

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

BY S. J. GOULD AND R. C. LEWONTIN

*Museum of Comparative Zoology, Harvard University,
Cambridge, Massachusetts 02138, U.S.A.*

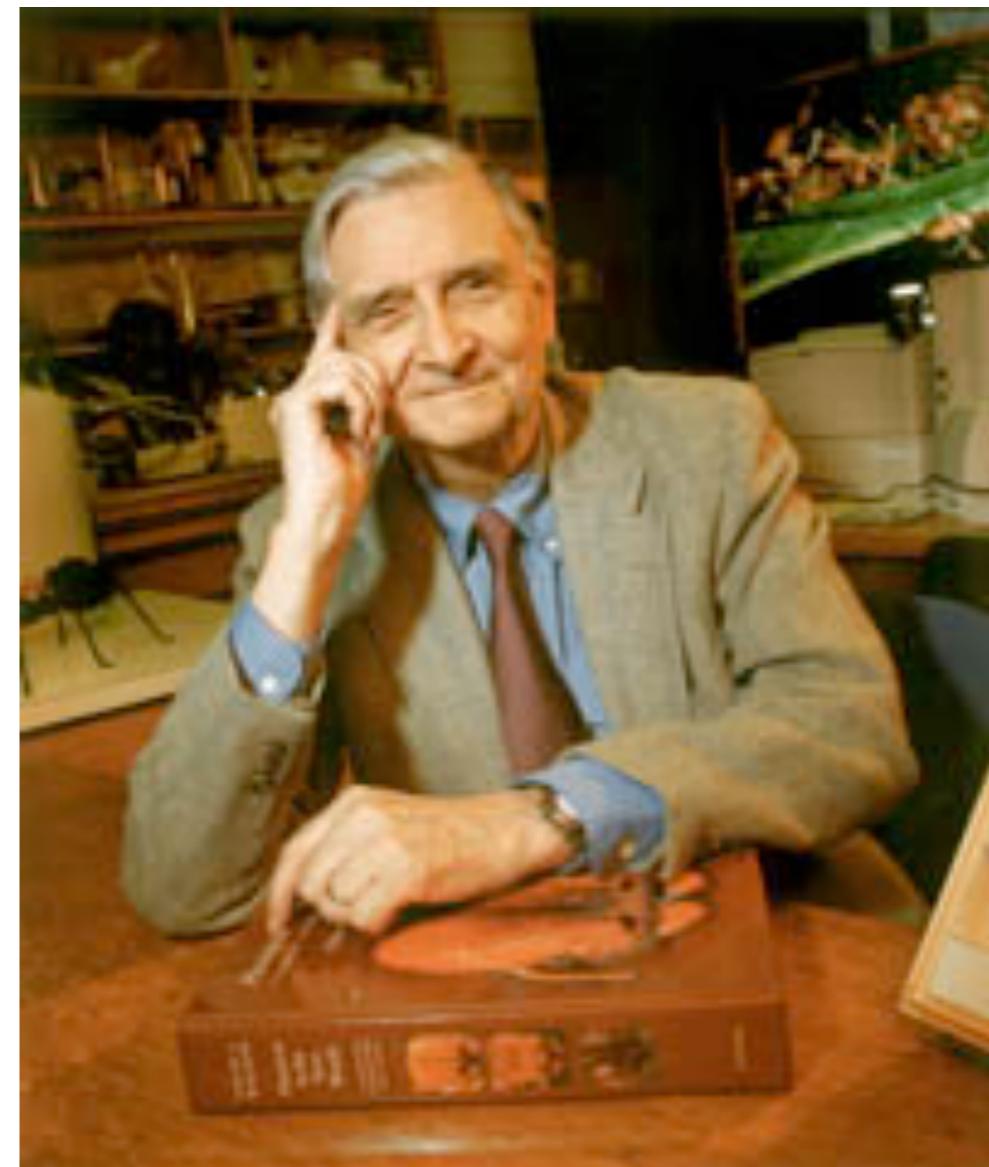
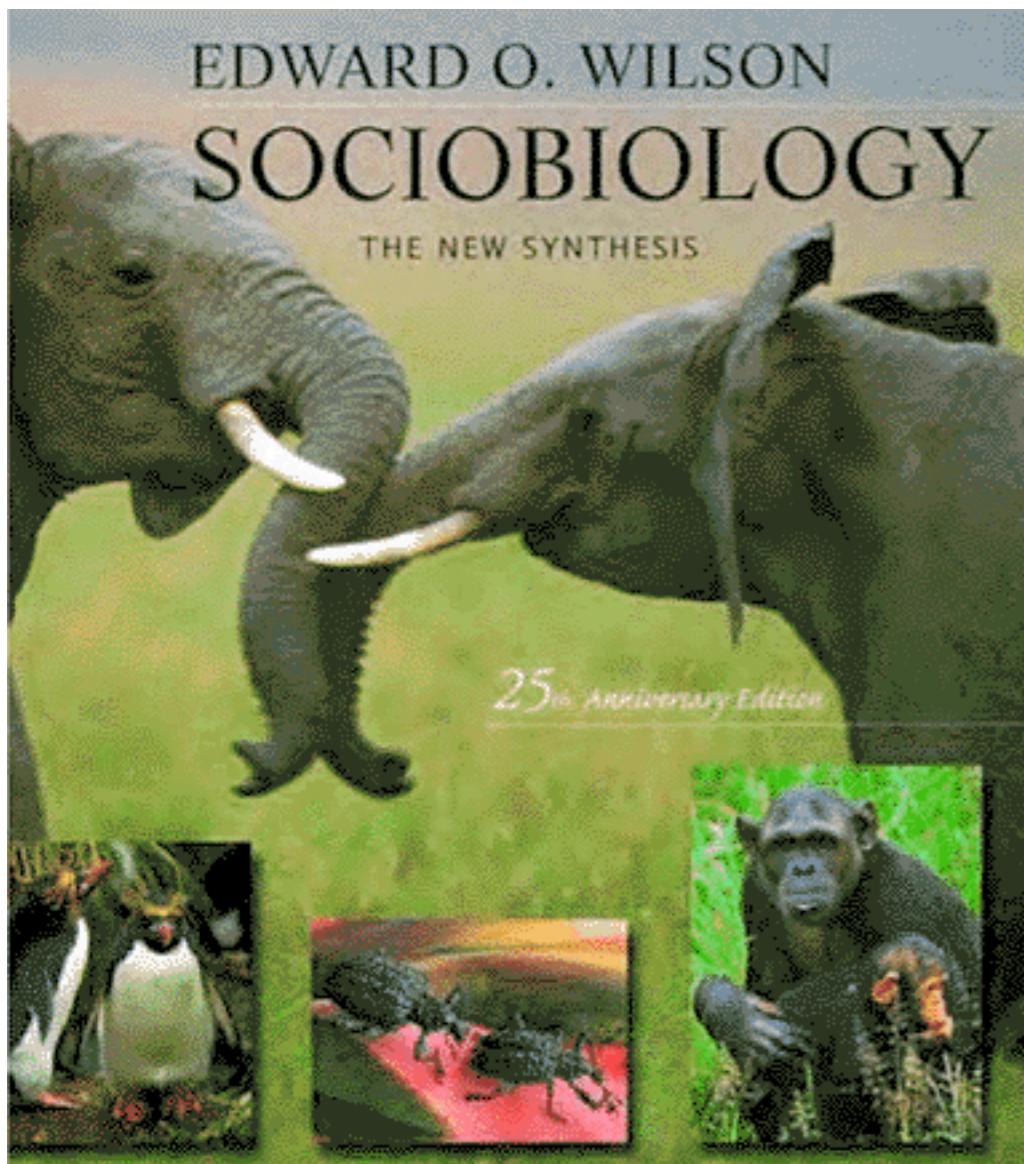


el optimista dr. Pangloss y el paradigma panglossiano



are... Everything is made for the best purpose. Our noses were made to carry spectacles, so we have spectacles. Legs were clearly intended for breeches, and we wear them.' Yet evolutionary biologists, in their tendency to focus exclusively on immediate adaptation to local conditions, do tend to ignore architectural constraints and perform just such an inversion of explanation.

An adaptationist programme has dominated evolutionary thought in England and the United States during the past 40 years. It is based on faith in the power of natural selection as an optimizing agent. It proceeds by breaking an organism into unitary ‘traits’ and proposing an adaptive story for each considered separately. Trade-offs among competing selective demands exert the only brake upon perfection; non-optimality is thereby rendered as a result of adaptation as well. We criticize this approach and attempt to reassert a competing notion (long popular in continental Europe) that organisms must be analysed as integrated wholes, with *Baupläne* so constrained by phyletic heritage, pathways of development and general architecture that the constraints themselves become more interesting and more important in delimiting pathways of change than the selective force that may mediate change when it occurs. We fault the adaptationist programme for its failure to distinguish current utility from reasons for origin (male tyrannosaurs may have used their diminutive front legs to titillate female partners, but this will not explain *why* they got so small); for its unwillingness to consider alternatives to adaptive stories; for its reliance upon plausibility alone as a criterion for accepting speculative tales; and for its failure to consider adequately such competing themes as random fixation of alleles, production of non-adaptive structures by developmental correlation with selected features (allometry, pleiotropy, material compensation, mechanically forced correlation), the separability of adaptation and selection, multiple adaptive peaks, and current utility as an epiphenomenon of non-adaptive structures. We support Darwin’s own pluralistic approach to identifying the agents of evolutionary change.



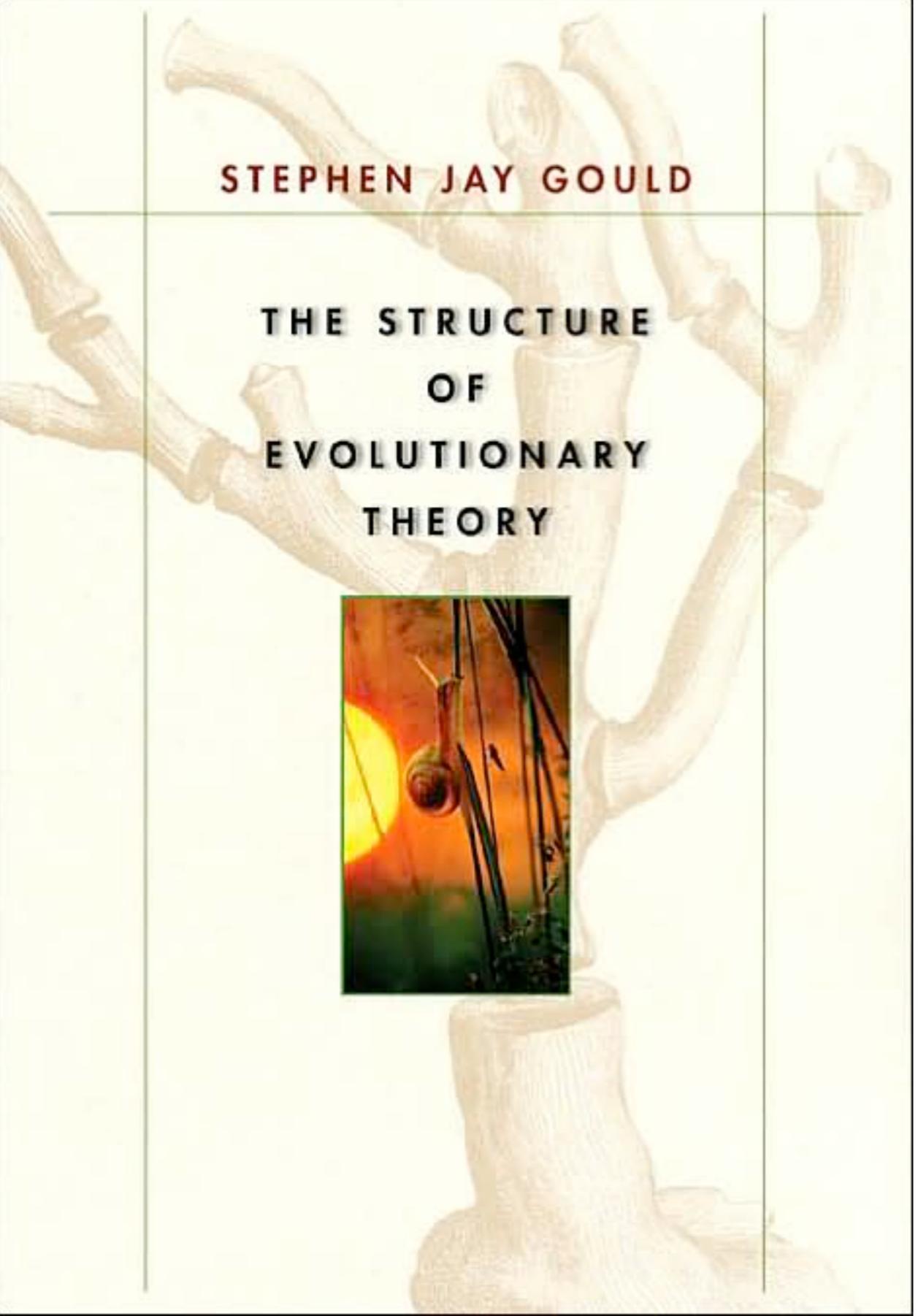
[\(<http://www.edge.org/conversation/the-false-allure-of-group-selection>\)](http://www.edge.org/conversation/the-false-allure-of-group-selection)

Exaptation—a missing term in the science of form

Stephen Jay Gould and Elisabeth S. Vrba*

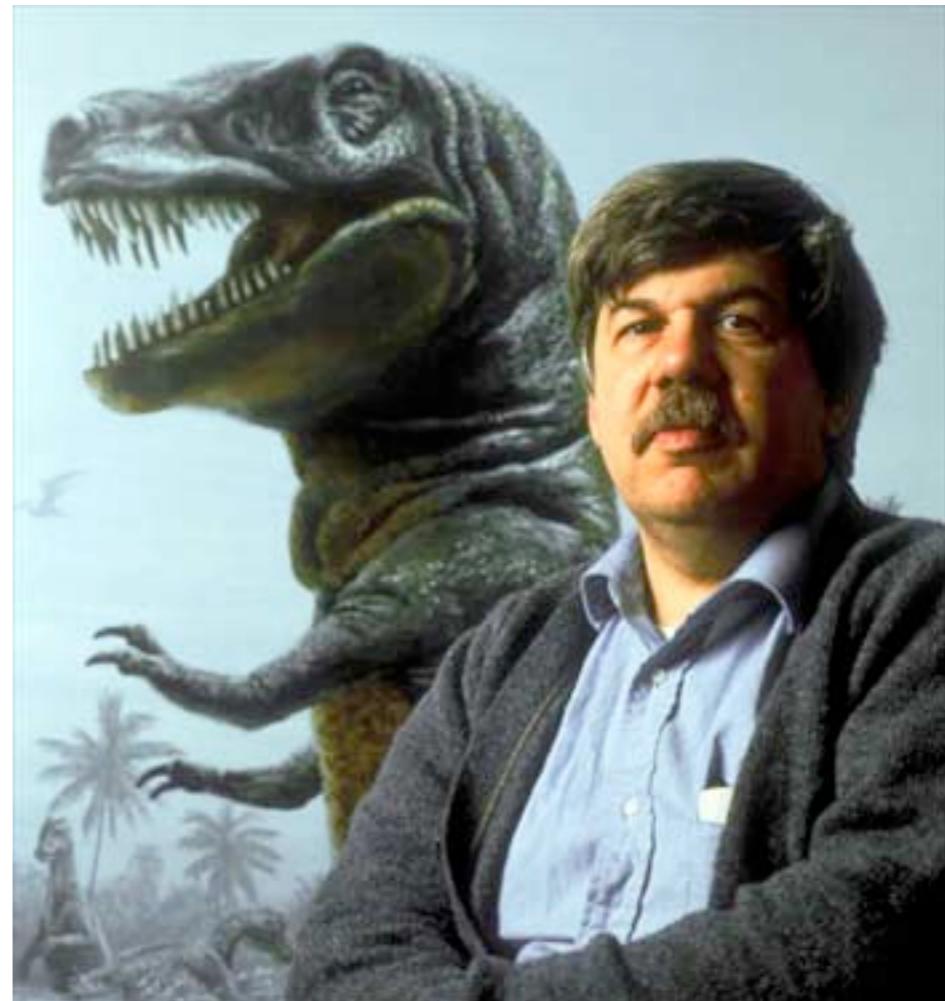
TABLE 1. A taxonomy of fitness.

Process	Character	Usage
Natural selection shapes the character for a current use—adaptation	adaptation	function
A character, previously shaped by natural selection for a particular function (an adaptation), is coopted for a new use—cooptation	exaptation	aptation
A character whose origin cannot be ascribed to the direct action of natural selection (a nonaptation), is coopted for a current use—cooptation		effect



STEPHEN JAY GOULD

THE STRUCTURE
OF
EVOLUTIONARY
THEORY



WHY ARE JUVENILES SMALLER THAN THEIR PARENTS?

NORMAN C. ELLSTRAND

Department of Botany and Plant Sciences, University of California, Riverside, California 92521

Received November 15, 1982. Revised December 14, 1982

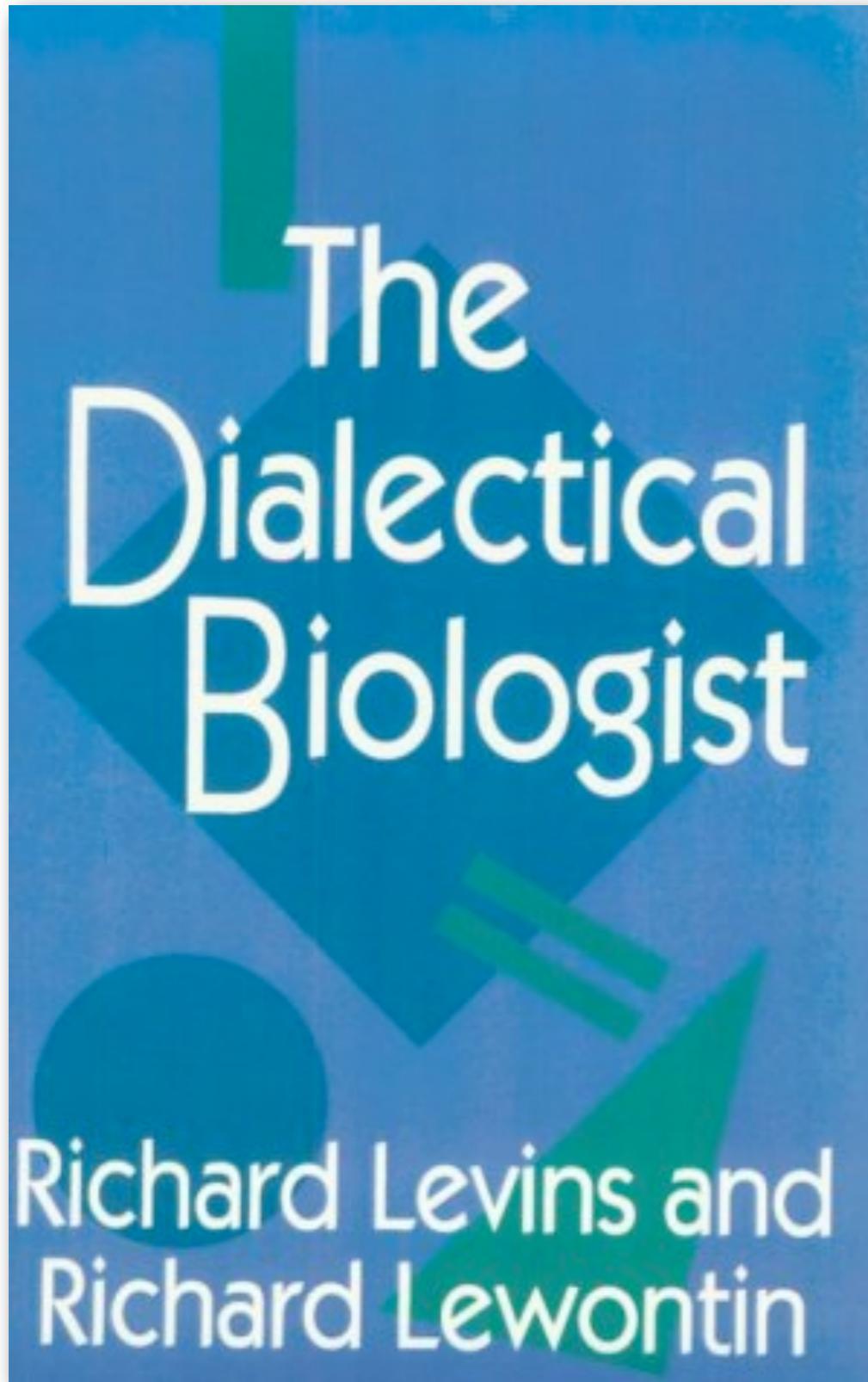
“Let’s get small.”

—S. Martin (1977)

The past 20 years have seen a burst of interest in life history traits and their evolution (e.g., Stearns 1976, 1977; Harper, 1977; Solbrig, 1980). Most studies either focus on adult traits such as reproductive effort, periodicity of reproduction, and timing of first reproduction, or they focus on whole life traits such as generation of time and shape of survivorship curves. Juvenile characters have not been so closely studied, yet differences between the life history traits of juveniles and adults can be profound (Pelton, 1953).

Furthermore, prereproductive traits are more sensitive to natural selection than those expressed later in the life cycle (Medawar, 1957; Cook, 1979; Emlen, 1980). Here I deal with the evolutionary significance of one such difference, the fact that juveniles at birth are usually smaller than adults, and I present a number of hypotheses of how selection might favor juveniles’ small size (JSS).

Small juveniles are indeed very common. The seeds of seed plants range from 2×10^{-6} g to about 27 kg (Harper et al., 1970) but are uniformly much smaller than the individuals which produce them. The dif-



by Richard Lewontin

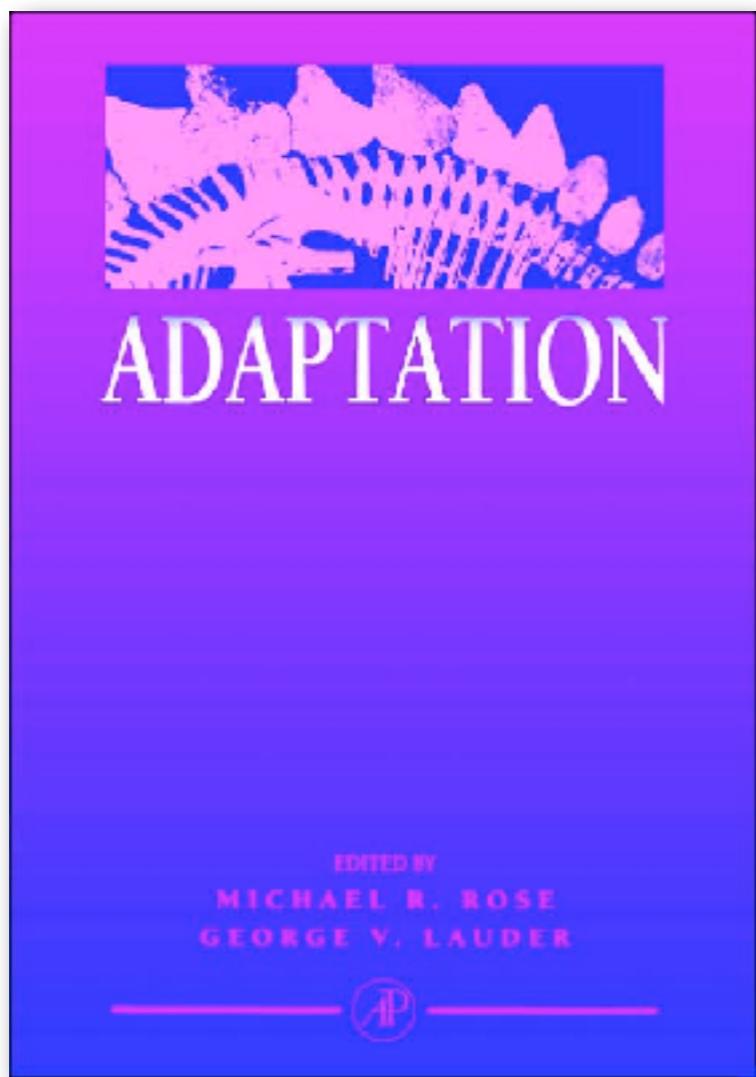
EVERY theory of the world that is at all powerful and covers a large domain of phenomena carries immanent within itself its own caricature. If it is to give a satisfactory explanation of a wide range of events in the world in a wide variety of circumstances, a theory necessarily must contain some logically very powerful element that is flexible enough to be applicable in so many situations. Yet the very logical power of such a system is also its greatest weakness, for a theory that can explain everything explains nothing. It ceases to be a theory of the contingent world and becomes instead a vacuous metaphysic that generates not only all possible worlds, but all conceivable ones. The narrow line that separates a genuinely fruitful and powerful theory from its sterile caricature is crossed over and over again by vulgarizers who seize upon the powerful explanatory element and, by using it indiscriminately, destroy its usefulness. In doing so, however, they reveal underlying weaknesses in the theories themselves, which can lead to their reformulation.

This element of immanent caricature is certainly present in three theoretical structures that have had immense effects on twentieth-century bourgeois thought: Marxism, Freudianism, and Darwinism.

ADAPTATION REVIEWED: A PHYLOGENETIC METHODOLOGY FOR STUDYING CHARACTER MACROEVOLUTION

DAVID A. BAUM AND ALLAN LARSON

*Department of Biology, Washington University,
St. Louis, Missouri 63130, USA*



Phylogenetic Systematics of Adaptation

ALLAN LARSON

JONATHAN B. LOSOS

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9 February 2012 Last updated at 04:59

2.6K Share

Zebra stripes evolved to keep biting flies at bay

By Victoria Gill

Science reporter, BBC Nature



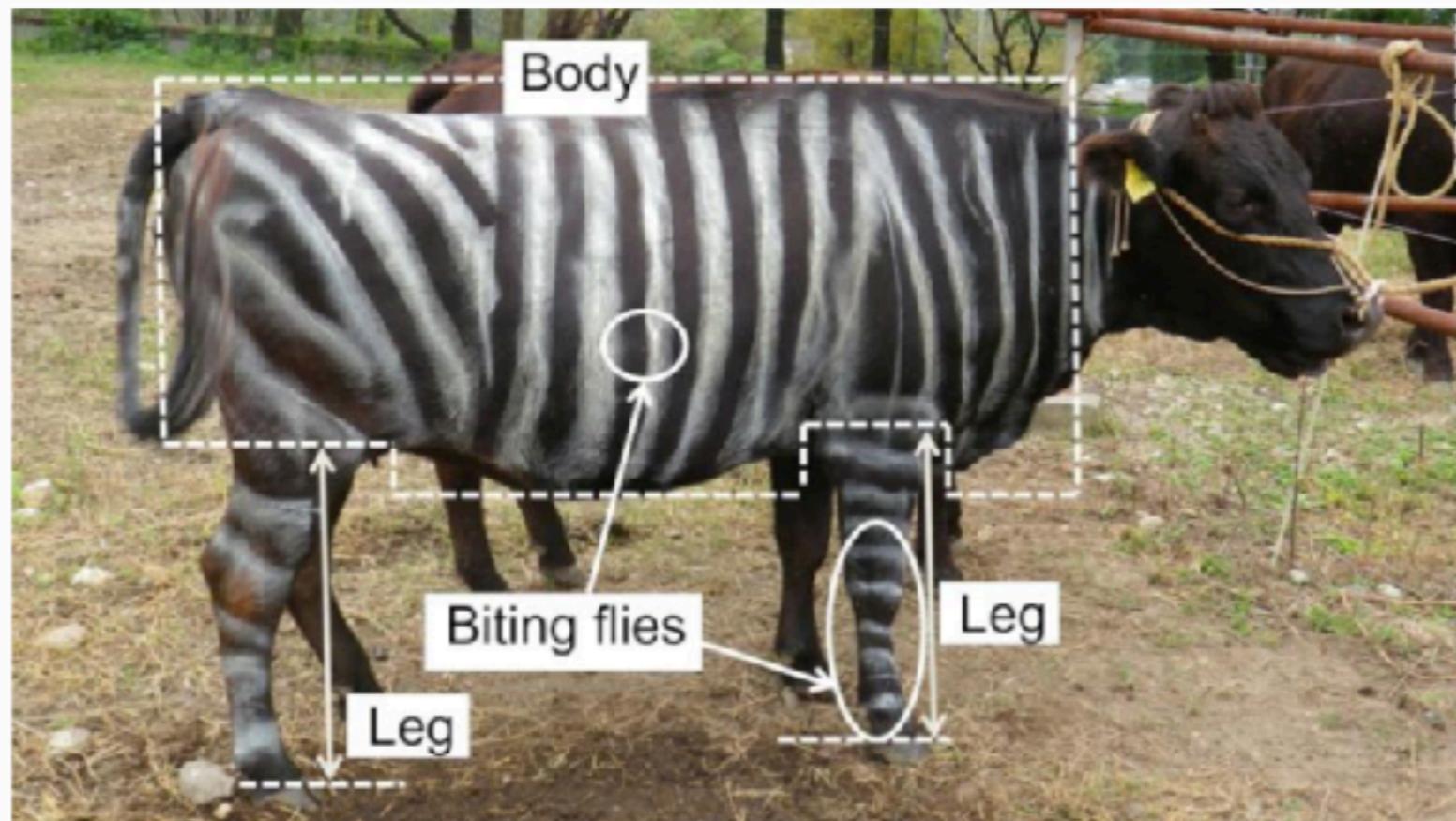
The team placed the sticky model horses in a fly-infested field

<http://www.bbc.co.uk/nature/16944753>

Cows painted like zebras can fend off flies better than their plain-coated counterparts

By Scottie Andrew, CNN

⌚ Updated 1519 GMT (2319 HKT) October 8, 2019



Zebra-striped cows might not look like the African wild horse, but they get the same benefits from their coloring. Stripes help cows avoid pesky fly bites, a new study found.

News & buzz



Arrest made in shooting of Joshua Brown, slain key witness in...

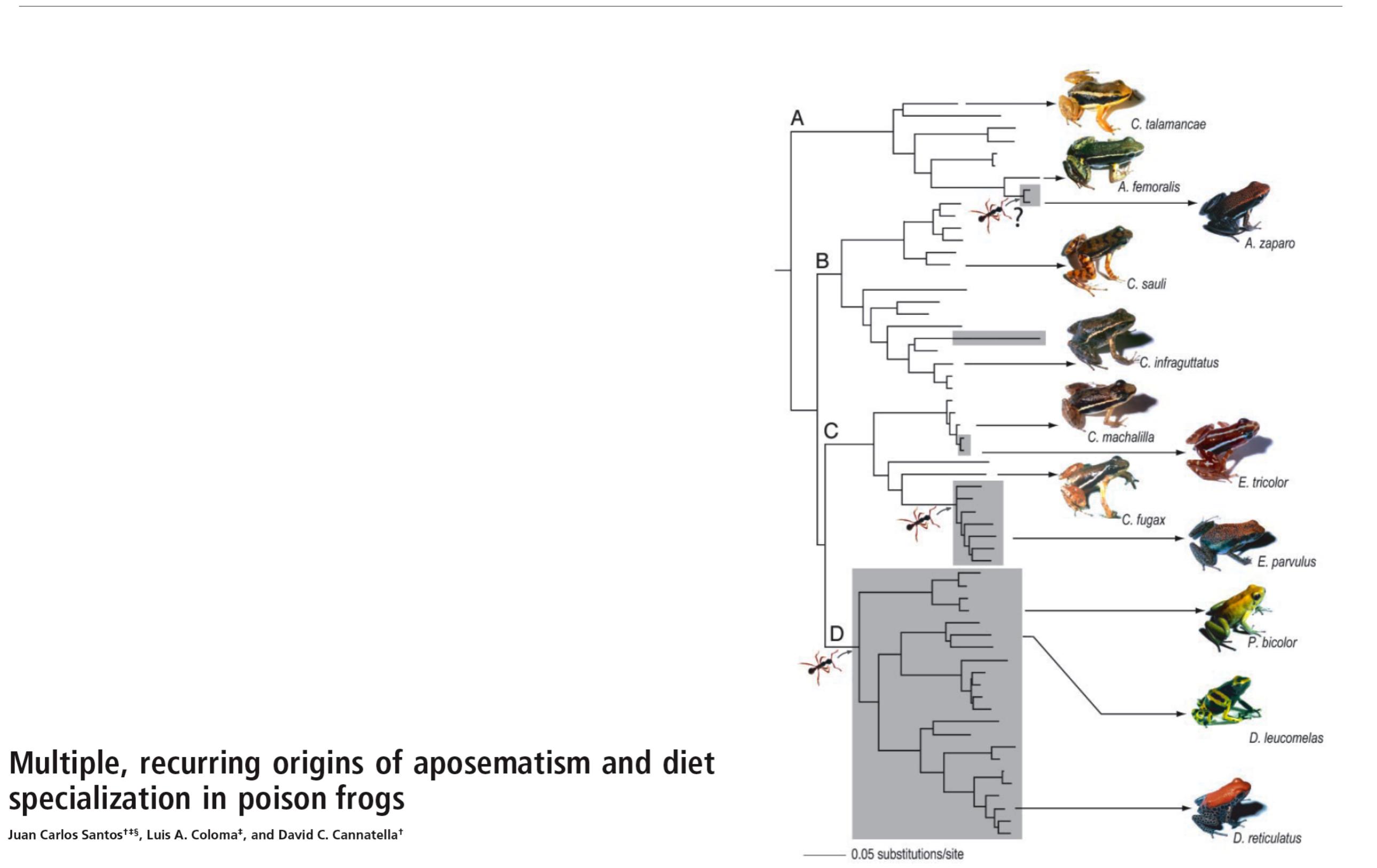


Despite 14 stitches and a black eye, Jimmy Carter is back...



Advertisement

patrones filogenéticos y la posibilidad de adaptación 1



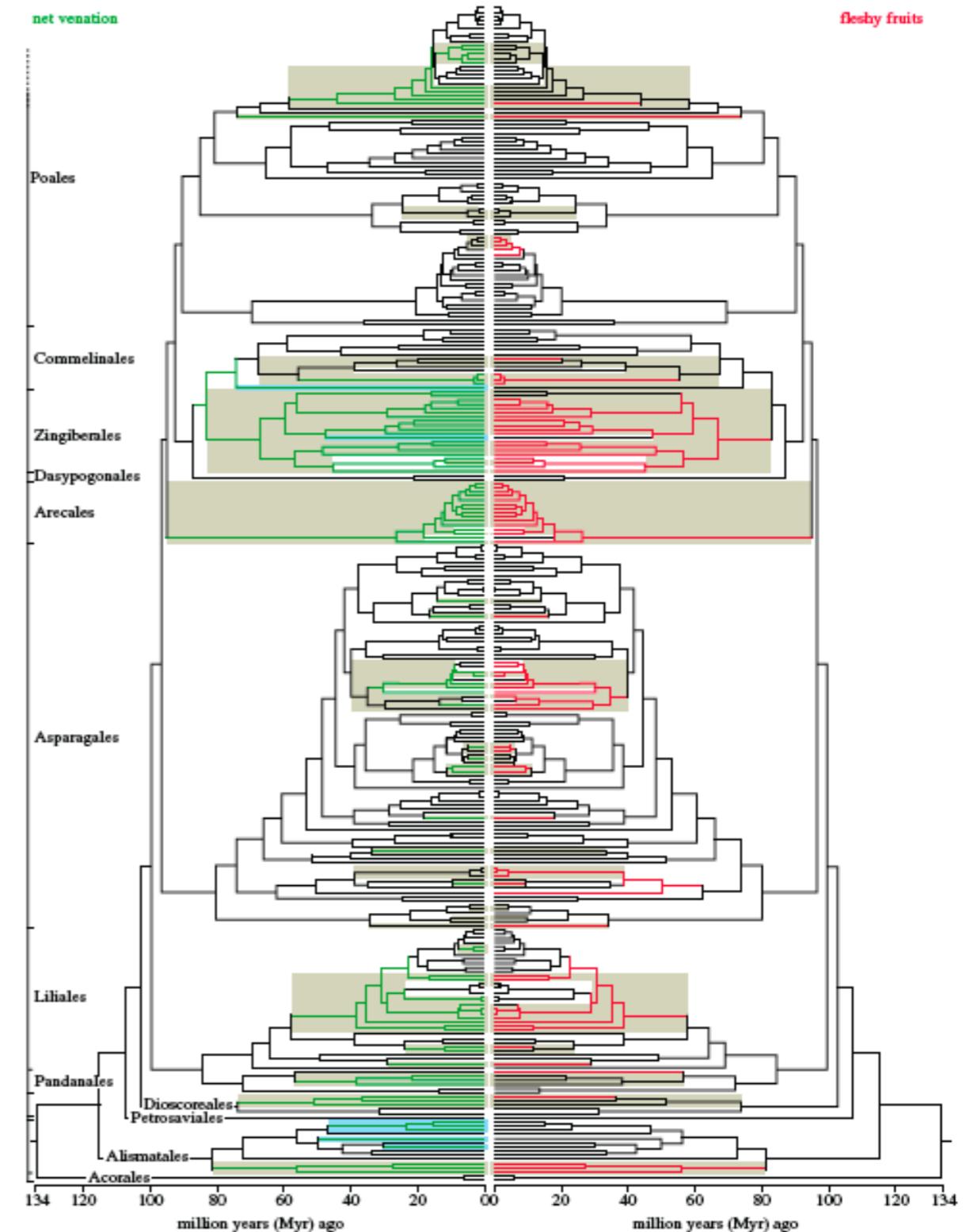
patrones filogenéticos y la posibilidad de adaptación 2

PROCEEDINGS
OF
THE ROYAL
SOCIETY B

Proc. R. Soc. B (2005) 272, 1481–1490
doi:10.1098/rspb.2005.3067
Published online 28 June 2005

Repeated evolution of net venation and fleshy fruits among monocots in shaded habitats confirms *a priori* predictions: evidence from an *ndhF* phylogeny

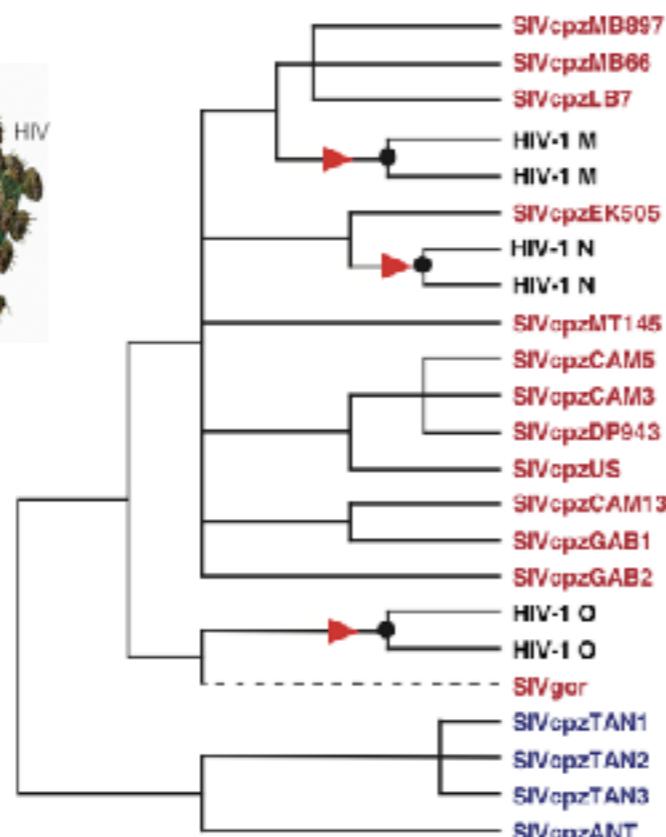
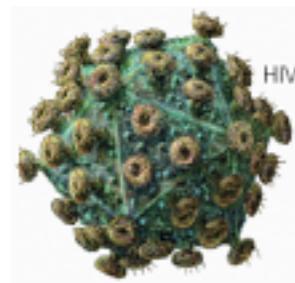
Thomas J. Givnish^{1,12,*}, J. Chris Pires², Sean W. Graham³,
Marc A. McPherson³, Linda M. Prince⁴, Thomas B. Patterson¹,
Hardeep S. Rai³, Eric H. Roalson⁵, Timothy M. Evans⁶, William J. Hahn⁷,
Kendra C. Millam¹, Alan W. Meerow⁸, Mia Molvray⁹, Paul J. Kores⁹,
Heath E. O'Brien³, Jocelyn C. Hall^{1,10}, W. John Kress¹¹
and Kenneth J. Sytsma¹



selección natural y evolución convergente del virus HIV

Adaptation of HIV-1 to Its Human Host

Louise V. Wain,¹ Elizabeth Bailes,¹ Frederic Bibollet-Ruche,² Julie M. Decker,² Brandon F. Keele,² Fran Van Heuverswyn,³ Yingying Li,² Jun Takehisa,² Eitel Mpoudi Ngole,⁴ George M. Shaw,² Martine Peeters,³ Beatrice H. Hahn,² and Paul M. Sharp¹



"as all three lineages of HIV-1 evolved from chimp-virus ancestors, each lineage acquired the same mutation encoding the same new amino acid in the same position in the same protein"

(Zimmer & Emlen 2013)

p17 Gag	26	30	34
HIV-1 group M ancestor	K	K	Y
HIV-1 group N ancestor	-	-	-
HIV-1 group O ancestor	-	-	-
SIVcpzPtt (MB66)	-	-	M
SIVcpzPtt (MB897)	-	-	M
SIVcpzPtt (LB7)	R	-	M
SIVcpzPtt (MT145)	-	-	M
SIVcpzPtt (EK505)	-	-	M
SIVcpzPtt (CAM13)	R	-	M
SIVcpzPtt (CAM3)	-	-	M
SIVcpzPtt (CAM5)	-	-	M
SIVcpzPtt (DP943)	-	-	M
SIVcpzPtt (GAB1)	R	-	M
SIVcpzPtt (GAB2)	R	-	M
SIVcpzPts (ANT)	-	-	I
SIVcpzPts (TAN1)	R	-	L
SIVcpzPts (TAN2)	R	-	L
SIVcpzPts (TAN3)	R	-	L
chimpanzee HIV-1 JC16	-	-	M
chimpanzee HIV-1 NC7	-	-	M

FIG. 2.—Species-specific adaptive changes in the matrix protein (Gag p17). Sequences from a region in the N-terminal basic domain of HIV-1/SIVcpz matrix proteins reveal a site (boxed) that differs between the HIV-1 group ancestors (R, Arg) and chimpanzee viruses (M, Met/L, Leu). Dashes indicate amino acid identity to the sequence at the top. Clones JC16 and NC7 were isolated from two chimpanzees experimentally infected with HIV-1 (Mwaengo and Novembre 1998).

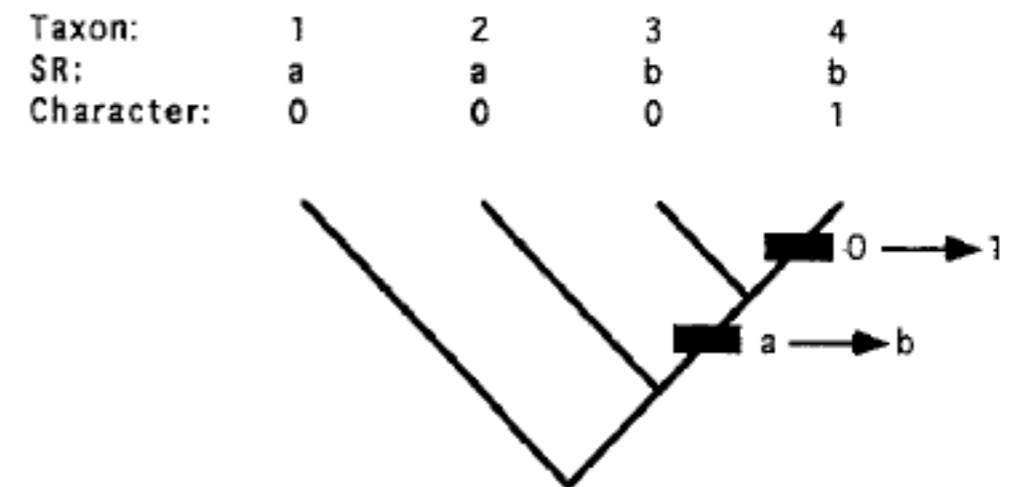
tarea para mañana:

busque en la literatura científica otro posible ejemplo de adaptación de patógenos o parásitos a presiones de selección asociadas con infectar seres humanos y analícelo a la luz de lo que veremos en lo que queda de la clase.

prueba filogenética de hipótesis de adaptación

Adaptación

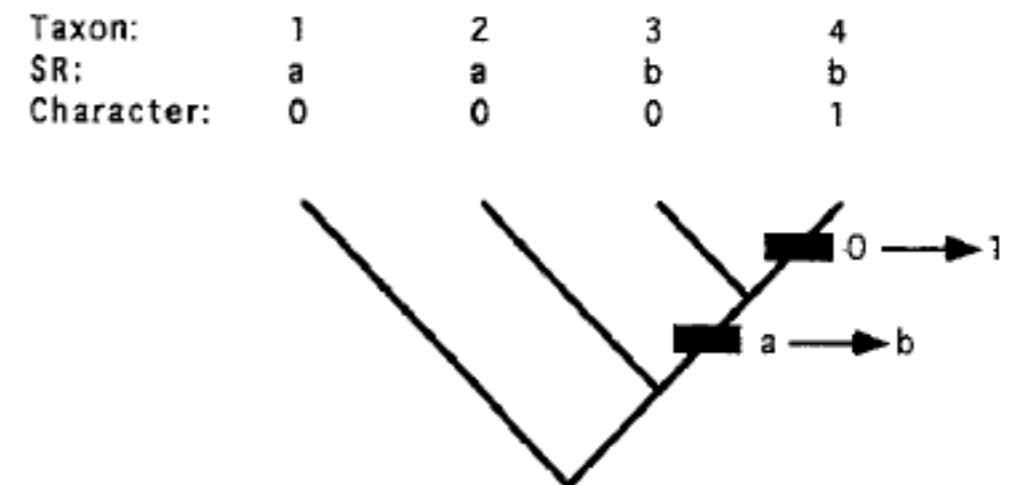
Rasgo de un organismo que ha sido originado mediante selección natural para una función biológica particular



prueba filogenética de hipótesis de adaptación

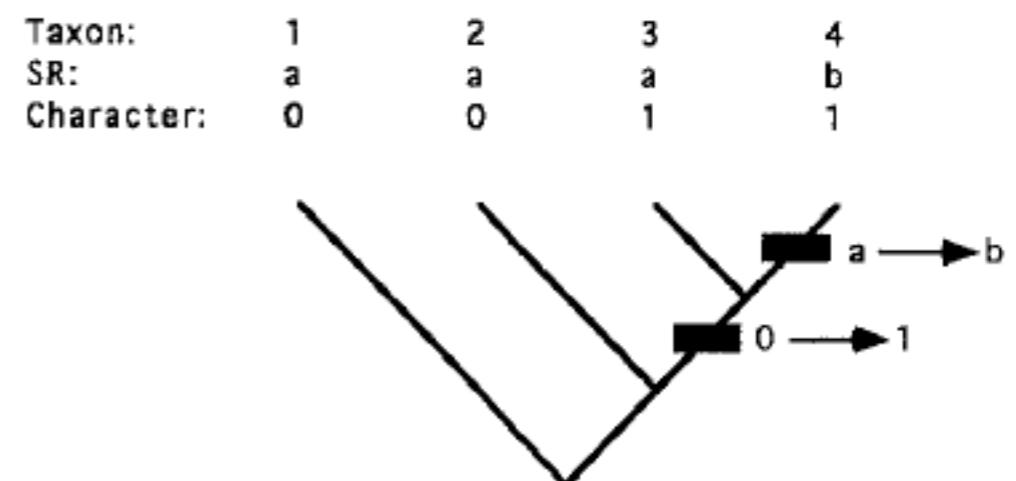
Adaptación

Rasgo de un organismo que ha sido originado mediante selección natural para una función biológica particular



Exaptación

Rasgo de un organismo que ha sido cooptado para una función diferente a su función original



prueba filogenética de hipótesis de adaptación

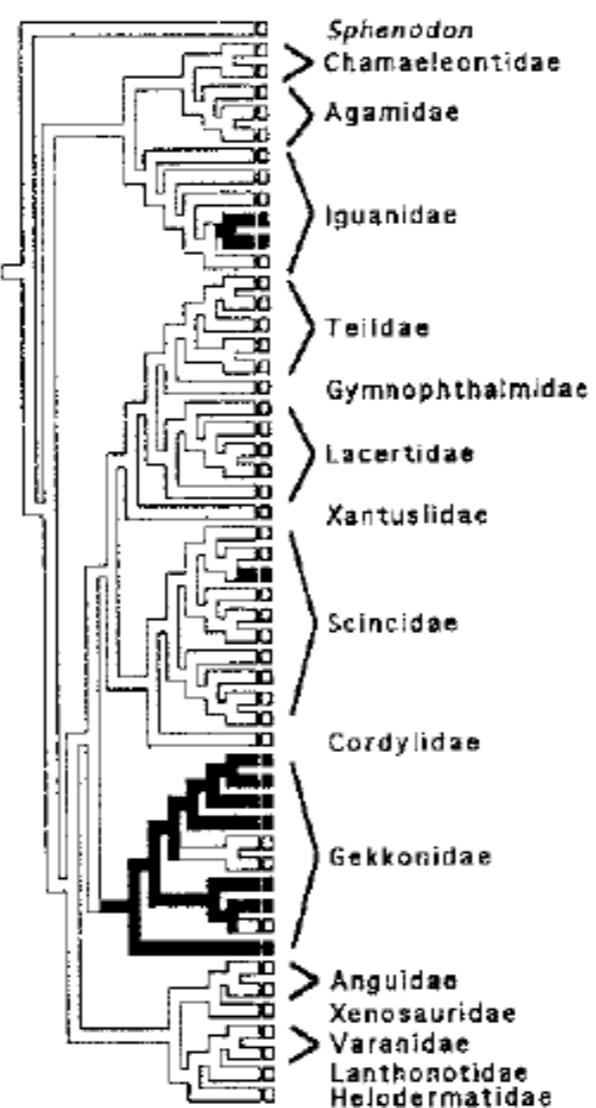
Predicción 1

El origen del rasgo está asociado con el origen del régimen selectivo al que supuestamente está adaptado, y su evolución es posterior al origen de ese régimen selectivo.



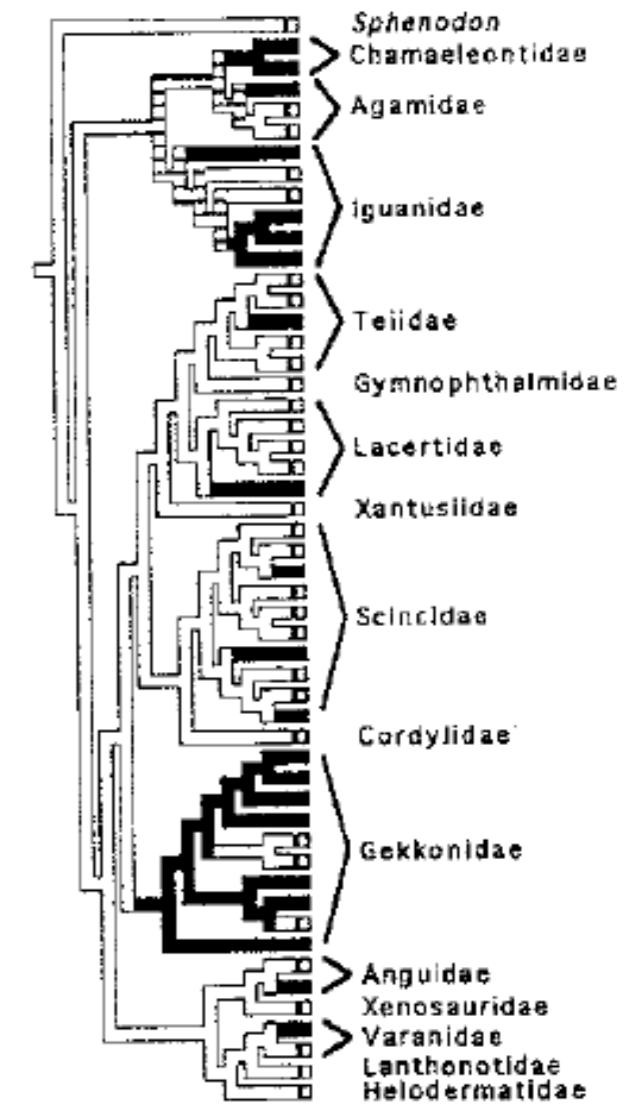
presencia de
ventosas & habilidad de
trepar

a



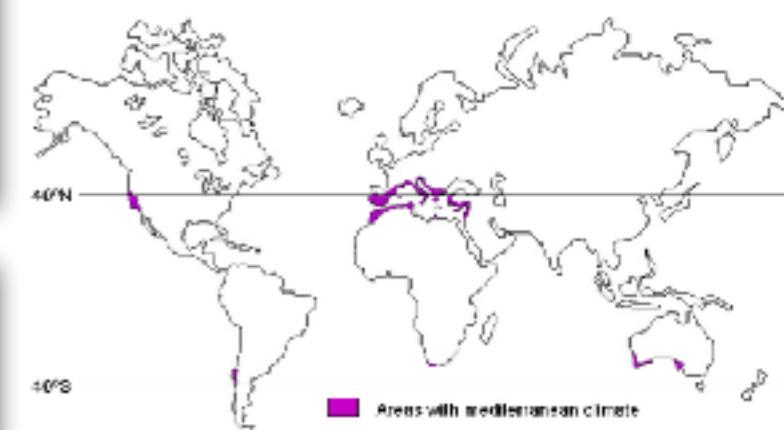
habitos
arbóreos

b

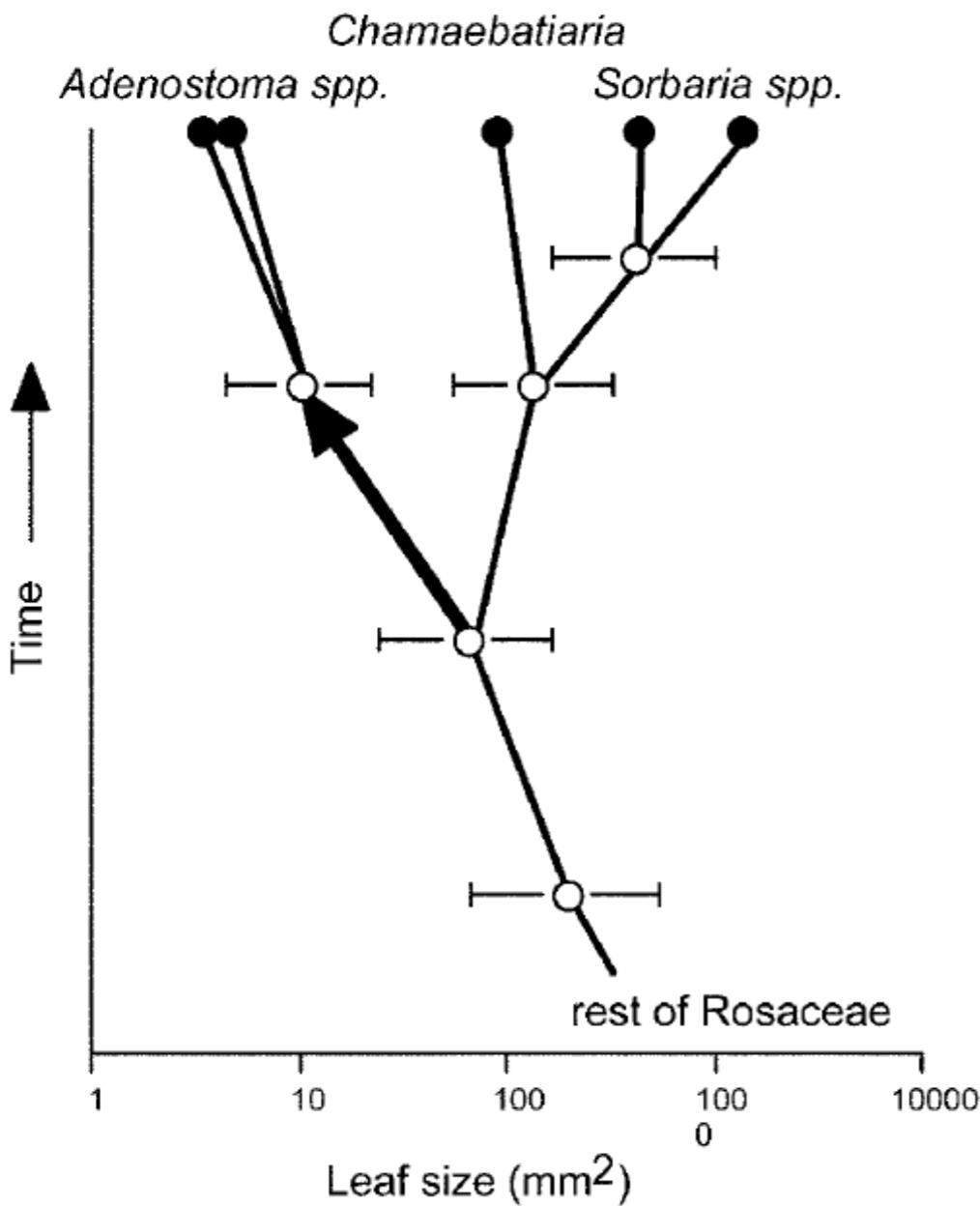


Larson & Losos (1996)

chaparral de California



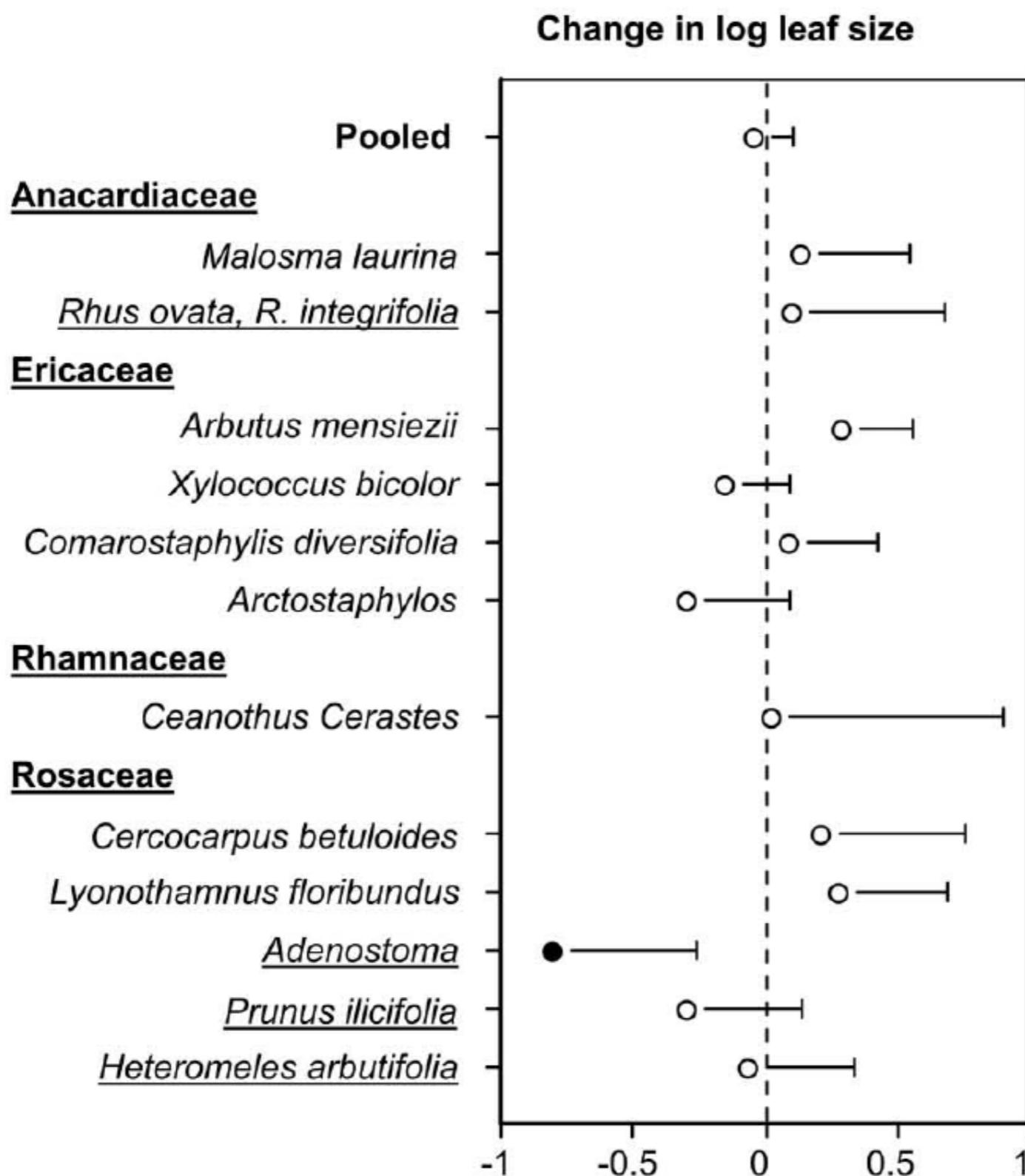
adaptación en chaparral de California



<http://www.botgard.ucla.edu>

Adaptation, Niche Conservatism, and Convergence:
Comparative Studies of Leaf Evolution in the
California Chaparral

(no) adaptación en chaparral de California



The function of zebra stripes

Tim Caro^{1,2}, Amanda Izzo¹, Robert C. Reiner Jr^{3,4}, Hannah Walker¹ & Theodore Stankowich⁵

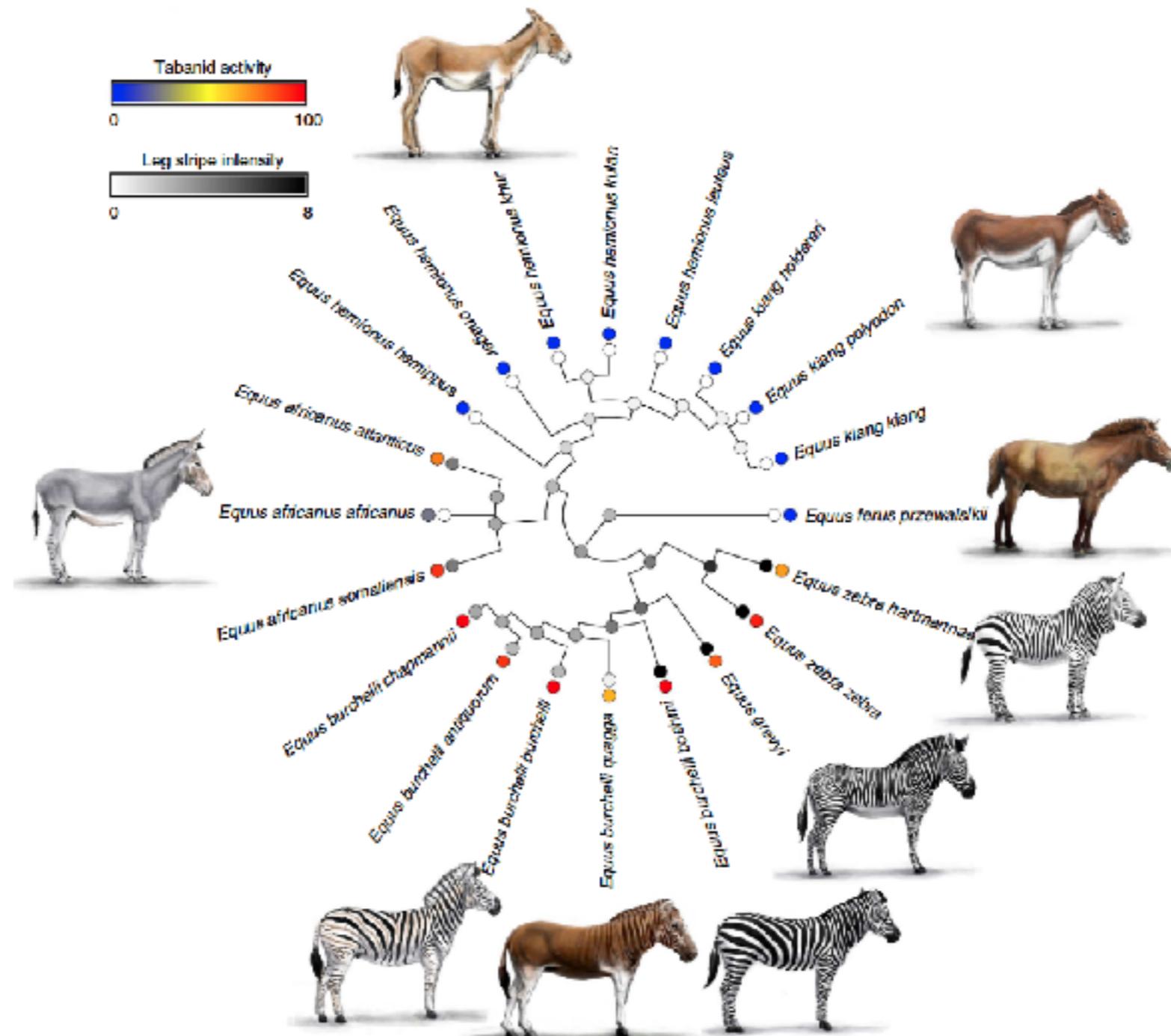
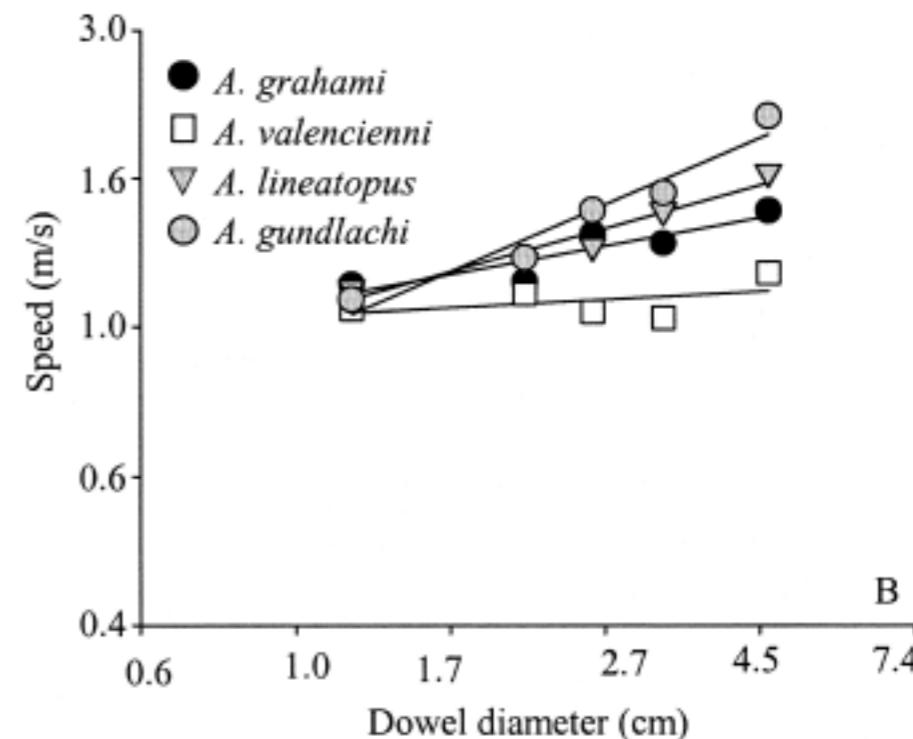
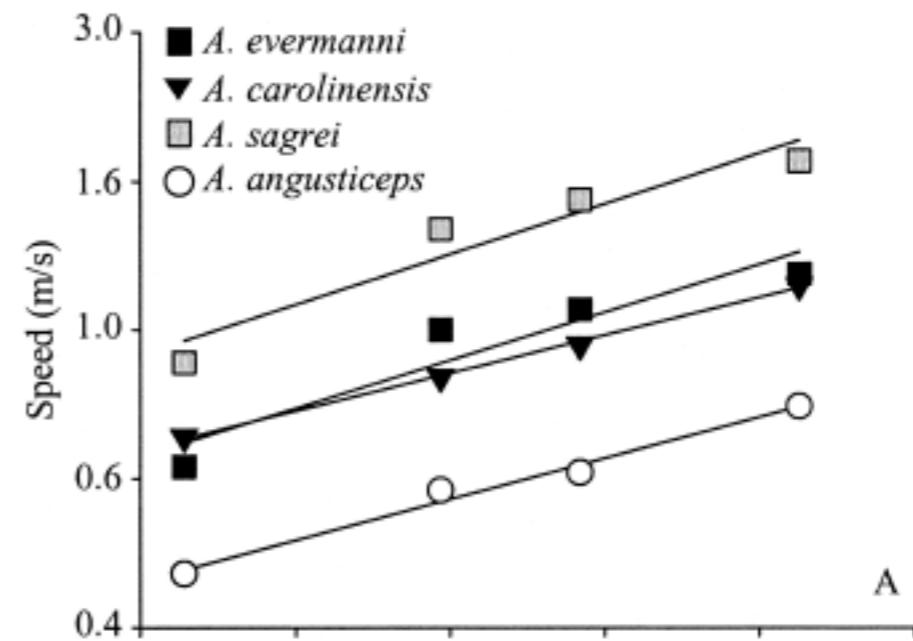


Figure 1 | Stripping and tabanid activity. Phylogenetic tree of equid subspecies showing leg stripe intensity (inside circles) and proportion of geographic range overlap with 7 consecutive months of temperature lying between 15 and 30 °C and humidity between 30 and 85% (outside circles). Drawings by Rickesh Patel.

prueba filogenética de hipótesis de adaptación

Predicción 2

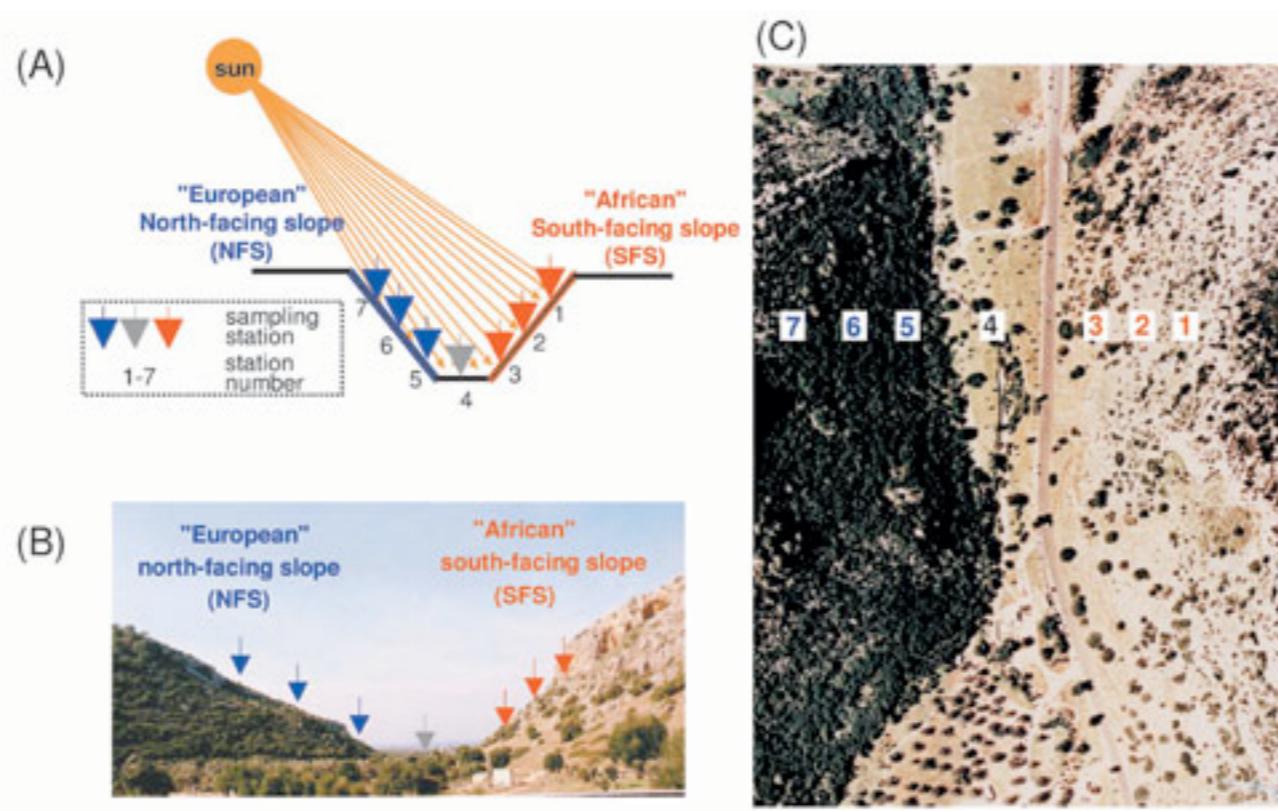
Los organismos que poseen el rasgo que supuestamente es una adaptación deben ser funcionalmente más aptos en su ambiente particular que los organismos que no poseen el rasgo y mantienen la condición ancestral.



Irschick (2002)

“¿funcionalmente más apto?”

"Evolution Canyon", Israel



crecimiento como proxy de aptitud funcional

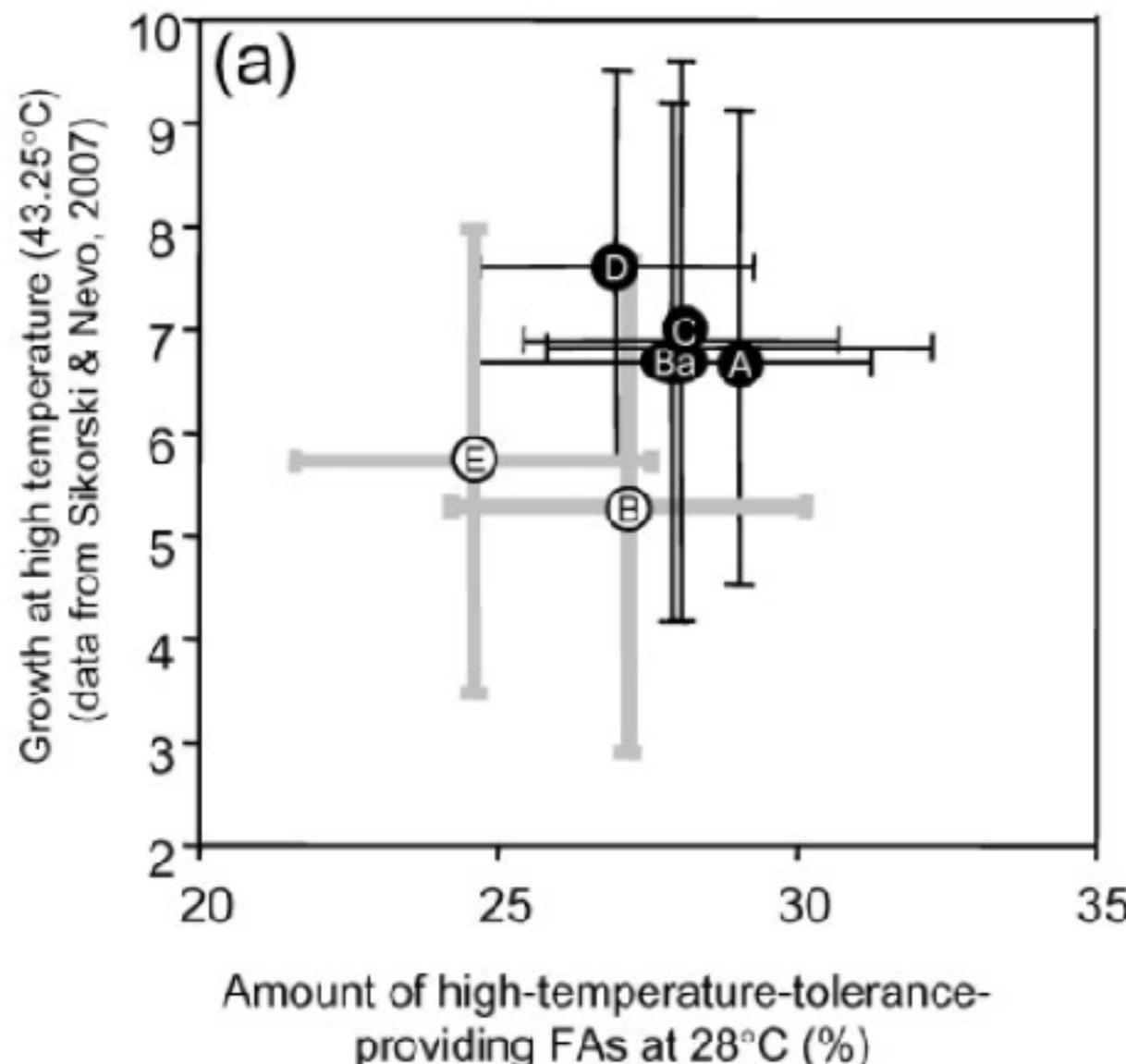


Fig. 6. Correlation plot of growth at high temperature (43.25 °C) and amount of heat-adaptive FAs at 28 °C of all 131 isolates. The growth values represent the integral of the growth curve between 60 and 540 min in rich liquid medium. Basically, the higher the growth value, the better is the growth; see Sikorski & Nevo (2007) for details. (a) Means and standard deviations of the strains of the evolutionary lineages as given in Fig. 1(e). (b) The letters indicate the evolutionary lineage as depicted in Fig. 1(e). 'African' strains are given in black (lineages A, Ba, C, D); 'European' strains are given in grey (lineages B and E). Lineages A, B, Ba, C, and lineages D, E represent the main genomic lineages GL1 and GL2, respectively (see Fig. 1).



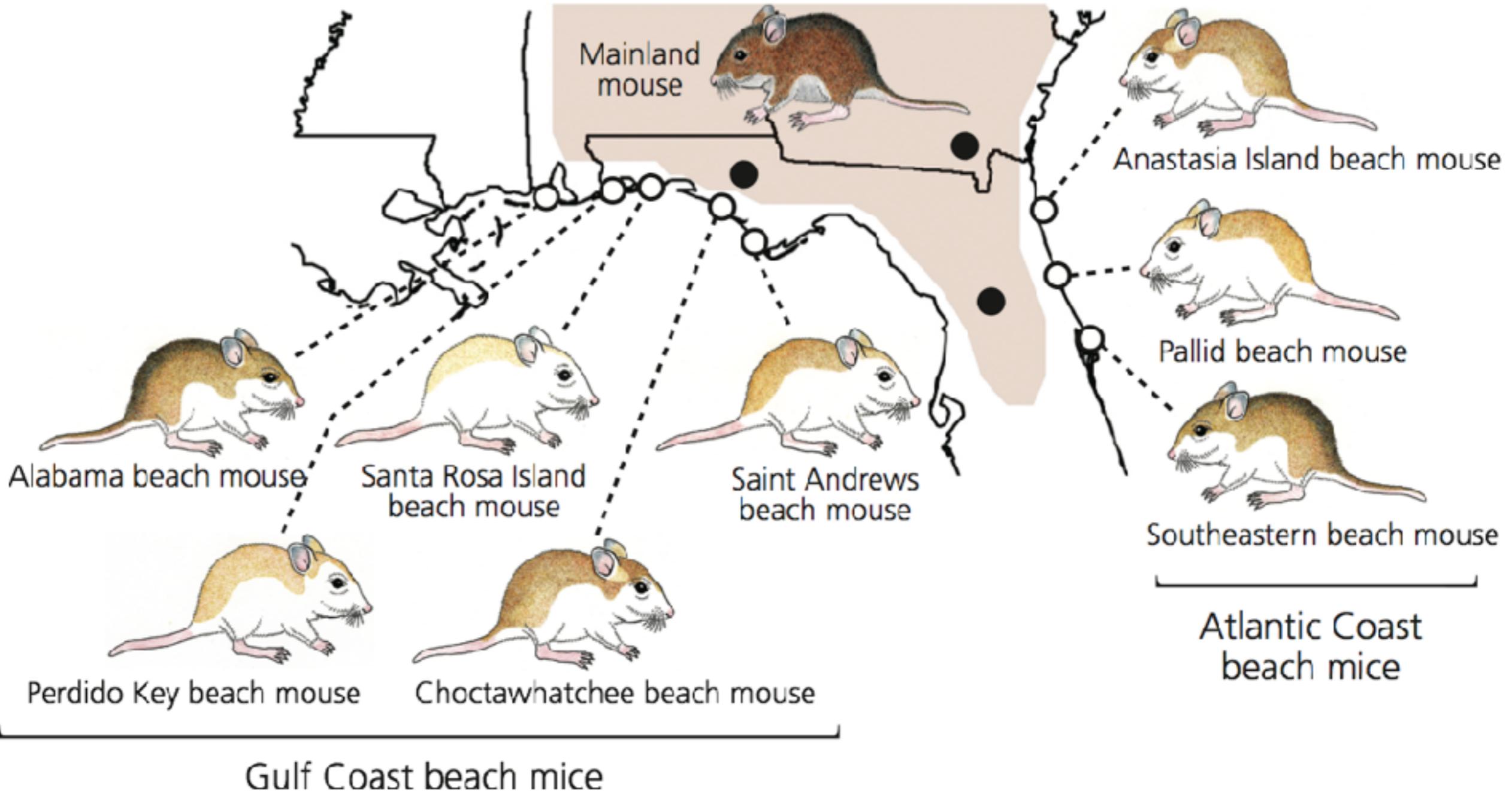
Microbiology (2008), 154, 2416–2426

The temperature-adaptive fatty acid content in *Bacillus simplex* strains from 'Evolution Canyon', Israel

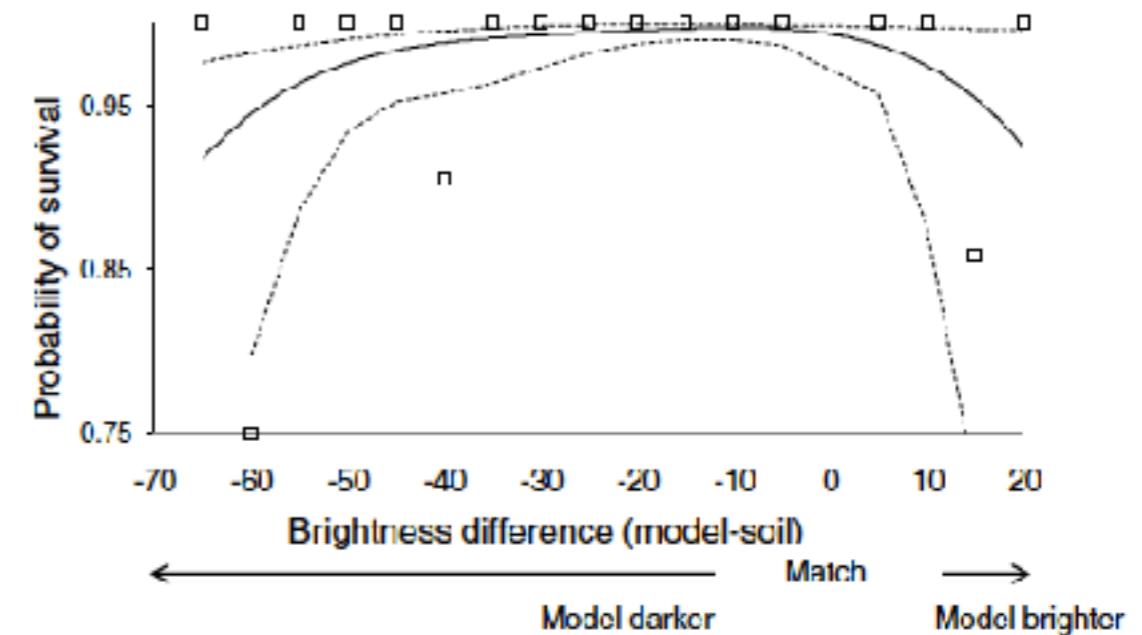
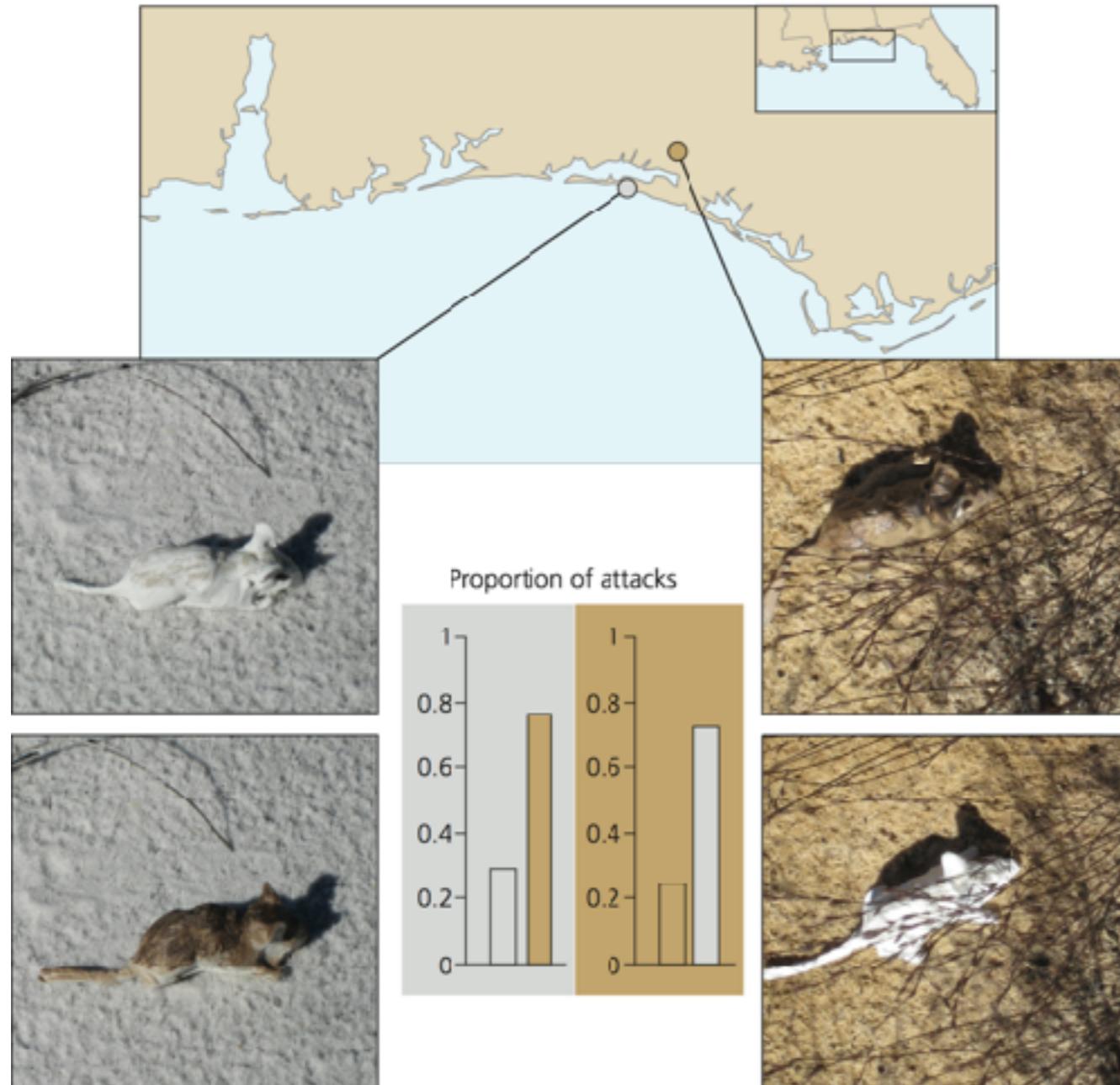
Johannes Sikorski,^{1,2} Evelyne Brambilla,¹ Reiner M. Kroppenstedt¹ and Brian J. Tindall¹



H. Hoekstra
Harvard University



fitness y adaptación



THE SELECTIVE ADVANTAGE OF CRYPTISIS IN MICE

Sacha N. Vignieri,^{1,2} Joanna G. Larson,¹ and Hopi E. Hoekstra¹

tarea 2: lean este blog (es corto!)

<https://www.theatlantic.com/science/archive/2019/01/unprecedentedly-thorough-evolution-experiment/581521/>



Linking a mutation to survival in wild mice

Rowan D. H. Barrett^{1,††}, Stefan Laurent^{2,††}, Ricardo Mallarino^{3,4,†§}, Susanne P. Pfeifer⁵, Charles C. Y. Xu¹, Matthieu Full⁶, Kazumasa Wakamatsu⁷, Jonathan S. Duke-Cohan⁸, Jeffrey D. Jensen⁵, Hopi E. Hockstra^{3,*¶}

Adaptive evolution in new or changing environments can be difficult to predict because the functional connections between genotype, phenotype, and fitness are complex. Here, we make these explicit connections by combining field and laboratory experiments in wild mice. We first directly estimate natural selection on pigmentation traits and an underlying pigment locus, *Agouti*, by using experimental enclosures of mice on different soil colors. Next, we show how a mutation in *Agouti* associated with survival causes lighter coat color through changes in its protein binding properties. Together, our findings demonstrate how a sequence variant alters phenotype and then reveal the ensuing ecological consequences that drive changes in population allele frequency, thereby illuminating the process of evolution by natural selection.

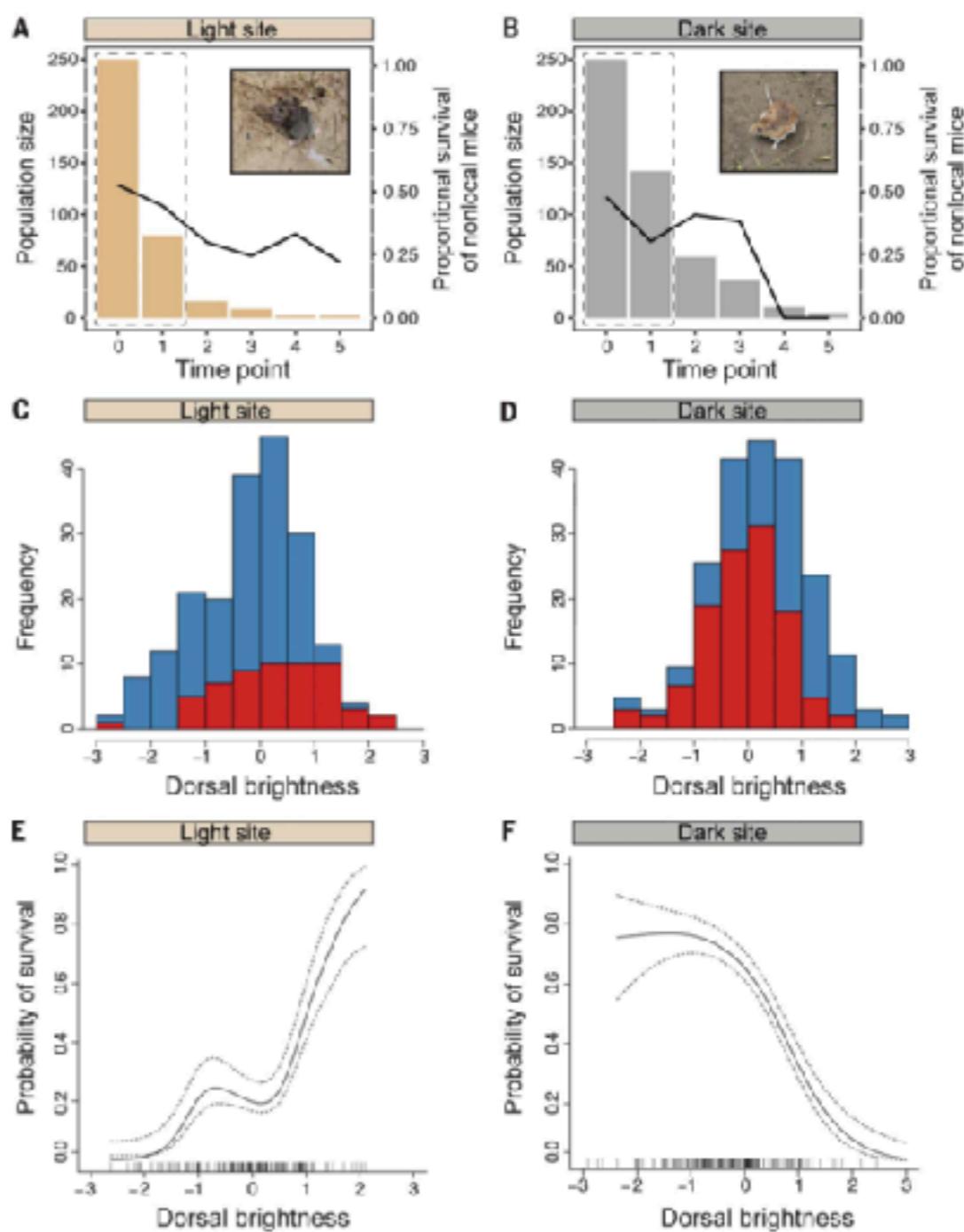
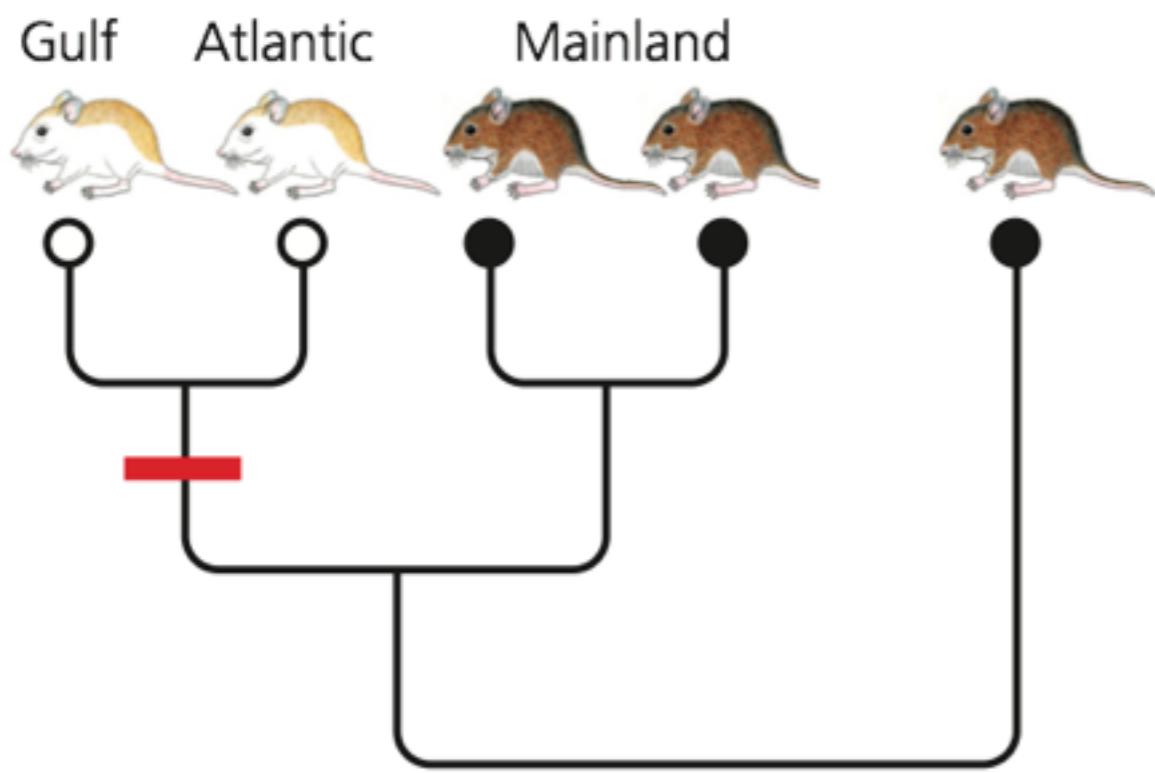
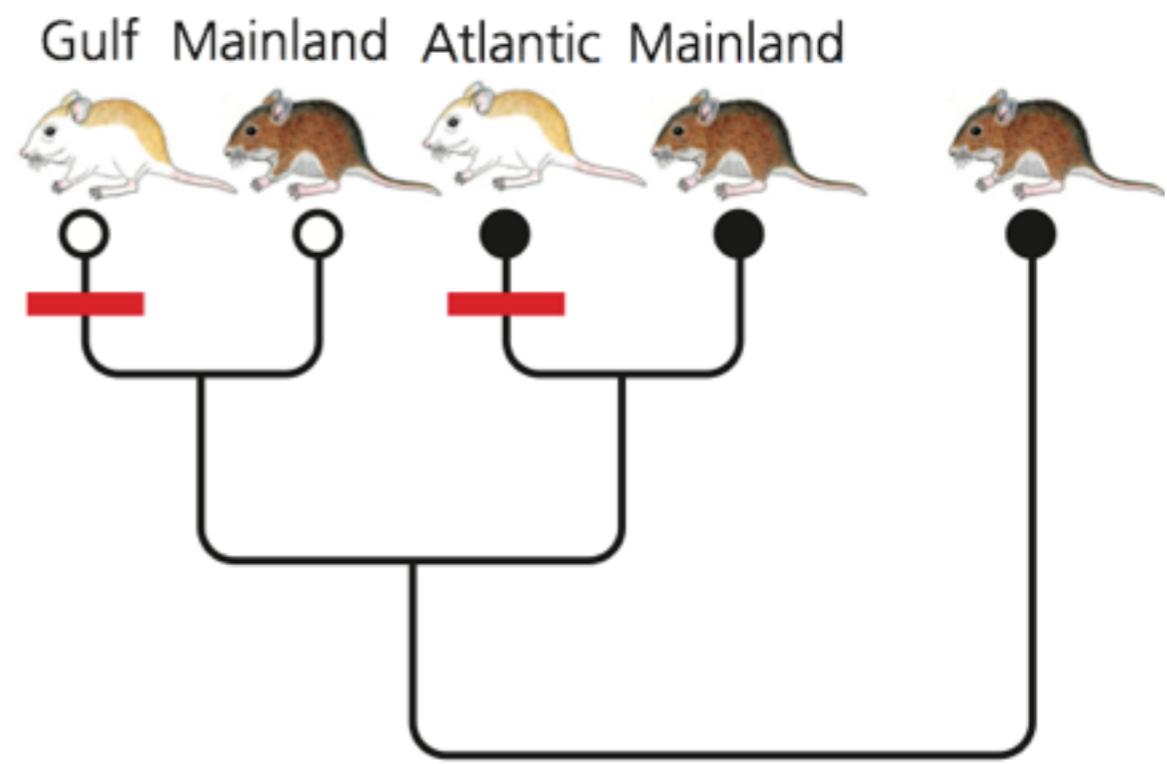


Fig. 2. Mortality and phenotypic change in the experimental populations. (A and B) Mortality in pooled enclosures at light (A) and dark (B) sites over five sequential episodes of selection (J8). Bars represent the number of surviving individuals (independent of coat color) at each time point. Black lines represent the proportion of surviving individuals that were originally caught on the opposite habitat type of the enclosure type they were placed in (mice from dark habitat in light enclosures and mice from light habitat in dark enclosures). Conspicuously colored mice are shown on typical substrate at each experimental site. Dashed boxes denote the time period used in selection analyses. (C and D) Distributions of dorsal brightness at time point 0 (blue) and time point 1 (red) at the light (C) and dark (D) sites. (E and F) Visualizations of selection on dorsal brightness at the light (E) and dark (F) sites between time point 0 and 1. Cubic spline plots are generated from predicted values. The solid lines represent the fitted spline, and the dotted lines represent ± 1 Bayesian SE.



Single origin of light color

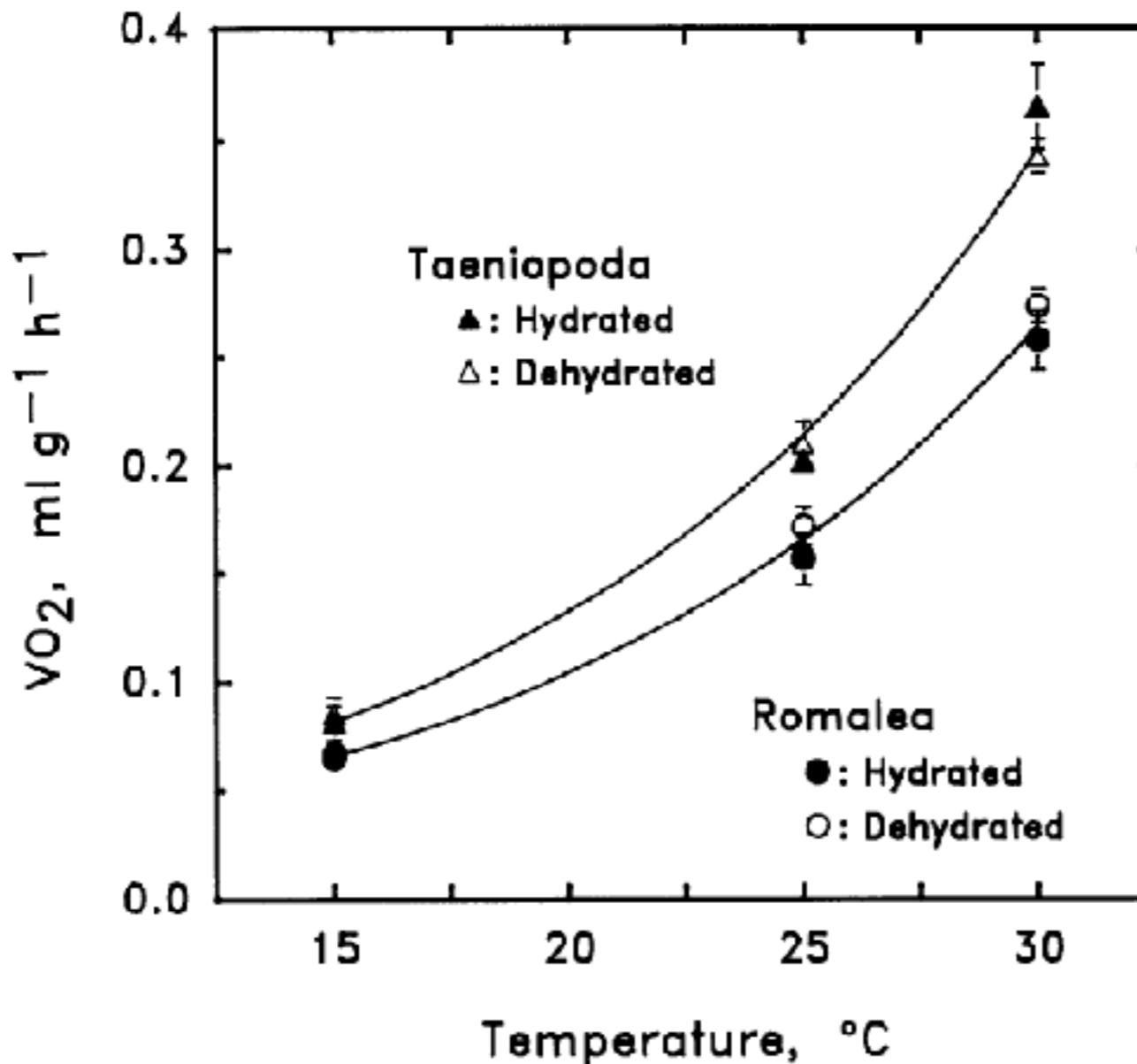
REJECTED



Multiple origins of light color

ACCEPTED

correlación fenotipo-ambiente a nivel de especies demuestra adaptación



Gas Exchange, Ventilatory Patterns, and Water Loss in Two Lubber Grasshoppers: Quantifying Cuticular and Respiratory Transpiration

Michael C. Quinlan*

Neil F. Hadley

correlación fenotipo-ambiente a nivel de especies no necesariamente demuestra adaptación

Invited Perspectives in Physiological Zoology

Why Not to Do Two-Species Comparative Studies: Limitations on Inferring Adaptation

Theodore Garland, Jr.¹

Stephen C. Adolph²

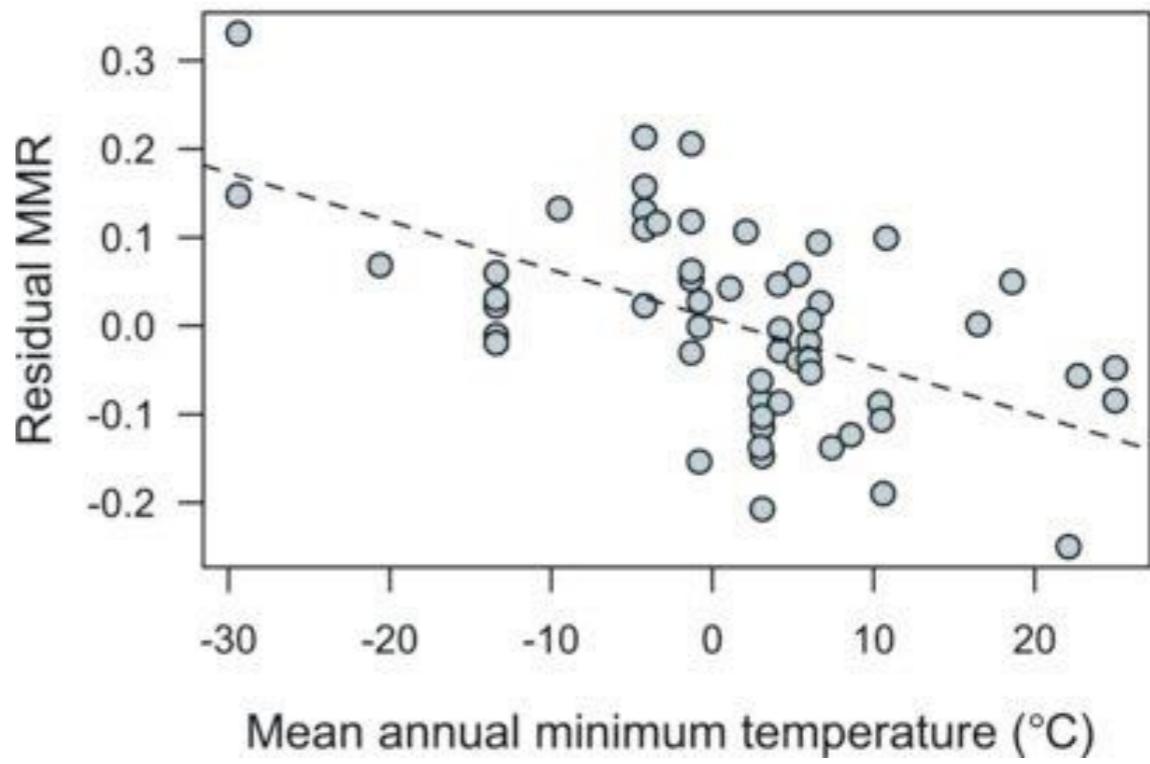
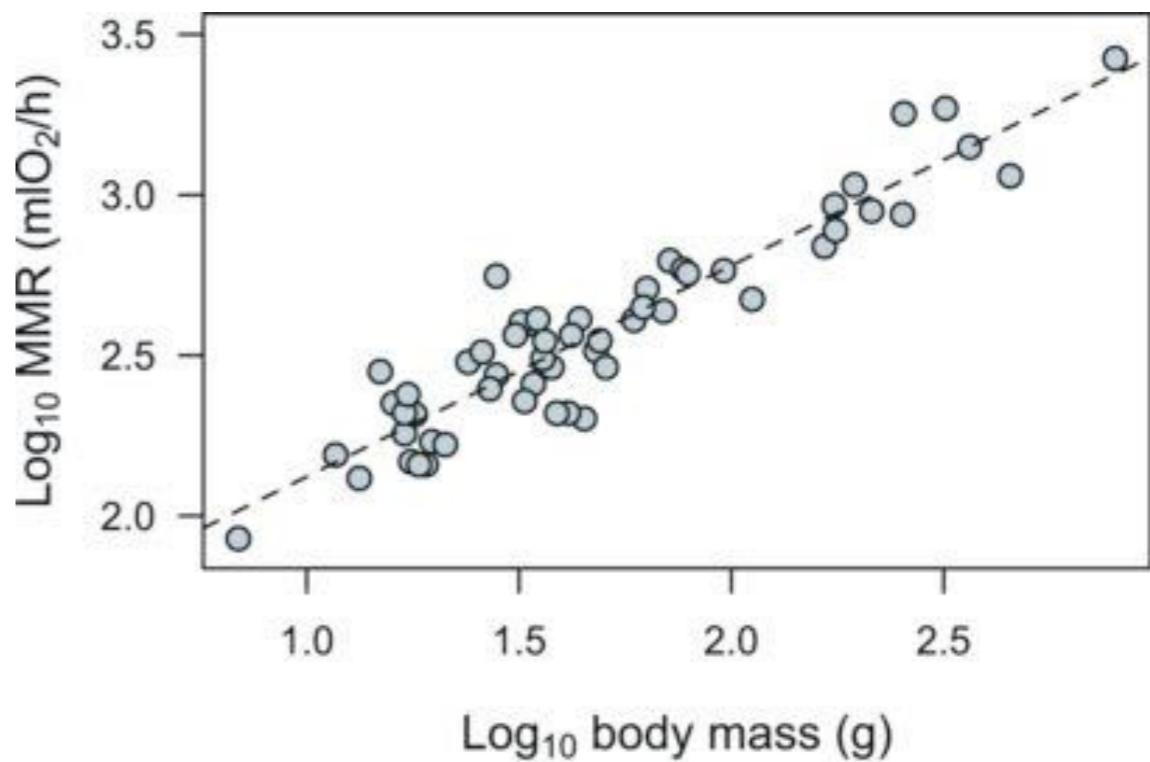
¹Department of Zoology, 430 Lincoln Drive, University of Wisconsin, Madison, Wisconsin 53706; ²Department of Biology, Harvey Mudd College, 301 E. Twelfth Street, Claremont, California 91711

Accepted 3/9/94

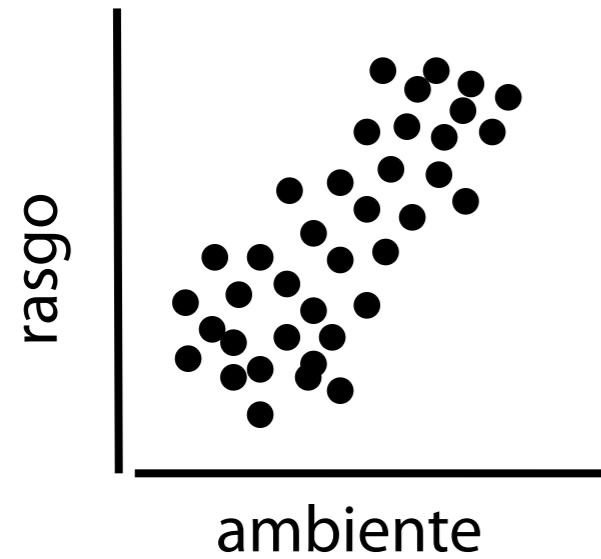
One thing cannot be evaluated unless it can be compared with another. This is, of course, why degrees of freedom in statistics are the number of observations minus one. [BRADSHAW 1987a, p. 71]

Adaptation can only be measured and indeed discussed on a comparative basis. . . . Adaptation is entirely a comparative concept. [BRADSHAW 1987a, p. 71]

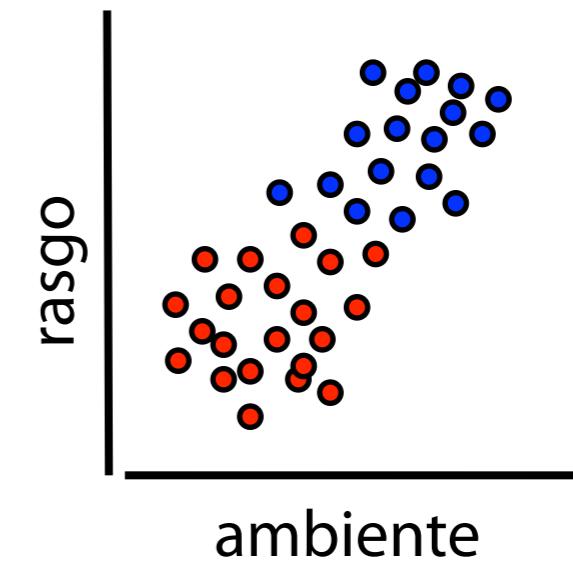
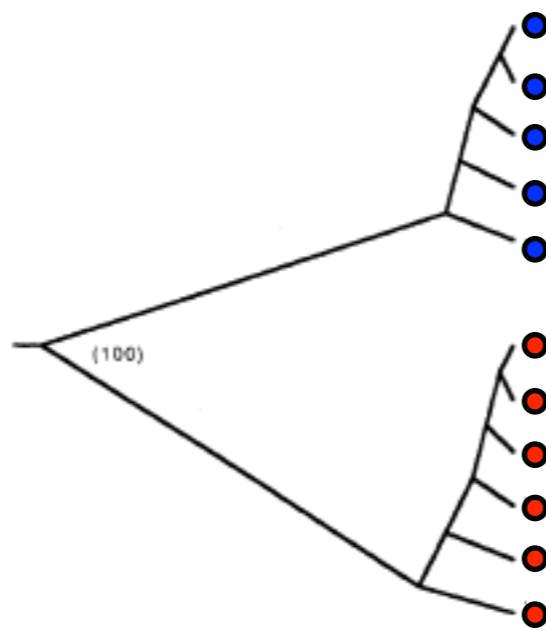
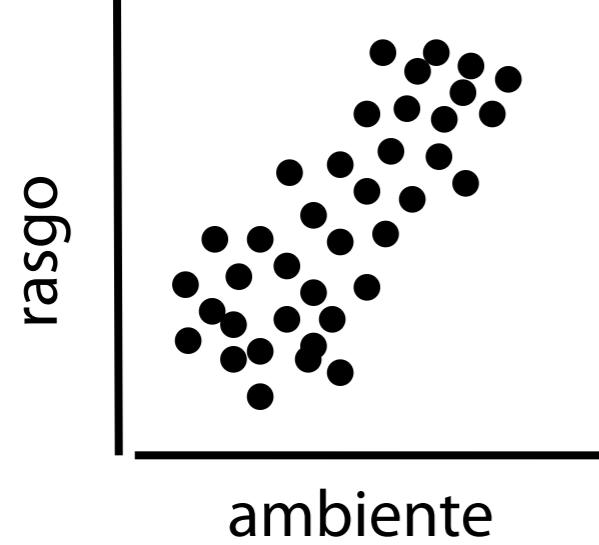
la importancia de tener especies como réplicas



el problema de usar especies como réplicas



el problema de usar especies como réplicas



¿cómo saber qué tanta confianza puedo tener en mi filogenia?

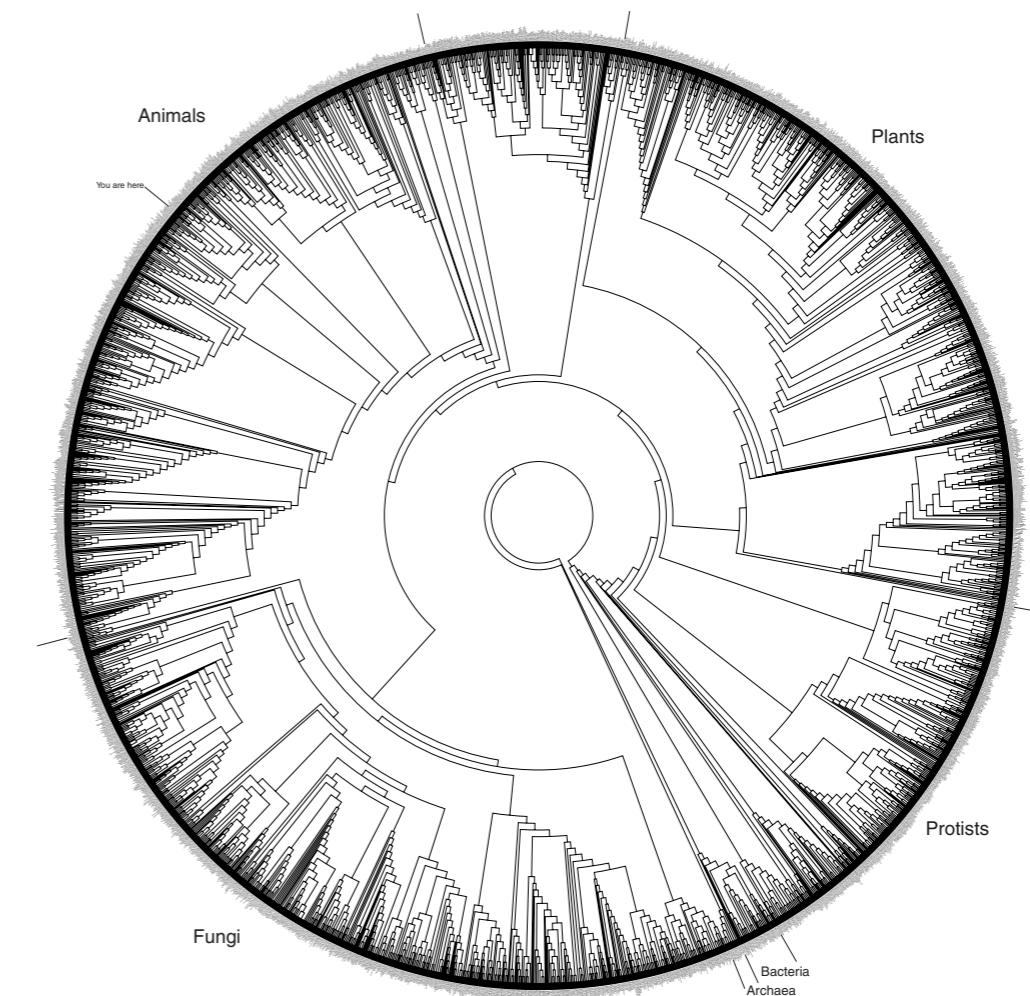
Evolution, 39(4), 1985, pp. 783-791

CONFIDENCE LIMITS ON PHYLOGENIES: AN APPROACH USING THE BOOTSTRAP

JOSEPH FELSENSTEIN

Department of Genetics SK-50, University of Washington, Seattle, WA 98195

Abstract.—The recently-developed statistical method known as the “bootstrap” can be used to place confidence intervals on phylogenies. It involves resampling points from one’s own data, with replacement, to create a series of bootstrap samples of the same size as the original data. Each of these is analyzed, and the variation among the resulting estimates taken to indicate the size of the error involved in making estimates from the original data. In the case of phylogenies, it is argued that the proper method of resampling is to keep all of the original species while sampling characters with replacement, under the assumption that the characters have been independently drawn by the systematist and have evolved independently. Majority-rule consensus trees can be used to construct a phylogeny showing all of the inferred monophyletic groups that occurred in a majority of the bootstrap samples. If a group shows up 95% of the time or more, the evidence for it is taken to be statistically significant. Existing computer programs can be used to analyze different bootstrap samples by using weights on the characters, the weight of a character being how many times it was drawn in bootstrap sampling. When all characters are perfectly compatible, as envisioned by Hennig, bootstrap sampling becomes unnecessary; the bootstrap method would show significant evidence for a group if it is defined by three or more characters.



[Confidence limits on phylogenies: an approach using the bootstrap](#)

J Felsenstein - *Evolution*, 1985 - JSTOR

The recently-developed statistical method known as the “**bootstrap**” can be used to place confidence intervals on phylogenies. It involves resampling points from one’s own data, with replacement, to create a series of **bootstrap** samples of the same size as the original data. ...

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deja vu

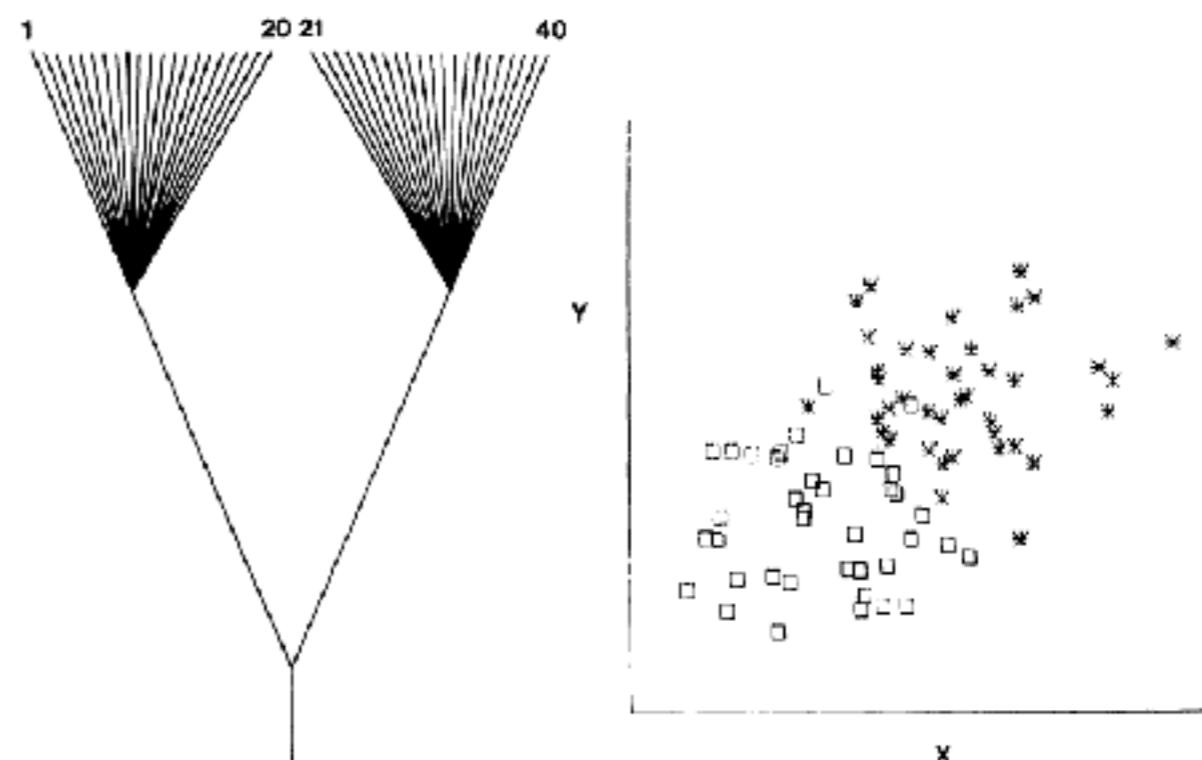
Vol. 125, No. 1

The American Naturalist

January 1985

PHYLOGENIES AND THE COMPARATIVE METHOD

JOSEPH FELSENSTEIN



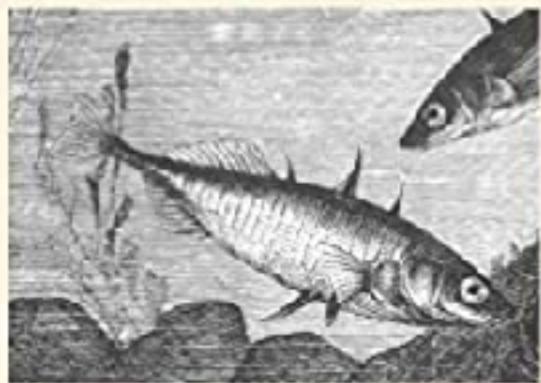
[PDF] [Phylogenies and the comparative method](#)
[J Felsenstein - American Naturalist, 1985 - JSTOR](#)

Comparative studies of the relationship between two phenotypes, or between a phenotype and an environment, are frequently carried out by invalid statistical **methods**. Most regression, correlation, and contingency table **methods**, including nonparametric **methods** ...
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PHYLOGENY, ECOLOGY, AND BEHAVIOR

A Research Program in Comparative Biology



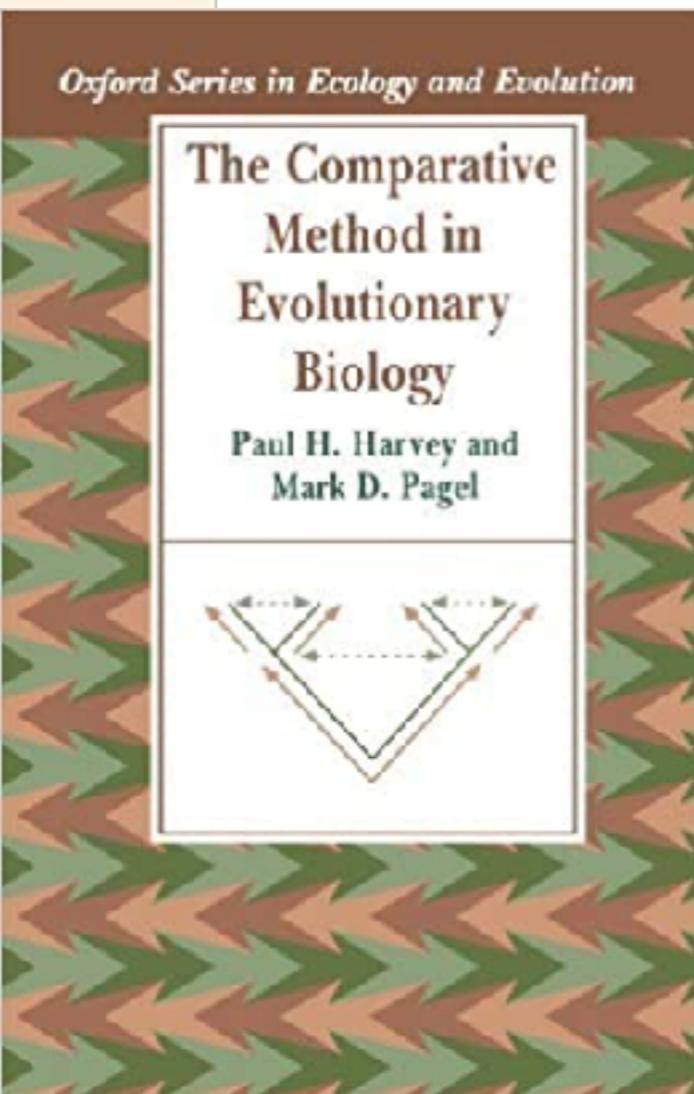
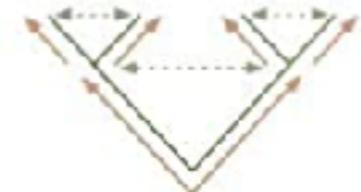
Daniel R. Brooks and
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Mark D. Pagel



Phylogenetic Comparative Methods

Learning from trees

Luke J Harmon



<https://ecoevorxiv.org/e3xnr/>

¿cómo reconstruir la historia si sólo tenemos datos del presente?



parsimony!

Reconstructing ancestral character states: a critical reappraisal

Clifford W. Cunningham

Kevin E. Omland

Todd H. Oakley

Box 1. Reconstructing ancestral states using parsimony

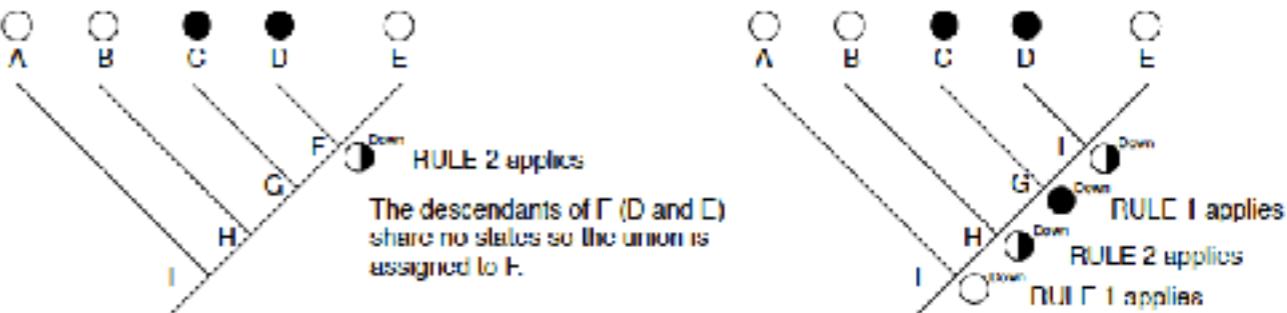
Ancestral states are often reconstructed using the parsimony criterion. The algorithm illustrated below identifies all unambiguous reconstructions for equally weighted, unordered characters⁴, and is implemented in commonly used computer packages such as MacClade 3.0 (Ref. 2).

The algorithm uses a 'downpass' and 'uppass' traversal (see Figures) to optimize ancestral states using two rules:

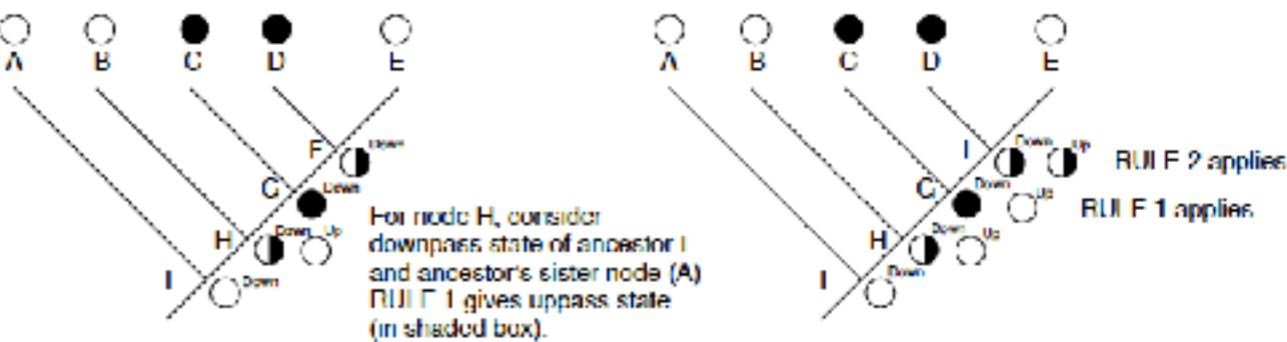
RULE 1: if descendant nodes share any states in common, assign the set of shared states to the ancestor.

RULE 2: if no states are shared in descendant nodes, assign the union of descendant's states to ancestor.

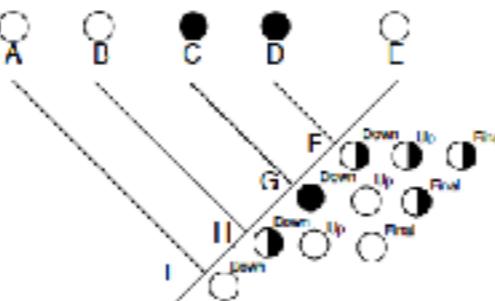
(1) Downpass optimization: proceed 'down' the tree towards the root, optimizing each ancestral node.



(2) Uppass optimization: proceed 'up' the tree away from the root, optimizing each ancestral node.



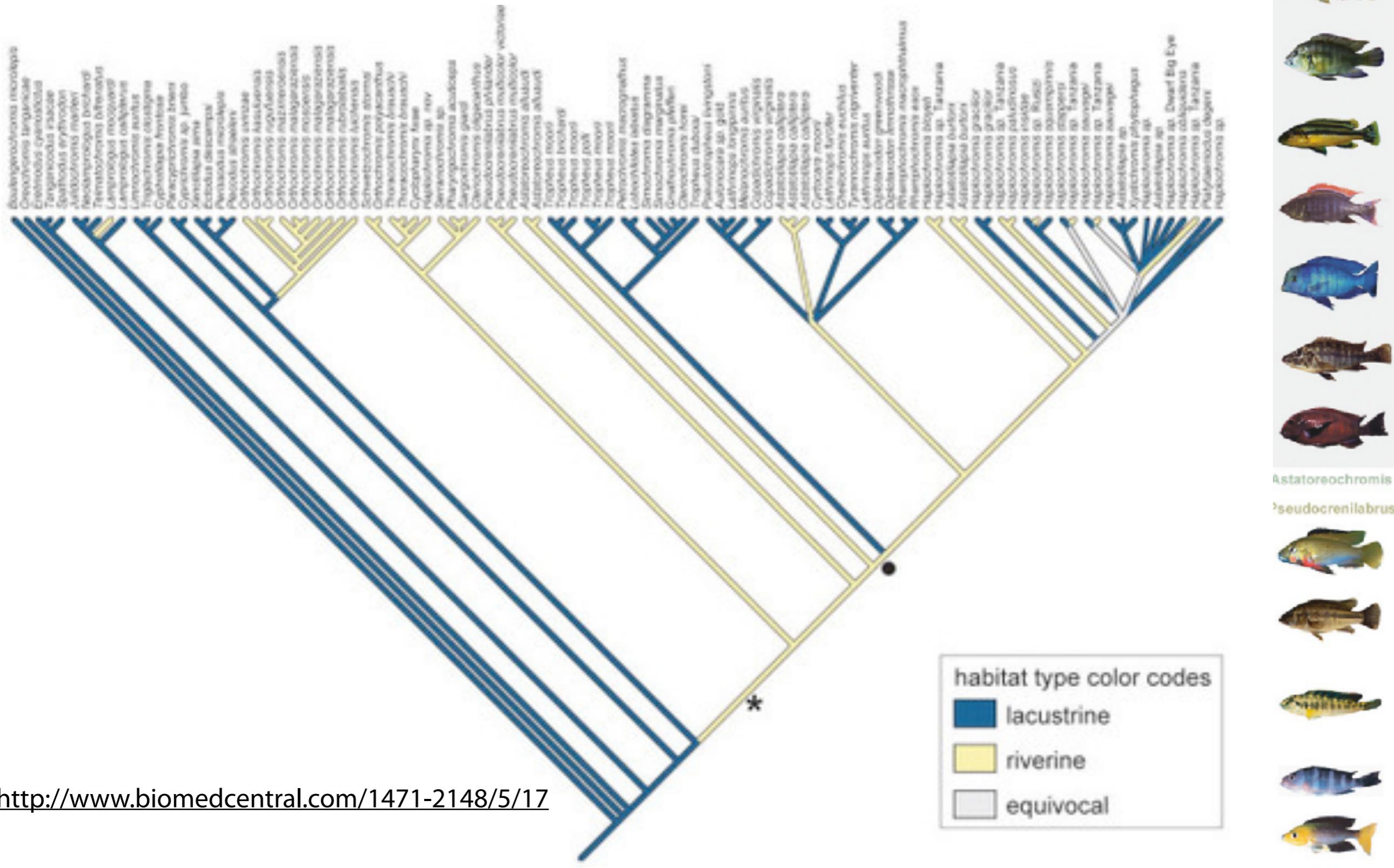
(3) Final optimization



Legend

- ○ Unambiguous reconstruction
- ● Ambiguous reconstruction
- ^{Down} Downpass reconstruction
- ^{Up} Uppass reconstruction
- ^{Final} Final reconstruction

For the final state of each node (e.g. node H), consider the uppass set of that node, and the downpass sets of its two descendant nodes (B and G). Choose the state that has the greatest number in all three sets. If none is in a majority, it remains ambiguous.



<http://www.biomedcentral.com/1471-2148/5/17>

parasitismo de cría



<http://forest.mtu.edu/classes/fw3020/images/cowbird.JPG>

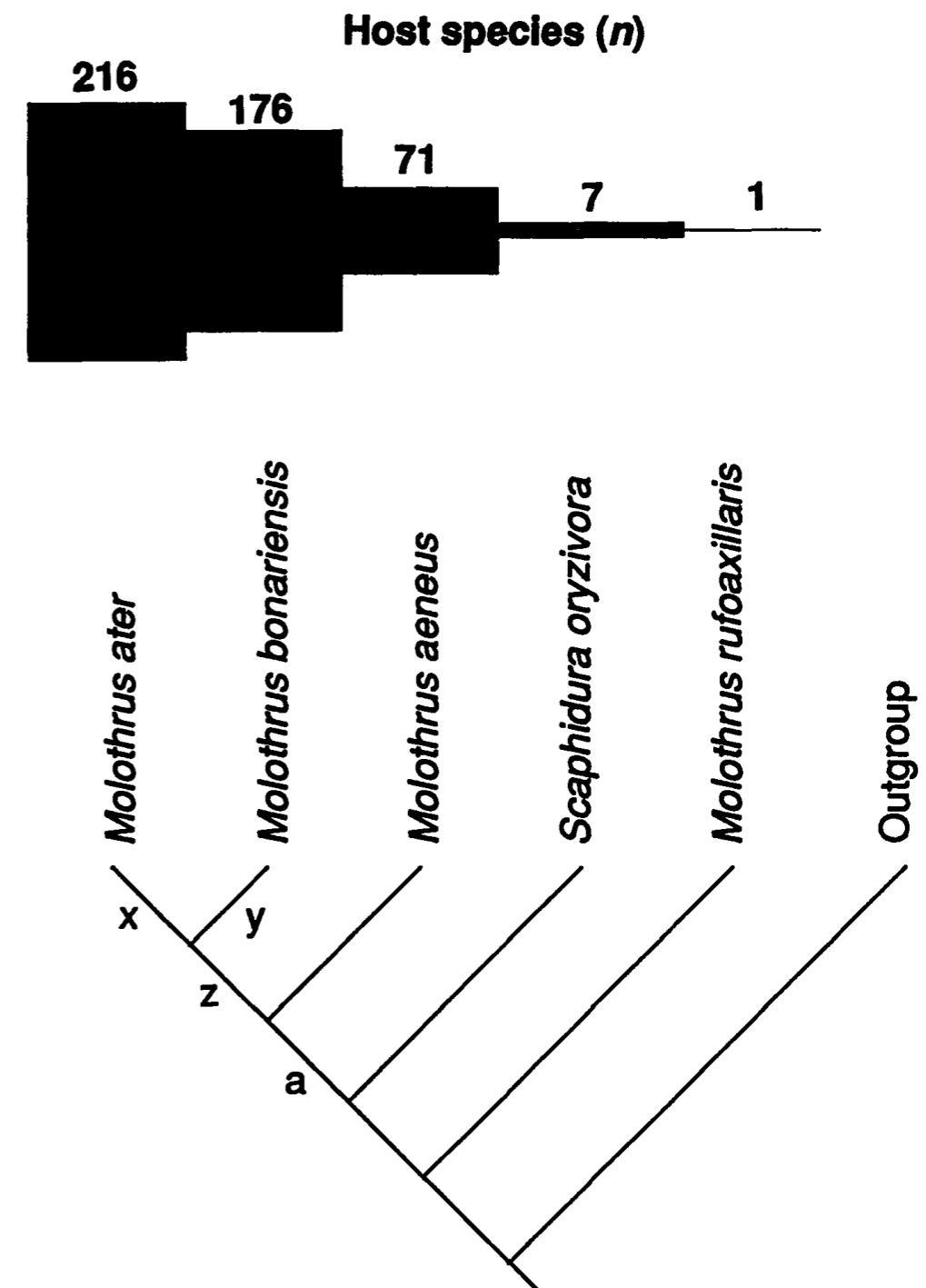


parsimonia y el paso de especialismo a generalismo

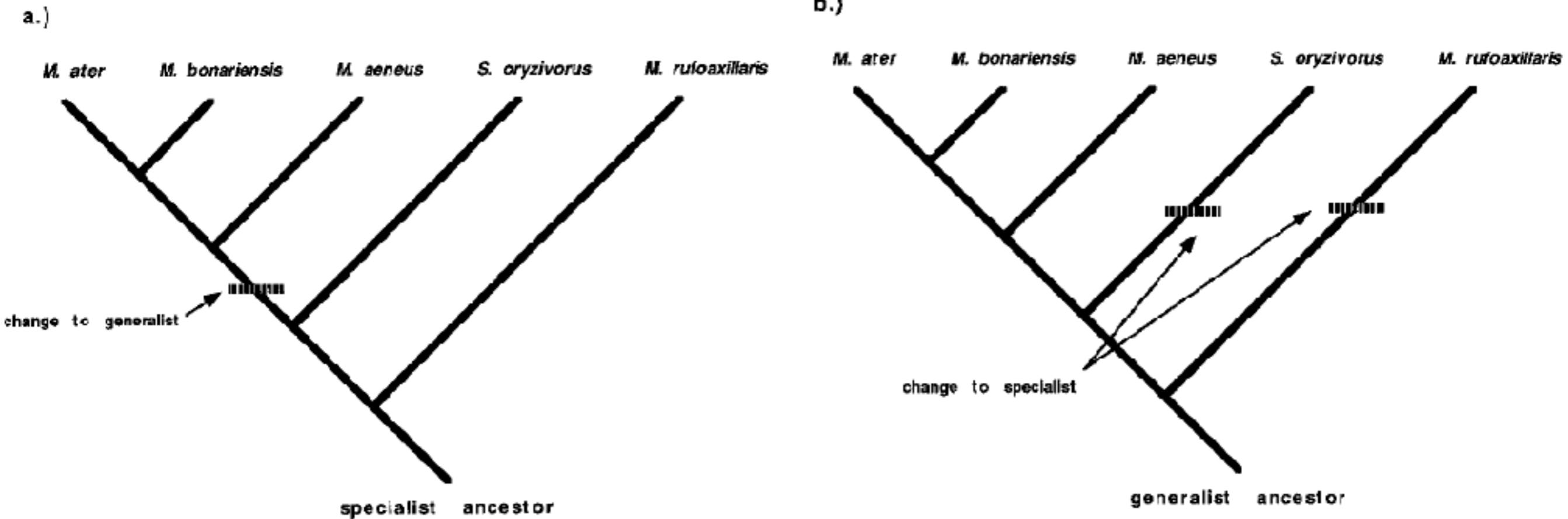


Interspecific Brood Parasitism in Blackbirds (Icterinae): A Phylogenetic Perspective

SCOTT M. LANYON



¿y si la evolución no es estrictamente parsimoniosa? ¿o si los cambios en distintas direcciones no son igualmente probables?



Behavioral Ecology Vol. 13 No. 1: 1–10

Phylogeny, specialization, and brood parasite-host coevolution: some possible pitfalls of parsimony

Stephen I. Rothstein,^a Michael A. Patten,^b and Robert C. Fleischer^c



Reconstructing the evolutionary history of the artiodactyl ribonuclease superfamily

Thomas M. Jermann, Jochen G. Opltz,
Joseph Stackhouse & Steven A. Benner

Department of Chemistry, ETH Zürich, CH-8092 Zürich, Switzerland

THE sequences of proteins from ancient organisms can be reconstructed from the sequences of their descendants by a procedure that assumes that the descendant proteins arose from the extinct ancestor by the smallest number of independent evolutionary events ('parsimony')^{1,2}. The reconstructed sequences can then be prepared in the laboratory and studied^{3,4}. Thirteen ancient ribonucleases (RNases) have been reconstructed as intermediates in the evolution of the RNase protein family in artiodactyls (the mammal order that includes pig, camel, deer, sheep and ox)⁵. The properties of the reconstructed proteins suggest that parsimony yields plausible ancient sequences. Going back in time, a significant change in behaviour, namely a fivefold increase in catalytic activity against double-stranded RNA, appears in the RNase reconstructed for the founding ancestor of the artiodactyl lineage, which lived about 40 million years ago⁶. This corresponds to the period when ruminant digestion arose in the artiodactyls, suggests that contemporary artiodactyl digestive RNases arose from a non-digestive ancestor, and illustrates how evolutionary reconstructions can help in the understanding of physiological function within a protein family⁷⁻⁹.



secuencias ancestrales inferidas por parsimonia

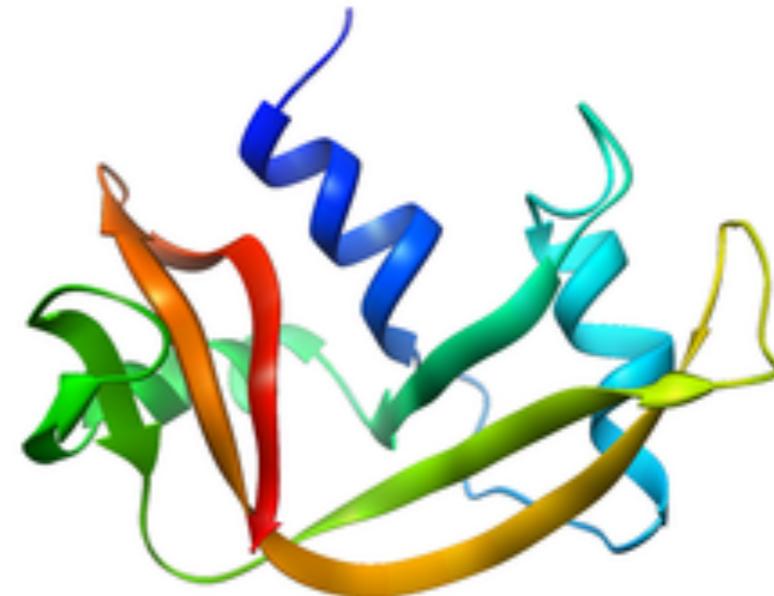
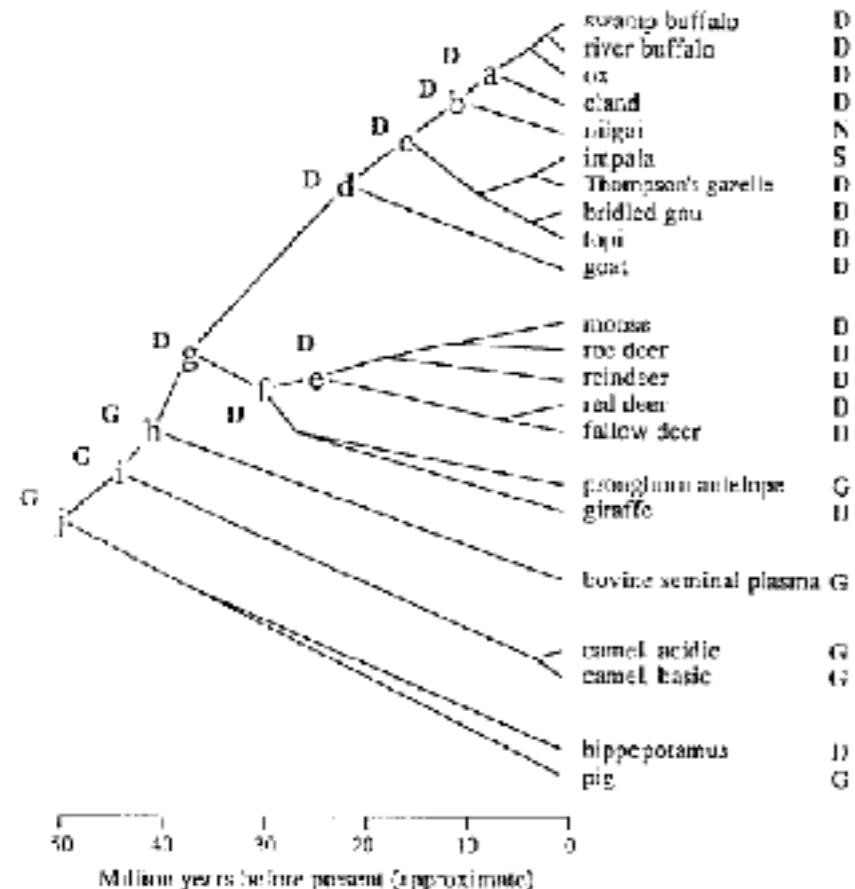


TABLE 1 Sequence changes in reconstructed ancient ribonucleases

	Hovine RNase A	a	b	c	d	e	f	g	h ₁	h ₂	i ₁	i ₂	j ₁	j ₂
3	Thr	Thr	Thr	Ser	Ser	Ser	Ser	Ser	Ser	Ser	Ser*	Thr*	Ser	Ser
6	Ala	Ala	Ala	Ala	Ala	Ala	Ala	Ala	Ala	Ala	Glu	Glu	Lys	Lys
15	Ser	Ser	Ser	Ser	Ser	Pro	Ser	Ser	Ser	Ser	Ser	Ser	Ser	Ser
16	Ser	Ser	Ser	Ser	Ser	Ser	Ser	Ser	Gly*	Gly*	Gly*	Gly*	Gly	Gly
17	Thr	Thr	Thr	Thr	Thr	Thr	Thr	Ser*	Thr*	Ser	Ser	Ser	Ser	Ser
19	Ala	Ser	Ser	Ser	Ser	Ser	Ser	Ser						
20	Ala	Ala	Ala	Ala	Ala	Ala	Ala	Ala	Ser	Ser	Ser	Ser	Ser	Ser
22	Ser	Ser	Ser	Ser	Ser	Ser	Ser	Ser	Ser	Ser	Asn*	Asn*	Asn	Asn
31	Lys	Lys	Lys	Lys	Lys	Gln	Lys	Lys	Lys	Lys	Lys	Lys	Lys*	Lys*
32	Ser	Ser	Ser	Ser	Ser	Ser	Ser	Ser	Ser	Ser	Ser	Arg	Arg	Arg
34	Asn	Asn	Asn	Asn	Asn	Asn	Asn	Asn*	Lys*	Lys*	Lys*	Lys*	Asn	Asn
35	Ieu	Met	Met	Leu	Leu	Leu	Leu	Leu*	Met	Met	Met	Met	Met	Met
37	Lys	Lys	Gln	Gln	Gln	Gln	Gln	Gln	Gln	Gln	Gln	Gln	Gln	Gln
38	Asp	Asp	Asp	Asp	Asp	Asp	Asp	Asp	Gly	Gly	Gly	Gly	Gly	Gly
59	Ser	Ser	Ser	Ser	Ser	Phe	Ser	Ser	Ser	Ser	Ser	Ser	Ser	Ser
64	Ala	Ala	Ala	Ala	Ala	Ala	Ala	Ala	Thr	Thr	Thr	Thr	Thr	Thr
70	Thr	Thr	Thr	Thr	Thr	Ser	Thr	Thr	Thr	Thr	Thr	Thr	Thr	Thr
76	Tyr	Tyr	Tyr	Tyr	Tyr	Asn	Tyr	Asn	Asn	Asn	Asn	Asn	Asn	Asn
78	Thr	Thr	Thr	Thr	Thr	Ala	Thr	Thr	Thr	Thr	Thr	Thr	Thr	Thr
80	Ser	Ser	Ser	Ser	Ser	His	Ser	Arg*	Arg*	Arg*	Arg*	His	His	His
96	Ala	Ala	Ala	Ala	Ala	Val	Ala	Ala	Ala	Ala	Ala	Ala	Ala	Ala
100	Thr	Thr	Thr	Thr	Thr	Thr	Thr	Thr	Thr	Thr	Ser	Ser	Ser	Ser
102	Ala	Ala	Ala	Ala	Ala	Ala	Ala	Ala	Val	Val	Val*	Val*	Val*	Glut*
103	Asn	Lys	Lys	Lys	Glu	Glu	Glu	Glu	Glu	Glu	Gln	Gln	Gln	Gln

secuencias ancestrales inferidas por parsimonia

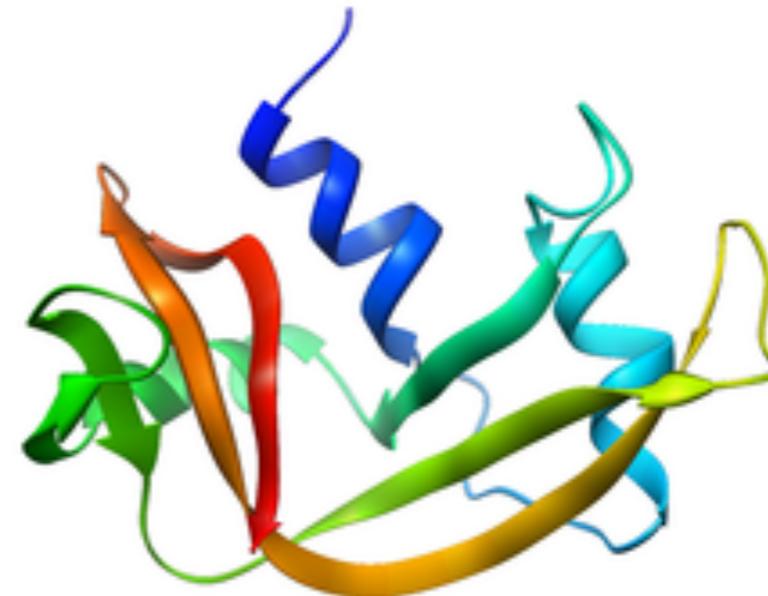
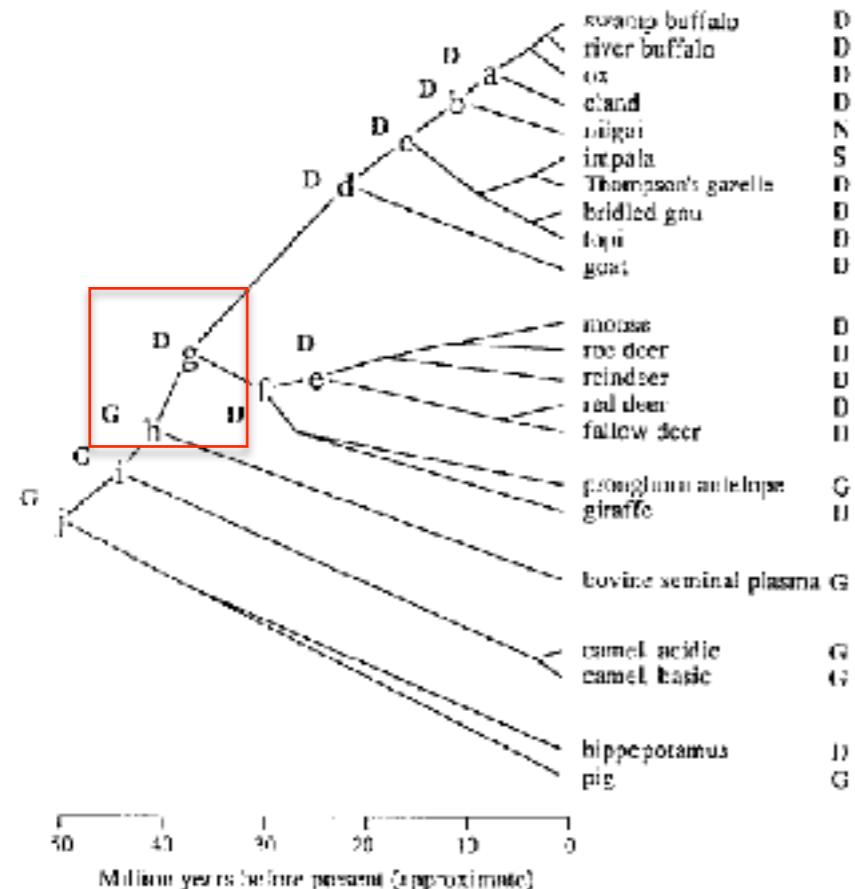


TABLE 1 Sequence changes in reconstructed ancient ribonucleases

	Hovine RNase A	a	b	c	d	e	f	g	h ₁	h ₂	i ₁	i ₂	j ₁	j ₂
3	Thr	Thr	Thr	Ser	Ser	Ser	Ser	Ser	Ser	Ser	Ser*	Thr*	Ser	Ser
6	Ala	Ala	Ala	Ala	Ala	Ala	Ala	Ala	Ala	Ala	Glu	Glu	Lys	Lys
15	Ser	Ser	Ser	Ser	Ser	Pro	Ser	Ser	Ser	Ser	Ser	Ser	Ser	Ser
16	Ser	Ser	Ser	Ser	Ser	Ser	Ser	Ser	Gly*	Gly*	Gly*	Gly*	Gly	Gly
17	Thr	Thr	Thr	Thr	Thr	Thr	Thr	Ser*	Thr*	Ser	Ser	Ser	Ser	Ser
19	Ala	Ser	Ser	Ser	Ser	Ser	Ser	Ser						
20	Ala	Ala	Ala	Ala	Ala	Ala	Ala	Ala	Ser	Ser	Ser	Ser	Ser	Ser
22	Ser	Ser	Ser	Ser	Ser	Ser	Ser	Ser	Ser	Ser	Asn*	Asn*	Asn	Asn
31	Lys	Lys	Lys	Lys	Lys	Gln	Lys	Lys	Lys	Lys	Lys	Lys	Lys*	Lys*
32	Ser	Ser	Ser	Ser	Ser	Ser	Ser	Ser	Ser	Ser	Arg	Arg	Arg	Arg
34	Asn	Asn	Asn	Asn	Asn	Asn	Asn	Asn*	Lys*	Lys*	Lys*	Lys*	Asn	Asn
35	Ieu	Met	Met	Leu	Leu	Leu	Leu	Leu*	Met	Met	Met	Met	Met	Met
37	Lys	Lys	Gln	Gln	Gln	Gln	Gln	Gln	Gln	Gln	Gln	Gln	Gln	Gln
38	Asp	Asp	Asp	Asp	Asp	Asp	Asp	Asp	Gly	Gly	Gly	Gly	Gly	Gly
59	Ser	Ser	Ser	Ser	Ser	Phe	Ser	Ser	Ser	Ser	Ser	Ser	Ser	Ser
64	Ala	Ala	Ala	Ala	Ala	Ala	Ala	Ala	Thr	Thr	Thr	Thr	Thr	Thr
70	Thr	Thr	Thr	Thr	Thr	Ser	Thr	Thr	Thr	Thr	Thr	Thr	Thr	Thr
76	Tyr	Tyr	Tyr	Tyr	Tyr	Asn	Tyr	Asn	Asn	Asn	Asn	Asn	Asn	Asn
78	Thr	Thr	Thr	Thr	Thr	Ala	Thr	Thr	Thr	Thr	Thr	Thr	Thr	Thr
80	Ser	Ser	Ser	Ser	Ser	His	Ser	Arg*	Arg*	Arg*	His	His	His	His
98	Ala	Ala	Ala	Ala	Ala	Val	Ala	Ala	Ala	Ala	Ala	Ala	Ala	Ala
100	Thr	Thr	Thr	Thr	Thr	Thr	Thr	Thr	Thr	Thr	Ser	Ser	Ser	Ser
102	Ala	Ala	Ala	Ala	Ala	Ala	Ala	Ala	Val	Val	Val*	Val*	Val*	Glut*
103	Asn	Lys	Lys	Lys	Glu	Glu	Glu	Glu	Glu	Glu	Gln	Gln	Gln	Gln

cambio de régimen selectivo y adaptación en funcionalidad de enzimas

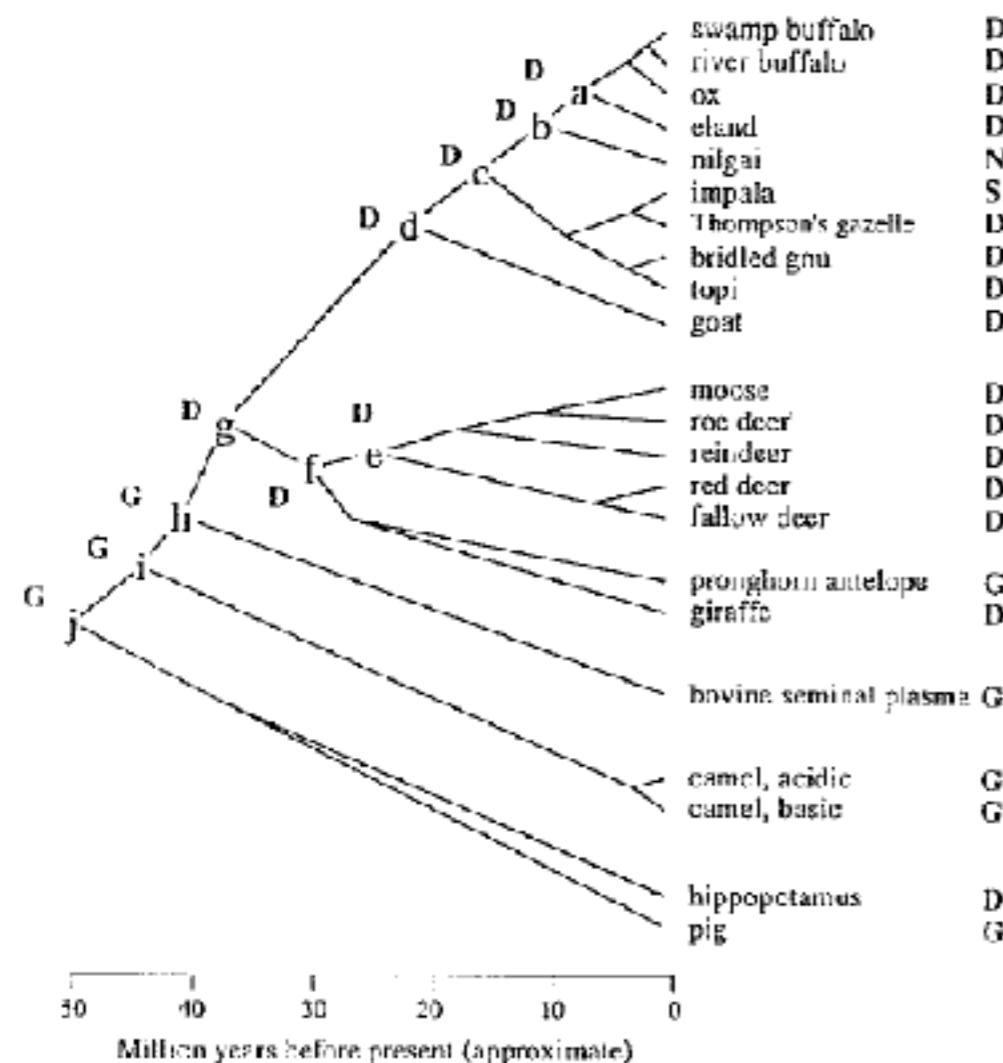
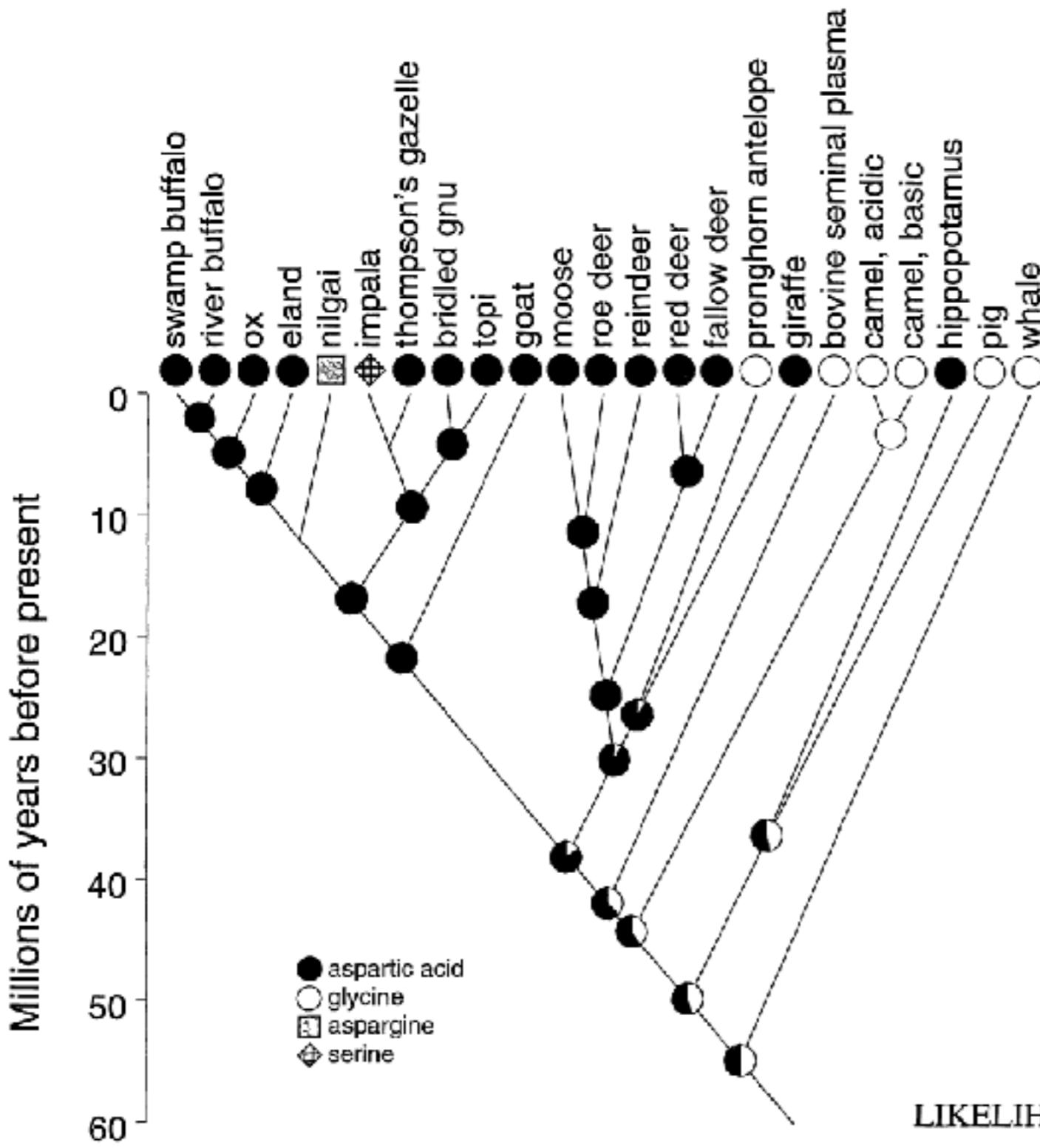


TABLE 2 Kinetic properties of reconstructed ancestral ribonucleases

RNase	Ancestor of	k_{cat}/K_m UpA $\times 10^5$	k_{cat}/K_m as % of RNase A	Poly(U) relative to RNase A	Poly(A)-poly(U) relative to RNase A
RNase A*		5.0	100	100	1.0
RNase A†		4.5	90	97	1.0
a	ox, buffalo, eland	6.1	122	106	1.4
b	ox, buffalo, eland, nilgai	5.9	118	112	1.0
c	b and the gazelles	4.5	91	97	0.8
d	Bovids	3.9	78	86	0.9
e	Deer	3.6	73	77	1.0
f	Deer, pronghorn, giraffe	3.3	67	103	1.0
g	Pecora	4.6	94	87	1.0
h ₁	Pecora and seminal RNase	5.5	111	106	5.2
h ₂	Pecora and seminal RNase	6.5	130	106	5.2
i ₁	Ruminata	4.5	90	96	5.0
i ₂	Ruminata	5.2	104	80	4.3
j ₁	Artiodactyla	3.7	74	73	4.6
j ₂	Artiodactyla	3.3	66	51	2.7

un momentico...



Evolution, 51(6), 1997, pp. 1699–1711

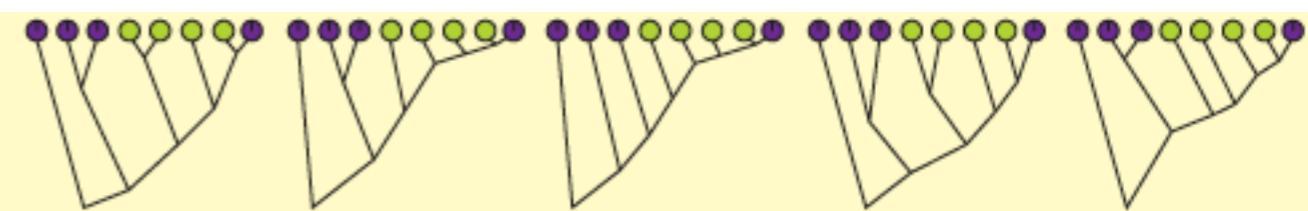
LIKELIHOOD OF ANCESTOR STATES IN ADAPTIVE RADIATION

DOLPH SCHLUTER,^{1,2} TREVOR PRICE,³ ARNE Ø. MOOERS^{1,4} AND DONALD LUDWIG^{1,5}

Phylogenetics Series

Bayesian inference of character evolution

Fredrik Ronquist



Box 1. Mapping uncertainty

We are interested in inferring the ancestral states of a character with two states, purple (0) or green (1). The states could, for example, represent particular behaviours, life-history traits or morphological features. The tree and the ages of the nodes are known; the scale is in amount of expected change.

Parsimony (Figure 1a) finds the reconstruction requiring the minimum amount of change between green and purple. In this case, there are two changes [marked (i) and (ii)] assuming gains and losses count equally. Ancestors are inferred as being either green or purple, but we do not know how certain these conclusions are. That is, we have not taken mapping uncertainty into account.

Likelihood analysis requires that we know the relative rates of $0 \rightarrow 1$ changes (π_1) and $1 \rightarrow 0$ changes (π_0). Assuming that these rates are

equal ($\pi_0 = \pi_1 = 0.5$), for instance, we can calculate the probability of each ancestor being either green or purple (Figure 1b). The ancestral state is uncertain for ancestors A, B and F because they are on long branches or close to regions of the tree where a state change is likely.

In Bayesian inference, π_1 does not have to be fixed. Instead, we specify a prior probability distribution on π_1 . In the absence of background information, we can assume that all possible values are equally likely (Figure 1c: prior). This enables us to infer ancestral states while weighting each π_1 value according to its probability given the data (Figure 1c: posterior). In our example, Bayesian inference simply adds a dash more uncertainty to the conditional probability values (Figure 1d; the effect is most notable for ancestor C).

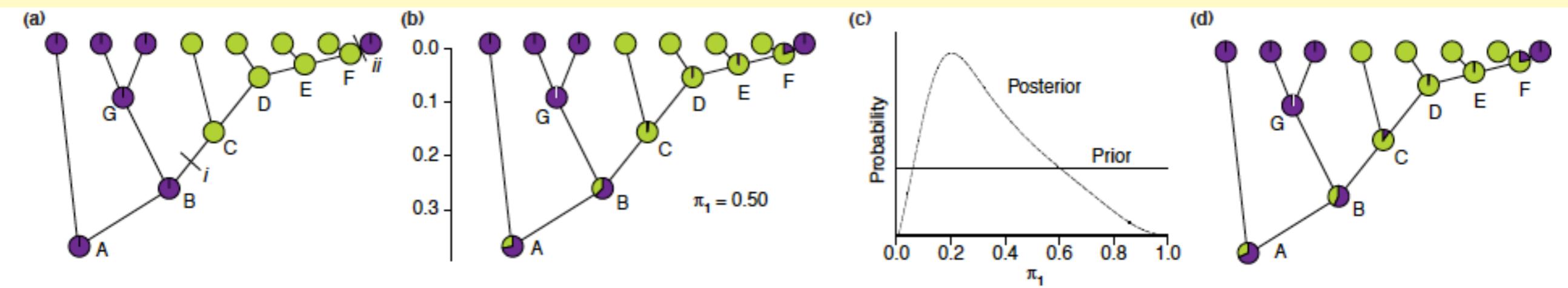


Figure 1.

11

Sexual selection has produced many of the most striking traits in animals, such as the antlers of this bull elk.



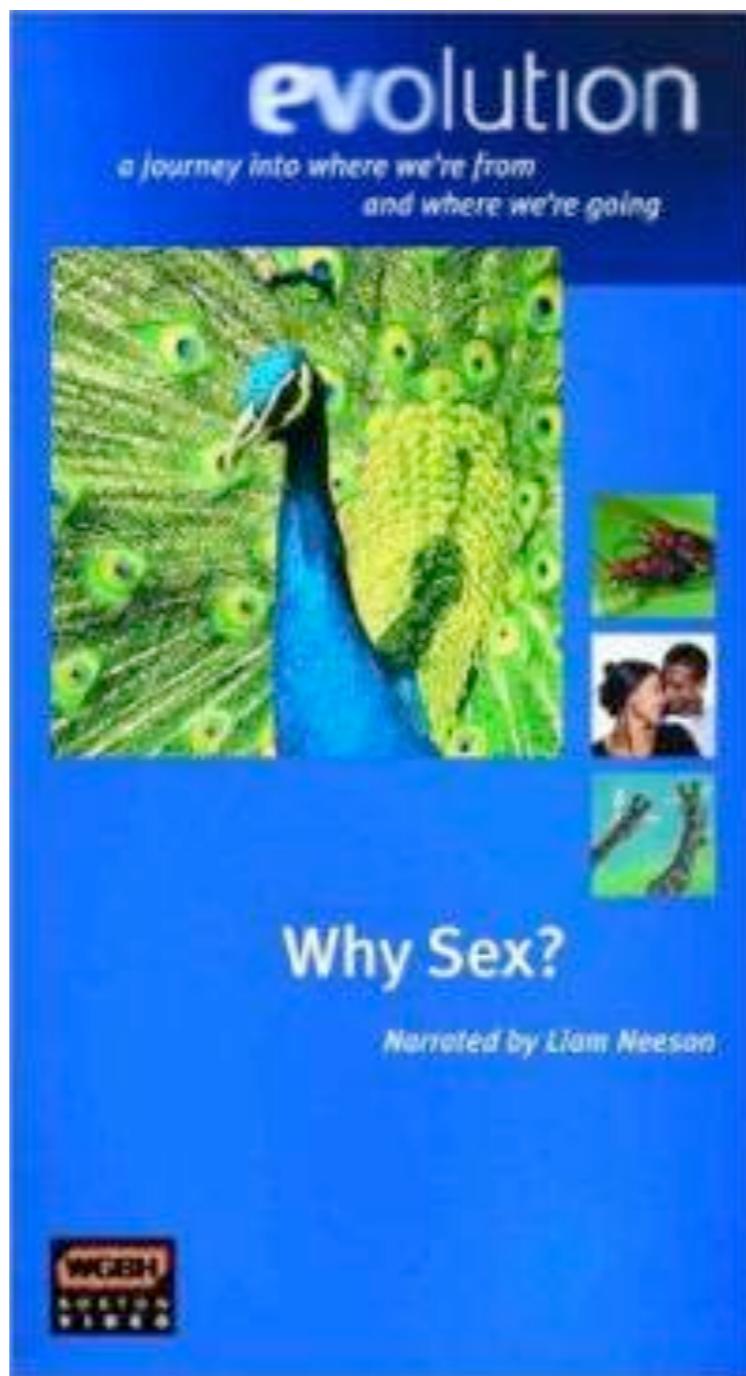
Sex

Causes and Consequences

Learning Objectives

- Define sex and identify possible mechanisms for the evolution of sex.
- Identify the genetic consequences of sexual and asexual reproduction.
- Explain the Red Queen effect.
- Explain why asexual organisms evolved alternatives to sex.
- Identify the different investments made in sexual reproduction by males and females.
- Explain how differential investment can result in conflicting selection pressure in males and females.
- Analyze how the different reproductive strategies of males and females lead to sexual selection.
- Explain why sexual dimorphism is an outcome of sexual selection.
- Identify the direct and indirect benefits of male choice.
- Apply Fisher's runaway model to a preexisting sensory bias for red.
- Compare and contrast the good genes and arbitrary choice models of sexual selection.
- Compare and contrast social monogamy with polygyny and polyandry.
- Analyze how competing interests of males and females in sexual reproduction may influence selection.

tarea



<https://youtu.be/JakdRczkmNo>