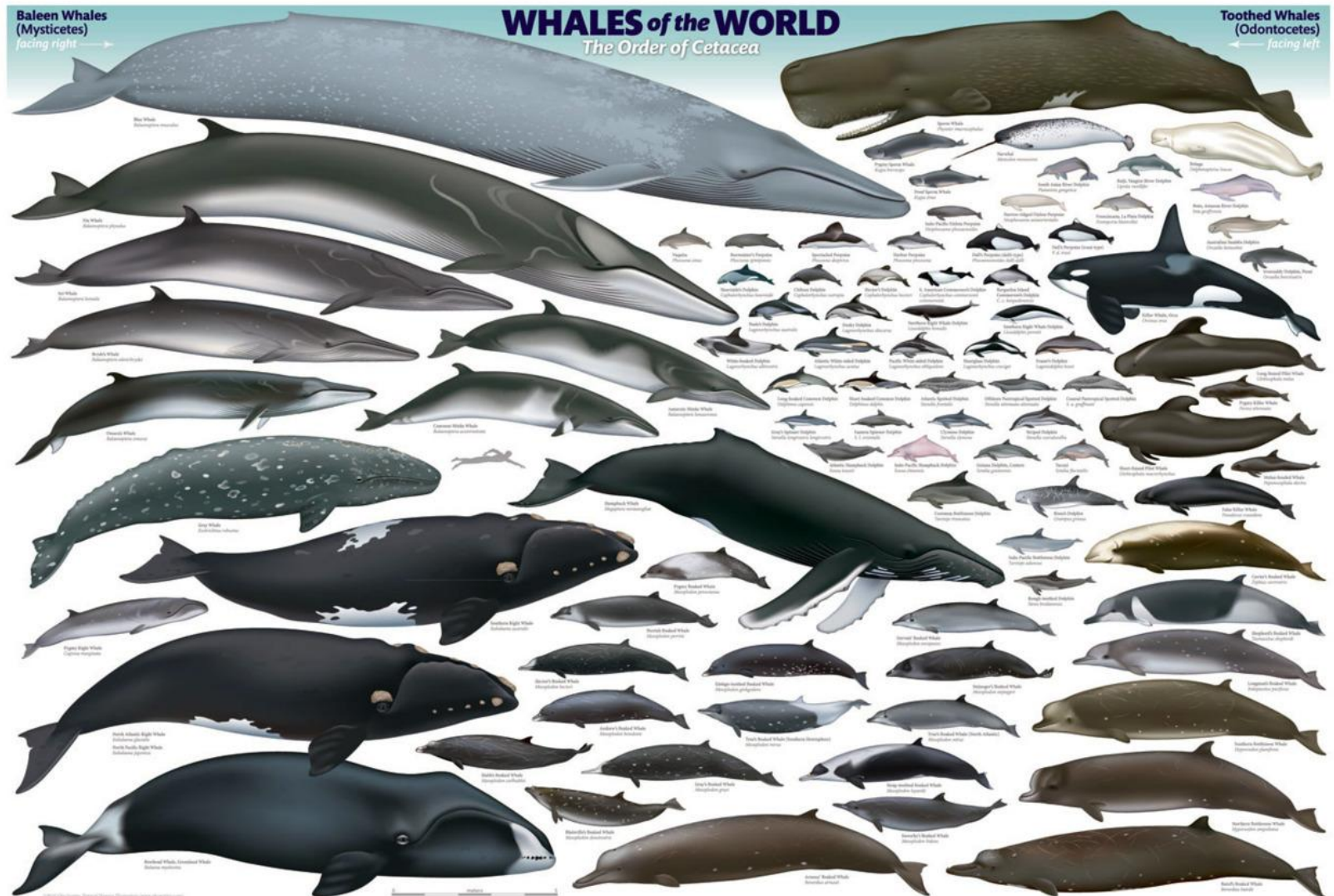


Генетические аспекты эволюции китобразных

П. Е. Гольдин

Институт зоологии им. И. И.
Шмальгаузена НАН Украины

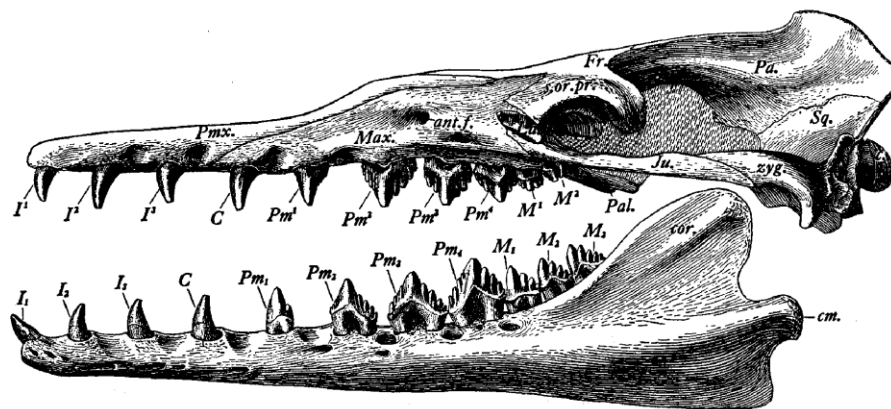
Китообразные (Cetacea)



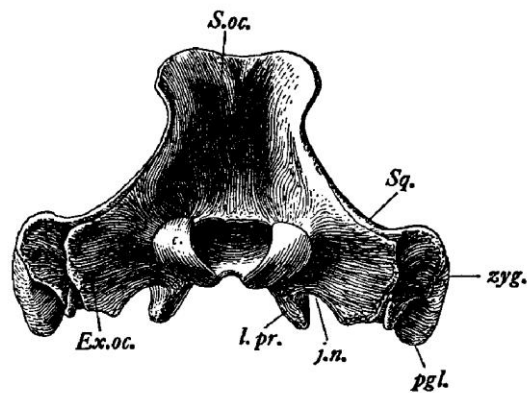
Усатые киты и зубатые киты

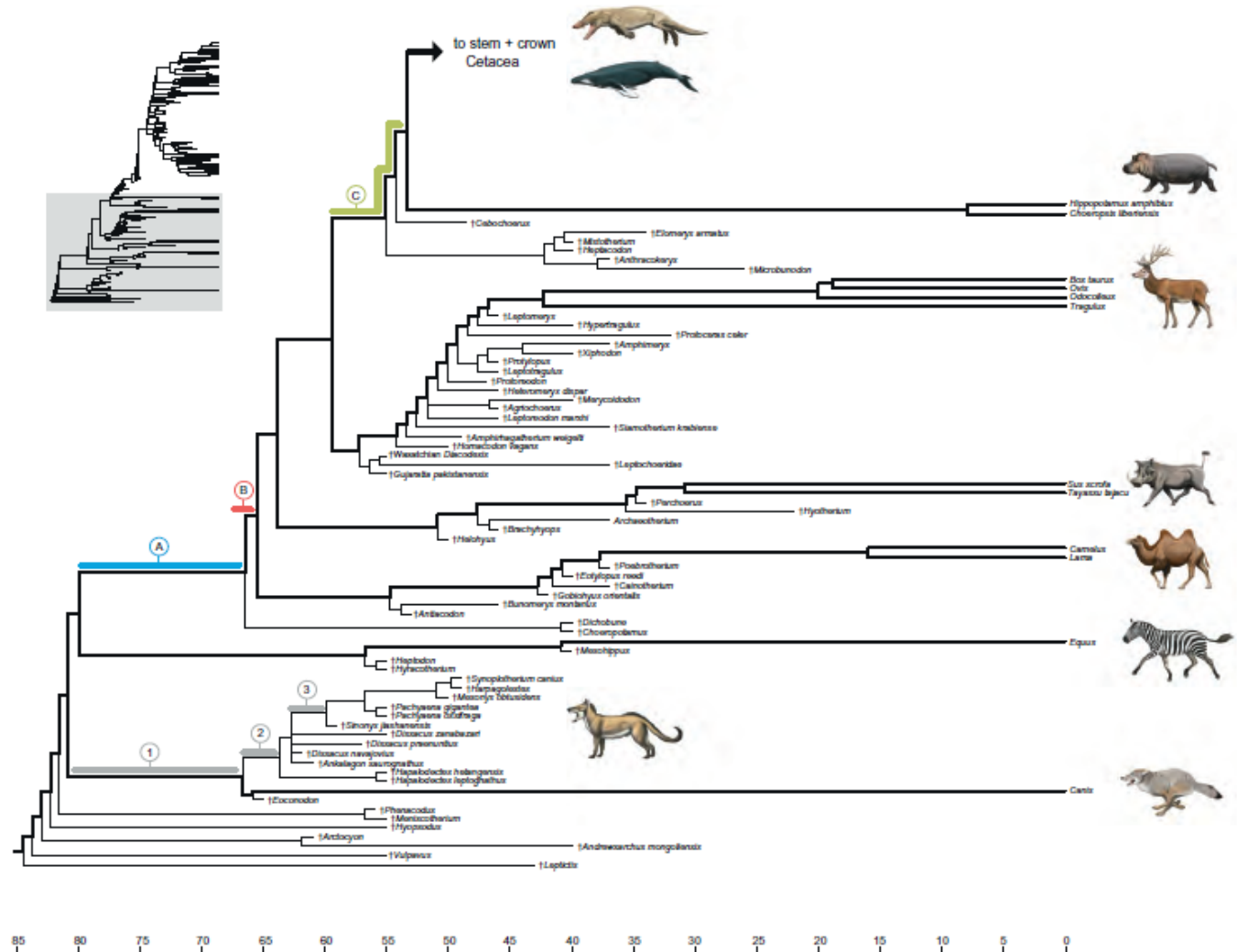


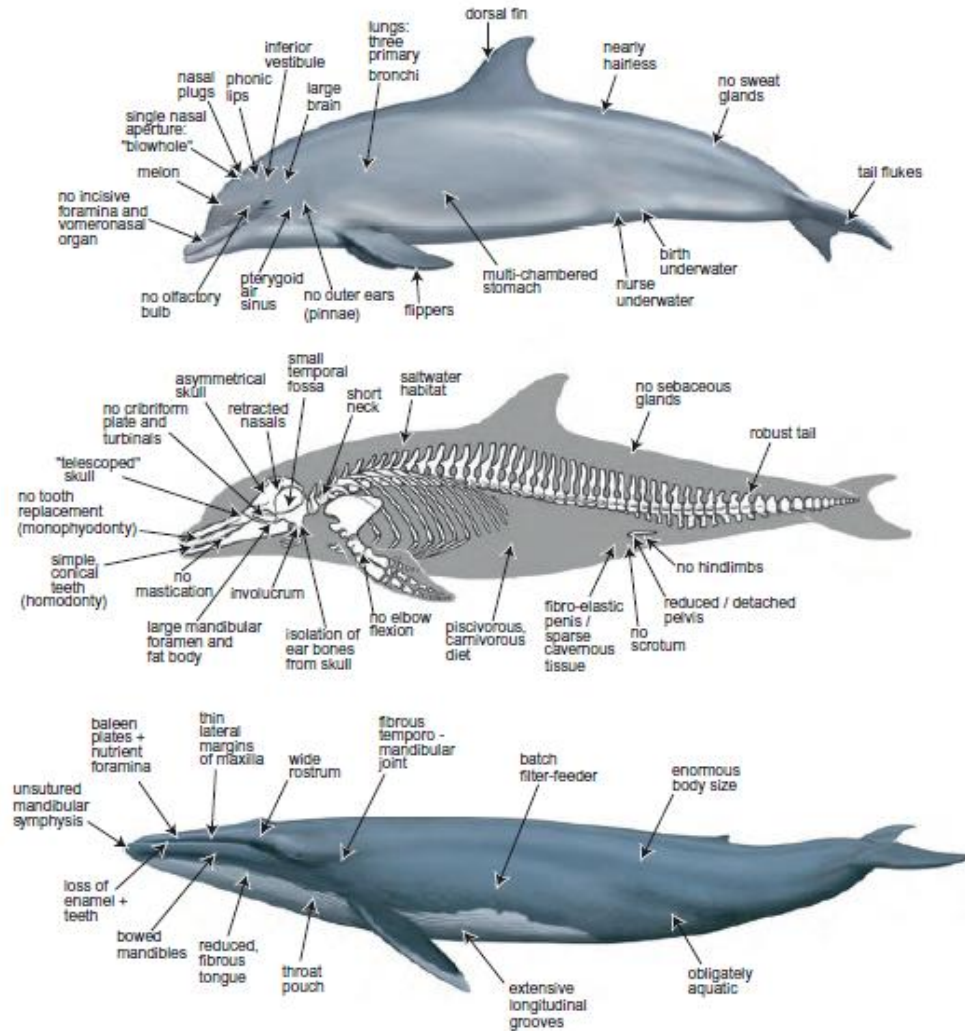
Парнокопытные и китообразные



from Kellogg, 1936







Big and Slow: Phylogenetic Estimates of Molecular Evolution in Baleen Whales (Suborder Mysticeti)

J. A. Jackson, C. S. Baker,*† M. Vant,† D. J. Steel,* L. Medrano-González,‡ and S. R. Palumbi§*

*Marine Mammal Institute, Hatfield Marine Science Center, Oregon State University; †School of Biological Sciences, Auckland University, Auckland, New Zealand; ‡Facultad de Ciencias, Universidad Nacional Autónoma de México, Circuito Exterior, Ciudad Universitaria, México, Mexico; and §Department of Biological Sciences, Hopkins Marine Station, Stanford University, Pacific Grove, CA

- скорость замен нуклеотидов у китообразных в 8-10 раз медленнее, чем в среднем у зверей
- эта закономерность выявлена и у зубатых, и у усатых китов; и в ядерных, и в митохондриальных генах
- частично это можно объяснить продолжительностью жизни, но – в пять раз медленнее, чем у человека!

Быстрое видообразование и разнообразие форм и размеров

- 15 современных видов усатых китов и около 300 известных (и еще 1000 неизвестных) ископаемых
- Открытие новых видов: кит Лонгмана (1966), шароголовый дельфин (1966), ремнезуб Перрина (2001), полосатик Омурь (2009)
- 4 экотипа косаток в Антарктике
- Диапазон размеров – от 30 до 170 000 кг

Расшифровка полных геномов

- Афалина
- Косатка
- Бесперая морская свинья
- Байцзи
- Кашалот
- Малый полосатик
- Гренландский кит

Dolphin genome provides evidence for adaptive evolution of nervous system genes and a molecular rate slowdown

**Michael R. McGowen, Lawrence I. Grossman
and Derek E. Wildman***

- положительный отбор генов эволюции нервной системы: число несинонимических замен выше, чем синонимических

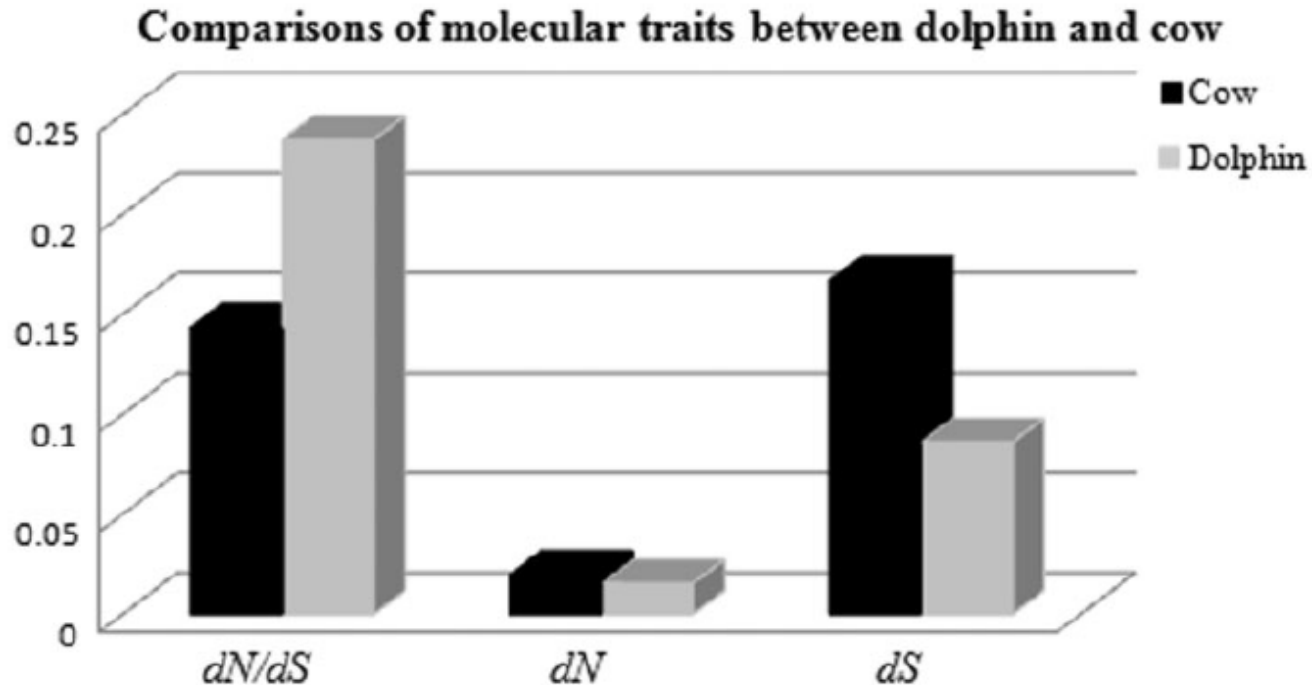
Дельфин афалина

gene symbol	gene name	dN/dS
<i>S100A9</i>	S100 calcium-binding protein A9	dS = 0
<i>AGRP</i>	agouti-related protein homologue (mouse)	dS = 0
<i>RNF182</i>	ring finger protein 182	dS = 0
<i>BAG2</i>	BCL2-associated athanogene 2	dS = 0
<i>ERCC8</i>	excision repair cross-complementing rodent repair deficiency, complementation group 8	7.8075
<i>CNPY1</i>	canopy 1 homologue (zebrafish)	2.6349
<i>ZNF597</i>	zinc finger protein 597	2.248
<i>C2orf40</i>	chromosome 2 open reading frame 40	2.0584
<i>APOO</i>	apolipoprotein O	1.8163
<i>SPINK5</i>	serine peptidase inhibitor, Kazal type 5	1.5892
<i>DMKN</i>	dermokine	1.5155
<i>EDN2</i>	endothelin 2	1.3248
<i>PCP4L1</i>	Purkinje cell protein 4-like 1	1.249
<i>DBI</i>	diazepam binding inhibitor (GABA receptor modulator, acyl-CoA binding protein)	1.2444
<i>BAALC</i>	brain and acute leukaemia, cytoplasmic	1.211
<i>KCNK18</i>	potassium channel, subfamily K, member 18	1.1874
<i>NMU</i>	neuromedin U	1.2147
<i>AGER</i>	advanced glycosylation end-product-specific receptor	1.2109
<i>TANK</i>	TRAF family member-associated NFKB activator	1.1617
<i>CD47</i>	CD47 molecule	1.1314
<i>AP4S1</i>	adaptor-related protein complex 4, sigma 1 subunit	1.1266
<i>LRFN1</i>	leucine-rich repeat and fibronectin type III domain containing 1	1.1158
<i>MAL</i>	mal, T-cell differentiation protein	1.1047
<i>MCPH1</i>	microcephalin 1	1.0707
<i>SYPL1</i>	synaptophysin-like 1	1.0364
<i>CNPY2</i>	canopy 2 homologue (zebrafish)	1.0188
<i>TTR</i>	transthyretin	1.0027

Другие гены – тоже!

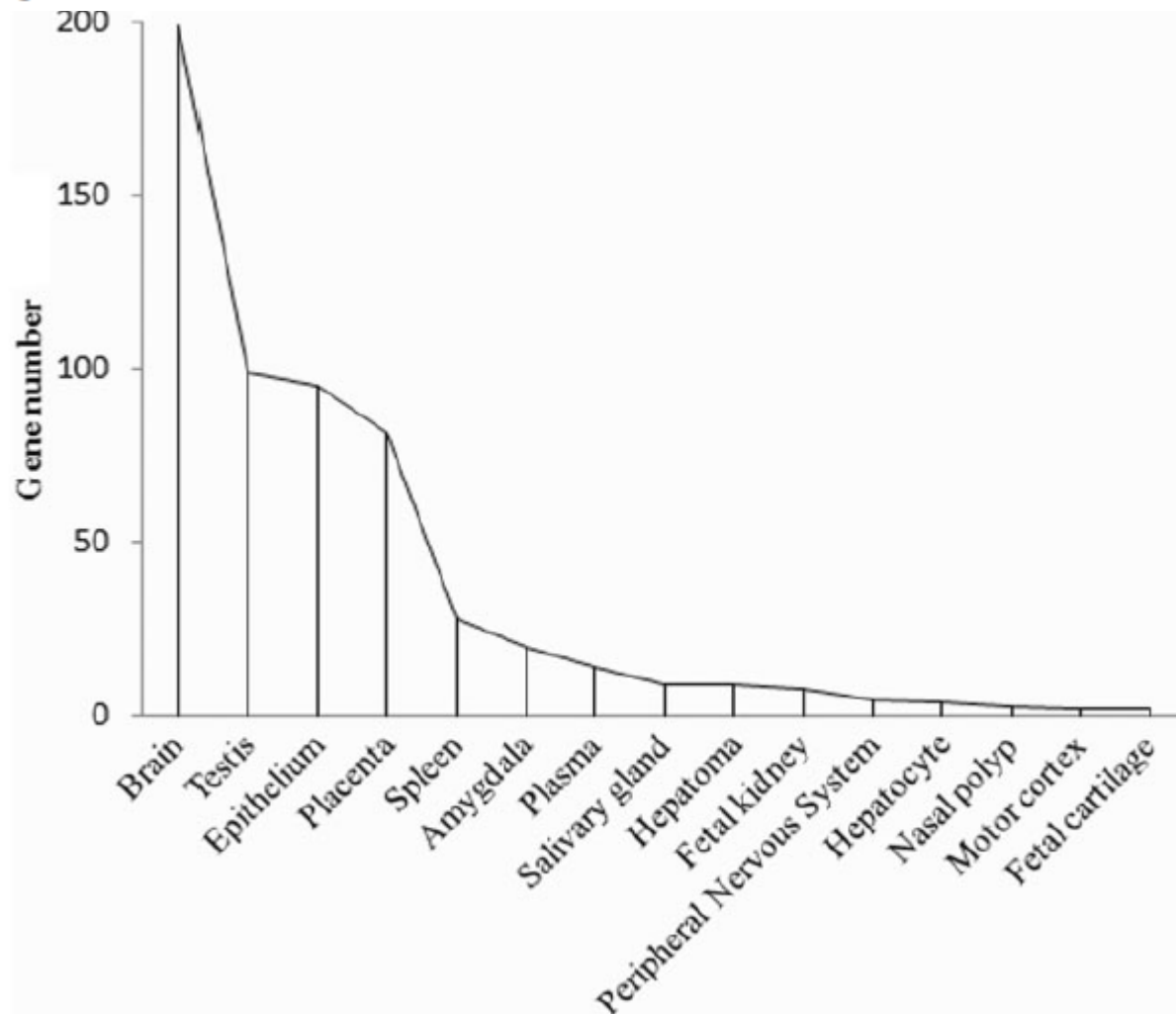
Genome-Wide Scans for Candidate Genes Involved in the Aquatic Adaptation of Dolphins

Yan-Bo Sun^{1,2,†}, Wei-Ping Zhou^{1,2,3,†}, He-Qun Liu^{1,2,4}, David M. Irwin^{1,5,6}, Yong-Yi Shen^{1,7,*}, and Ya-Ping Zhang^{1,2,*}



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НВ: об эволюции мозга

STEPHEN H. MONTGOMERY ET AL.

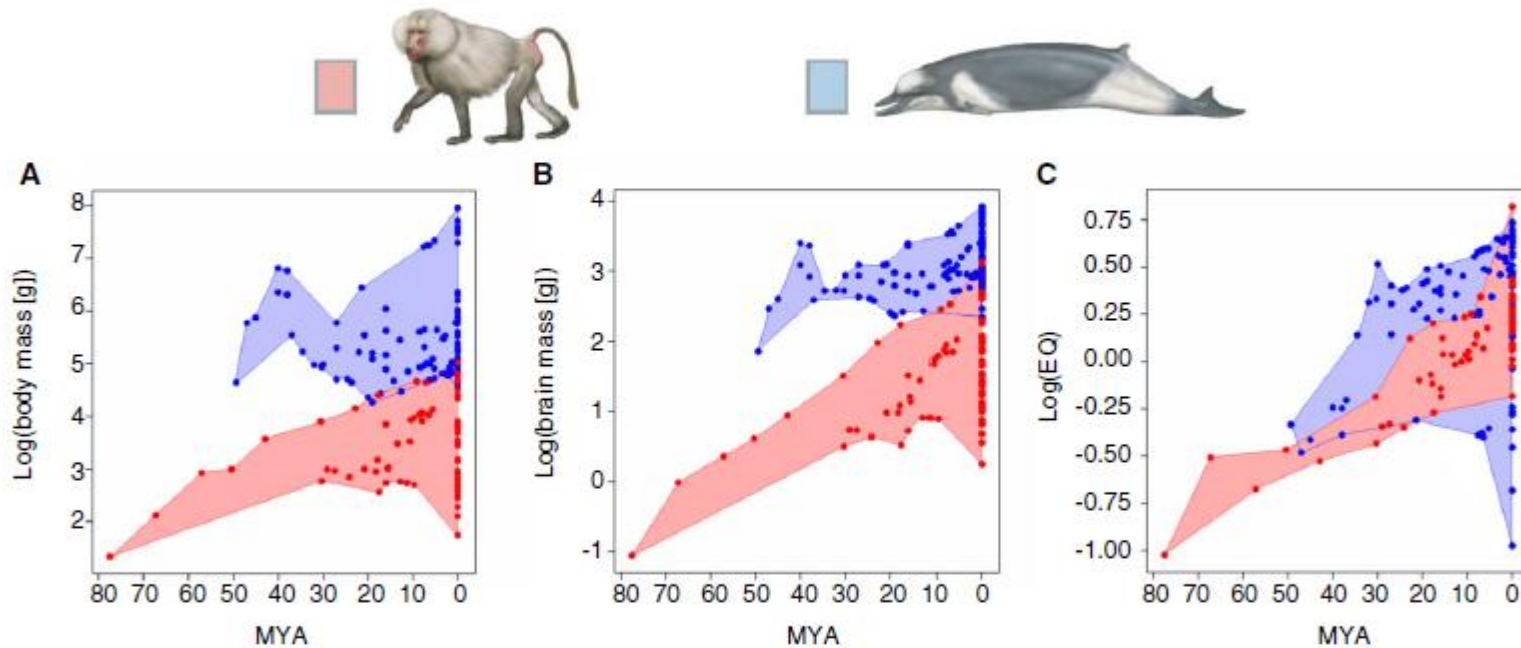


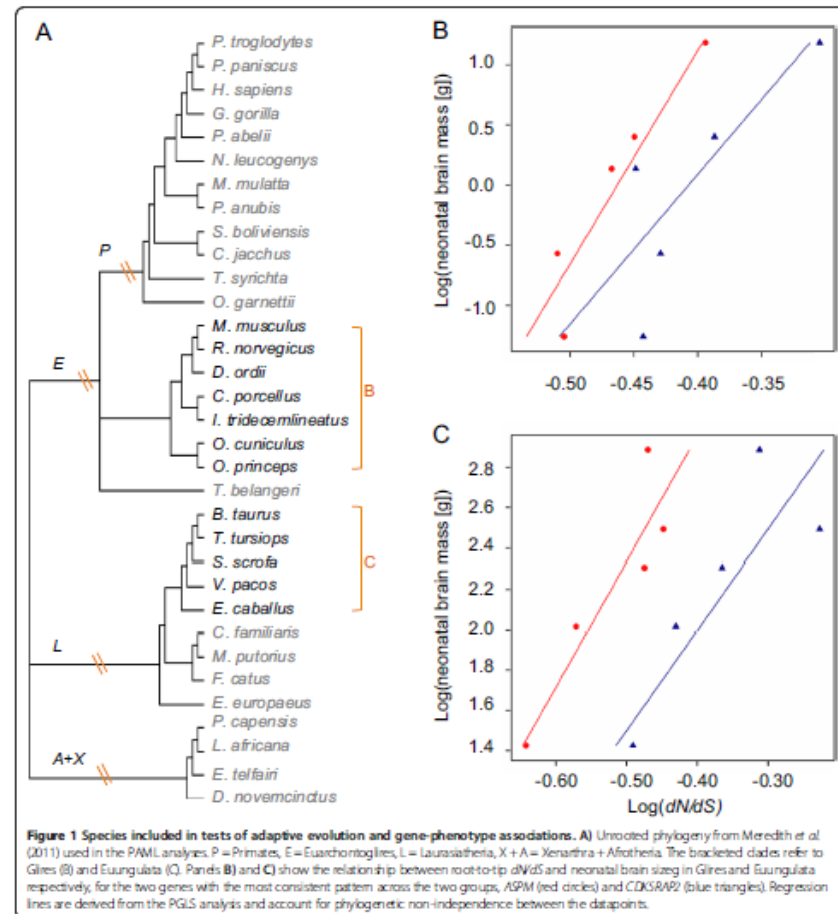
Figure 5. Distribution of log(body mass [g]) (A), log(brain mass [g]) (B), and log(EQ) (C) through time for cetaceans (blue) and primates (red) from their origins to present day (x-axis is millions of years ago [MYA]). Scatterplots include data for extant species, extinct taxa, and ancestral states reconstructed at internal nodes of the tree in Figure 1. Paintings are by Carl Buell.

Microcephaly genes evolved adaptively throughout the evolution of eutherian mammals

Stephen H Montgomery^{1*} and Nicholas I Mundy²

Montgomery and Mundy *BMC Evolutionary Biology* 2014, **14**:120
<http://www.biomedcentral.com/1471-2148/14/120>

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Sun et al.: Категории генов, подвергшихся положительному отбору, - по функциям

- Метаболизм жиров и отложение подкожного жира
- Метаболизм мышечной ткани и мышечное сокращение
- Слух
- Пищеварение

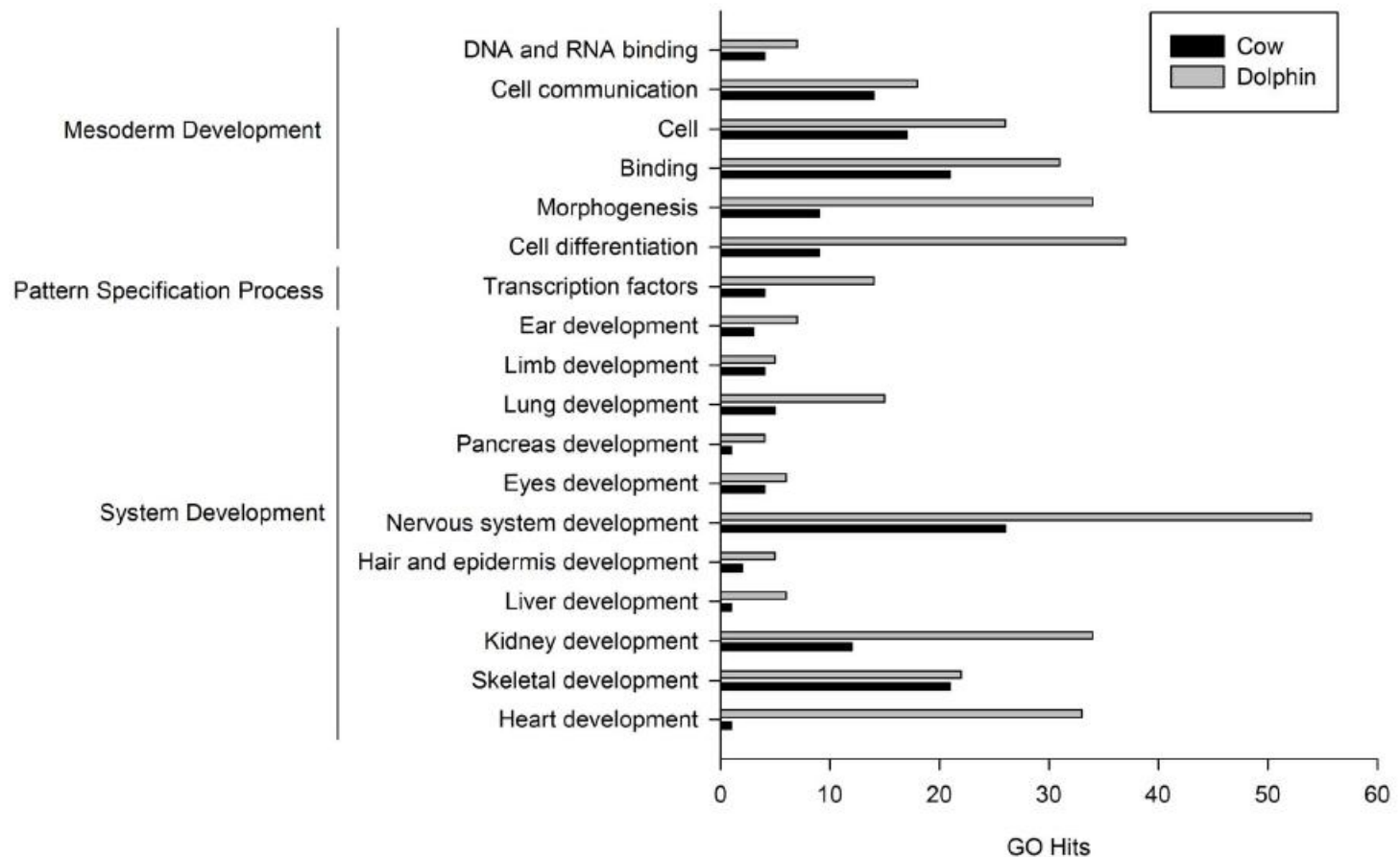
Увеличение числа генов в семействах

- Немногочисленны и мало исследованы
- DYNEIN HEAVY CHAIN DOMAIN CONTAINING 1
DYNEIN HEAVY CHAIN DOMAIN 1 PROTEIN
CCDC35 ENSFM00550000743164 – три гена вместо одного: адаптация к плаванию???
- Зато: уменьшение числа генов И инактивация (превращение в псевдогены) – обоняние у зубатых китов, развитие зубов у усатых китов

How to Make a Dolphin: Molecular Signature of Positive Selection in Cetacean Genome

Mariana F. Nery^{1,2*}, Dimar J. González¹, Juan C. Opazo^{1*}

- 376 генов, подвергшихся положительному отбору



Baiji genomes reveal low genetic variability and new insights into secondary aquatic adaptations

Xuming Zhou^{1,2,*}, Fengming Sun^{3,*}, Shixia Xu^{1,*}, Guangyi Fan³, Kangli Zhu¹, Xin Liu³, Yuan Chen¹, Chengcheng Shi³, Yunxia Yang¹, Zhiyong Huang³, Jing Chen³, Haolong Hou³, Xuejiang Guo⁴, Wenbin Chen³, Yuefeng Chen¹, Xiaohong Wang¹, Tian Lv³, Dan Yang¹, Jiajian Zhou³, Bangqing Huang³, Zhengfei Wang¹, Wei Zhao³, Ran Tian¹, Zhiqiang Xiong³, Junxiao Xu¹, Xinming Liang³, Bingyao Chen¹, Weiqing Liu³, Junyi Wang³, Shengkai Pan³, Xiaodong Fang³, Ming Li², Fuwen Wei², Xun Xu³, Kaiya Zhou¹, Jun Wang^{3,5,6} & Guang Yang¹

- Положительный отбор – благодаря замедлению скорости эволюции!
Синонимических замен мало, что повышает значение несинонимических.

The transcriptome of the bowhead whale *Balaena mysticetus* reveals adaptations of the longest-lived mammal

Inge Seim¹, Siming Ma¹, Xuming Zhou¹, Maxim V. Gerashchenko¹, Sang-Goo Lee¹, Robert Suydam², John C. George², John W. Bickham³, Vadim N. Gladyshev¹

Table 7. Positively selected genes in the bowhead whale.

Gene symbol (mouse)	Ensembl transcript ID	Gene description
<i>BC026585</i>	ENSMUST00000046743	quinone oxidoreductase-like protein 2-like
<i>Cyfp1</i>	ENSMUST00000032629	cytoplasmic FMR1 interacting protein 1
<i>Ecm1</i>	ENSMUST00000117507	extracellular matrix protein 1
<i>Gsk3a</i>	ENSMUST00000071739	glycogen synthase kinase 3 alpha
<i>Gtf2i</i>	ENSMUST00000059042	general transcription factor II I
<i>Hp</i>	ENSMUST00000074898	haptoglobin
<i>Mtus1</i>	ENSMUST00000059115	mitochondrial tumor suppressor 1
<i>Prune</i>	ENSMUST00000015855	prune exopolyphosphatase

Convergent evolution of the genomes of marine mammals

Andrew D Foote^{1,2,16}, Yue Liu^{3,16}, Gregg W C Thomas^{4,16}, Tomáš Vinař^{5,16}, Jessica Alföldi⁶, Jixin Deng³, Shannon Dugan³, Cornelis E van Elk⁷, Margaret E Hunter⁸, Vandita Joshi³, Ziad Khan³, Christie Kovar³, Sandra L Lee³, Kerstin Lindblad-Toh^{6,9}, Annalaura Mancia^{10,11}, Rasmus Nielsen¹², Xiang Qin³, Jiabin Qu³, Brian J Raney¹³, Nagarjun Vijay², Jochen B W Wolf^{2,9}, Matthew W Hahn^{4,14}, Donna M Muzny³, Kim C Worley³, M Thomas P Gilbert^{1,15} & Richard A Gibbs³

Table 1 Positively selected genes that encode parallel substitution in all three marine mammal lineages

Gene	Branch along which positive selection was detected (<i>P</i> value)	Position ^a	Convergent amino acid substitution
<i>MYH7B</i>	Combined marine mammals (0.0335)	1	Lys→Gln
<i>TBC1D15</i>	Combined marine mammals (0.0278)	15	Asn→Ser
<i>MGP</i>	Combined marine mammals (0.0014)	57	Leu→Ile
<i>SMPX</i>	Combined marine mammals (0.0315)	49	Ser→Leu
<i>GCLC</i>	Combined marine mammals (0.0002) and walrus (<0.0001)	220	Val→Met
<i>SERPINC1</i>	Combined marine mammals (0.0241), walrus (0.0400) and cetacean (0.0009)	435	Asn→Ser
<i>M6PR</i>	Combined marine mammals (0.0227) and cetacean (0.0242)	102	Asn→Ser
<i>S100A9</i>	Combined marine mammals (0.0007) and manatee (0.0051)	72	Ala→Gly
<i>IRAK2</i>	Cetacean (0.0091)	481	Asp→Glu
<i>CHRM5</i>	Cetacean (0.0449)	270	Arg→Gln
<i>GPR97</i>	Manatee (0.0466)	135	Ser→Arg
<i>ESD</i>	Manatee (0.0144)	66	Asp→Glu
<i>SIAE</i>	Manatee (0.0452)	415	Ile→Val
<i>DUSP27</i>	Walrus (0.0121)	850	Asn→Ser
<i>C7orf62</i>	Walrus (0.0101)	78	Ser→Asn

^aPosition of the amino acid substitution within the encoded product of the ortholog.

Genome-culture coevolution promotes rapid divergence of killer whale ecotypes

Andrew D. Foote^{1,2,3,*}, Nagarjun Vijay^{1,*}, María C. Ávila-Arcos^{2,4}, Robin W. Baird⁵, John W. Durban⁶, Matteo Fumagalli⁷, Richard A. Gibbs⁸, M. Bradley Hanson⁹, Thorfinn S. Korneliussen², Michael D. Martin², Kelly M. Robertson⁶, Vitor C. Sousa³, Filipe G. Vieira², Tomáš Vinař¹⁰, Paul Wade¹¹, Kim C. Worley⁸, Laurent Excoffier³, Phillip A. Morin⁶, M. Thomas P. Gilbert^{2,12} & Jochen B.W. Wolf^{1,13,14}

- Скорость молекулярной эволюции (замен) – обычна для китообразных
- Генетическая дифференциация – высокая за счет дрейфа генов (изоляция в малых группах)
- В некоторых генах (пищеварение, жиронакопление) – положительный отбор
- Причина разнообразия форм – социальная организация

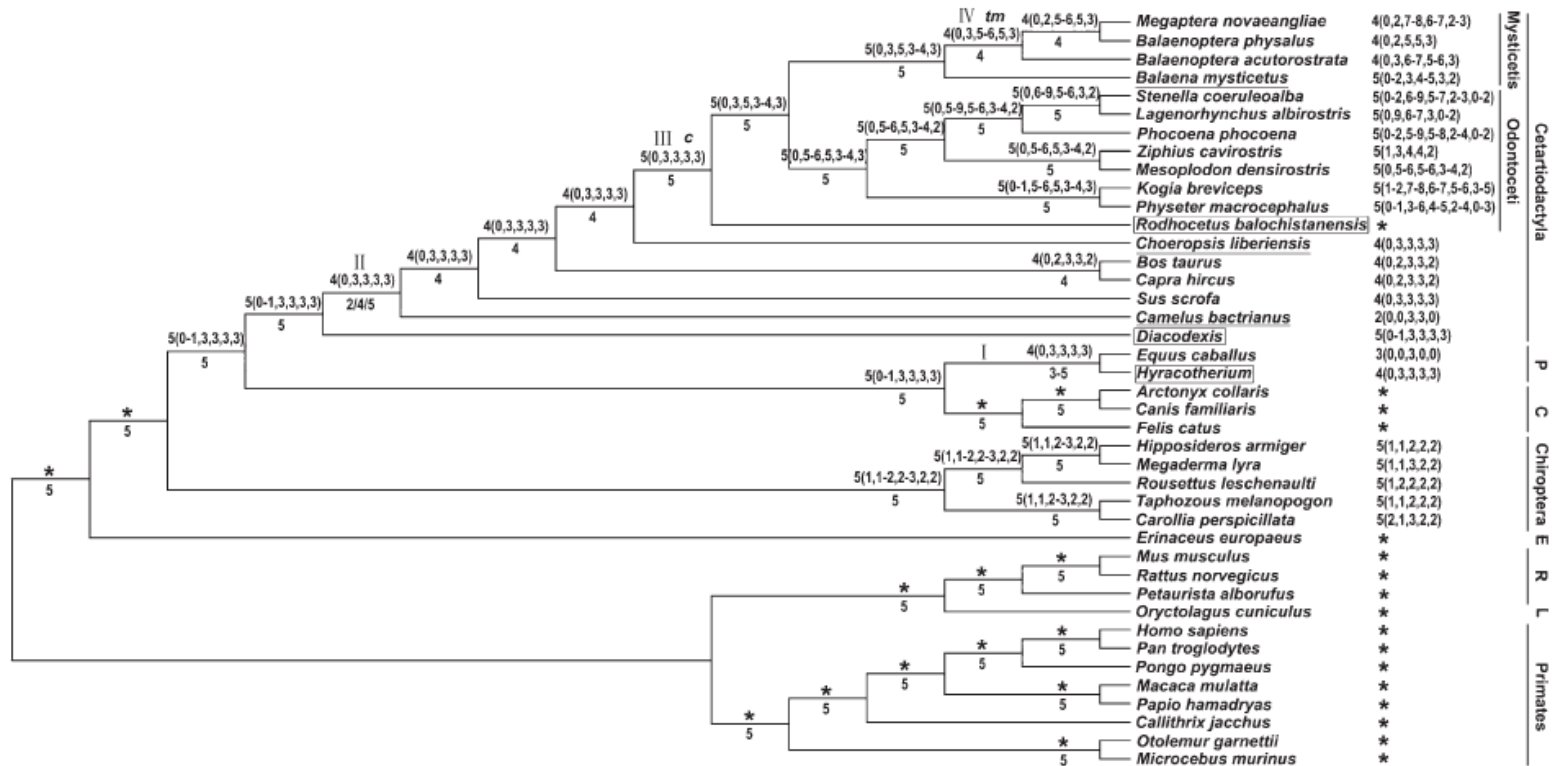
Проблемы

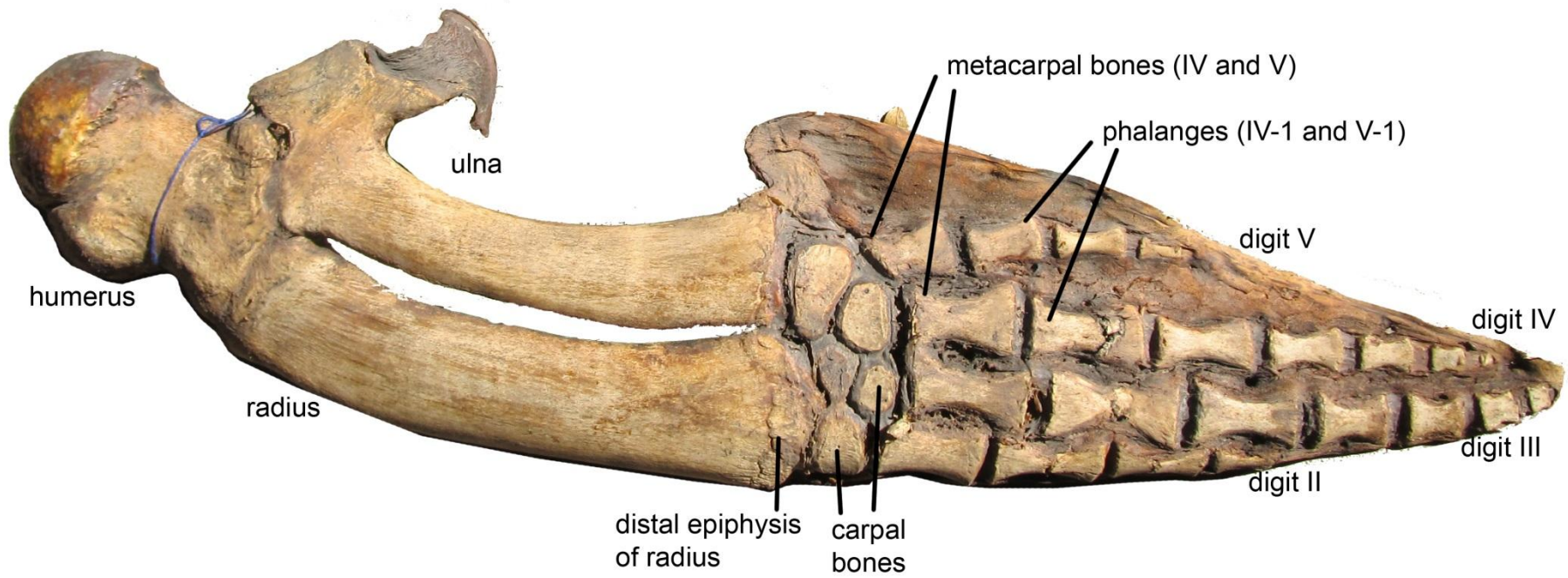
- Интерпретация реальных процессов, происходящих под действием положительного отбора
- Быстрая эволюция в группах со слабой социальной организацией

Регуляторные гены

Adaptive Evolution of 5' *HoxD* Genes in the Origin and Diversification of the Cetacean Flipper

Zhe Wang,* Lihong Yuan,† Stephen J. Rossiter,‡ Xueguo Zuo,* Binghua Ru,* Hui Zhong,*
 Naijian Han,§ Gareth Jones,|| Paul D. Jepson,¶ and Shuyi Zhang*





Bmp4

Bmp4

Orc

MI PGNRMLMVLLCQVLLGGASHASLI PETGKKKVAEIQGHAGGRRSGQSHELLRDFEATLLQMFGLRRRPQPSKSTVVPDYMRDLYRLQSGEEEGE QIHSIGLEYPERPASRANTVRSFHHEEHLENI PGTSENSAFRFLNLSI PENEVISSAELRRLFREQVDQGPDWEQGFHRIN IYEVMPKPAEVPVPGHLITRLLDTRLVHHNVTRWETF DVS PAVLRWTRKQPNYGLAIEVTHLHQTRTRQGQHVRISRSLPQSGDWAQLRPLLVTFGHDGRGHALTRRRRAKRS PKHHPQ RARKKNKNCRRHS LYVDFSDVGWNDWIVAPPGYQAFYCHGDCPFFLADHLNSTNHAI VQ TLVNSVNSSI PKACCVPELSAISMLYLDEYDKVVLKNYQEMVVEGCGCR

Minke

MDCYYMPCFLDTMI PGNRMLMVLLCQVLLGGASHASLI PETGKKKVAEIQGHAGGRRSGQSHELLRDFEATLLQMFGLRRRPQPSKSAVVVDYMRDLYRLQSGEEEEEQIHSIGLEYPERPASRANTVRSFHHEEHLENI PGTSENSAFRFLNLSI PENEVISSAELRRLFREQVDQ GPDWEQGFHRINIYEVMPKPAEVPVPGHLITRLLDTRLVHHNVTRWETF DVS PAVLRWTRKQPNYGLAIEVTHLHQTRTRQGQHVRISRSLPQSGDWAQLRPLLVTFGHDGWGHALTRRRRAKRS PKHHPQ RARKKNKNCRRHS LYVDFSDVGWNDWIVAPPGYQAFYCHGDCPFFLADHLNSTNHAI VQ TLVNSVNSSI PKACCVPELSAISMLYLDEYDKVVLKNYQEMVVEGCGCR

Cow

MI PGNRMLMVLLCQVLLGGASHASLI PETGKKKVAEIQGHAGGRRSGQSHELLRDFEATLLQMFGLRRRPQPSKSAVIIDYMRDLYRLQSGEEEEEQIQGIGLEYPERPASRANTVRSFHHEEHLENI PGTSENSAFRFLNLSI PENEVISSAELRRLFREQVDQGPDWQGFHRINIYEVMPKPAEVPVPGHLITRLLDTRLVHHNVTRWETF DVS PAVLRWTRKQPNYGLAIEVTHLHQTRTHQGQHVRISRSLPQSGDWAQLRPLLVTFGHDGRGHALTRRRRAKRS PKHHPQ RARKKNKNCRRHS LYVDFSDVGWNDWIVAPPGYQAFYCHGDCPFFLADHLNSTNHAI VQ TLVNSVNSSI PKACCVPELSAISMLYLDEYDKVVLKNYQEMVVEGCGCR

Homo

MI PGNRMLMVLLCQVLLGGASHASLI PETGKKKVAEIQGHAGGRRSGQSHELLRDFEATLLQMFGLRRRPQPSKSAVIIDYMRDLYRLQSGEEEEEQIHSIGLEYPERPASRANTVRSFHHEEHLENI PGTSENSAFRFLNLSI PENEVISSAELRRLFREQVDQGPDWERGFRINIYEVMPKPAEVPVPGHLITRLLDTRLVHHNVTRWETF DVS PAVLRWTRKQPNYGLAIEVTHLHQTRTHQGQHVRISRSLPQSGDWAQLRPLLVTFGHDGRGHALTRRRRAKRS PKHHSQ RARKKNKNCRRHS LYVDFSDVGWNDWIVAPPGYQAFYCHGDCPFFLADHLNSTNHAI VQ TLVNSVNSSI PKACCVPELSAISMLYLDEYDKVVLKNYQEMVVEGCGCR

Manatee

MI PGNRMLMVLLCQVLLGGASHASLI PETGKKKVAEIQGHAGGRRSGQSHELLRDFEATLLQMFGLRRRPQPSKSAVIIDYMRDLYRLQSGEEEEEQIHSIGLEYPERPASRANTVRSFHHEEHLENI PGNSSENSAFRFLNLSI PENEVISSAELRRLFREQVDQGPDWEQGFHRINIYEVMPKPAEVPVPGHLITRLLDTRLVHHNVTRWETF DVS PAVLRWTRKQPNYGLAIEVTHLYQTRTHQGQHVRISRSLPQSGDWAQLRPLLVTFGHDGRGHALTRRRRAKRS PKHHPQ RARKKNKNCRRHS LYVDFSDVGWNDWIVAPPGYQAFYCHGDCPFFLADHLNSTNHAI VQ TLVNSVNSSI PKACCVPELSAISMLYLDEYDKVVLKNYQEMVVEGCGCR

Opossum

MI PGNRMLMVLLCQVLLGGVSHASLI PETGKKKVTIQHSGGRRPGQNHHELLRDFEATLLQMFGLRRRPQPSKSAVIIDYMRDLYRLQSGEEVEKEQILNITLEYPERSTSRANTVRCFHHEEHLESIPGTRENPAFRFLNLSI PENEVISSAELRLYREQVDQGSDELGFHRINIYEVMPKPAEVPVPGHLITRLLDTRLVHHNVTRWETF DVS PAVLRWTRKQPNYGLAIEVTHLHQTRTHQGQHVRISRSLPQSGDWAQFRPLLVTFGHDGRGHTLIQHRRRAKRS PKHHPQ RPRKKGKNCRRHPLYVDFSDVGWNDWIVAPPGYHAFYCHGDCPFFLADHLNSTNHAI VQ TLVNSVNSSI PKACCVPELSAISMLYLDEYDKVVLKNYQEMVVEGCGCR

