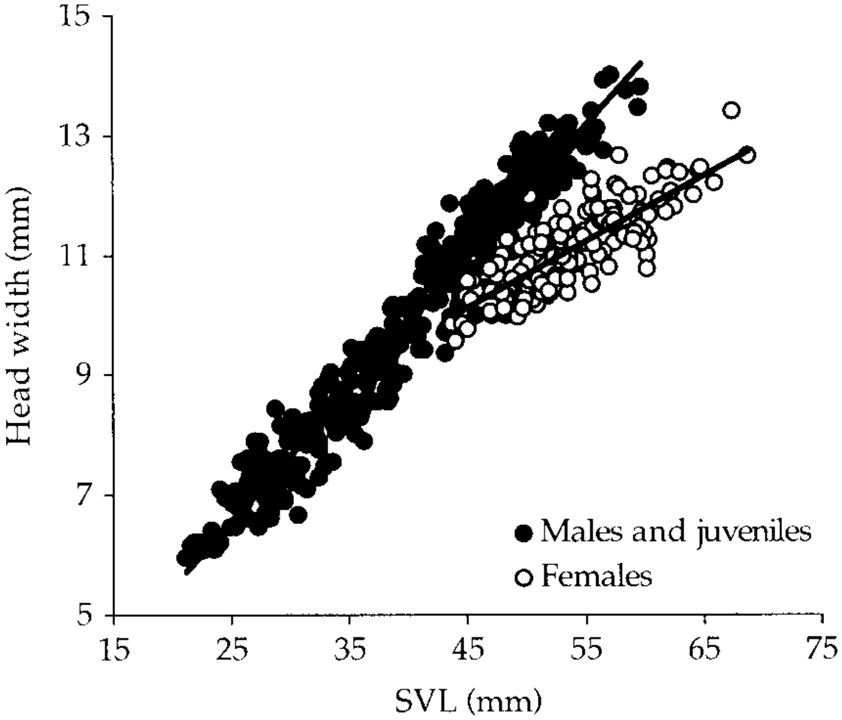


Figure 1 Relative size at sex change varies widely among animals. **a**, Distribution of relative size at sex change (L_{50}/L_{max}) for 52 species of fish used by Allsop and West[7,8]. **b**, Distribution of relative size at sex change for 77 hypothetical species generated by our null model. **c**, Log–log plot of average size at sex change (L_{50}) against maximum size (L_{max}) for 77 hypothetical species. The null data generate apparent invariance in relative size at sex change (b, c). **d**, Size at maturity (L_{mat}) plotted against maximum size: green circles, $L_{mat} = 33\%\ L_{max}$; blue squares, $L_{mat} = 66\%\ L_{max}$; red triangles, $L_{mat} = 100\%\ L_{max}$. Average size at sex change must fall within these constraints. **e**, Log–log plot of the data shown in d. From **d**, **e**, it is evident that more stringent constraints generate more apparent invariance.

Sex change and relative body size in animals

Arising from: Allsop, D. J. & West, S. A. *Nature* **425**, 783–784 (2003)

Výběr „měřítka“ je zásadní pro pochopní evolučních procesů



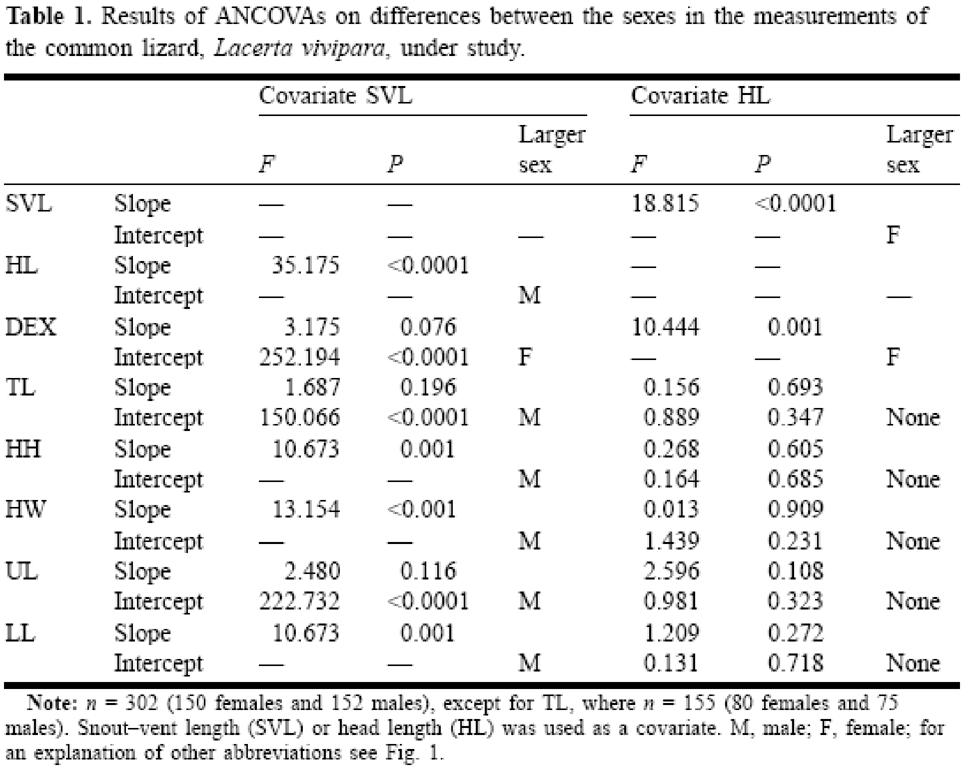


Table 1. Results of ANCOVAs on differences between the sexes in the measurements of the common lizard, *Lacerta vivipara*, under study.

		Covariate SVL			Covariate HL		
		F	*P*	Larger sex	*F*	*P*	Larger sex
SVL	Slope	—	—		18.815	<0.0001	
	Intercept	—	—	—	—	—	F
HL	Slope	35.175	<0.0001		—	—	
	Intercept	—	—	M	—	—	—
DEX	Slope	3.175	0.076		10.444	0.001	
	Intercept	252.194	<0.0001	F	—	—	F
TL	Slope	1.687	0.196		0.156	0.693	
	Intercept	150.066	<0.0001	M	0.889	0.347	None
HH	Slope	10.673	0.001		0.268	0.605	
	Intercept	—	—	M	0.164	0.685	None
HW	Slope	13.154	<0.001		0.013	0.909	
	Intercept	—	—	M	1.439	0.231	None
UL	Slope	2.480	0.116		2.596	0.108	
	Intercept	222.732	<0.0001	M	0.981	0.323	None
LL	Slope	10.673	0.001		1.209	0.272	
	Intercept	—	—	M	0.131	0.718	None

Note: n = 302 (150 females and 152 males), except for TL, where n = 155 (80 females and 75 males). Snout–vent length (SVL) or head length (HL) was used as a covariate. M, male; F, female; for an explanation of other abbreviations see Fig. 1.

Misinterpretation of character scaling: a tale of sexual dimorphism in body shape of common lizards

Can. J. Zool. 81: 1112–1117 (2003)

Lukáš Kratochvíl, Michael Fokt, Ivan Rehák, and Daniel Frynta

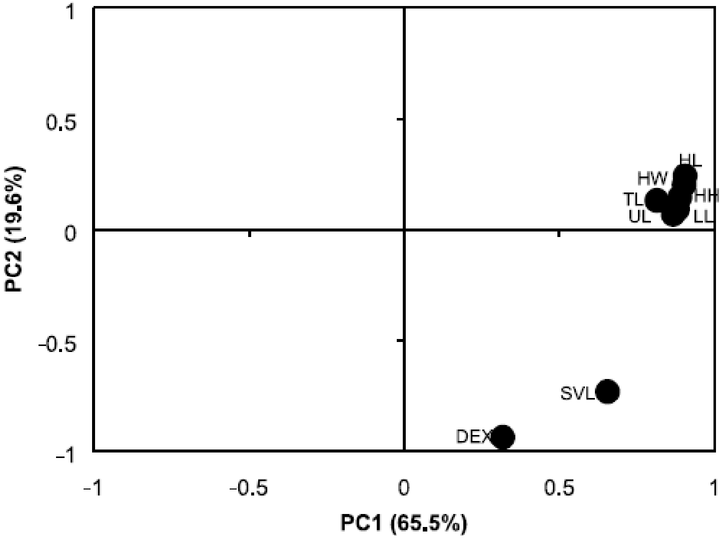
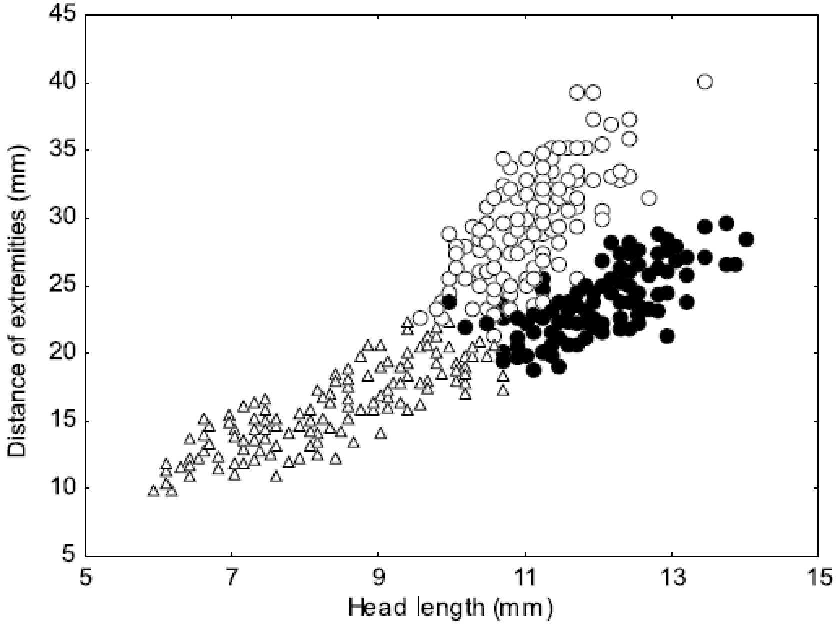
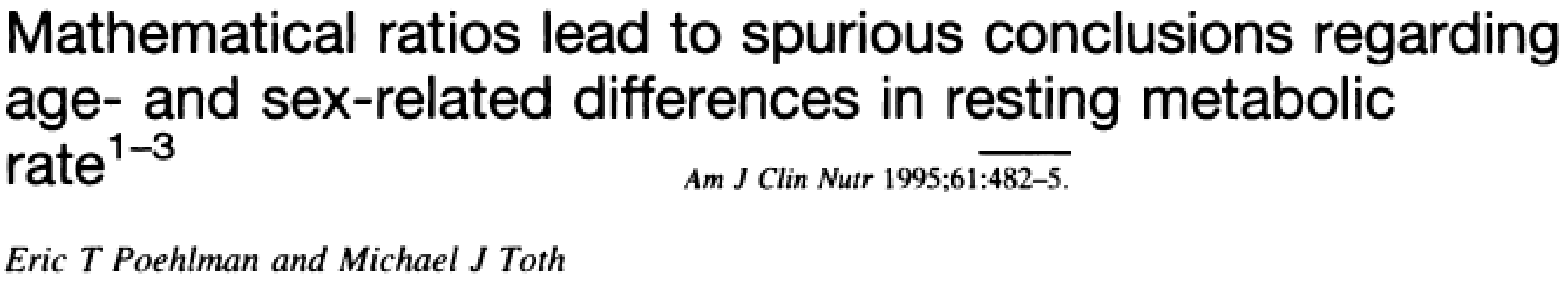


Fig. 2. Scatterplot of distances between the extremities versus head length for the common lizard, according to sex and maturity. Juveniles from Central Europe (n = 211) were added to show the ontogenetic trajectory of component development (●, males; ○, females; △, juveniles).



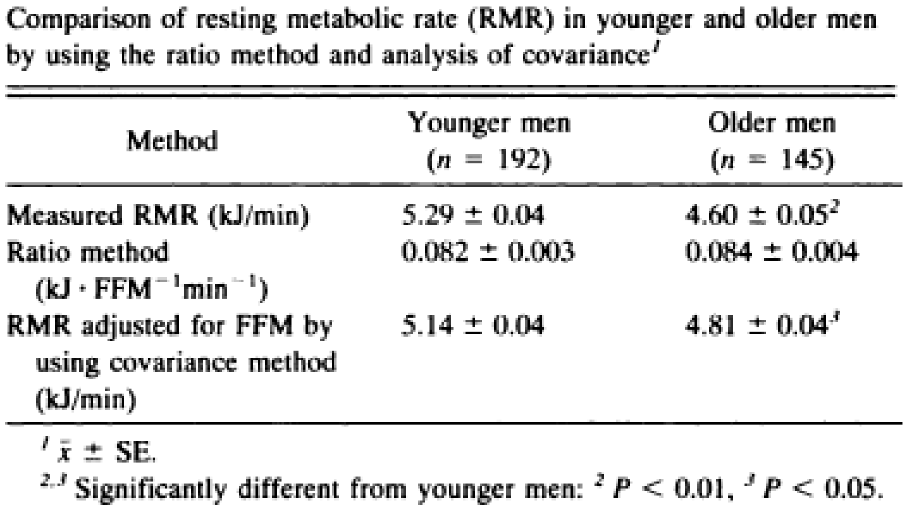
Proč nepoužívat poměry při studiu alometrických změn?



Mathematical ratios lead to spurious conclusions regarding age- and sex-related differences in resting metabolic rate[1–3]

Am J Clin Nutr 1995;61:482–5.

Eric T Poehlman and Michael J Toth



Comparison of resting metabolic rate (RMR) in younger and older men by using the ratio method and analysis of covariance[1]

Method	Younger men (n = 192)	Older men (n = 145)
Measured RMR (kJ/min)	5.29 ± 0.04	4.60 ± 0.05[2]
Ratio method ($kJ \cdot FFM^{-1} min^{-1}$)	0.082 ± 0.003	0.084 ± 0.004
RMR adjusted for FFM by using covariance method (kJ/min)	5.14 ± 0.04	4.81 ± 0.04[3]

[1] $\bar{x}$ ± SE.

[2,3] Significantly different from younger men: [2] $P < 0.01$, [3] $P < 0.05$.

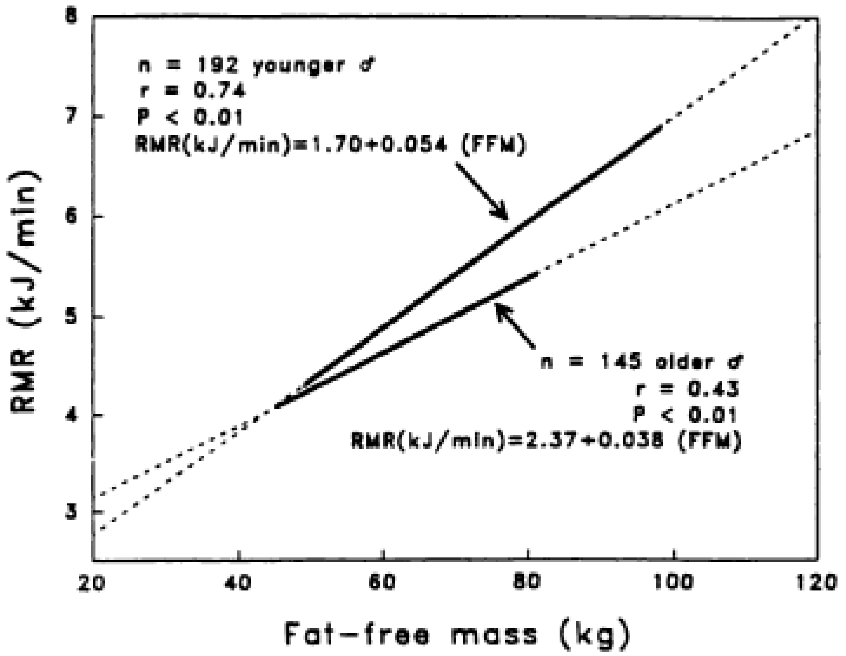


FIGURE 1. Relationship between resting metabolic rate (RMR) and fat-free mass (FFM) in younger and older men. The solid line represents the relationship between RMR and FFM within the range of FFM examined, whereas the dotted line represents an extrapolation of the regression line.

Proč nepoužívat poměry?

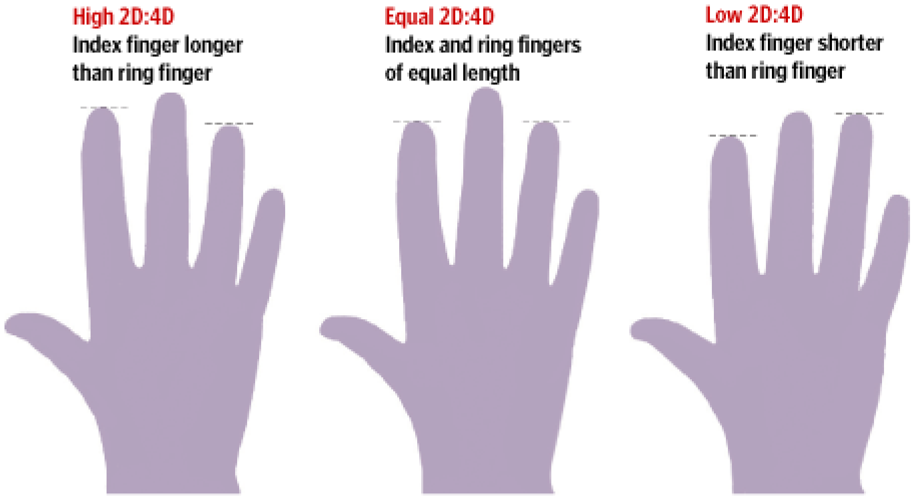
b i o l o g y
letters

Biol. Lett. (2009) 5, 643–646
doi:10.1098/rsbl.2009.0346
Published online 24 June 2009

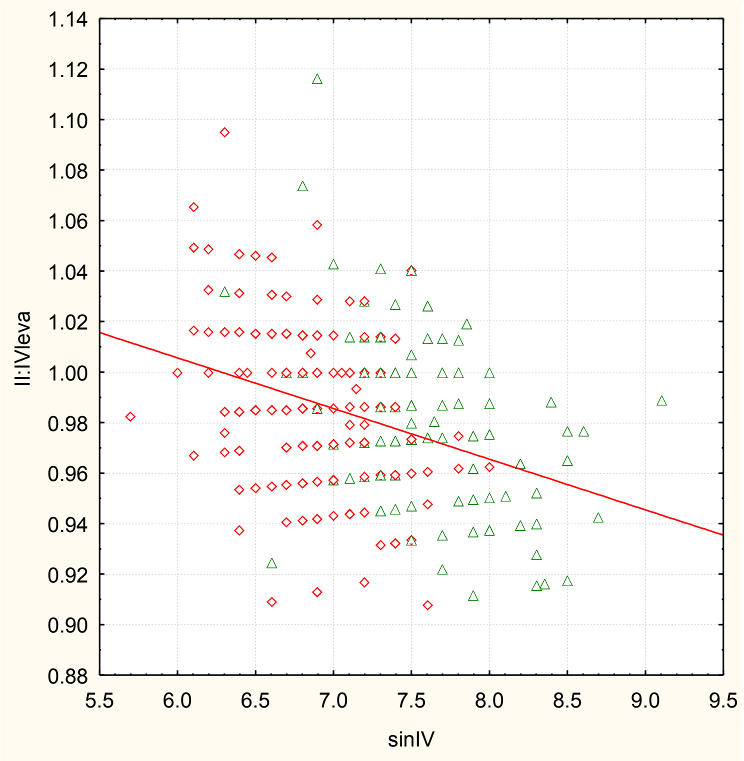
Evolutionary biology

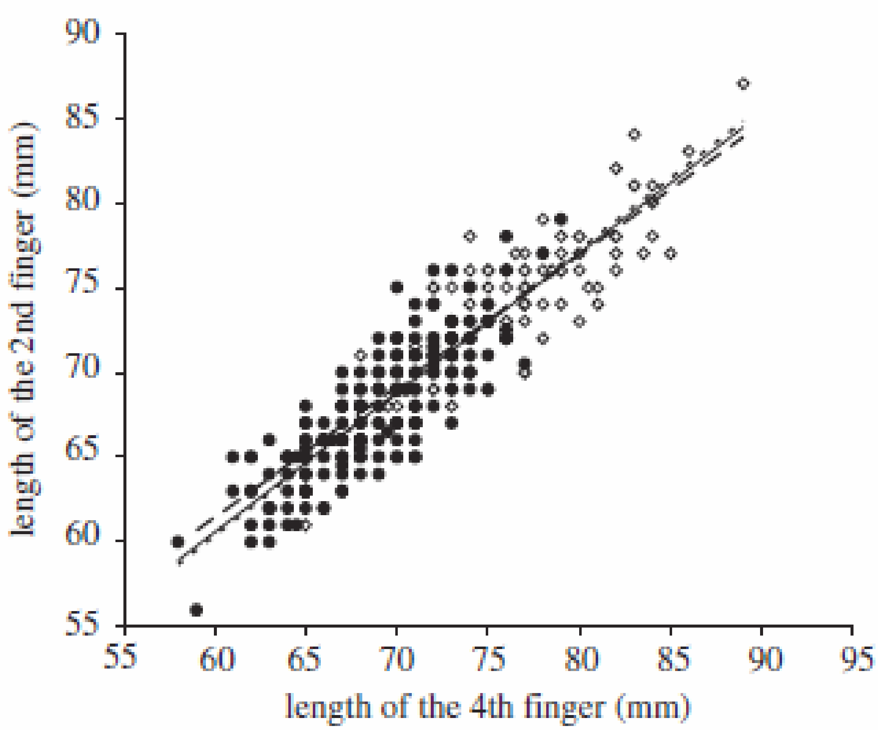
Differences in the 2nd to 4th digit length ratio in humans reflect shifts along the common allometric line

Lukáš Kratochvíl[1,*] and Jaroslav Flegr[2]



Many studies have looked at the relationship between the length of the second digit (2D) and the fourth (4D). A new study finds that women who have index fingers shorter than their ring fingers (i.e., have "Low 2D:4D" as shown on hand at right, above) are more likely to have athletic skills. Most women have equal 2D:4D.





Shrnutí

- omezení jsou někdy způsobena fyzikálními (mechanickými) principy, často však vznikají důsledkem předchozích adaptací

- korelace mezi znaky může být právě takovýmto omezením

- alometrické vztahy je někdy složité interpretovat (např. potíže s výběrem znaku, ke kterému alometrickou změnu vztahovat; výběr funkce popisující data; interpretace alometrických změn na velkých škálách…)