«Evo-Devo в контексте филогении, или что мы знаем о «немодельных» видах».

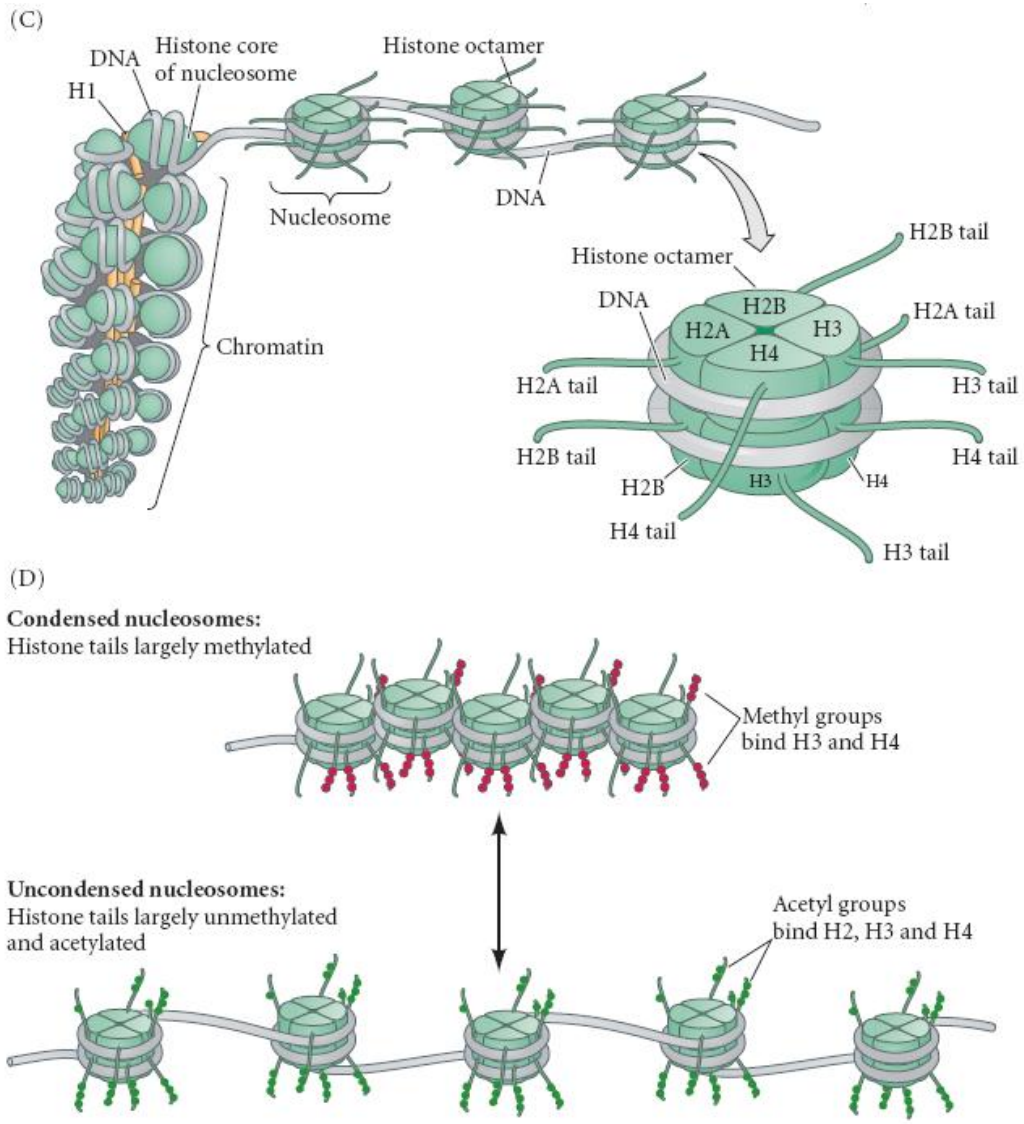
Николай Мюге
ИБР/ВНИРО

Транскрипционные факторы
(из Gilbert 2010)

TABLE 2.1 Some major transcription factor families and subfamilies

Family	Representative transcription factors	Some functions
Homeodomain:		
Hox	Hoxa1, Hoxb2, etc.	Axis formation
POU	Pit1, Unc-86, Oct-2	Pituitary development; neural fate
LIM	Lim1, Forkhead	Head development
Pax	Pax1, 2, 3, 6, etc.	Neural specification; eye development
Basic helix-loop-helix (bHLH)	MyoD, MITF, daughterless	Muscle and nerve specification; *Drosophila* sex determination; pigmentation
Basic leucine zipper (bZip)	C/EBP, AP1	Liver differentiation; fat cell specification
Zinc finger:		
Standard	WT1, Krüppel, Engrailed	Kidney, gonad, and macrophage development; *Drosophila* segmentation
Nuclear hormone receptors	Glucocorticoid receptor, estrogen receptor, testosterone receptor, retinoic acid receptors	Secondary sex determination; craniofacial development; limb development
Sry-Sox	Sry, SoxD, Sox2	Bend DNA; mammalian primary sex determination; ectoderm differentiation

Регуляция экспрессии: метилирование и ацетилирование гистонов



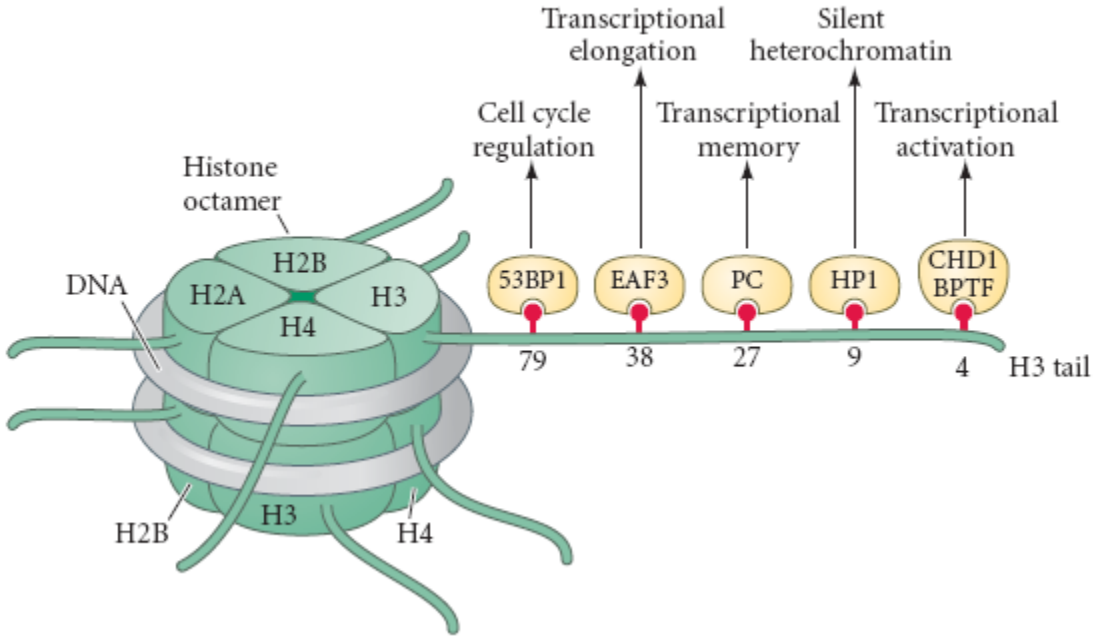
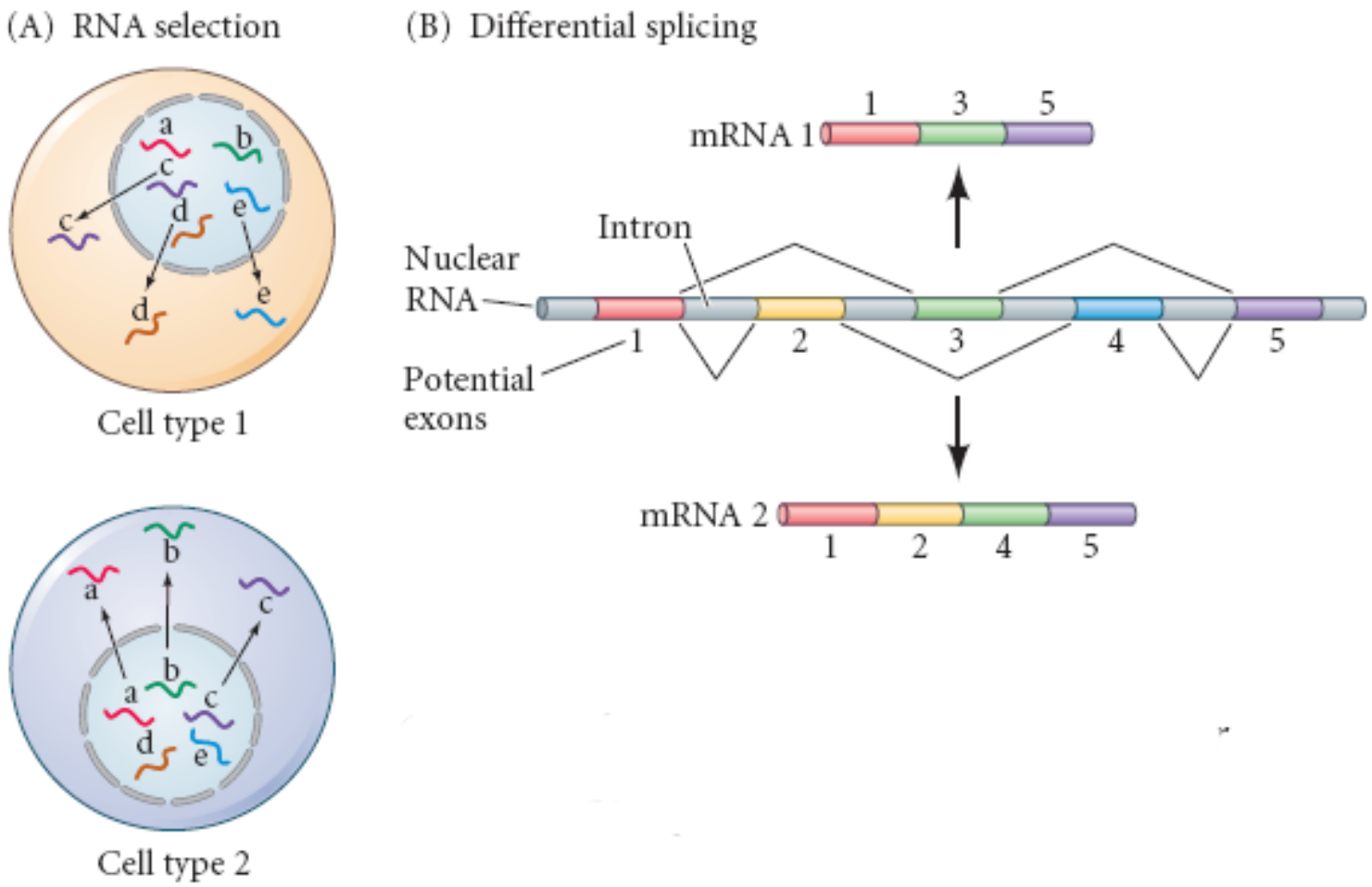
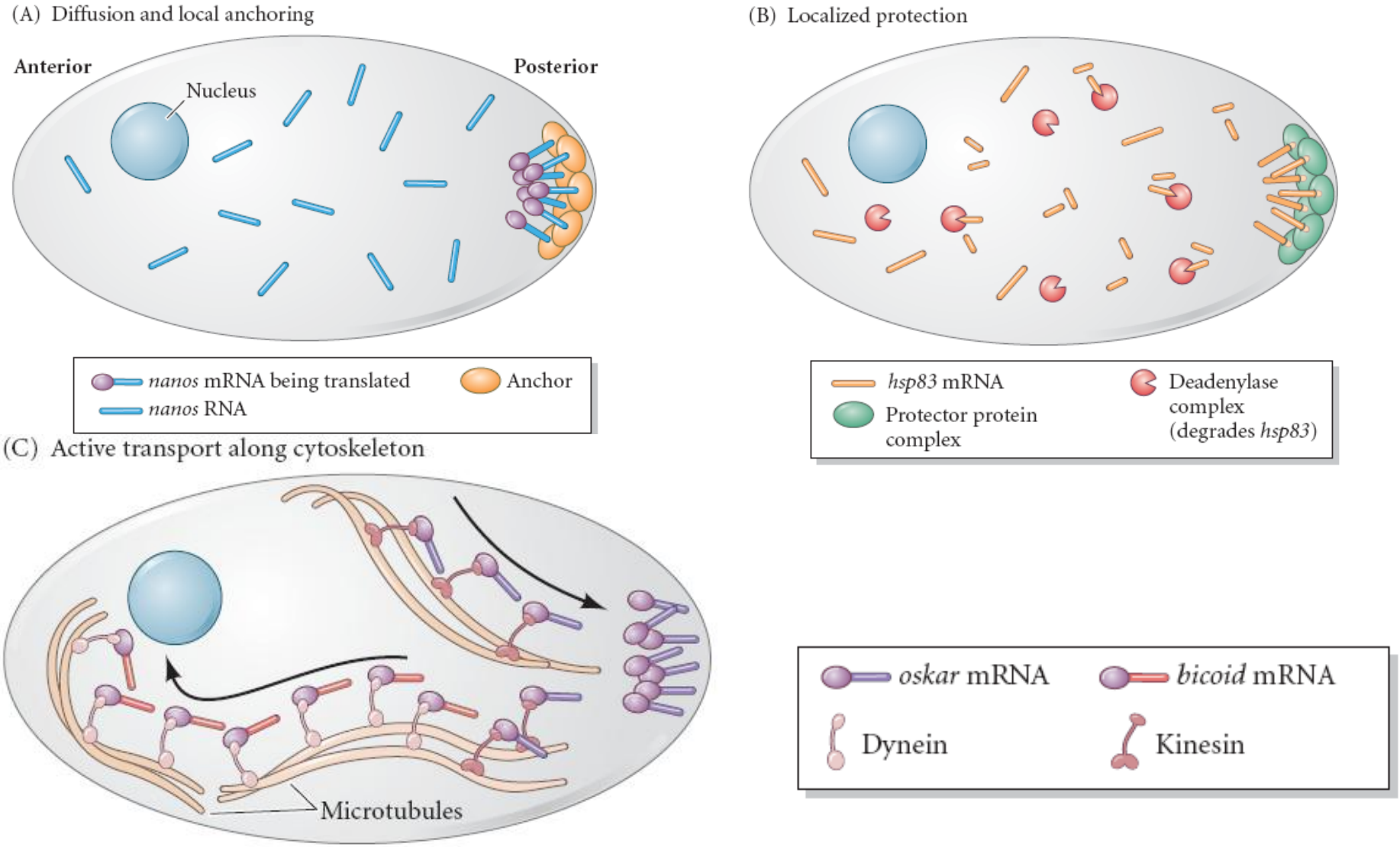


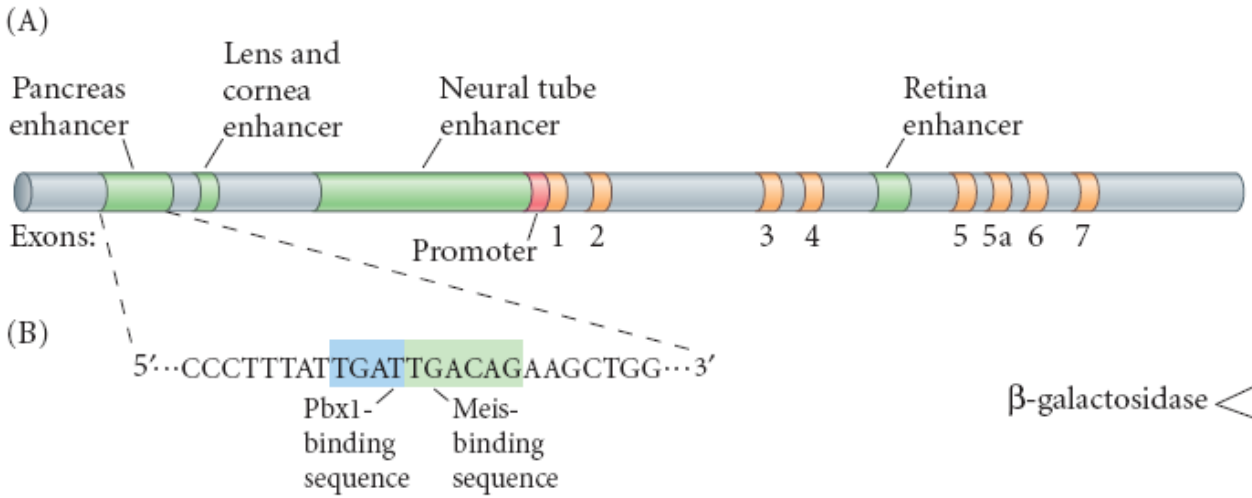
FIGURE 2.4 Histone methylations on histone H3. The tail of histone H3 (its aminomost sequence, at the beginning of the protein) sticks out from the nucleosome and is capable of being methylated or acetylated. Here, lysines can be methylated and recognized by particular proteins. Methylated lysine residues at positions 4, 38, and 79 are associated with gene activation, whereas methylated lysines at positions 9 and 27 are associated with repression. The proteins binding these sites (not shown to scale) are represented above the methyl group. (After Kouzarides and Berger 2007.)

РНК –селекция и альтернативный сплайсинг



Локализация мРНК в яйце дрозофилы (Gilbert, 2010)





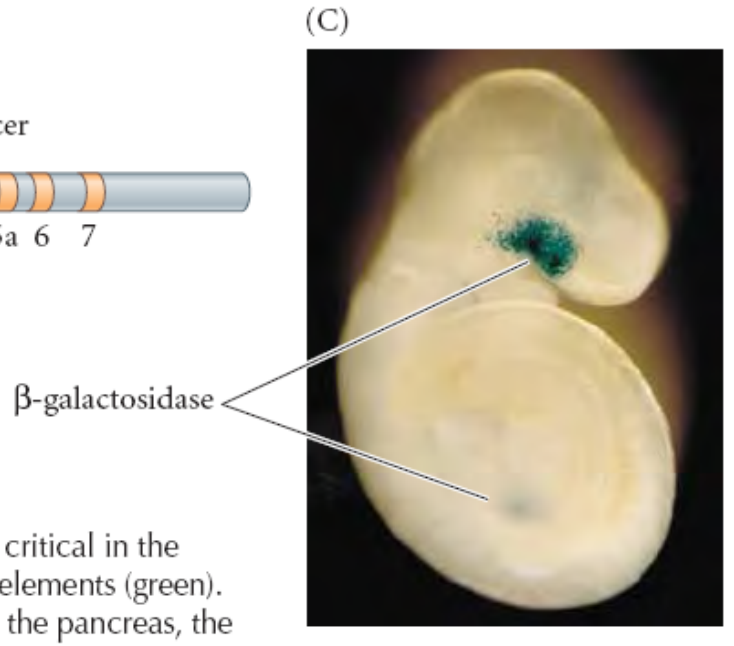
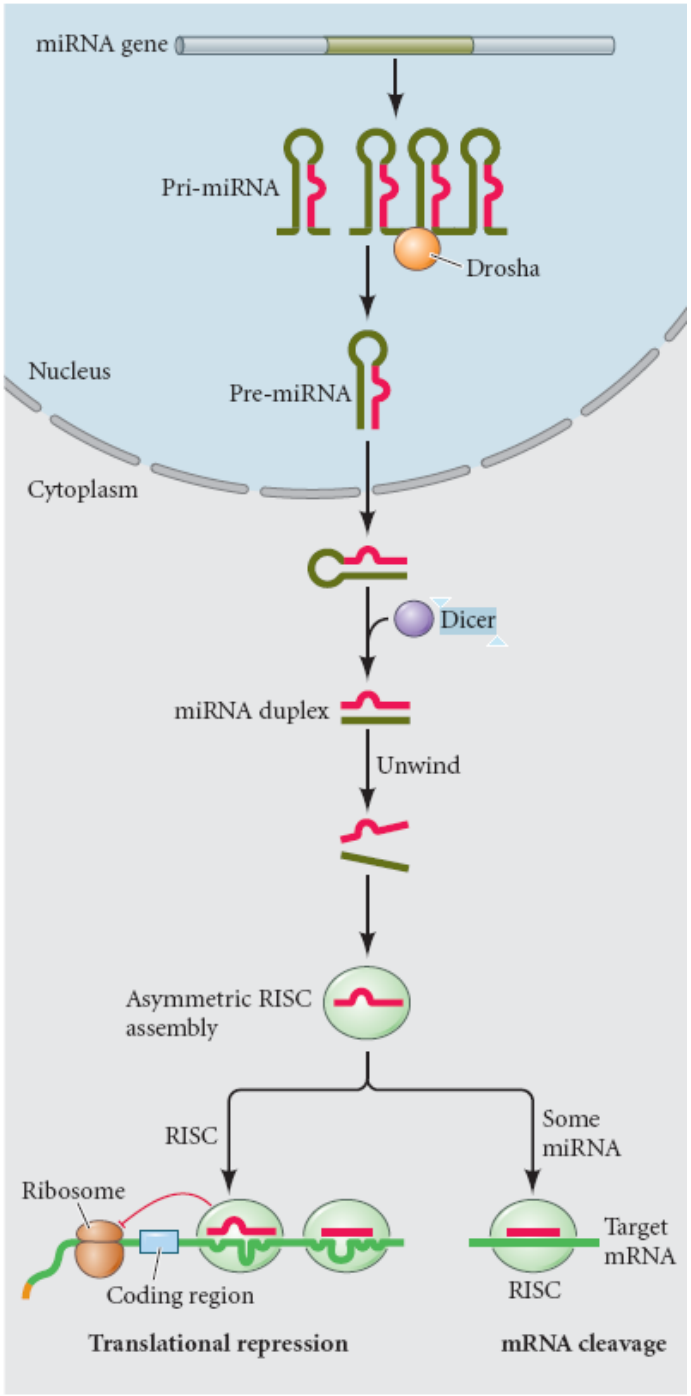
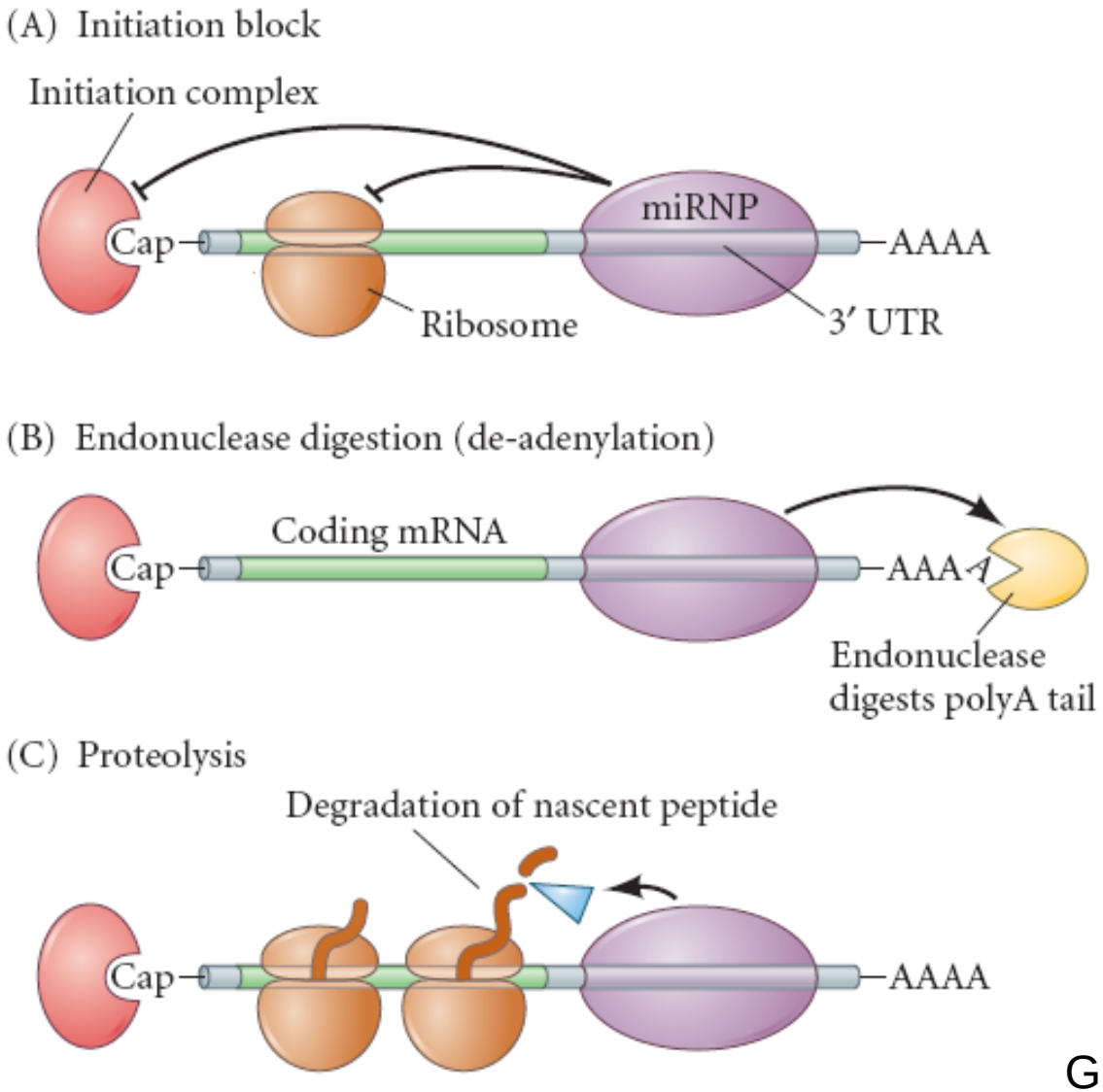


FIGURE 2.9 Enhancer region modularity. (A) The gene for Pax6, a protein critical in the development of a number of widely different tissues, has several enhancer elements (green). These enhancers direct *Pax6* expression (yellow exons 1–7) differentially in the pancreas, the lens and cornea of the eye, the retina, and the neural tube. (B) A portion of the DNA sequence of the pancreas-specific enhancer element. This sequence has binding sites for the Pbx1 and Meis transcription factors; both must be present in order to activate the *Pax6* gene in the pancreas.(C) When the gene for bacterial β-galactosidase is fused to *Pax6* enhancers for expression in the pancreas and the lens/cornea, this enzyme (which is easily stained) can be seen in those tissues. (C from Williams et al. 1998, courtesy of R. A. Lang.)


miRNA gene
Pri-miRNA
Drosha
Nucleus
Pre-miRNA
Cytoplasm
Dicer
miRNA duplex
Unwind
Asymmetric RISC assembly
RISC
Some miRNA
Ribosome
Target mRNA
Coding region
RISC
Translational repression
mRNA cleavage

Принцип работы малых РНК



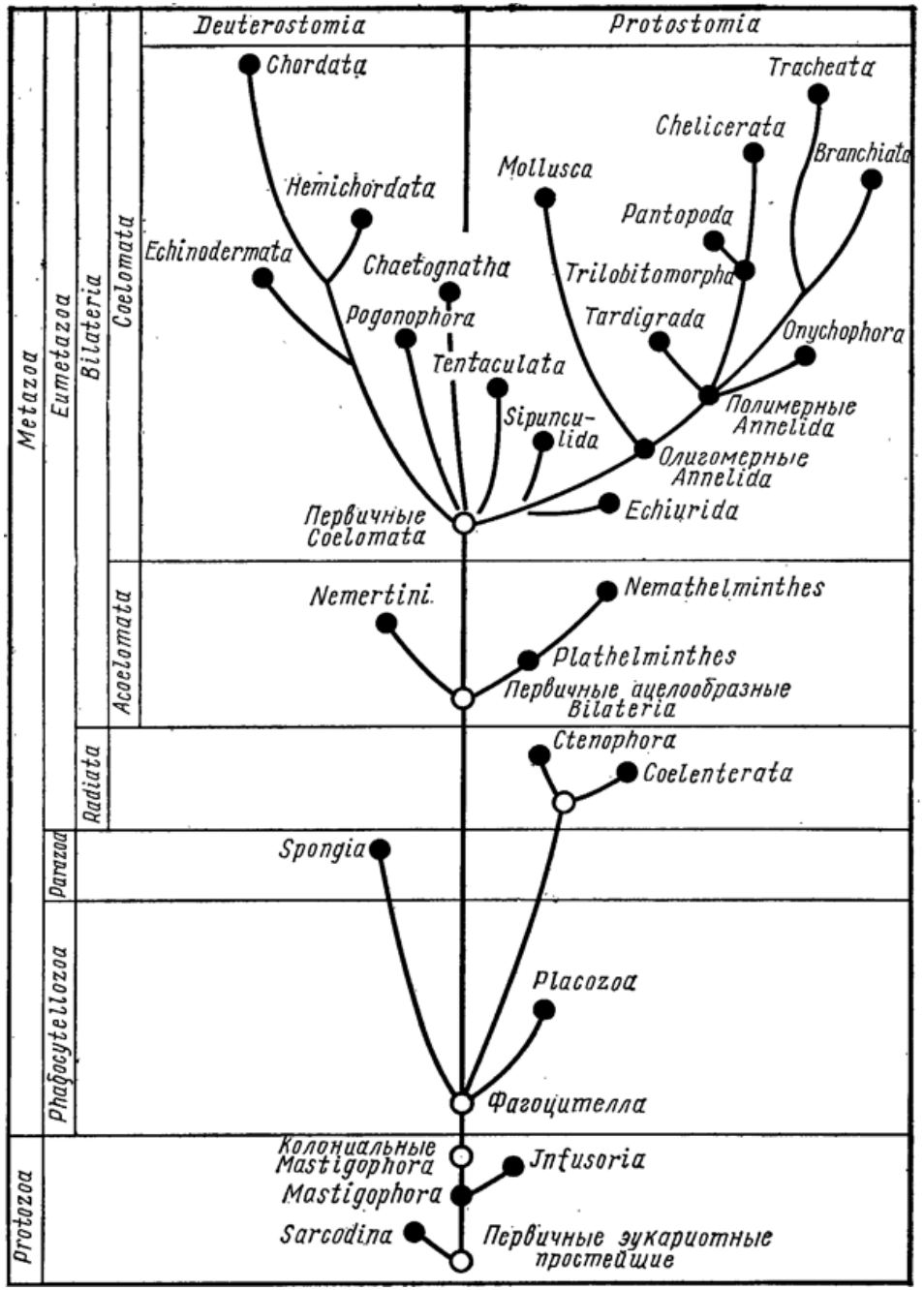
А. Блокировка трансляции

Б. Активация эндонуклеаз (обычно – с поли-А хвоста)

В. Активация протеолиза синтезируемого пептида dicer

Gilbert 2010 after Filipowicz 2008

современные «молекулярные революции» в филогении



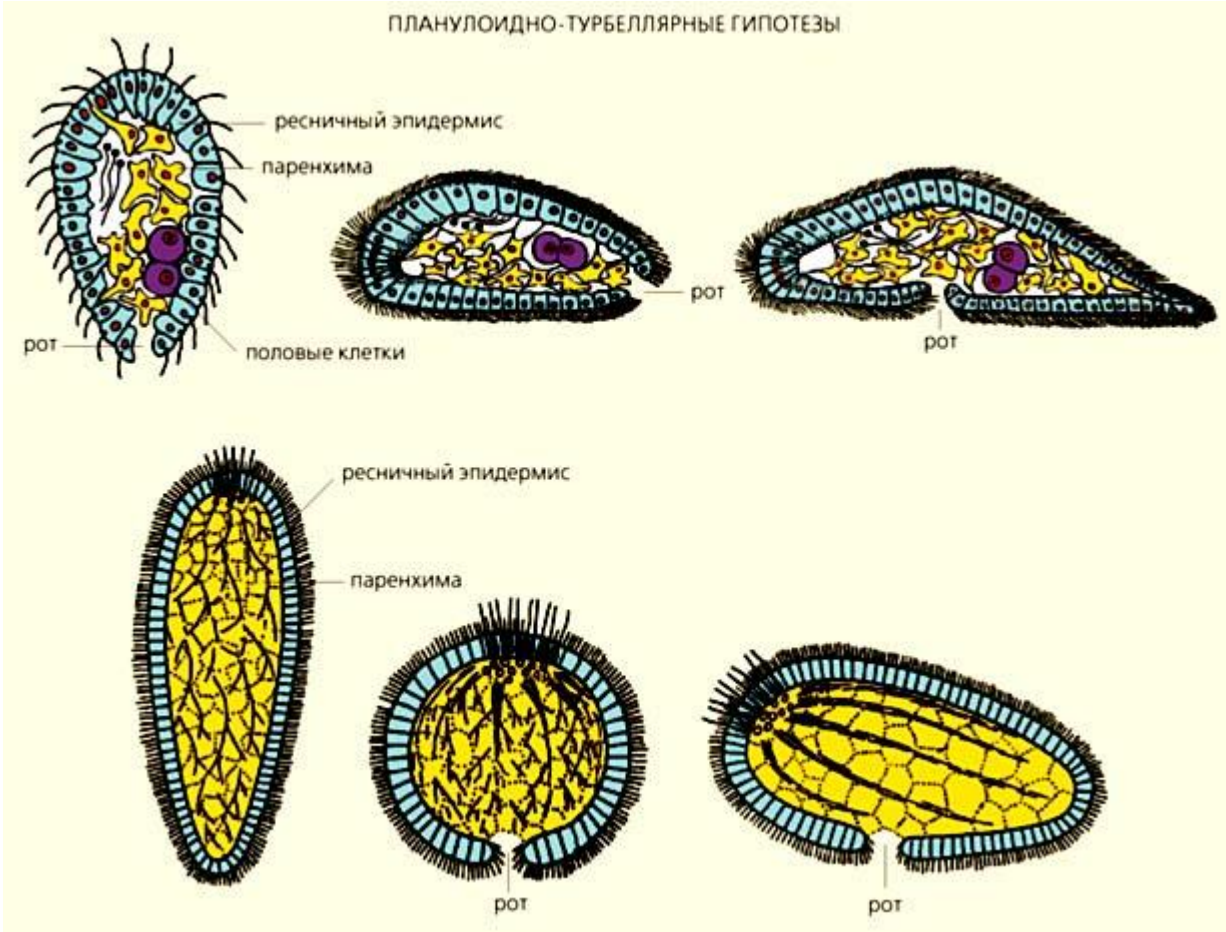
В·А·ДОГЕЛЬ

ЗООЛОГИЯ БЕСПОЗВОНОЧНЫХ

ИЗДАНИЕ СЕДЬМОЕ,
ПЕРЕРАБОТАННОЕ
И ДОПОЛНЕННОЕ

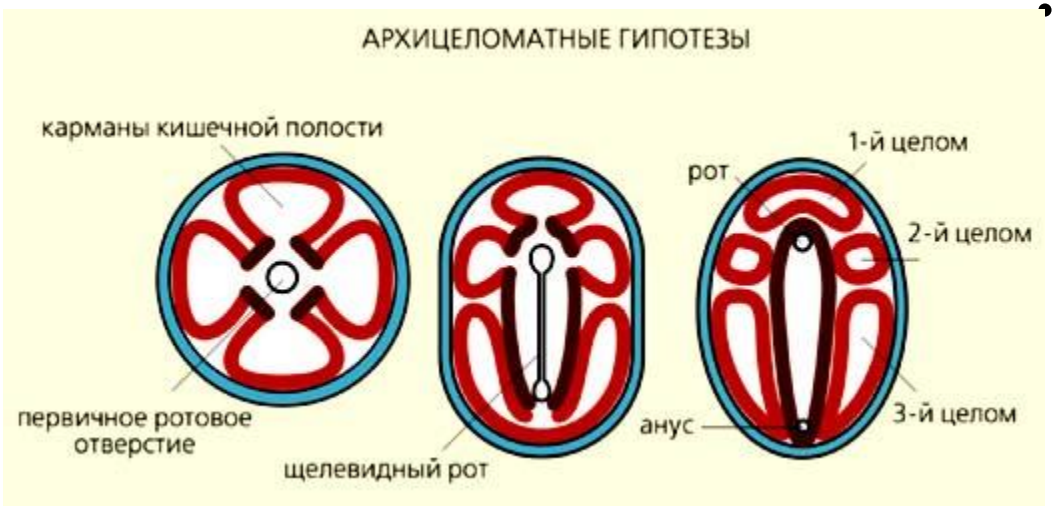
Под общей редакцией
чл.-корр. АН СССР Ю. И. Полянского

Согласно классическим представлениям, все билатерии, имеющие целом (вторичную полость тела), происходят от общего предка и противопоставляются «доцеломическим» билатериям, таким как плоские и круглые черви. Целоматы подразделяются на первичноротых (кольчатые черви, моллюски, членистоногие и др.) и вторичноротых.(хордовые, полухордовые, иглокожие). Кольчатые черви считались предками членистоногих.



- **По мнению сторонников планулоидно-турбеллярных гипотез (*вверху*), предками билатерий были организмы, напоминающие личинок современных кишечнополостных животных (планул). По одной из версий (верхний ряд), брюшная сторона первичных билатерий образовалась из бокового сектора планулоидного предка , по другой, - из ротовой поверхности.**

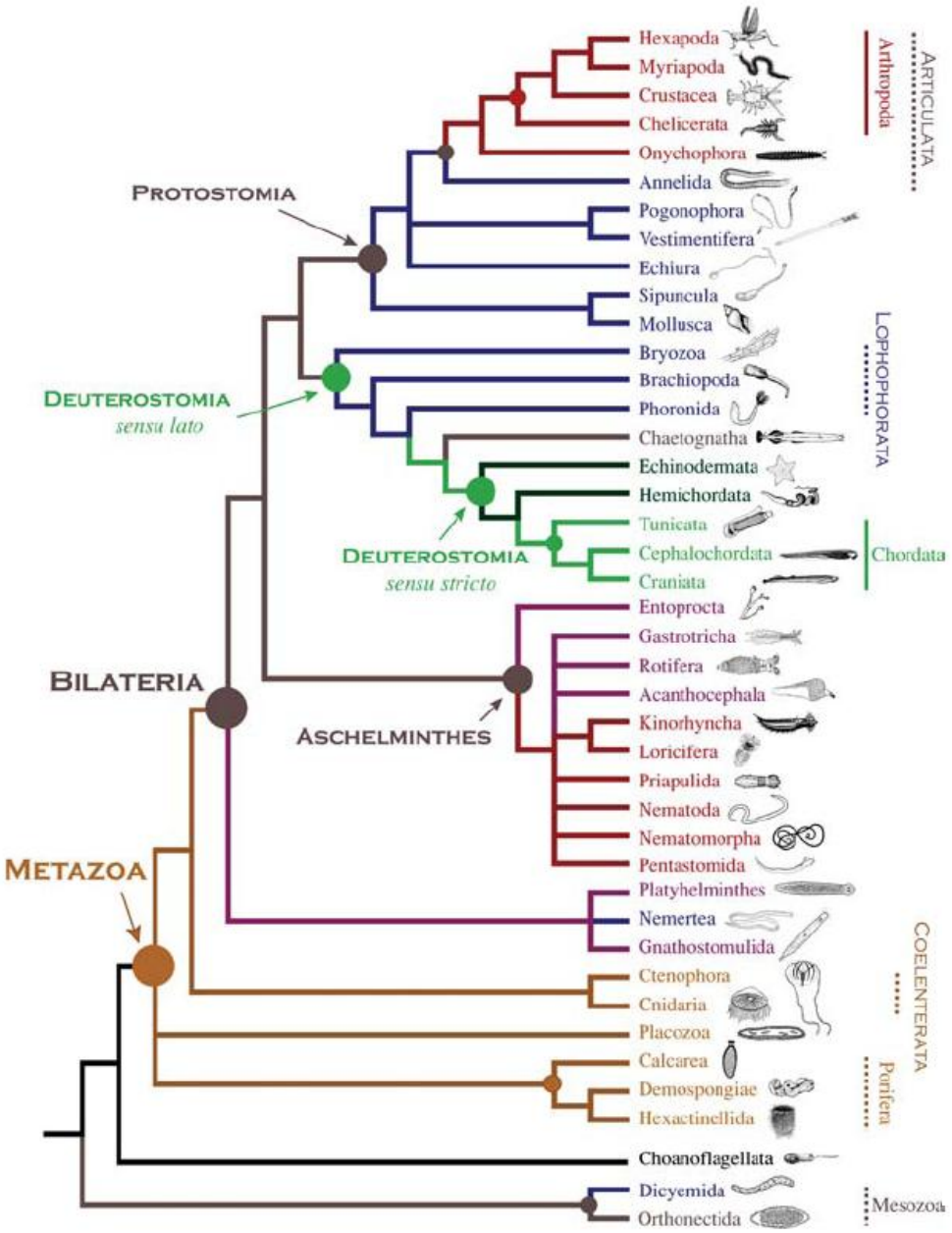
Из: Малахов В.В. Новый взгляд на происхождение билатерий. Природа 2004



Согласно архицеломатным гипотезам (*слева)*, билатерии произошли от четырехлучевых коралловых полипов, кишечная полость которых разделена на четыре камеры

Метамерные животные произошли(*Sedgwick ,1884)* **от многолучевых кораллов (вид сверху и сбоку [***Beneden E. van.1881***], а также со стороны ротовой поверхности**

Из: Малахов В.В. Новый взгляд на происхождение билатерий. Природа 2004



Систематика беспозвоночных до начала эры «молекулярных революций»

Annu. Rev. Ecol. Evol. Syst. 2004. 35:229–56
doi: 10.1146/annurev.ecolsys.35.112202.130124
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First published online as a Review in Advance on September 2, 2004

THE NEW VIEW OF ANIMAL PHYLOGENY

Kenneth M. Halanych
Department of Biological Sciences, Auburn University, Auburn, Alabama 36849; email: ken@auburn.edu

Molecular Phylogeny of the Animal Kingdom

KATHARINE G. FIELD, GARY J. OLSEN, DAVID J. LANE, STEPHEN J. GIOVANNONI, MICHAEL T. GHISELIN, ELIZABETH C. RAFF, NORMAN R. PACE, RUDOLF A. RAFF*

- Впервые систематика анализировалась пол данным сиквенса 18s РНК.
- Также впервые был применен адекватный набор методов анализа сиквенсов

Science 1988 (239) 748-753

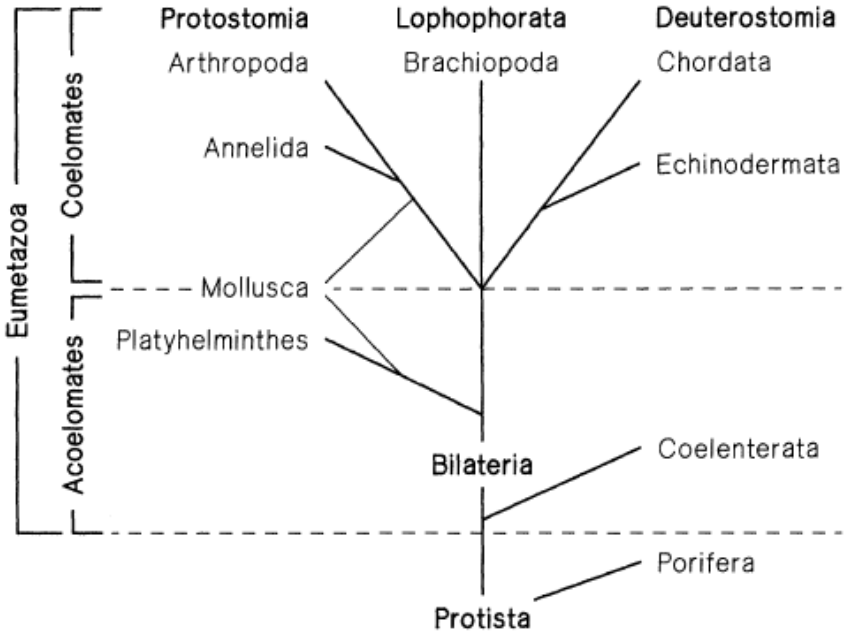

Fig. 1. Phylogenetic tree for the Metazoa, based on the views of Hyman (*5*). This phylogeny is based on morphology of both adults and embryos. Phylum names are shown in lightface lettering.

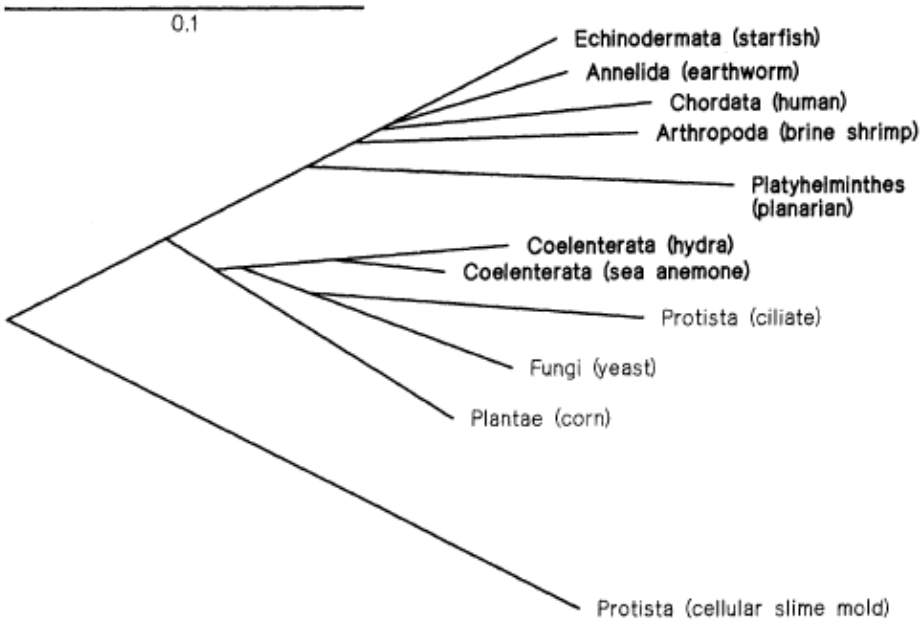

Fig. 2. An evolutionary tree for animals that is based on partial sequences of 18*S* rRNAs. The tree is read from left to right. The root of the tree is provided by the most distantly related organism, the cellular slime mold. The

Rapid Radiation of Four Coelomate Groups

Within the Bilateria, an early split separated Platyhelminthes (flatworms) from coelomate animals (Fig. 2). The close relationship among eucoelomate lineages renders it implausible that the coelom originated more than once (*2a*). Our data suggest a rapid radiation of coelomates, resulting in the divergence of four major groups: (i) Chordata, (ii) Echinodermata, (iii) Arthropoda, and (iv) "eucoelomate protostomes," a group consisting of Annelida, Mollusca, Brachiopoda, Sipuncula, and Pogonophora (Vestimentifera). The

Annu. Rev. Ecol. Evol. Syst. 2004. 35:229–56
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First published online as a Review in Advance on September 2, 2004

THE NEW VIEW OF ANIMAL PHYLOGENY

Kenneth M. Halanych
Department of Biological Sciences, Auburn University, Auburn, Alabama 36849; email: ken@auburn.edu

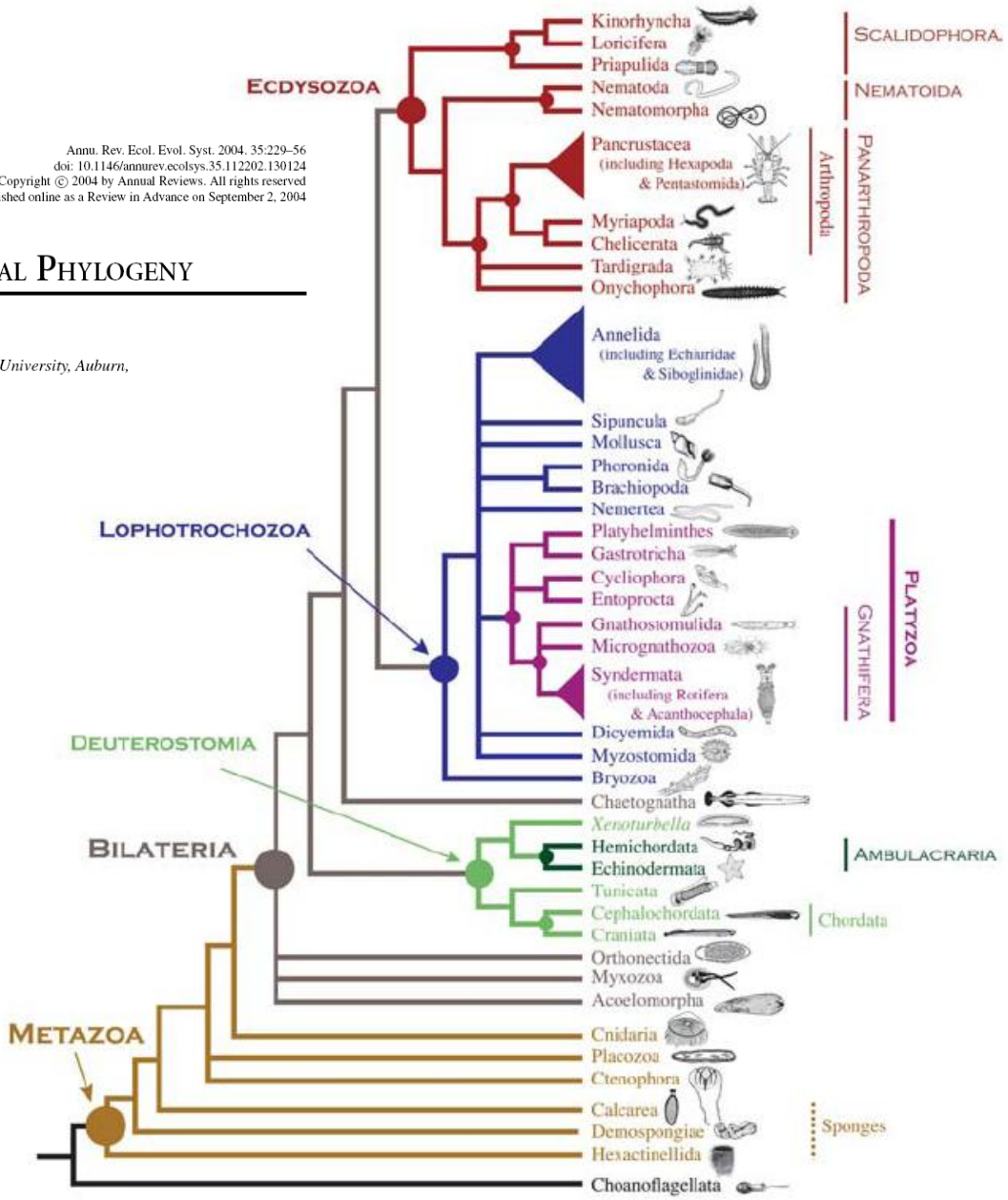
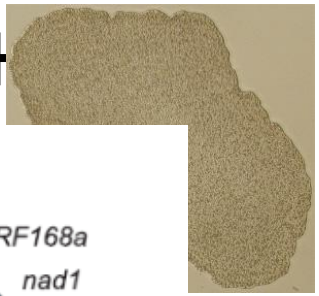
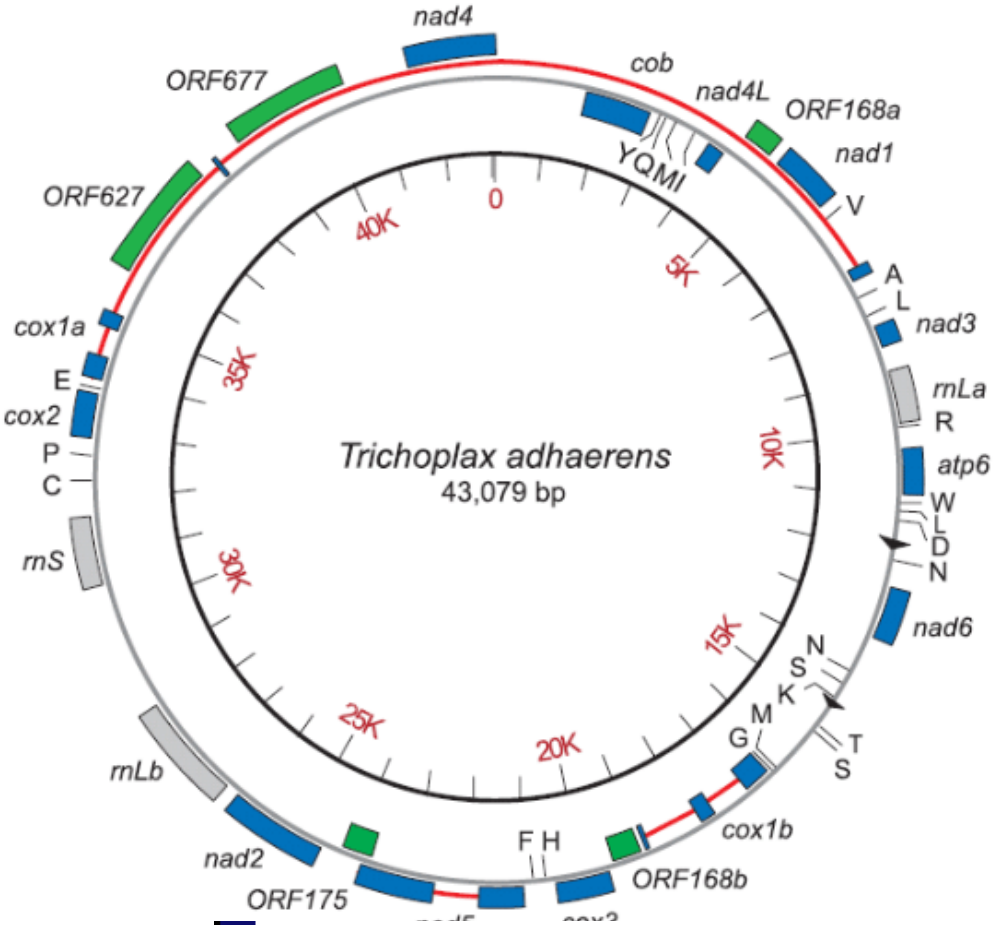


Figure 2 Modern synthesis. The new view of animal phylogeny based largely on molecular data. Details and support for various clades are discussed in the text. This

Трихоплакс – полный мт ге



У трихоплакса митохондриальный геном очень велик — 43 079 пар нуклеотидов, Некодирующие участки занимают около половины генома, как у хоанофлагеллят (у животных — не более 25%). Имеется как минимум три интрона (у воротничкового жгутиконосца *Monosiga* — четыре, у большинства животных — ни одного, за исключением некоторых кишечнополостных, имеющих 1-2 интрона). Имеется пять генов, кодирующих неизвестные белки (у *Monosiga* — шесть, у животных — обычно ни одного). Гены рибосомных белков, однако, отсутствуют — этот признак отличает трихоплакса от хоанофлагеллят и грибов и сближает его с животными.



Mitochondrial genome of *Trichoplax adhaerens* supports Placozoa as the basal lower metazoan phylum

Stephen L. Dellaporta*†, Anthony Xu*, Sven Sagasser‡, Wolfgang Jakob‡, Maria A. Moreno*, Leo W. Buss§¶, and Bernd Schierwater*‡

*Department of Molecular, Cellular, and Developmental Biology, Yale University, New Haven, CT 06520-8104; ‡Division of Ecology and Evolution Institut für Tierökologie und Zellbiologie, Tieraerztliche Hochschule Hannover, Bünteweg 17d, D-30559 Hannover, Germany; and Departments of §Ecology and Evolutionary Biology and ¶Geology and Geophysics, Yale University, New Haven, CT 06520-8106

Edited by W. Ford Doolittle, Dalhousie University, Halifax, NS, Canada, and approved April 24, 2006 (received for review March 15, 2006)

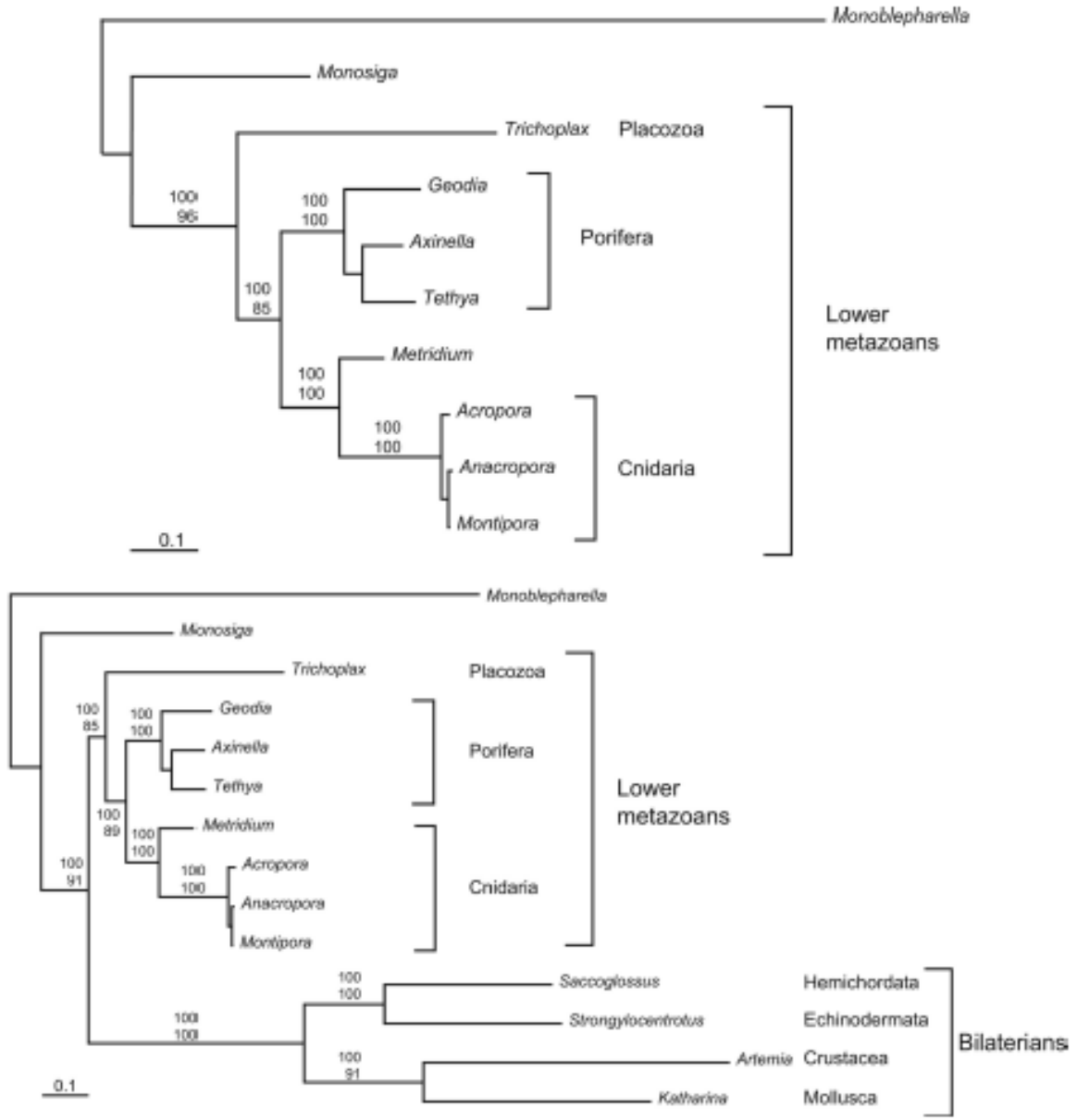


Fig. 2. Phylogenetic analysis of concatenated mitochondrial proteins. The data set consisted of a total of 2,730 amino acid positions concatenated from 12

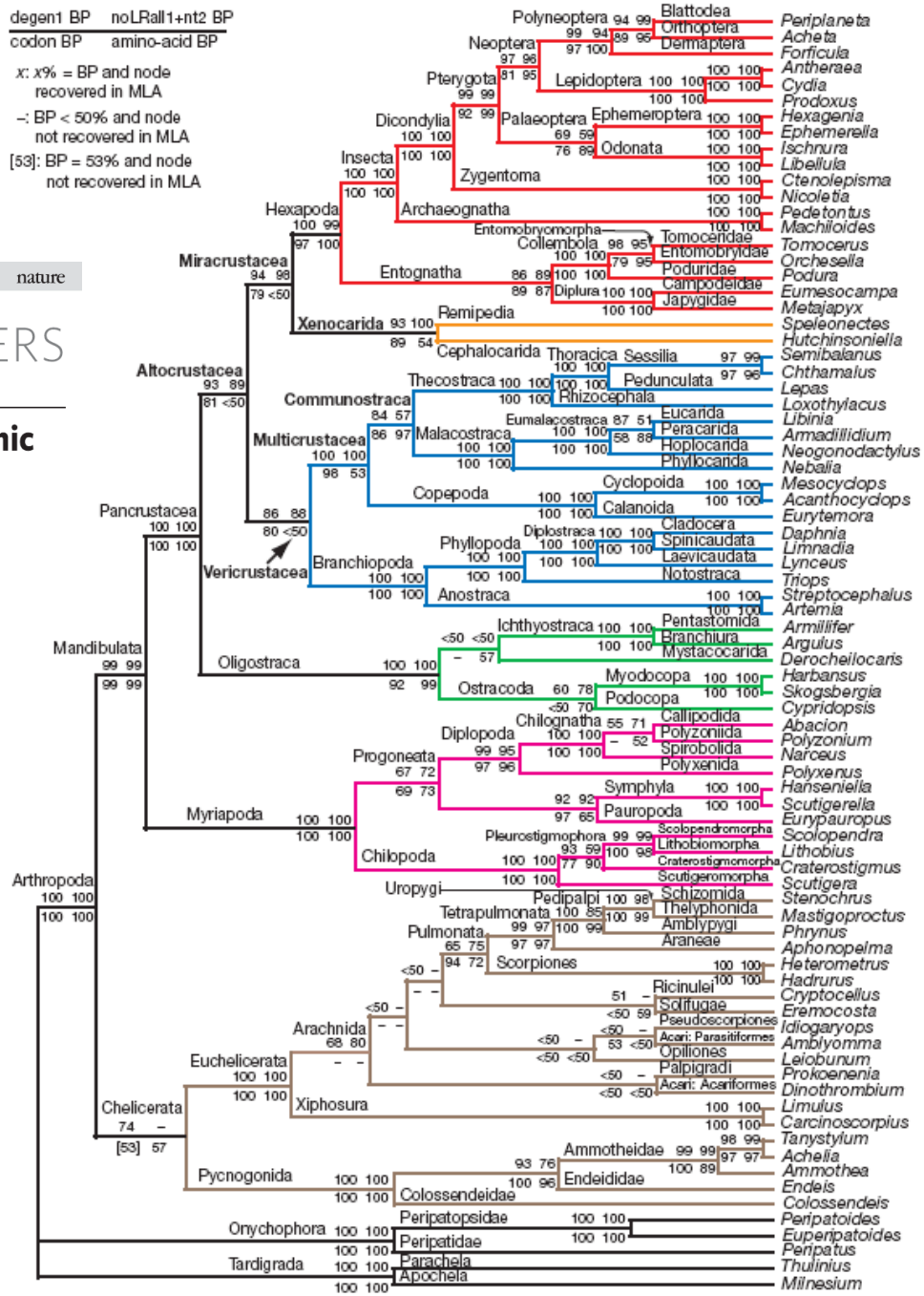
PNAS 2006

doi:10.1038/nature08742 nature

LETTERS

Arthropod relationships revealed by phylogenomic analysis of nuclear protein-coding sequences

Jerome C. Regier[1], Jeffrey W. Shultz[1,2,3], Andreas Zwick[1], April Hussey[1], Bernard Ball[4], Regina Wetzer[5], Joel W. Martin[5] & Clifford W. Cunningham[4]



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Our results strongly support Pancrustacea (Hexapoda plus Crustacea) but also strongly favour the traditional morphology-based Mandibulata11 (Myriapoda plus Pancrustacea) over the molecule-based Paradoxopoda (Myriapoda plus Chelicerata)2,5,12. In addition to Hexapoda, Pancrustacea includes three major extant lineages of ‘crustaceans’, each spanning a significant range of morphological disparity. These are Oligostraca (ostracods, mystacocarids, branchiurans and pentastomids), Vericrustacea (malacostracans, thecostracans, copepods and branchiopods) and Xenocarida (cephalocarids and remipedes). Finally,within Pancrustacea we identify Xenocarida as the long-sought sister group to theHexapoda, a result confirming that ‘crustaceans’ are notmonophyletic.

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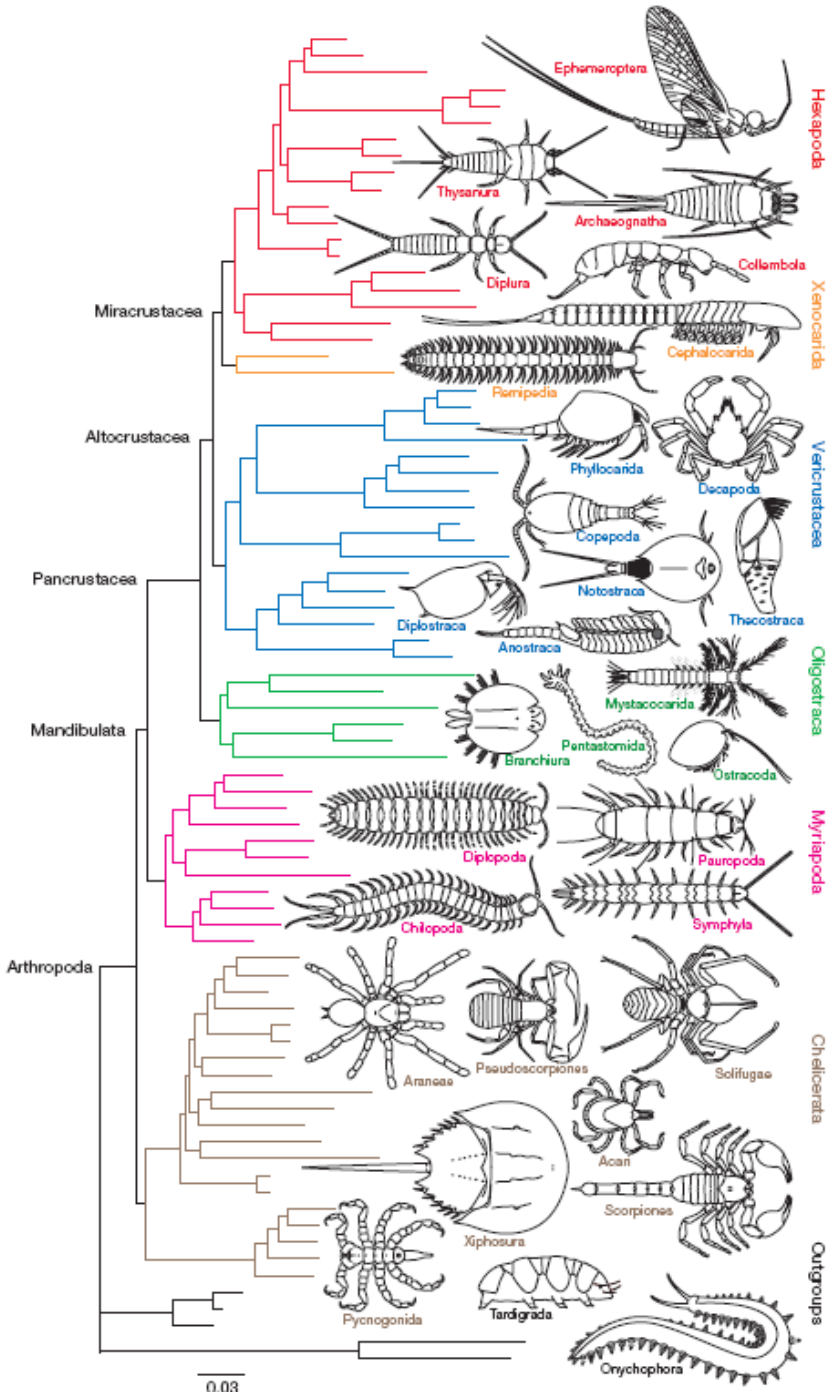

- 1. Ракообразные – полифилетичная группа, состоящая из трех таксонов (Oligostraca, Vericrustacea Xenocarida)
- 2. Xenocarida – сестринская группа насекомым
- 3. Многоножки ближе к ракам чем к паукам (таксон Mandibulata)

doi:10.1038/nature08742 nature

LETTERS

Arthropod relationships revealed by phylogenomic analysis of nuclear protein-coding sequences

Jerome C. Regier[1], Jeffrey W. Shultz[1,2,3], Andreas Zwick[1], April Hussey[1], Bernard Ball[4], Regina Wetzer[5], Joel W. Martin[5] & Clifford W. Cunningham[4]

История зверька Xenoturbella

- Описаны из фьордов Швеции в 1949 г. по сборам 1915 года

  (Westblad, E. (1949). *Xenoturbella bocki* n.g., n.sp., a peculiar, primitive turbellarian type. *Arkiv för Zoologi, 1, 3-29.)*

- Отнесены к бескишечным турбеллариям (Acoelomortpha)

До 4 см в длину. У них нет пищеварительного тракта, половой системы и централизованного мозга или нервного узла.[1] Имеется орган равновесия (статоцист), диффузная нервная система (расположена под эпидермисом), мешкообразная кишка (без заднего прохода) образует единственную полость тела, обнаружены гаметы. Морские червеобразные животные, найденные у побережья Швеции (на глубине 60-100 м в фьордах), Шотландии, Исландии.

- Молекулярные исследования (1997) – близкое родство с моллюсками. Гипотеза о неотеничной трохофоре, перешедшей к ползанию на дне и питанию. Noren & Jondelius, 1997

Michael Norén, Ulf Jondelius
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Xenoturbella's molluscan relatives...

Despite detailed morphological studies[1–4], the phylogenetic relationships of *Xenoturbella bocki* Westblad 1949 have remained unclear. The marine, worm-like *X. bocki* was first described as an acoel flatworm[5]. Later it was proposed to be a deuterostome[1], and most recently as the sister taxon of the Bilateria[6]. Here we present DNA sequence data that place *X. bocki* within the protostome clade Eutrochozoa.

We used standard DNA extraction, polymerase chain reaction (PCR) and sequencing techniques to sequence 1,759 nucleotides of the small-subunit ribosomal RNA gene (18S rRNA) and 708 base pairs of the protein-coding mitochondrial cytochrome *c* oxidase subunit I gene (COI) from five specimens of *X. bocki* collected on the west coast of Sweden. We sequenced the corresponding COI fragment from the flatworm *Graffilla buccinicola* for comparison. We used these and sequences obtained from GenBank to construct two matrices for cladistic analysis.

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Noren & Jondelius, 1997 – 18s tree

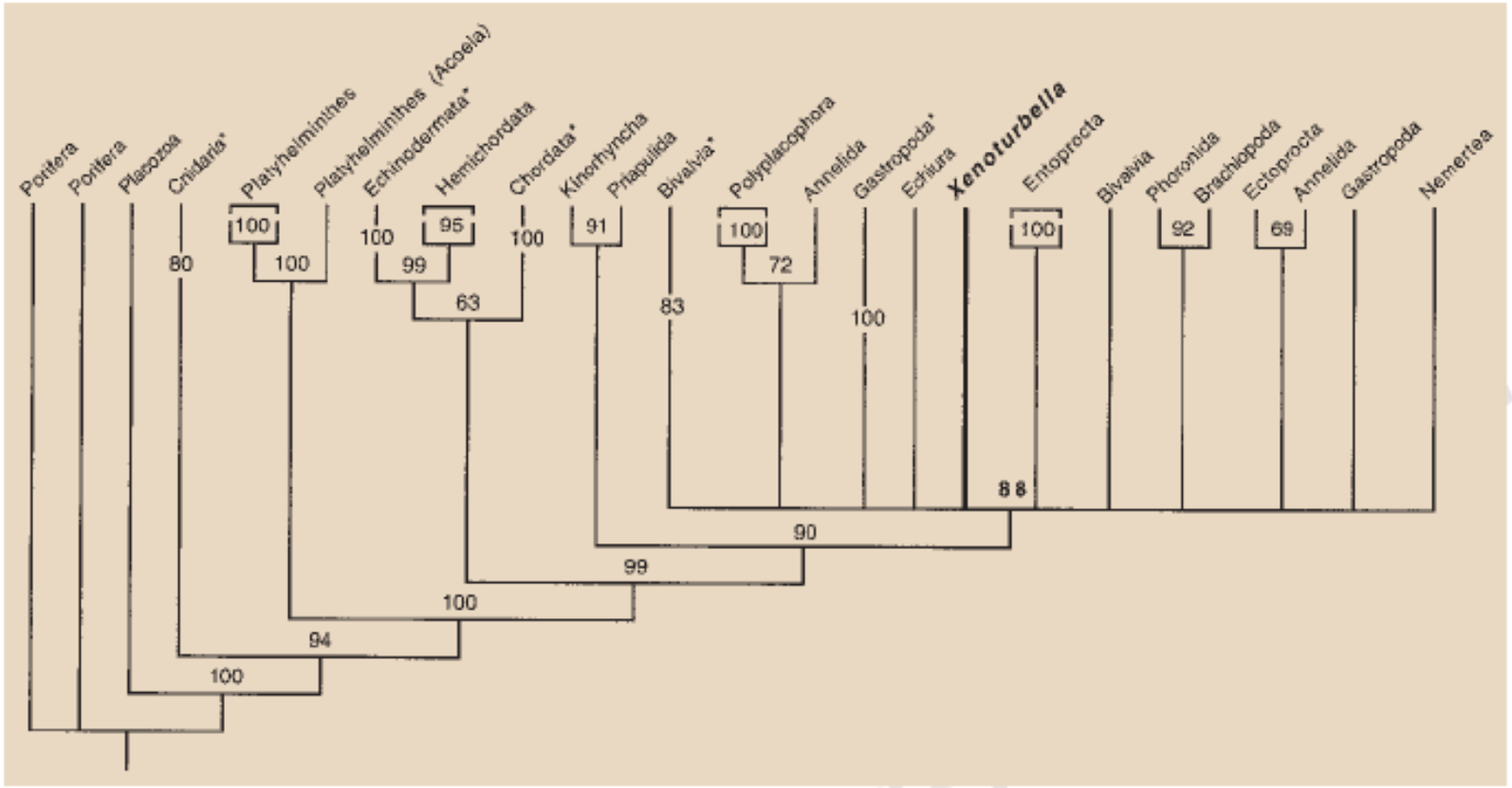

Figure 1 Consensus tree showing groups present in 60% of jack-knife replicates from analysis of 18S rRNA matrix (successive weighting of characters, 10 iterations with 100 replicates each, deletion frequency e^{-1}). Labels indicate jack-knife frequencies. Clades marked with asterisks represent multiple terminals.

Noren & Jondelius, 1997 – COI tree

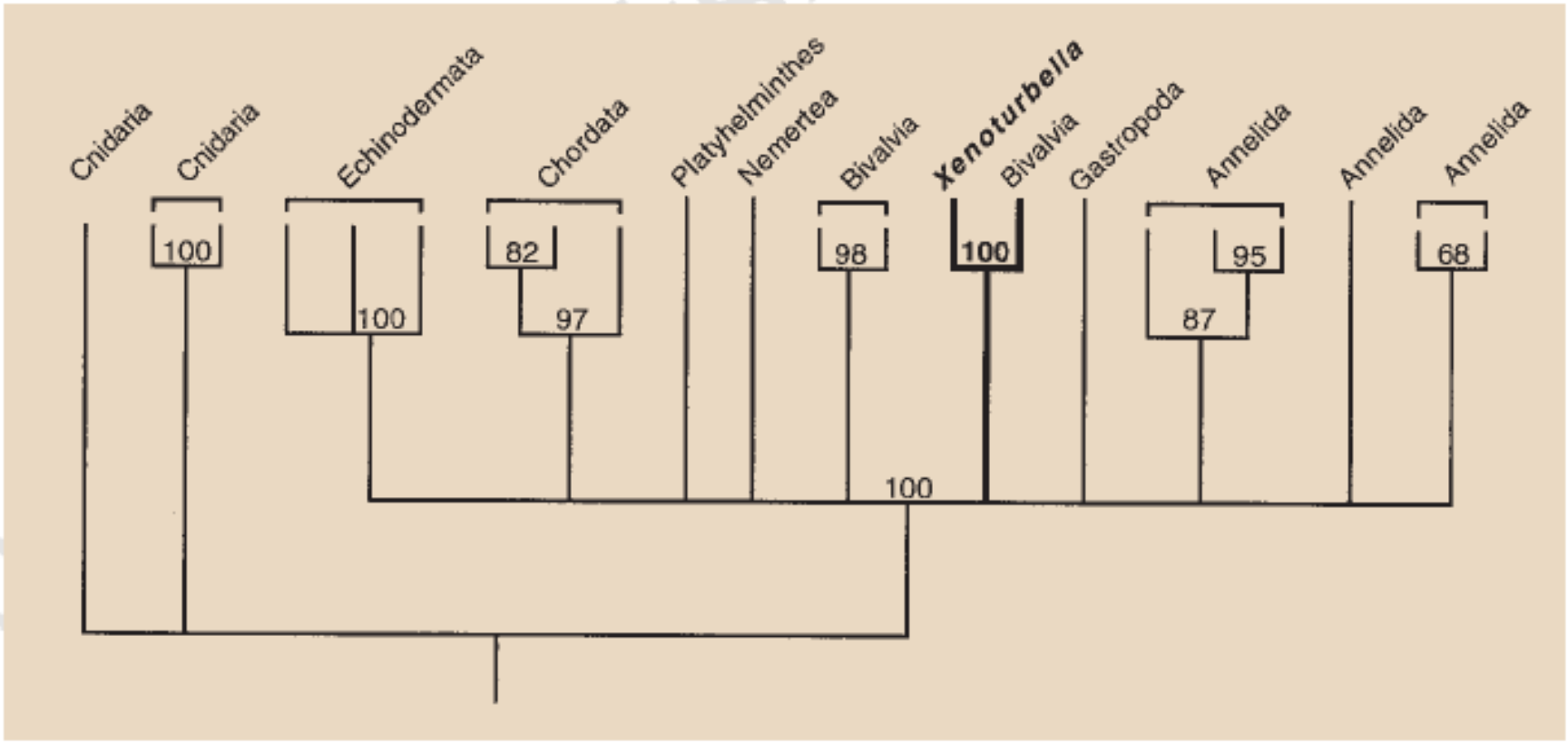

Figure 2 Consensus tree showing groups present in 60% of jack-knife replicates from analysis of COI matrix (3,000 replicates, 5 random additions and branch swapping, deletion frequency e^{-1}). Labels indicate jack-knife frequencies. Full details of tree topology and sequence alignment are available from the authors.

...and molluscan embryogenesis

Xenoturbella bocki Westblad[1] is a strange animal — a 2-cm-long, slowly moving ciliated bag with no anus and no organs except for a position-sensing statocyst containing flagellated statoconia[2]. Despite the animal's peculiarities, it has been neglected by most textbooks. I now report a study of oogenesis in *X. bocki* which, together with the nucleotide data of Norén and Jondelius[3], contradicts earlier hypotheses as to the phylogeny of the animal and instead suggests a molluscan relationship close to or within the protobranch bivalves.

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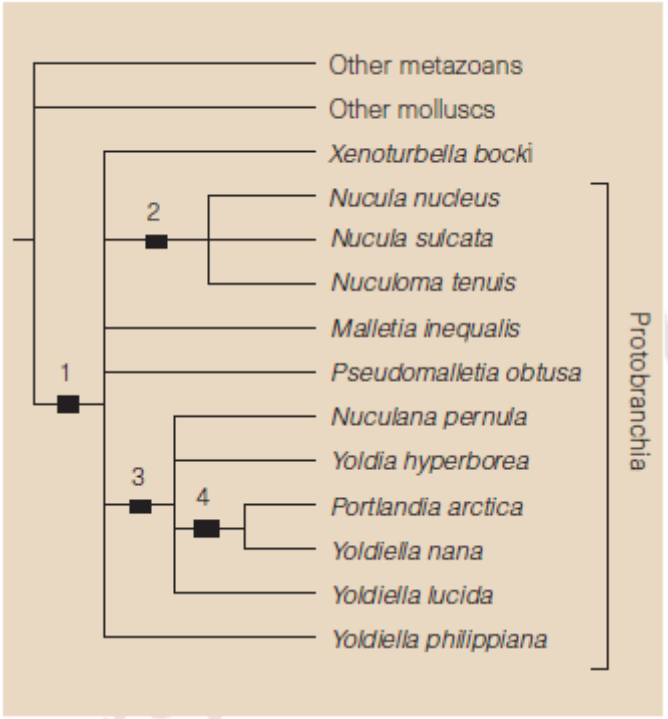

Figure 2 Cladistic analyses of oogenesis indicates that *Xenoturbella bocki* is a sister group or a subgroup of protobranch bivalves. The analysed characters, with their apomorphic states, are: **1,**

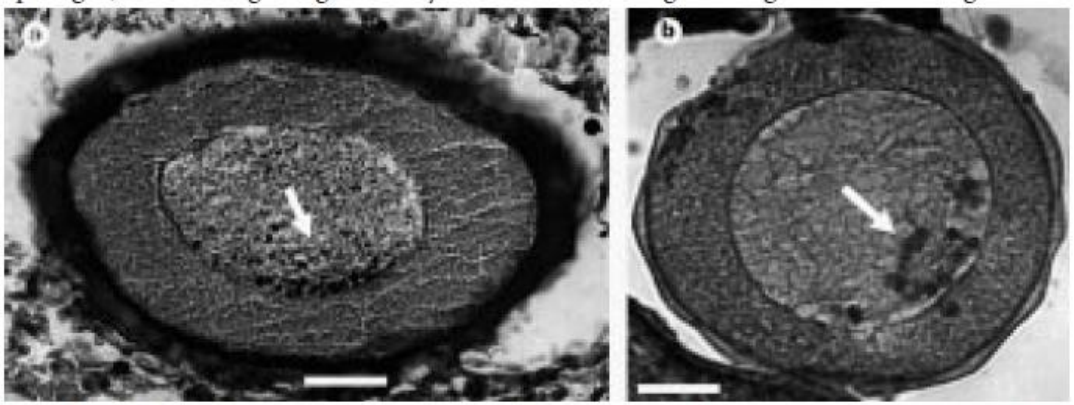

Figure 1 Relationship of *Xenoturbella bocki* to molluscs. Late vitellogenous oocytes of **a,** *Xenoturbella bocki* and **b,** the protobranch mollusc *Nucula nucleus*. Scale bars, 20 μm.

Nature © Macmillan Publishers Ltd 1997

2003 новые молекулярные данные

Xenoturbella is a deuterostome that eats molluscs

Sarah J. Bourlat[1], Claus Nielsen[2], Anne E. Lockyer[3], D. Timothy J. Littlewood[3] & Maximilian J. Telford[1]

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[2]*Zoological Museum (University of Copenhagen), Universitetsparken 15, DK-2100 Copenhagen, Denmark*
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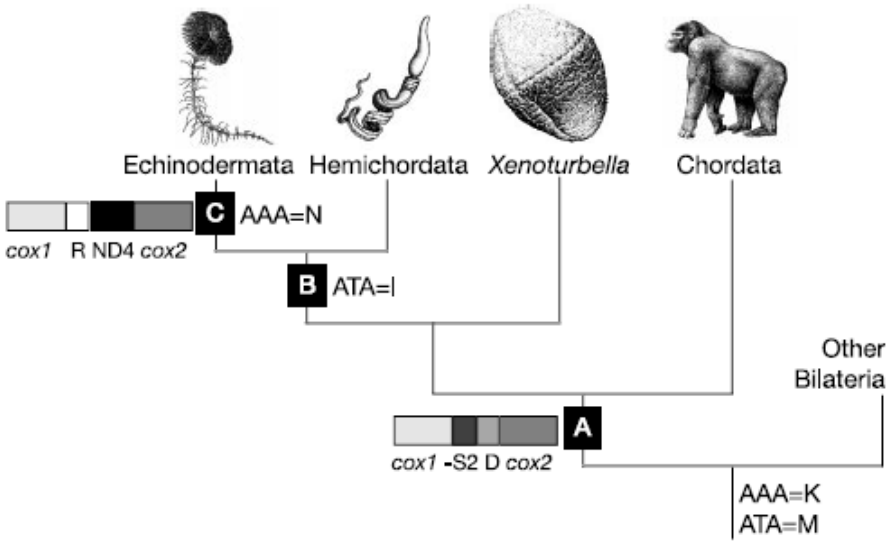

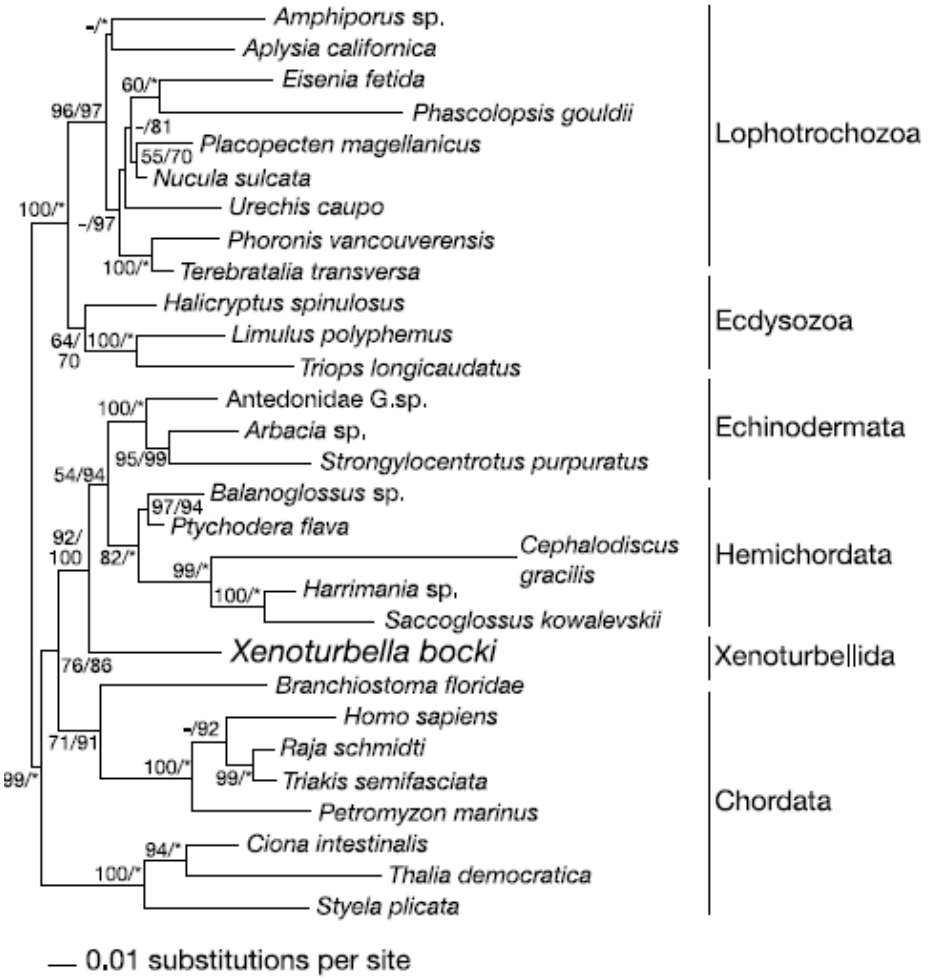

Figure 2 Position of *Xenoturbella* within the deuterostomes as suggested by our analyses of *SSU* and mitochondrial data. The distribution of synapomorphic molecular character

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2006

Deuterostome phylogeny reveals monophyletic chordates and the new phylum Xenoturbellida

Sarah J. Bourlat[1], Thorhildur Juliusdottir[2], Christopher J. Lowe[3], Robert Freeman[4], Jochanan Aronowicz[3], Mark Kirschner[5], Eric S. Lander[4,6], Michael Thorndyke[7], Hiroaki Nakano[7], Andrea B. Kohn[8], Andreas Heyland[8], Leonid L. Moroz[8], Richard R. Copley[2] & Maximilian J. Telford[1]

and urochordates, meaning that chordates are paraphyletic[2]. To study the relationships among all deuterostome groups, we have assembled an alignment of more than 35,000 homologous amino acids, including new data from a hemichordate, starfish and *Xenoturbella*. We have also sequenced the mitochondrial genome of *Xenoturbella*. We support the clades Olfactores (urochordates and vertebrates) and Ambulacraria (hemichordates and echinoderms[6]). Analyses using our new data, however, do not support a cephalochordate and echinoderm grouping and we conclude that chordates are monophyletic. Finally, nuclear and mitochondrial data place *Xenoturbella* as the sister group of the two ambulacrarian phyla[1]. As such, *Xenoturbella* is shown to be an independent phylum, Xenoturbellida, bringing the number of living deuterostome phyla to four.

NATURE|Vol 444|2 November 2006

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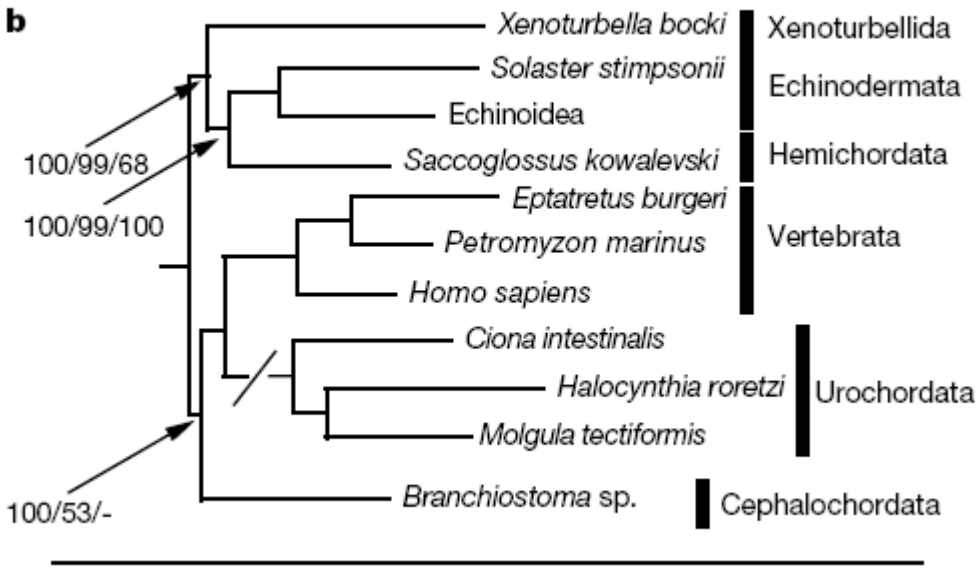

- Figure 1 | Phylogenetic analyses of 170 nuclear proteins and 13 mitochondrial proteins support a monophyletic chordate clade and an independent deuterostome phylum of Xenoturbellida.

b Bayesian analysis of nuclear
data after the addition of asteroid, hemichordate and xenoturbellid data. The new sequences join the branch to the echinoderm, and the cephalochordates now join the chordate branch. This indicates that the previous result is due to systematic error. Xenoturbella is the sister group of the Ambulacraria (echinoderms plus hemichordates).

- .

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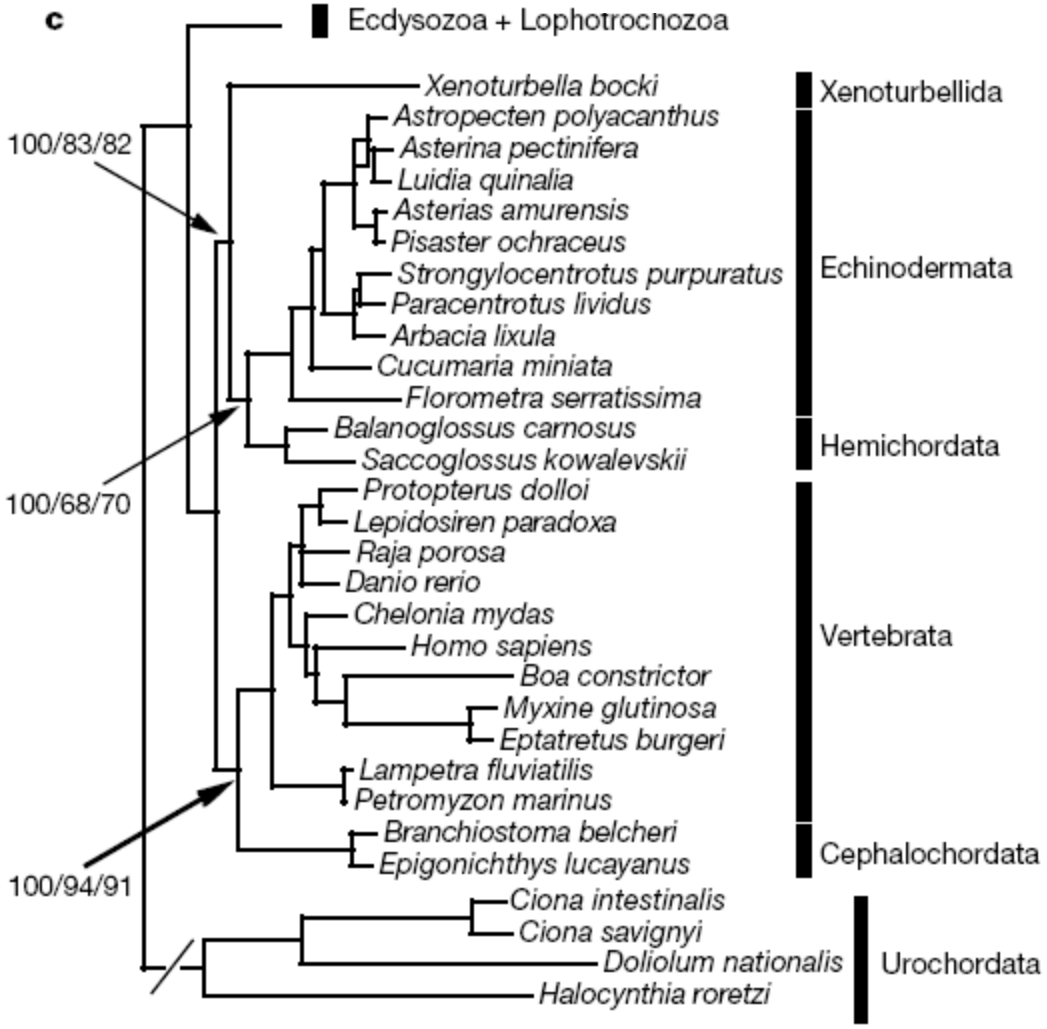


- C. Bayesian analysis of mitochondrial data with the amino acids M, I, N and K recoded as missing data places the cephalochordates with vertebrates; Xenoturbella is the sister group of Ambulacraria.

EVOLUTION & DEVELOPMENT 9:5, 409–415 (2007)

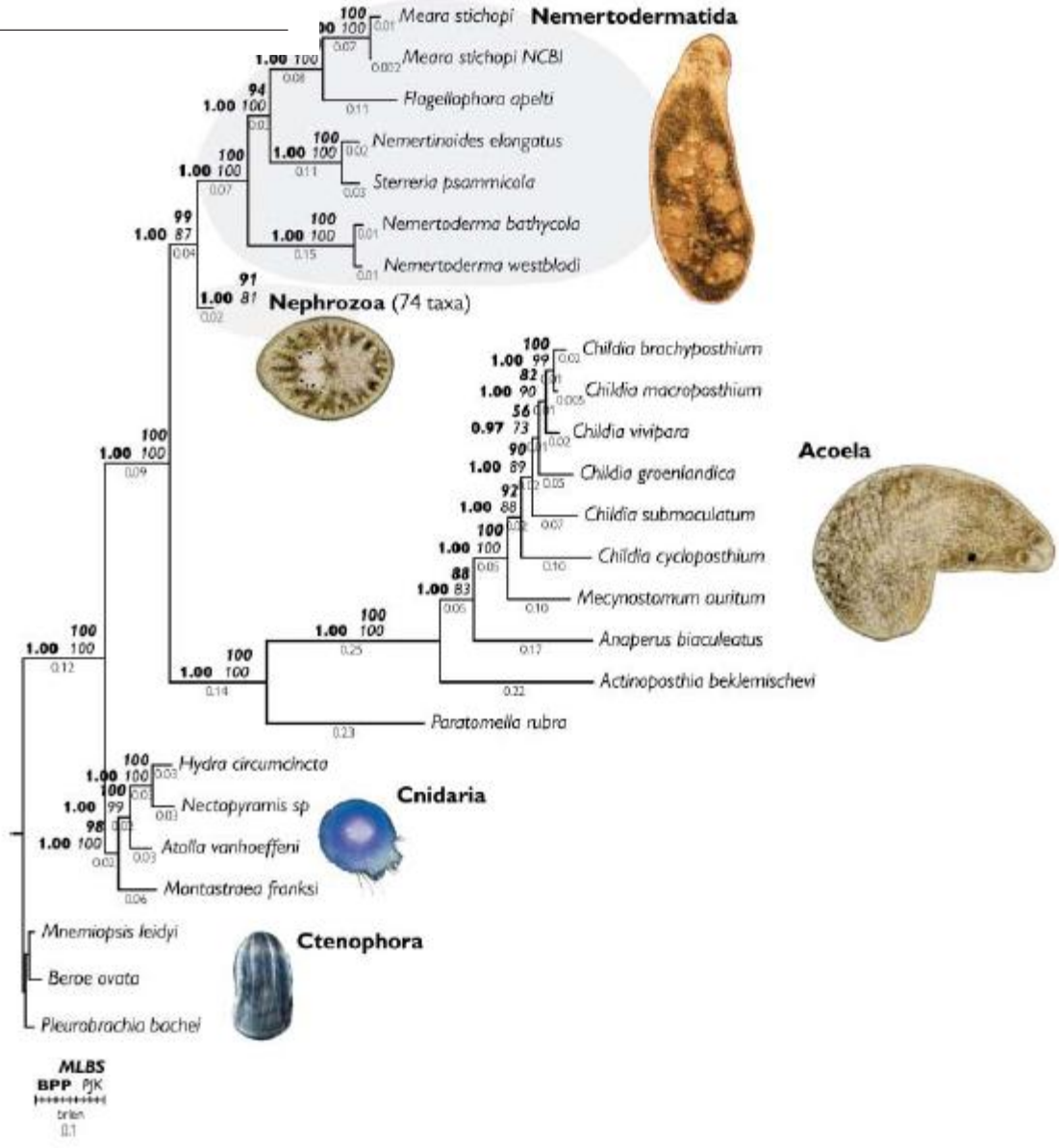
Phylogenetic distribution of microRNAs supports the basal position of acoel flatworms and the polyphyly of Platyhelminthes

Lorenzo F. Sempere,[a] Pedro Martinez,[b,c] Charles Cole,[a,d] Jaume Baguñà,[b] and Kevin J. Peterson[e,*]

SUMMARY Phylogenetic analyses based on gene sequences suggest that acoel flatworms are not members of the phylum Platyhelminthes, but instead are the most basal branch of triploblastic bilaterians. Nonetheless, this result has been called into question. An alternative test is to use qualitative molecular markers that should, in principle, exclude the possibility of convergent (homoplastic) evolution in unrelated groups. microRNAs (miRNAs), noncoding regulatory RNA molecules that are under intense stabilizing selection, are a newly discovered set of phylogenetic markers that can resolve such taxonomic disputes. The acoel *Childia* sp. has recently been shown to possess a subset of the conserved core of miRNAs found across deuterostomes and protostomes, whereas a polyclad flatworm—in addition to this core subset—possesses miRNAs restricted to just protostomes. Here, we examine another acoel, *Symsagittifera roscoffensis*, and three other platyhelminths. Our results show that the distribution of miRNAs in *S. roscoffensis* parallels that of *Childia*. In addition, two of 13 new miRNAs cloned from a triclad flatworm are also found in other lophotrochozoan protostomes, but not in ecdysozoans, deuterostomes, or in basal metazoans including acoels. The limited set of miRNAs found in acoels, intermediate between the even more reduced set in cnidarians and the larger and expanding set in the rest of bilaterians, is compelling evidence for the basal position of acoel flatworms and the polyphyly of Platyhelminthes.

Dismissal of Acoelomorpha: Acoela and Nemertodermatida are separate early bilaterian clades

Andreas Wallberg, Marco Curini-Galletti, Afsaneh Ahmadzadeh & Ulf Jondelius



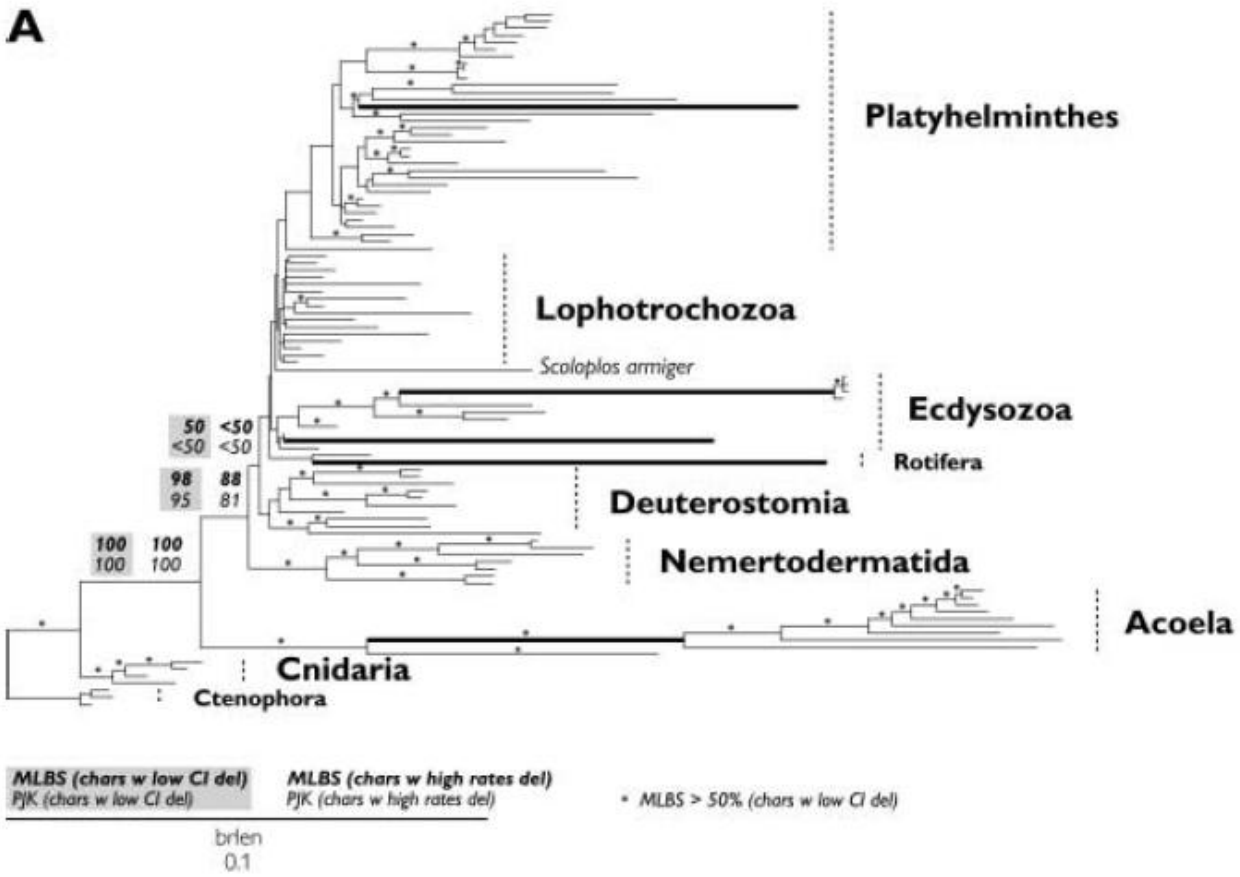


Fig. 5 A, B. The positions of Acoela and Nemertodermatida as separate braches are not artefacts of globally fast evolving characters. Maximum likelihood non-parametric bootstrap values (MLBS; bold italics; 200 pseudoreplicates, GTR + Γ + I model, PHYML) and parsimony jackknife values (PJK; italics; 1000 pseudoreplicates, 10 random addition sequences and TBR branch swapping, TNT) relevant for Acoela and Nemertodermatida are displayed above branches. MLBS frequencies over 50% for nodes in other parts of the trees when characters with low CI were removed are indicated with a star. 'Rouge' taxa recovered outside their expected major group are indicated using their full name. The five longest branches are indicated as bold lines. —A. Phylogram reconstructed from a maximum likelihood analysis of 18S and 28S ribosomal data when the fastest 25% of the data was removed. Values in grey boxes are resampling support values recovered when characters where removed according to their consistency index; the other values are resampling support values recovered from removing characters according to their maximum likelihood rates. Resolution is lost within Nephrozoa. —B. Removing characters according to their Shannon–Wiener variability index results in general loss of resolution within Bilateria and potential LBA artefacts.

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PLoS one

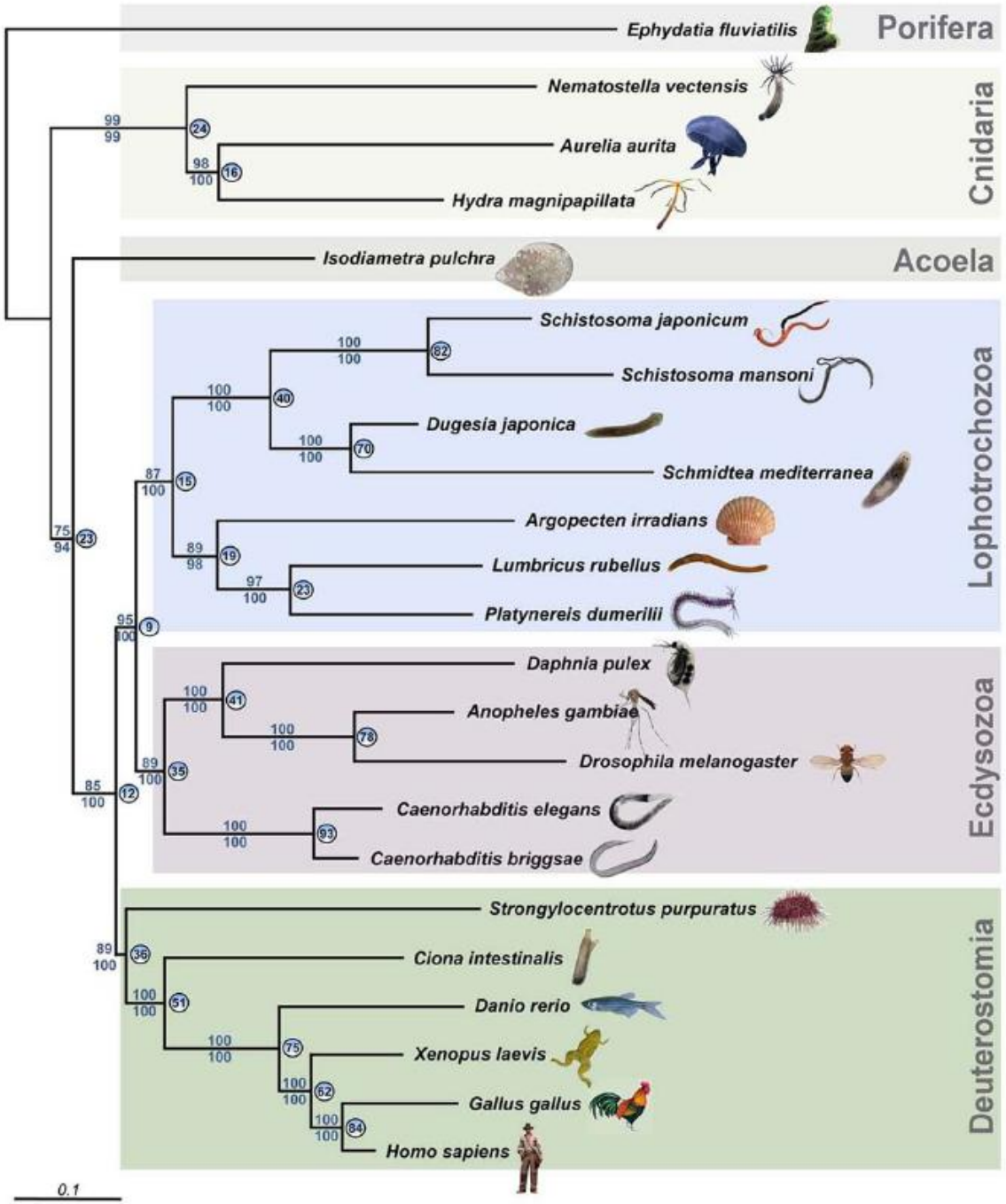
To Be or Not to Be a Flatworm: The Acoel Controversy

Bernhard Egger[1☯], Dirk Steinke[2☯], Hiroshi Tarui[3☯], Katrien De Mulder[4☯], Detlev Arendt[5], Gaëtan Borgonie[4], Noriko Funayama[8], Robert Gschwentner[1], Volker Hartenstein[6], Bert Hobmayer[1], Matthew Hooge[7], Martina Hrouda[8], Sachiko Ishida[9], Chiyoko Kobayashi[3,10], Georg Kuales[1], Osamu Nishimura[3], Daniela Pfister[1], Reinhard Rieger[1], Willi Salvenmoser[1], Julian Smith, III[11], Ulrich Technau[12], Seth Tyler[7]*, Kiyokazu Agata[8]*, Walter Salzburger[13]*, Peter Ladurner[1]*

Abstract

Since first described, acoels were considered members of the flatworms (Platyhelminthes). However, no clear synapomorphies among the three large flatworm taxa - the Catenulida, the Acoelomorpha and the Rhabditophora - have been characterized to date. Molecular phylogenies, on the other hand, commonly positioned acoels separate from other flatworms. Accordingly, our own multi-locus phylogenetic analysis using 43 genes and 23 animal species places the acoel flatworm *isodiametra pulchra* at the base of all Bilateria, distant from other flatworms. By contrast, novel data on the distribution and proliferation of stem cells and the specific mode of epidermal replacement constitute a strong synapomorphy for the Acoela plus the major group of flatworms, the Rhabditophora. The expression of a *piwi*-like gene not only in gonadal, but also in adult somatic stem cells is another unique feature among bilaterians. These two independent stem-cell-related characters put the Acoela into the Platyhelminthes-Lophotrochozoa clade and account for the most parsimonious evolutionary explanation of epidermal cell renewal in the Bilateria. Most available multigene analyses produce conflicting results regarding the position of the acoels in the tree of life. Given these phylogenomic conflicts and the contradiction of developmental and morphological data with phylogenomic results, the monophyly of the phylum Platyhelminthes and the position of the Acoela remain unresolved. By these data, both the inclusion of Acoela within Platyhelminthes, and their separation from flatworms as basal bilaterians are well-supported alternatives.

Egger B, Steinke D, Tarui H, De Mulder K, Arendt D, et al. (2009) To Be or Not to Be a Flatworm: The Acoel Controversy. PLoS ONE 4(5): e5502. doi:10.1371/journal.pone.0005502


Ephydatia fluviatilis
Porifera
Nematostella vectensis
Aurelia aurita
Hydra magnipapillata
Cnidaria
Isodiametra pulchra
Acoela
Schistosoma japonicum
Schistosoma mansoni
Dugesia japonica
Schmidtea mediterranea
Argopecten irradians
Lumbricus rubellus
Platynereis dumerilii
Lophotrochozoa
Daphnia pulex
Anopheles gambiae
Drosophila melanogaster
Caenorhabditis elegans
Caenorhabditis briggsae
Ecdysozoa
Strongylocentrotus purpuratus
Ciona intestinalis
Danio rerio
Xenopus laevis
Gallus gallus
Homo sapiens
Deuterostomia
0.1

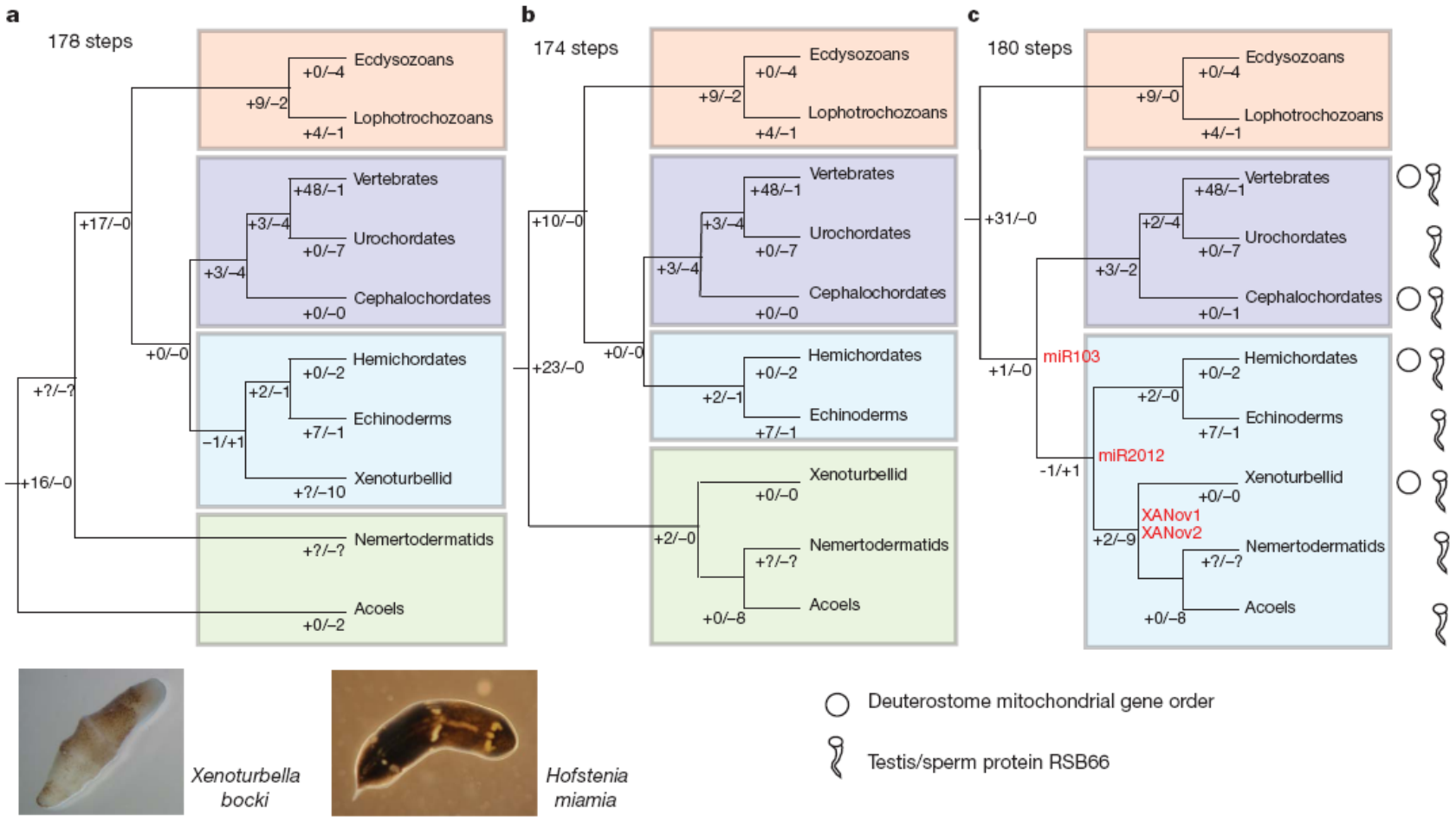
LETTER

doi:10.1038/nature09676

Acoelomorph flatworms are deuterostomes related to *Xenoturbella*

Hervé Philippe[1], Henner Brinkmann[1], Richard R. Copley[2], Leonid L. Moroz[3], Hiroaki Nakano[4]†, Albert J. Poustka[5], Andreas Wallberg[6], Kevin J. Peterson[7] & Maximilian J. Telford[8]

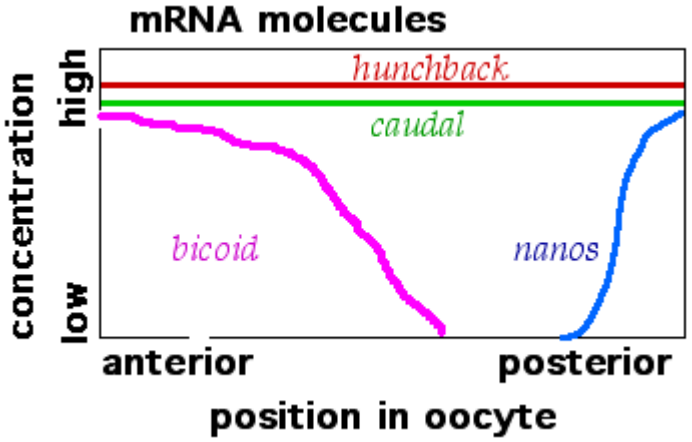
Xenoturbellida and Acoelomorpha are marine worms with contentious ancestry. Both were originally associated with the flatworms (Platyhelminthes), but molecular data have revised their phylogenetic positions, generally linking Xenoturbellida to the deuterostomes[1,2] and positioning the Acoelomorpha as the most basally branching bilaterian group(s)[3–6]. Recent phylogenomic data suggested that Xenoturbellida and Acoelomorpha are sister taxa and together constitute an early branch of Bilateria[7]. Here we assemble three independent data sets—mitochondrial genes, a phylogenomic data set of 38,330 amino-acid positions and new microRNA (miRNA) complements—and show that the position of Acoelomorpha is strongly affected by a long-branch attraction (LBA) artefact. When we minimize LBA we find consistent support for a position of both acoelomorphs and *Xenoturbella* within the deuterostomes. The most likely phylogeny links *Xenoturbella* and Acoelomorpha in a clade we call Xenacoelomorpha. The Xenacoelomorpha is the sister group of the Ambulacraria (hemichordates and echinoderms). We show that analyses of miRNA complements[8] have been affected by character loss in the acoels and that both groups possess one miRNA and the gene *Rsb66* otherwise specific to deuterostomes. In addition, *Xenoturbella* shares one miRNA with the ambulacrarians, and two with the acoels. This phylogeny makes sense of the shared characteristics of Xenoturbellida and Acoelomorpha, such as ciliary ultrastructure and diffuse nervous system, and implies the loss of various deuterostome characters in the Xenacoelomorpha including coelomic cavities, through gut and gill slits.

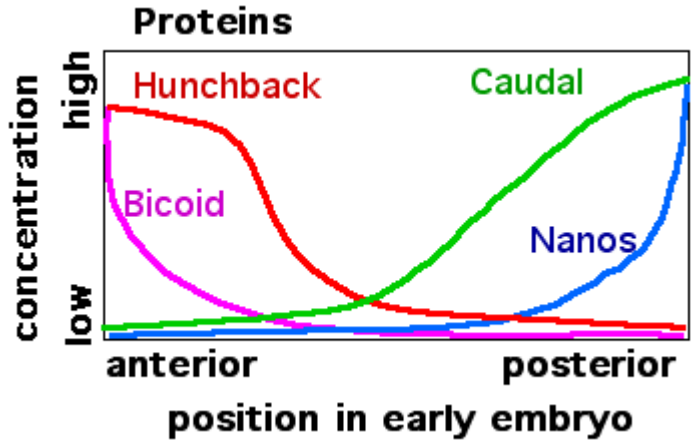

a
178 steps
Ecdysozoans
Lophotrochozoans
Vertebrates
Urochordates
Cephalochordates
Hemichordates
Echinoderms
Xenoturbellid
Nemertodermatids
Acoels
+0/–4
+9/–2
+4/–1
+48/–1
+3/–4
+0/–7
+0/–0
+2/–1
+7/–1
+?/–10
+?/–?
+0/–2
+17/–0
+0/–0
+?/–?
+16/–0
–1/+1
b
174 steps
+10/–0
+23/–0
+2/–0
+?/–?
+0/–8
c
180 steps
+31/–0
+1/–0
+3/–2
+2/–4
+0/–1
miR103
miR2012
-1/+1
+2/–9
XANov1
XANov2
Xenoturbella bocki
Hofstenia miamia
Deuterostome mitochondrial gene order
Testis/sperm protein RSB66

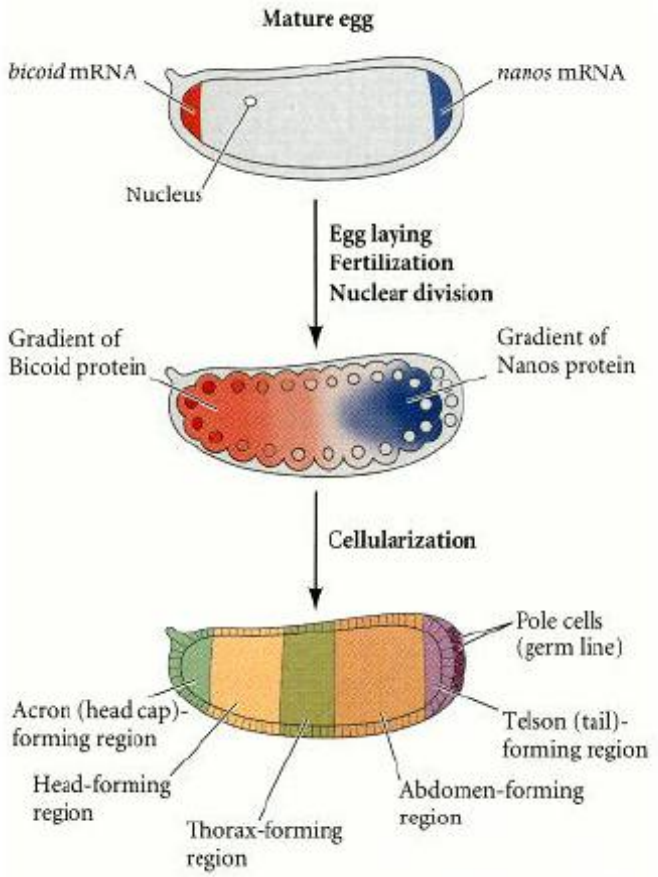
Some major transcription factor families and subfamilies

Family	Representative transcription factors	Some functions
Homeodomain:		
Hox	Hoxa-1, Hoxb-2, etc.	Axis formation
POU	Pit-1, Unc-86, Oct-2	Pituitary development; neural fate
LIM	Lim-1, Forkhead	Head development
Pax	Pax1, 2, 3, etc.	Neural specification; eye development
Basic helix-loop-helix (bHLH)	MyoD, achaete, daughterless	Muscle and nerve specification; *Drosophila* sex determination
Basic leucine zipper (bZip)	C/EBP, AP1	Liver differentiation; fat cell specification
Zinc finger:		
Standard	WT1, Krüppel, Engrailed	Kidney, gonad, and macrophage development; *Drosophila* segmentation
Nuclear hormone receptors	Glucocorticoid receptor, estrogen receptor, testosterone receptor, retinoic acid receptors	Secondary sex determination; craniofacial development; limb development
Sry-Sox	Sry, SoxD, Sox2	Bend DNA; mammalian primary sex deter- mination; ectoderm differentiation

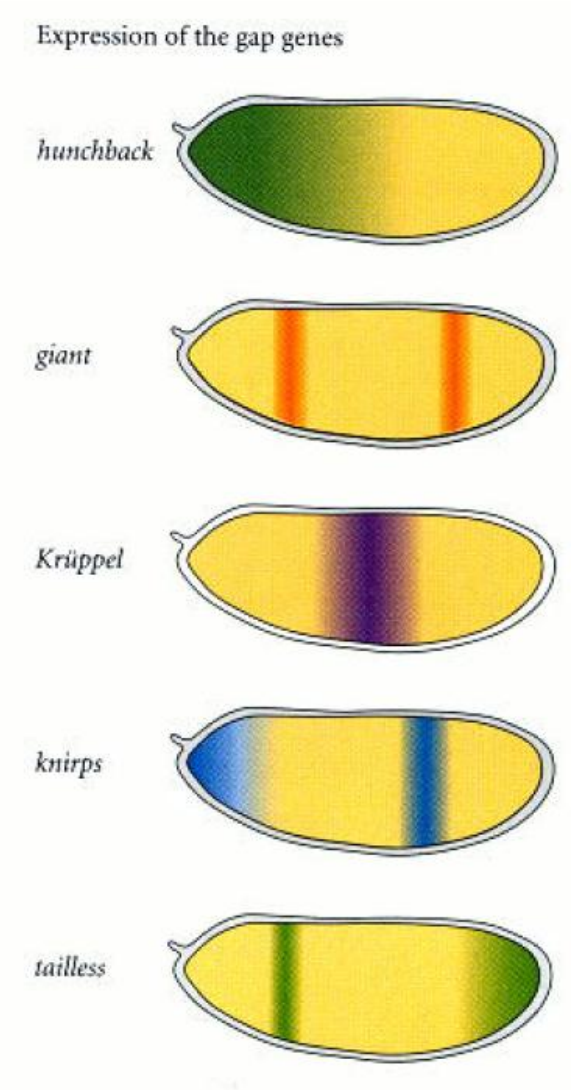
Локализация мРНК в яйце дрозофилы (Gilbert, 2000)

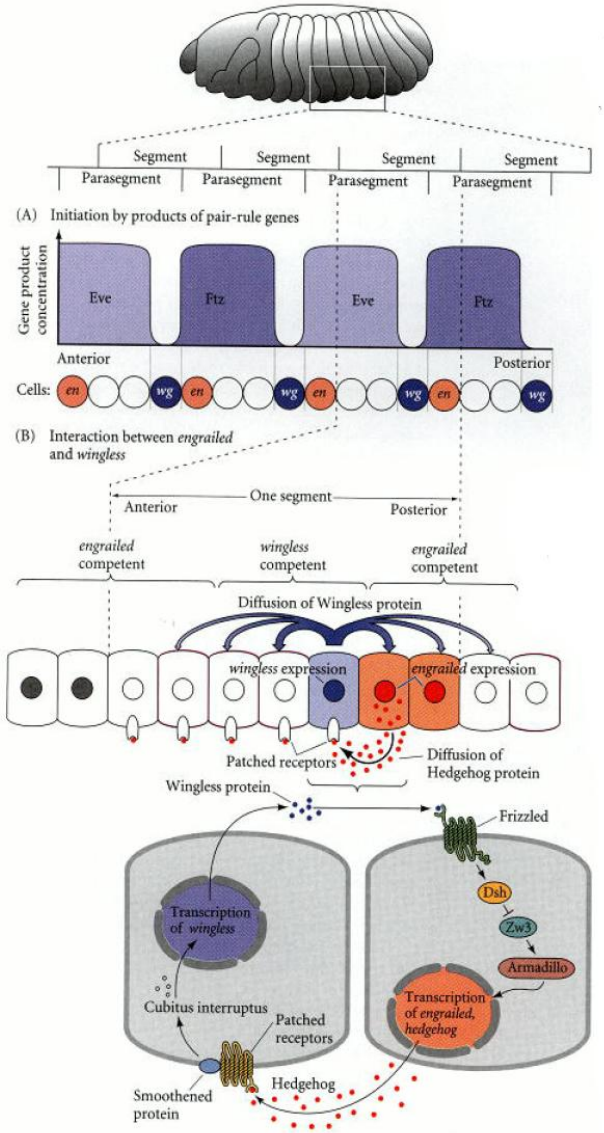






Экспрессия Gap-genes и формирование границ сегментов

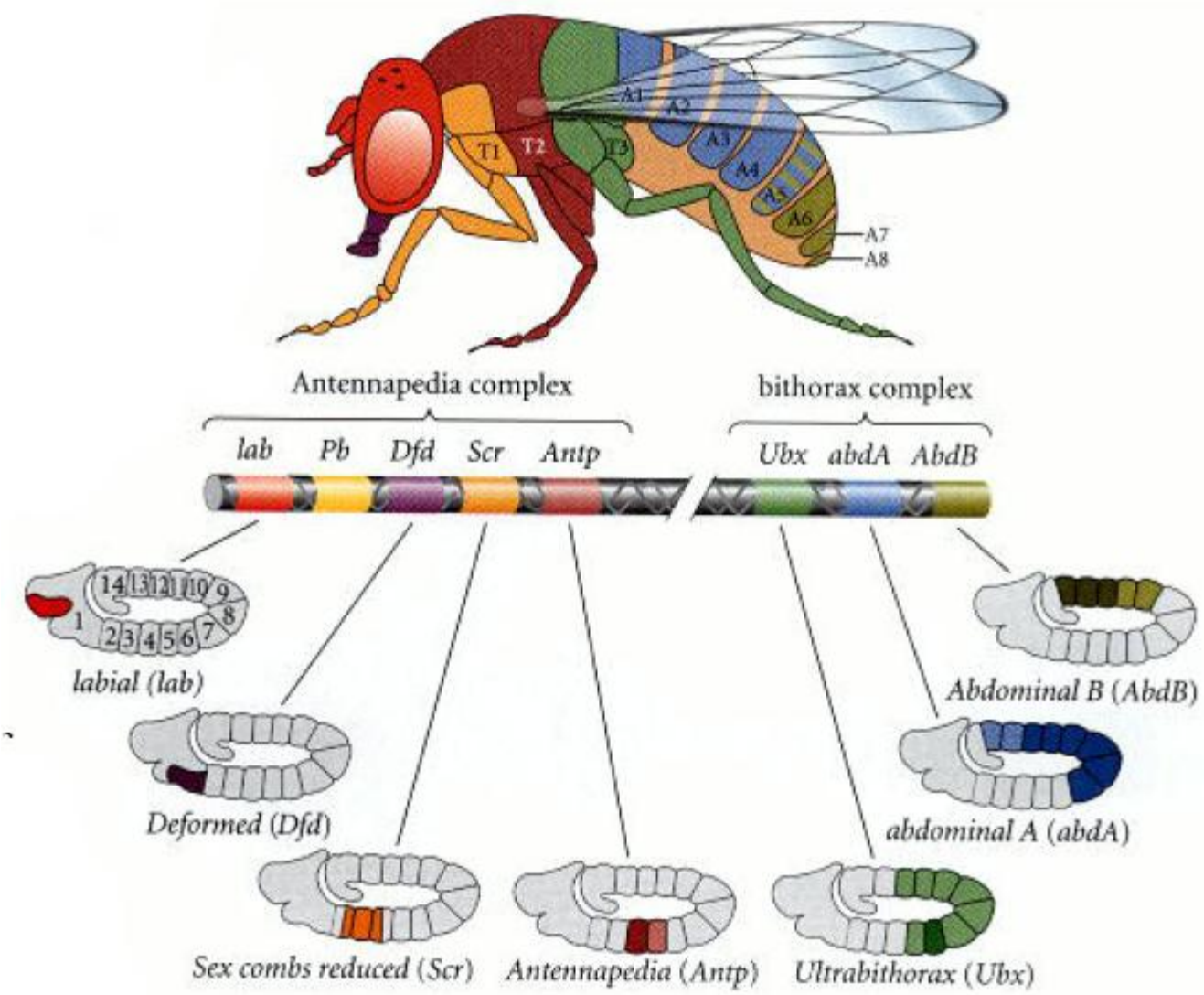




Основные гены сегментации мухи

(из Gilbert, 2000)

Category		Category	
Gap genes	*Krüppel (Kr)*	Pair-rule genes Secondary	*fushi tarazu (ftz)*
	knirps (kni)		*odd-paired (opa)*
	hunchback (hb)		*odd-skipped (slp)*
	giant (gt)		*sloppy-paired (slp)*
	tailless (tll)		*paired (prd)*
	huckendein (hkb)		
	buttonhead (btd)	Segment	*engrailed (en)*
	empty spiracles (ems)	polarity genes	*wingless (wg)*
	orthodenticle (otd)		*cubitus interruptus*^{D} (*ci*^{D})
			hedgehog (hh)
Pair-rule genes Primary	*hairy (h)*		*fused (fu)*
	even-skipped (eve)		*armadillo (arm)*
	runt (run)		*patched (ptc)*
			gooseberry (gsb)
			pangolin (pan)


T1
T2
T3
A1
A2
A3
A4
A5
A6
A7
A8
Antennapedia complex
bithorax complex
lab
Pb
Dfd
Scr
Antp
Ubx
abdA
AbdB
labial (lab)
Deformed (Dfd)
Sex combs reduced (Scr)
Antennapedia (Antp)
Ultrabithorax (Ubx)
abdominal A (abdA)
Abdominal B (AbdB)

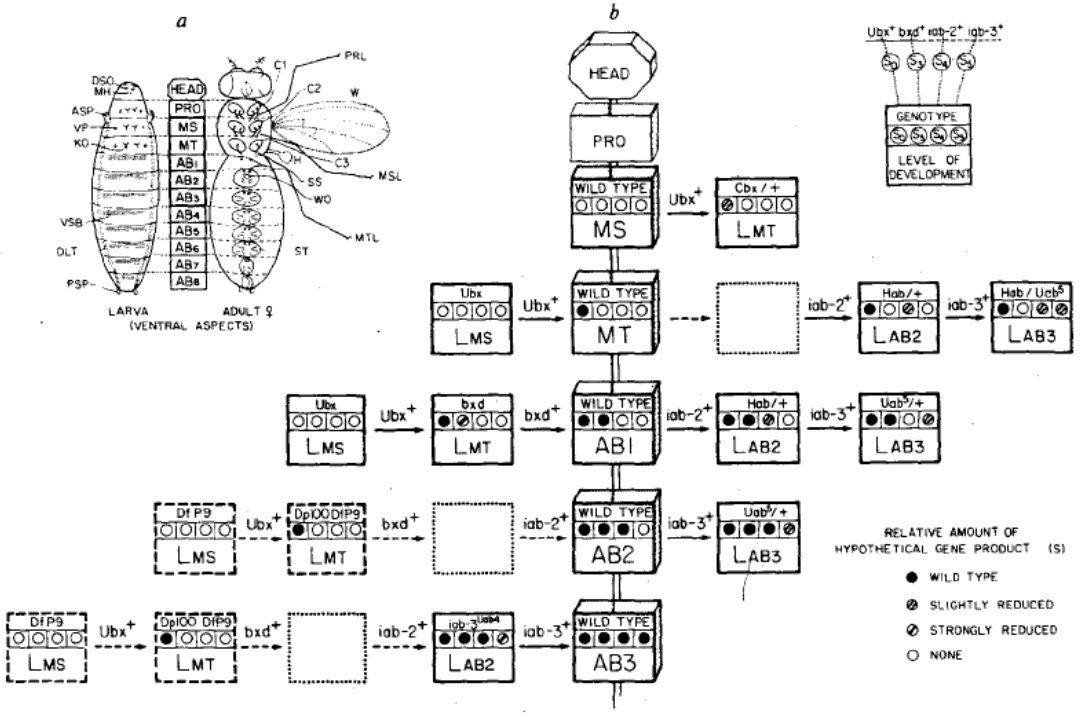
A gene complex controlling segmentation in *Drosophila*

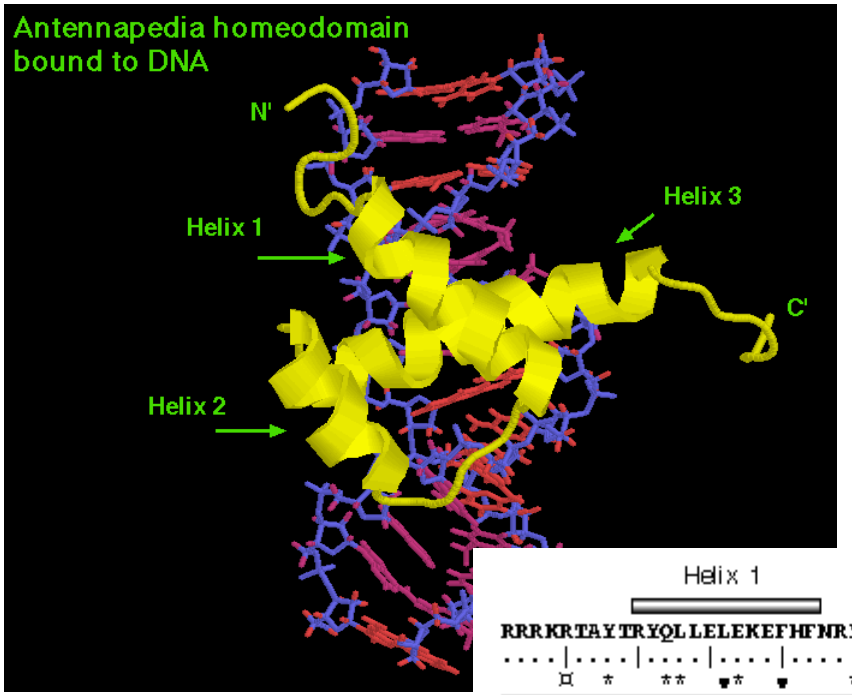
E. B. Lewis

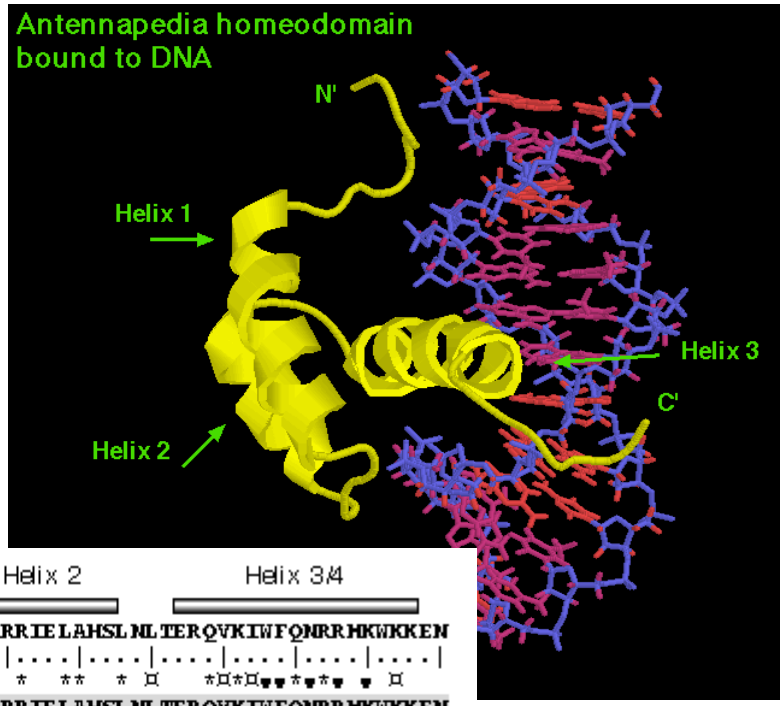
Division of Biology, California Institute of Technology, Pasadena, California 91125

The bithorax gene complex in Drosophila *contains a minimum of eight genes that seem to code for substances controlling levels of thoracic and abdominal development. The state of repression of at least four of these genes is controlled by* cis*-regulatory elements and a separate locus (Polycomb) seems to code for a repressor of the complex. The wild-type and mutant segmentation patterns are consistent with an antero-posterior gradient in repressor concentration along the embryo and a proximo-distal gradient along the chromosome in the affinities for repressor of each gene's* cis*-regulatory element.*

Nature Vol. 276 7 December 1978





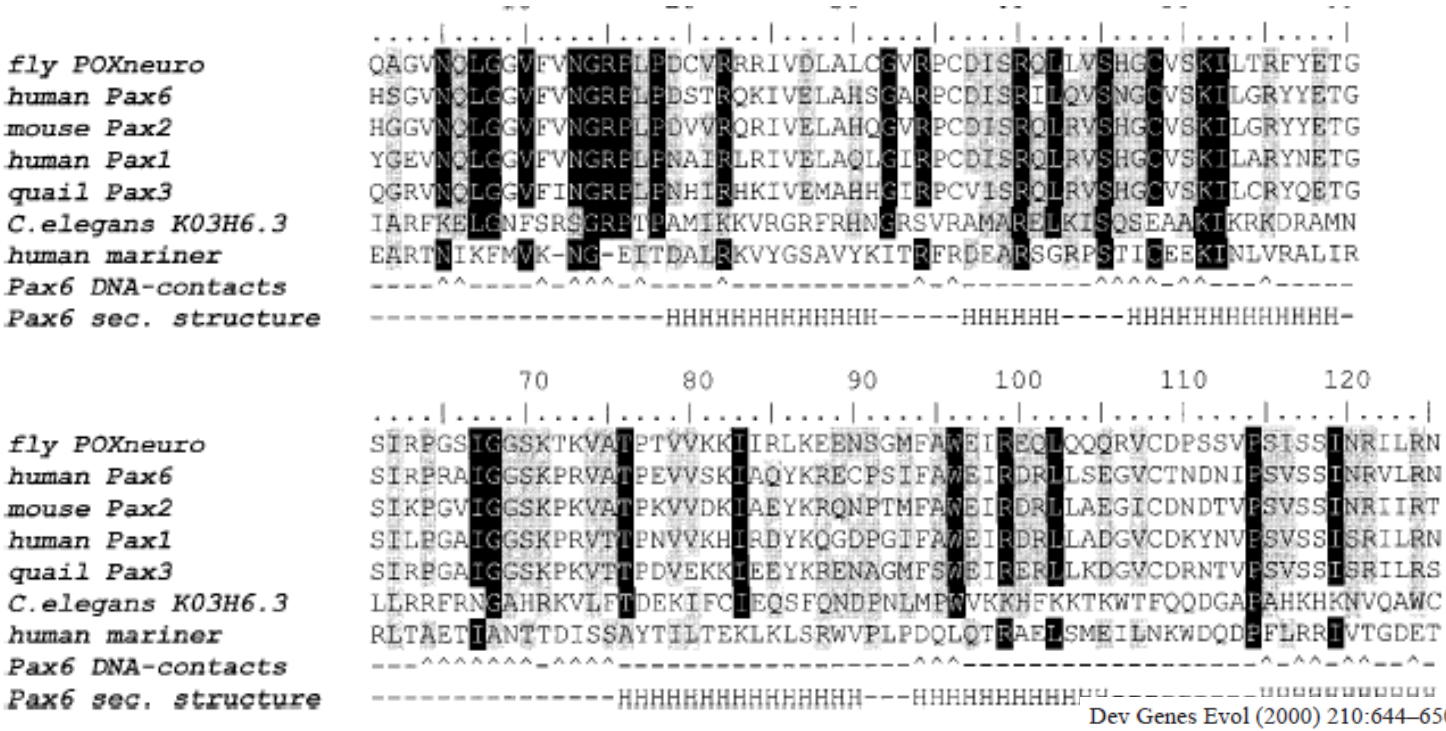


Helix 1 Helix 2 Helix 3/4

```
RRRKRTAYTRYQLLELEKEFHFNRYLTRRRRIELAHSLNLTERQVKIWFQNRRMKWKKEN
....|....|....|....|....|....|....|....|....|....|....|....|
    ¤  *   **  ▪*  ▪   *¤    *  **  * ¤   *¤*¤▪▪*▪*▪ ▪ ¤
RRRKRTAYTRYQLLELEKEFHFNRYLTRRRRIELAHSLNLTERQVKIWFQNRRMKWKKEN
KKKPGQTFSKEVTAA KRAYLQSKKPSAAEIEQISAATGHSDTVIRV  C K ARERRQS
PNSG CPIETSAVER RNK QKQPFIDIPKKARV NEIC NKAR QT  S H Q L QDT
GSGS VSLKSAIIRT  QH ERTQNVNKQDLVSH RTVS EPET T   K A T Q  HQ
SDAA AV DAH KVV  AR AEKHR CVET LHF QL Q PHS         Y H  LK
N  R KN  DQ RGS  SS RYCH  ASKH TA  SR D KQK         V A  IE
Q  T RI  VK  TI  TY KTEN  VEDA QN  EK H DTD         S I  RH
T  V  L  NF  QQ  HF NADS   GHQ KK  DH K R          N H  AV
E  L  R  QT  K   EC FSHV   PL  RD  KN R                Y  VR
D  I     PN  D       SI A   LY  S   LQ E                D  SL
A  Y     GL  F       GV E     S  Y   TV A                F  KA
L  N     YD  Y       DL       T  F    I                 K  N
V  Q     EP  H       YN       F  C    D                 T
   H      R          HH          H
   H
```

No. of amino acids encountered: ▪ 1-2; ¤ 3-5; * 6-9

- Происхождение гомеобоксных генов:
- Возможно, семейство Pax генов приобретено на заре метазой от транспозазы.

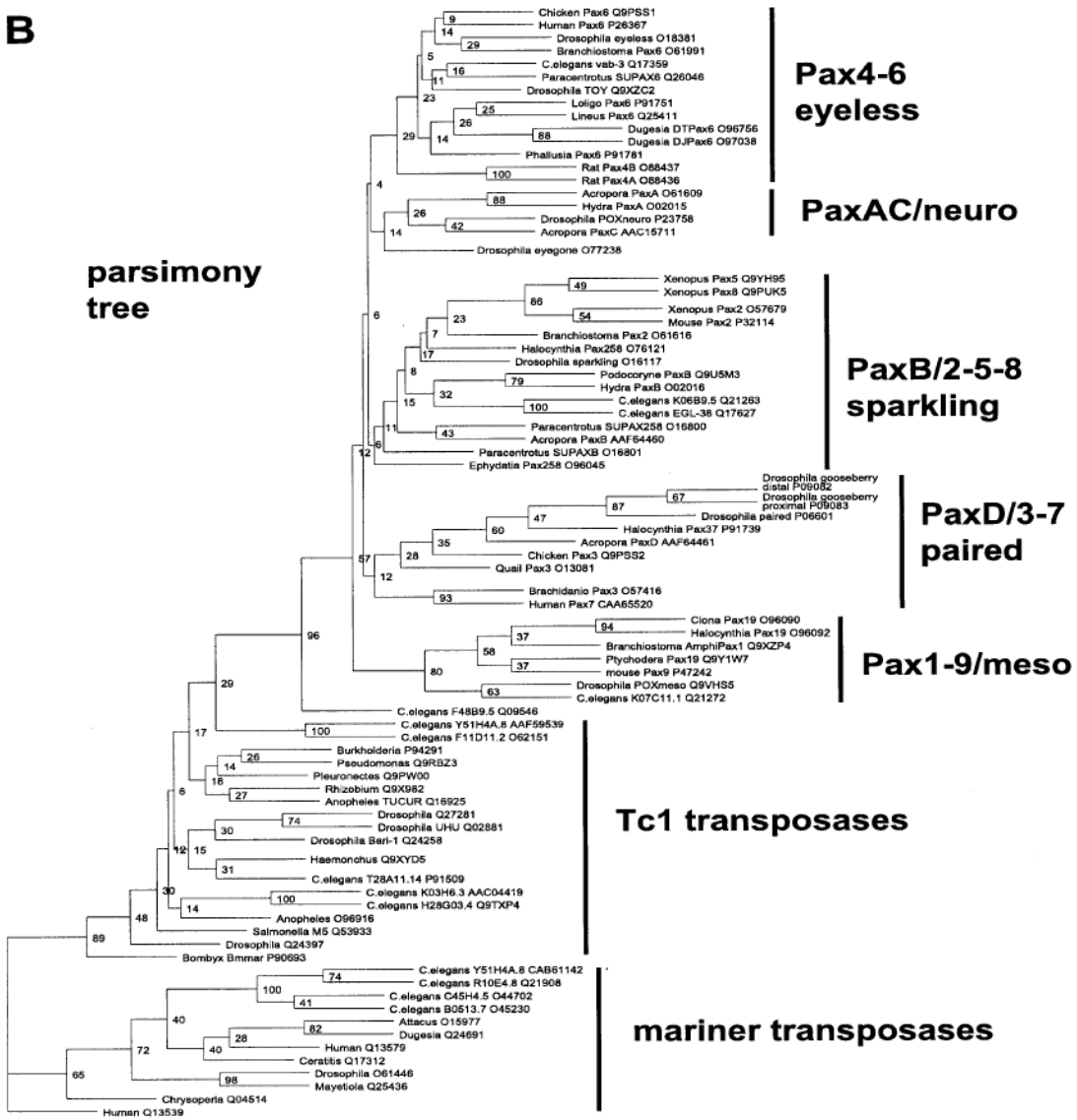


Dev Genes Evol (2000) 210:644–650

SEQUENCE CORNER

Rainer Breitling · Josef-Karl Gerber

Origin of the paired domain



- Предполагается, что изначально приобретена единичная копия гена, затем ген дуплицировался.

Dev Genes Evol (2000) 210:644–650

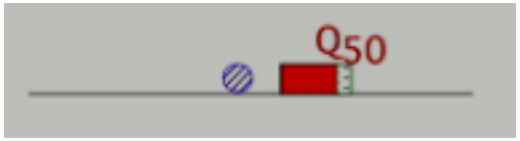
SEQUENCE CORNER

Rainer Breitling · Josef-Karl Gerber

Origin of the paired domain

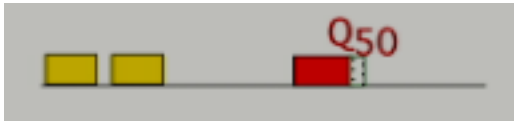
Все HOX-гены формируют один кластер

HOX



PAIRED

LIM

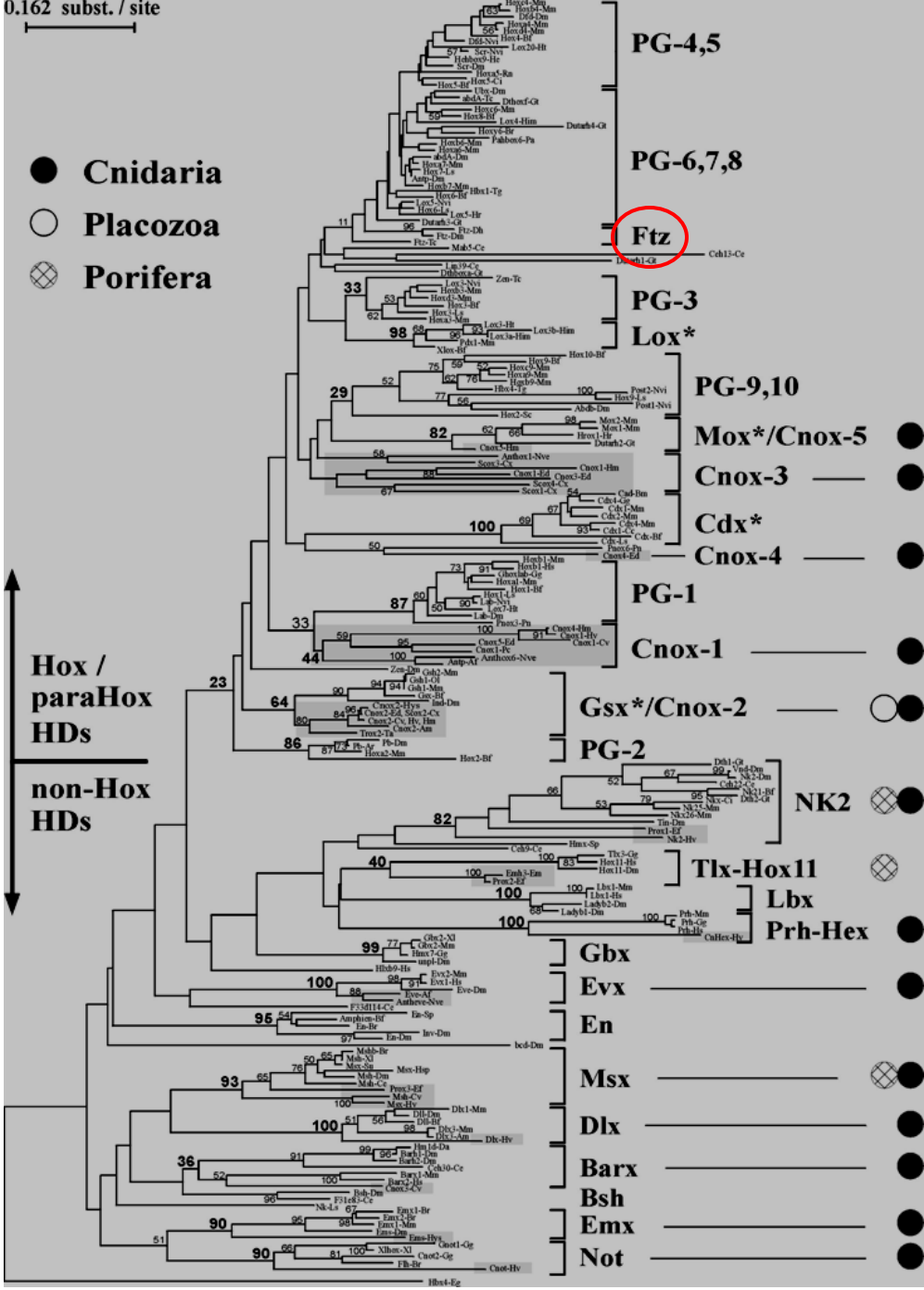


HOX –кластер также содержит негомеозисные гены

Fushi-tarazu (Ftz)
Bicoid (Bcd)
Zerknüllt (Zen1 and Zen2)

Эти гены внутри кластера, но утеряли у мух свою гомеозисную функцию и колинеарную экспрессию относительно недавно

У более примитивных насекомых (прямокрылые) эти гены выполняют гомеозисную функуию.



Sonic hadgehog регулирует передне-заднюю ось конечностей и крыльев.

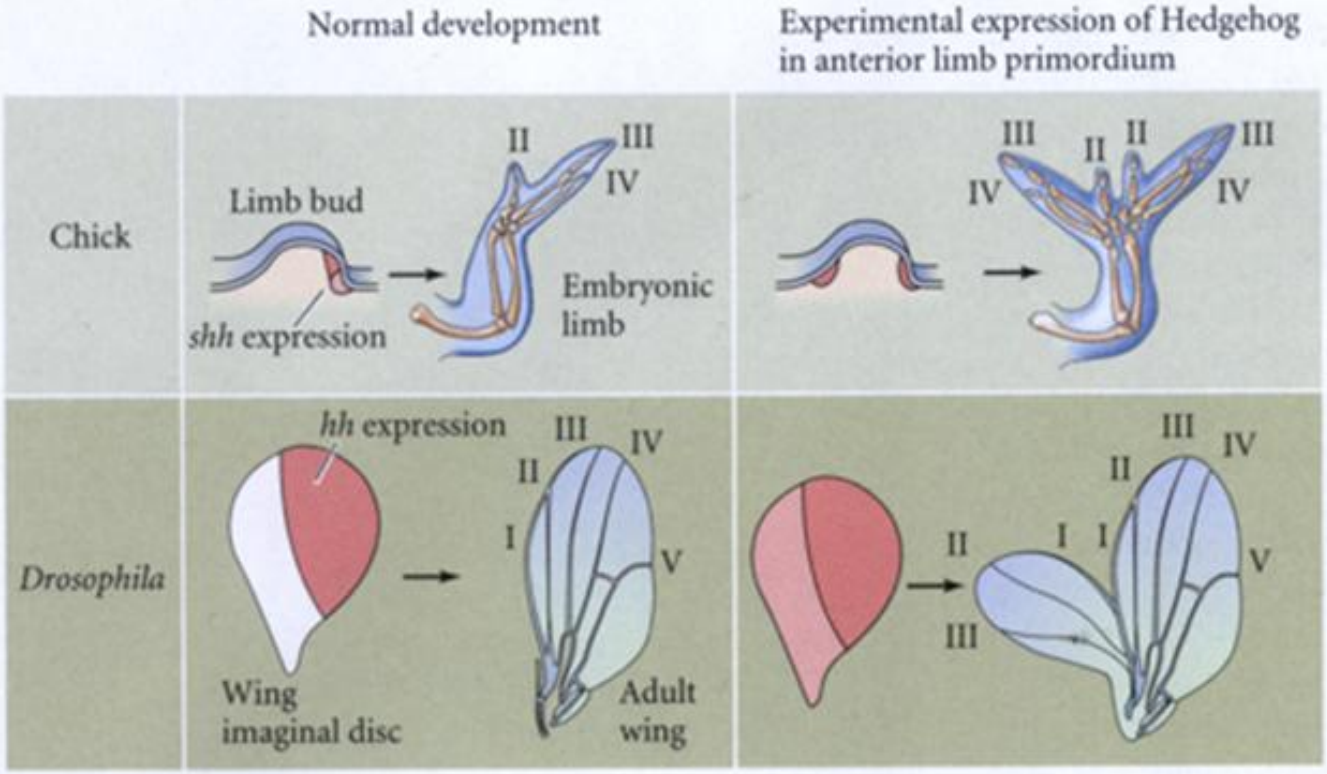
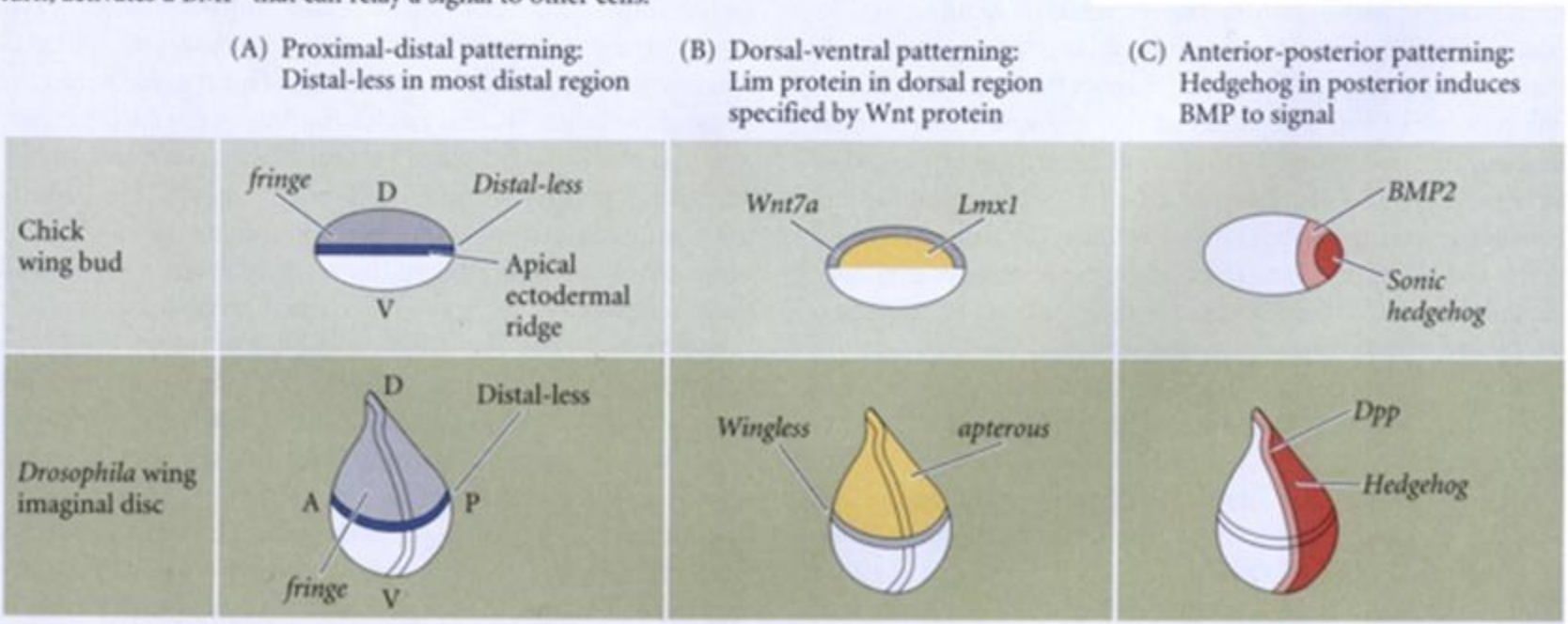


Figure 22.15
Homology of process in the formation of the anterior-posterior axes in *Drosophila* and chick appendages. A chick limb bud expresses Sonic hedgehog in its posterior region. If Sonic hedgehog is also expressed in an anterior region, the limb develops a mirror-image duplication of the anterior-posterior axis. A *Drosophila* wing disc expresses Hedgehog in its posterior compartment. If Hedgehog is expressed in the anterior compartment as well, the wing develops a mirror-image duplication of the anterior-posterior axis. (After Ingham 1994.)

Sonic the Hedgehog, as he appears in *Sonic the Hedgehog 4*

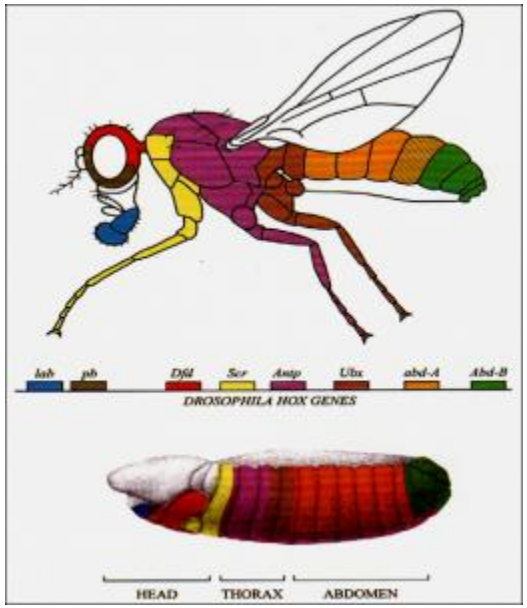
Другие оси конечностей цыпленка и крыльев мухи также определяются экспрессией гомологичных генов

Deep homology of the limbs. The same set of proteins is used to establish the polarity of limbs in both deuterostomes (chick) and protostomes (*Drosophila*). The top panels represent chick limb buds with the dorsal region on top and the apical ectodermal ridge facing the viewer. The bottom panels represent the *Drosophila* wing disc with its dorsal region upward and its anterior side to the left. (A) Proximal-distal axes are specified by the Distal-less protein in the most distal region of the limb bud or disk. This protein forms at the junction where the Fringe-containing dorsal cells meet the ventral cells. (B) Dorsal-ventral patterning is specified by the expression of a LIM protein, either Apterous (*Drosophila*) or Lmx1 (chick), in the dorsal portion of the disk or bud. A Wnt protein (Wingless in *Drosophila*, Wnt7A in the chick) induces this expression. (C) Anterior-posterior patterning is accomplished by the expression of Hedgehog in the posterior of the disk or bud. Hedgehog, in turn, activates a BMP that can relay a signal to other cells.

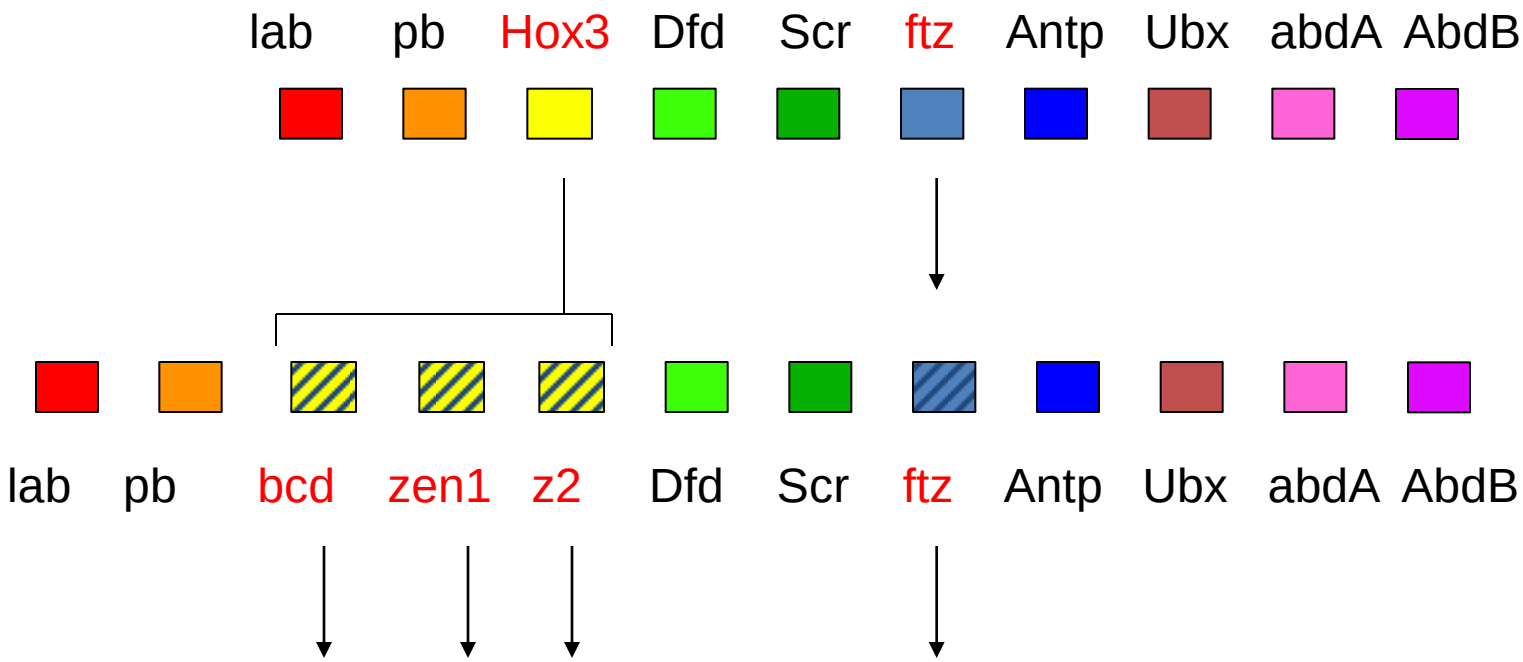


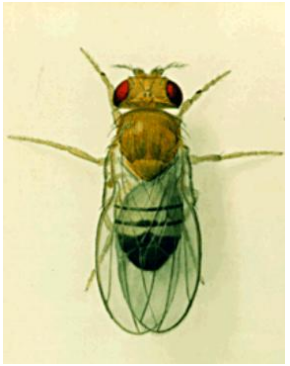
Гомеозисные гены

HOX и PARAHOX



Предковый набор Hox генов членистоногих имел 10 генов

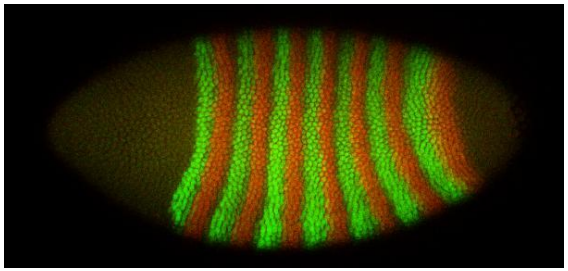




Maternal effect gene

Extra embryonic ammniosera

Pair rule gene

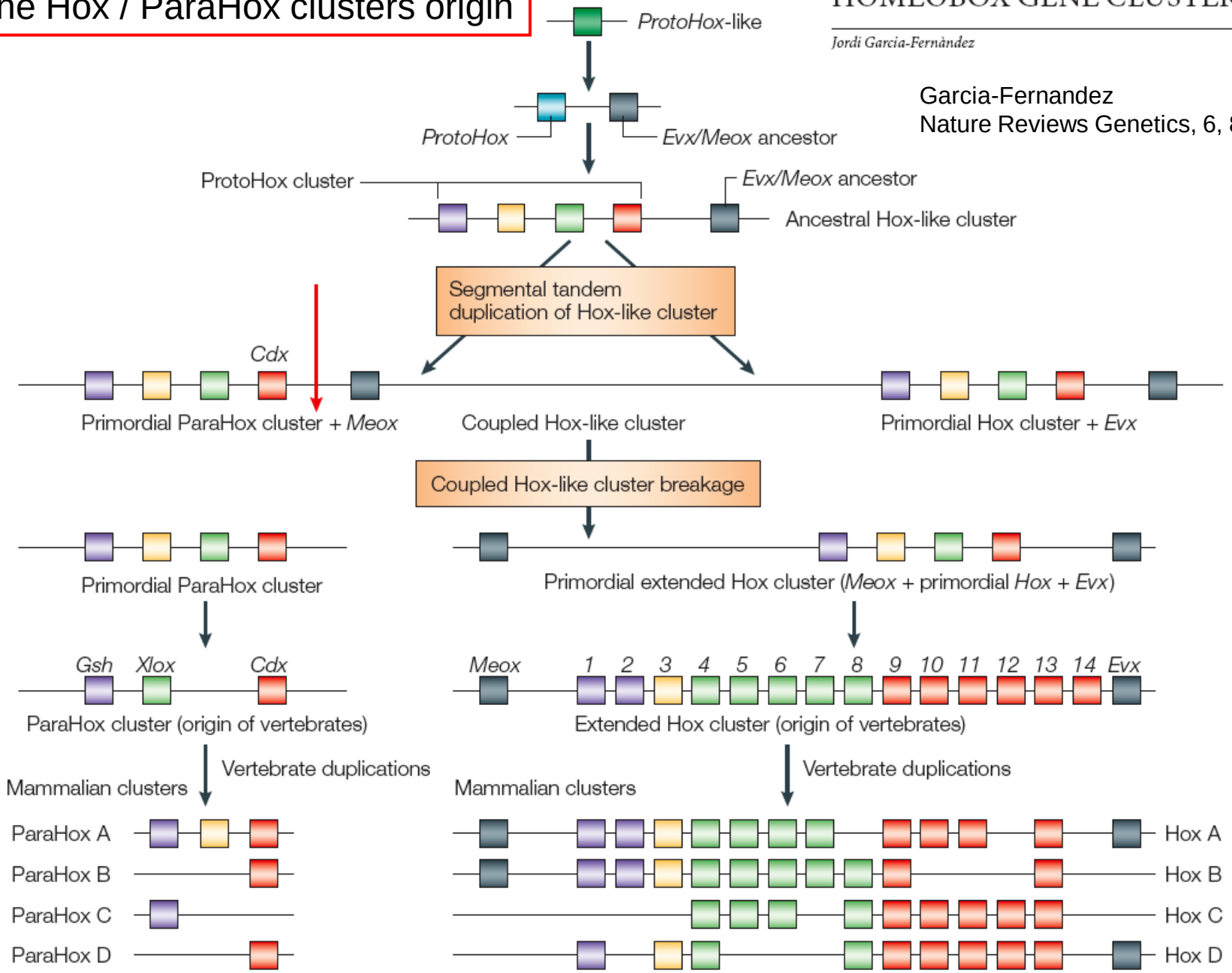


The Hox / ParaHox clusters origin

THE GENESIS AND EVOLUTION OF HOMEOBOX GENE CLUSTERS

Jordi Garcia-Fernàndez

Garcia-Fernandez
Nature Reviews Genetics, 6, 881, 2005



Heredity (2005) 94, 145–152
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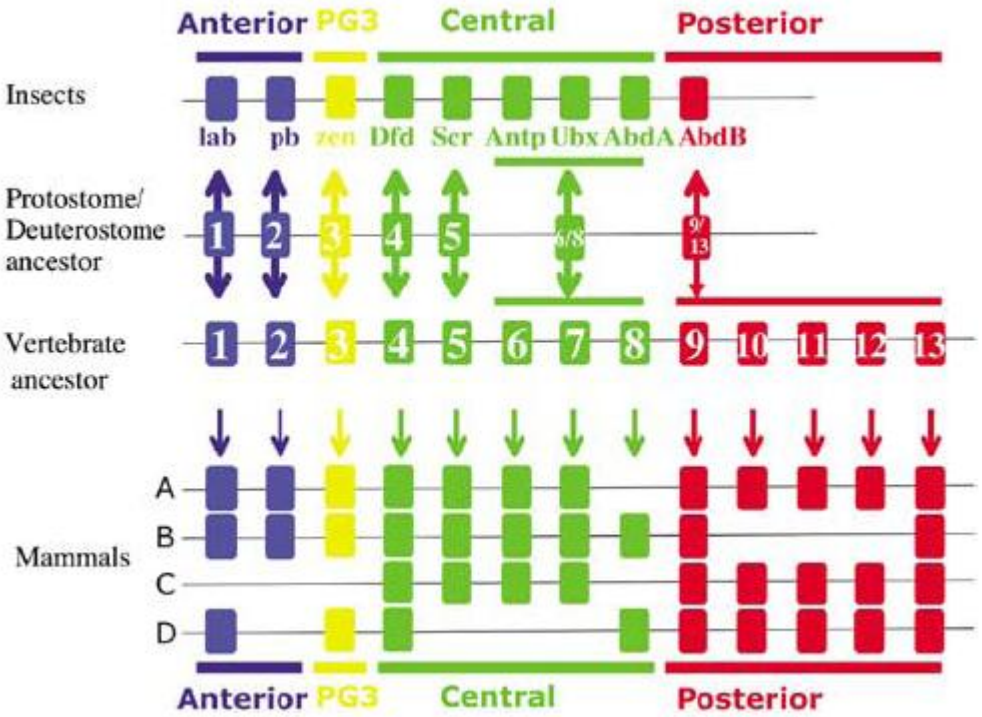
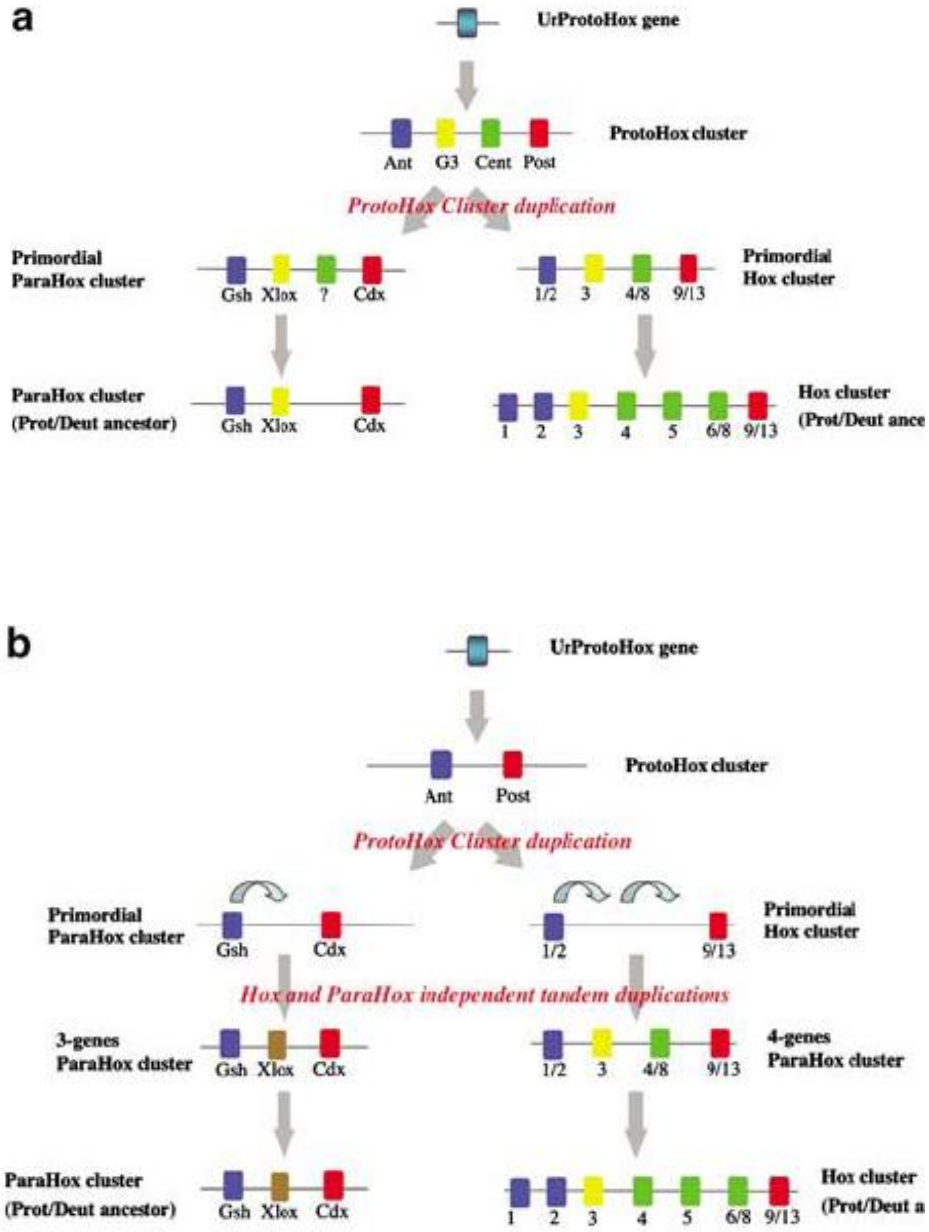
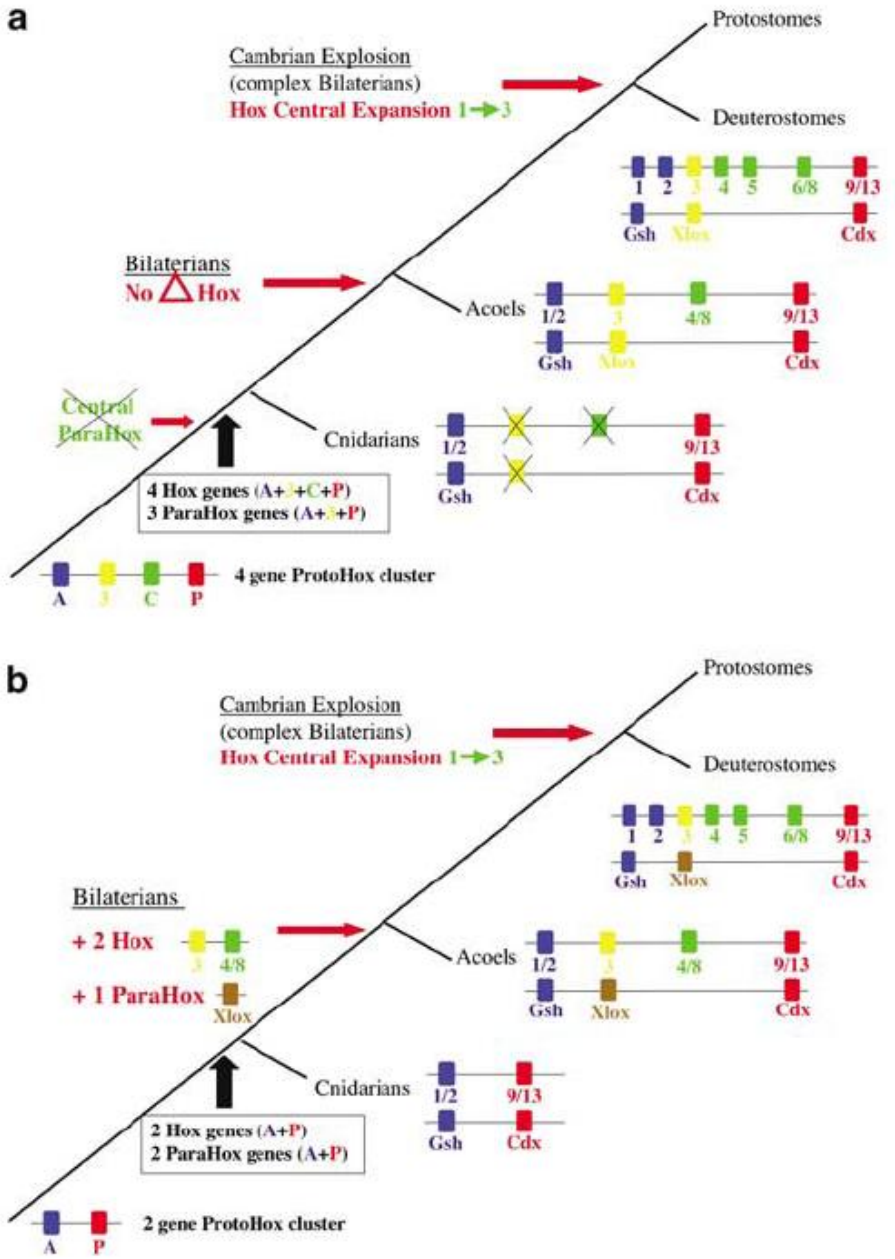
REVIEW

Hox, ParaHox, ProtoHox: facts and guesses

J Garcia-Fernàndez
Departament de Genètica, Facultat de Biologia, Universitat de Barcelona, Av. Diagonal, 645, E-08028, Barcelona, Spain




a
UrProtoHox gene
ProtoHox cluster
Ant G3 Cent Post
ProtoHox Cluster duplication
Primordial ParaHox cluster
Gsh Xlox ? Cdx
1/2 3 4/8 9/13
Primordial Hox cluster
ParaHox cluster (Prot/Deut ancestor)
Gsh Xlox Cdx
1 2 3 4 5 6/8 9/13
Hox cluster (Prot/Deut ance
b
UrProtoHox gene
ProtoHox cluster
Ant Post
ProtoHox Cluster duplication
Primordial ParaHox cluster
Gsh Cdx
1/2 9/13
Primordial Hox cluster
Hox and ParaHox independent tandem duplications
3-genes ParaHox cluster
Gsh Xlox Cdx
1/2 3 4/8 9/13
4-genes ParaHox cluster
ParaHox cluster (Prot/Deut ancestor)
Gsh Xlox Cdx
1 2 3 4 5 6/8 9/13
Hox cluster (Prot/Deut a


a
Protostomes
Cambrian Explosion
(complex Bilaterians)
Hox Central Expansion 1→3
Deuterostomes
1 2 3 4 5 6/8 9/13
Gsh Xlox Cdx
Bilaterians
No Hox
Acoels
1/2 3 4/8 9/13
Gsh Xlox Cdx
Central ParaHox
Cnidarians
1/2 9/13
Gsh Cdx
4 Hox genes (A+3+C+P)
3 ParaHox genes (A+3+P)
A 3 C P
4 gene ProtoHox cluster
b
Protostomes
Cambrian Explosion
(complex Bilaterians)
Hox Central Expansion 1→3
Deuterostomes
1 2 3 4 5 6/8 9/13
Gsh Xlox Cdx
Bilaterians
+ 2 Hox
3 4/8
+ 1 ParaHox
Xlox
Acoels
1/2 3 4/8 9/13
Gsh Xlox Cdx
Cnidarians
1/2 9/13
Gsh Cdx
2 Hox genes (A+P)
2 ParaHox genes (A+P)
A P
2 gene ProtoHox cluster

Evolution of Antp-class genes and differential expression of *Hydra Hox/paraHox* genes in anterior patterning

Dominique Gauchat*, Françoise Mazet*, Cédric Berney*†, Michèl Schummer‡§, Sylvia Kreger‡, Jan Pawlowski*†, and Brigitte Galliot*¶‖

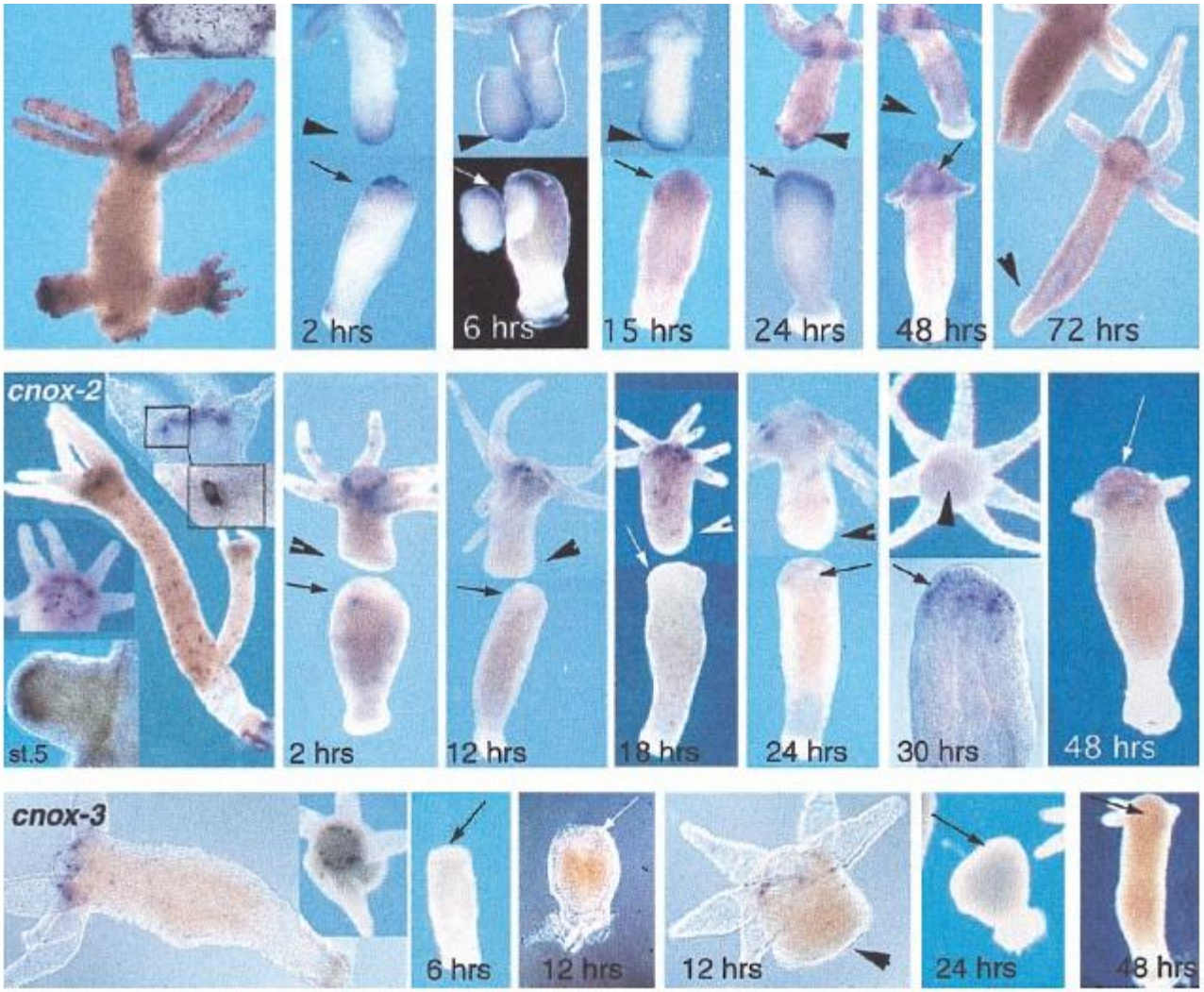


Fig. 5. Expression pattern of the *Hv Hox/paraHox* genes, *cnox-1* (*Top*), *cnox-2* (*Middle*), and *cnox-3* (*Bottom*) in adult (*Left*) and regenerating *Hydra*. Time points after cutting are given; arrowheads and arrows indicate foot- and head-regenerating stumps, respectively. st, budding stage.

Трихоплак

Wolfgang Jakob · Sven Sagasser · Stephen Dellaporta ·
Peter Holland · Kerstin Kuhn · Bernd Schierwater

The *Trox-2* Hox/ParaHox gene of *Trichoplax* (Placozoa) marks an epithelial boundary

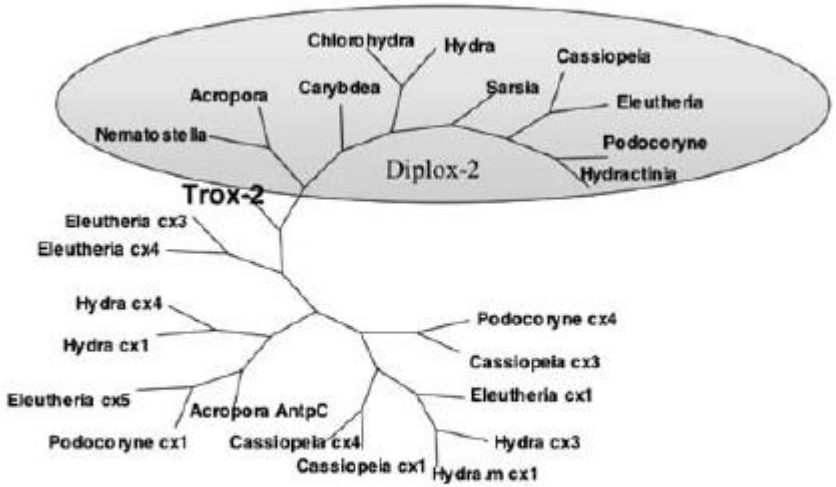
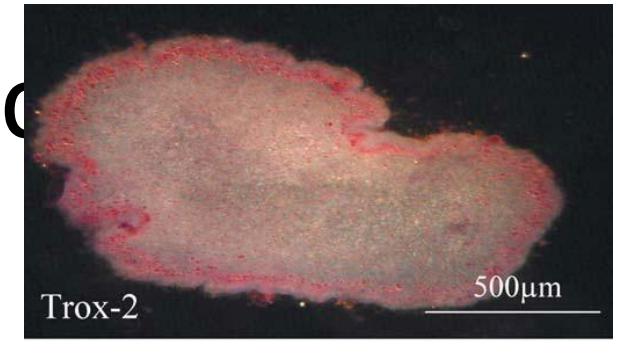
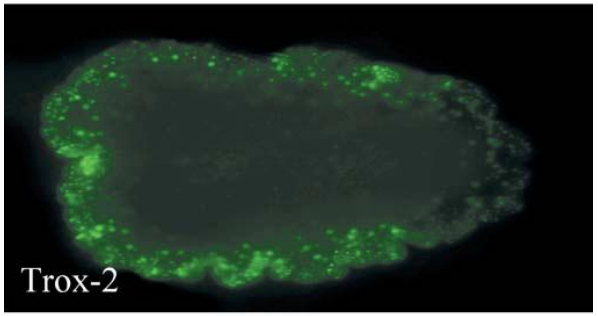
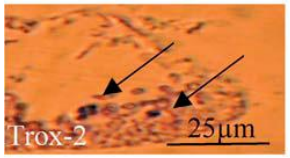


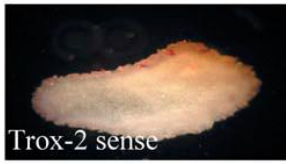
Fig. 2 Neighbour-Joining tree of all known full-length Diplox gene homeodomains. *Trox-2* groups at the base of known *Cnox-2* genes from Cnidaria (*Diplox-2* group, *highlighted*), while all other *Diplox* genes are separated on different clades. The tree is intended to

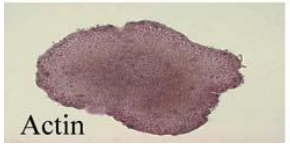
Dev Genes Evol (2004) 214:170–175

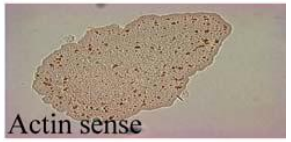




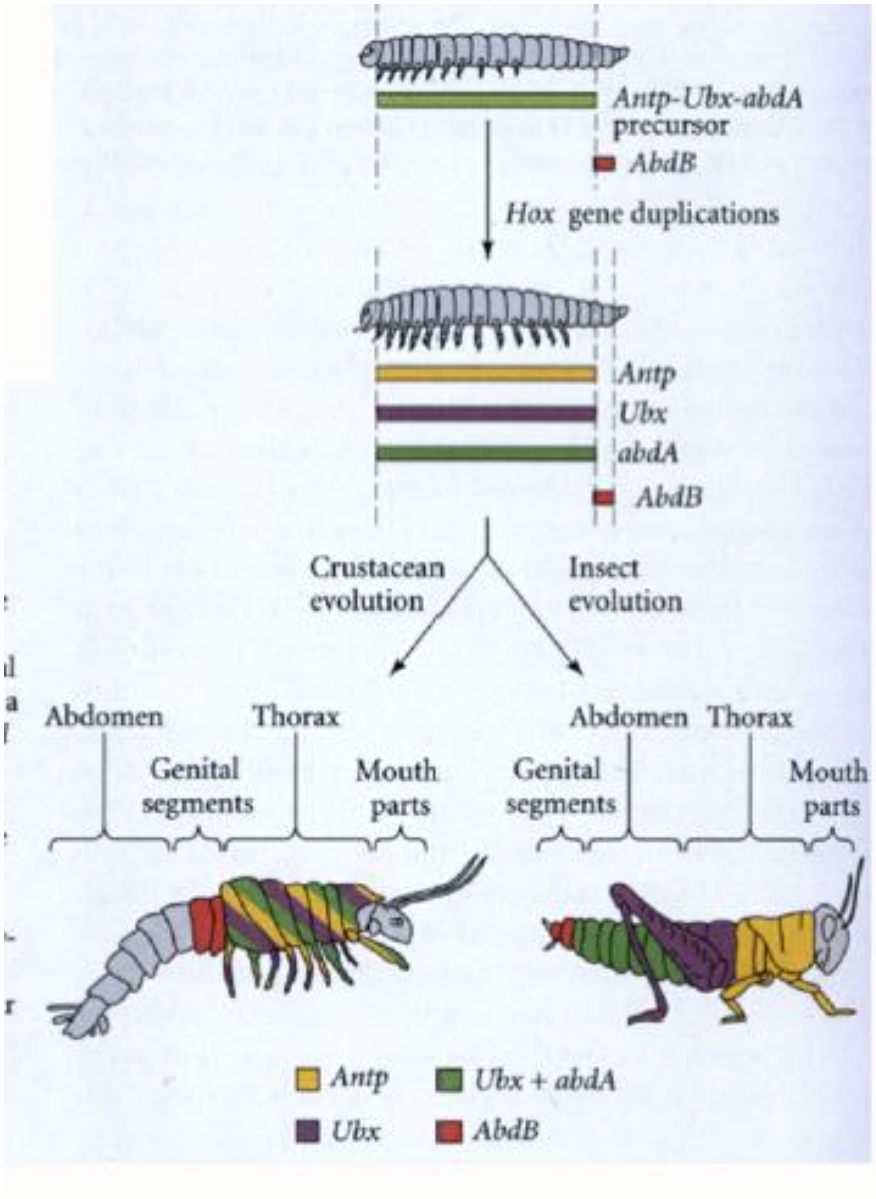








Trox-2 expression in Trichoplax adhaerens.



Averof and Akam, 1995: дупликация Hox-генов привела к формированию отделов тела у насекомых, но не у раков. Раки «изобрели» хвост самостоятельно

Где у раков «шея»?

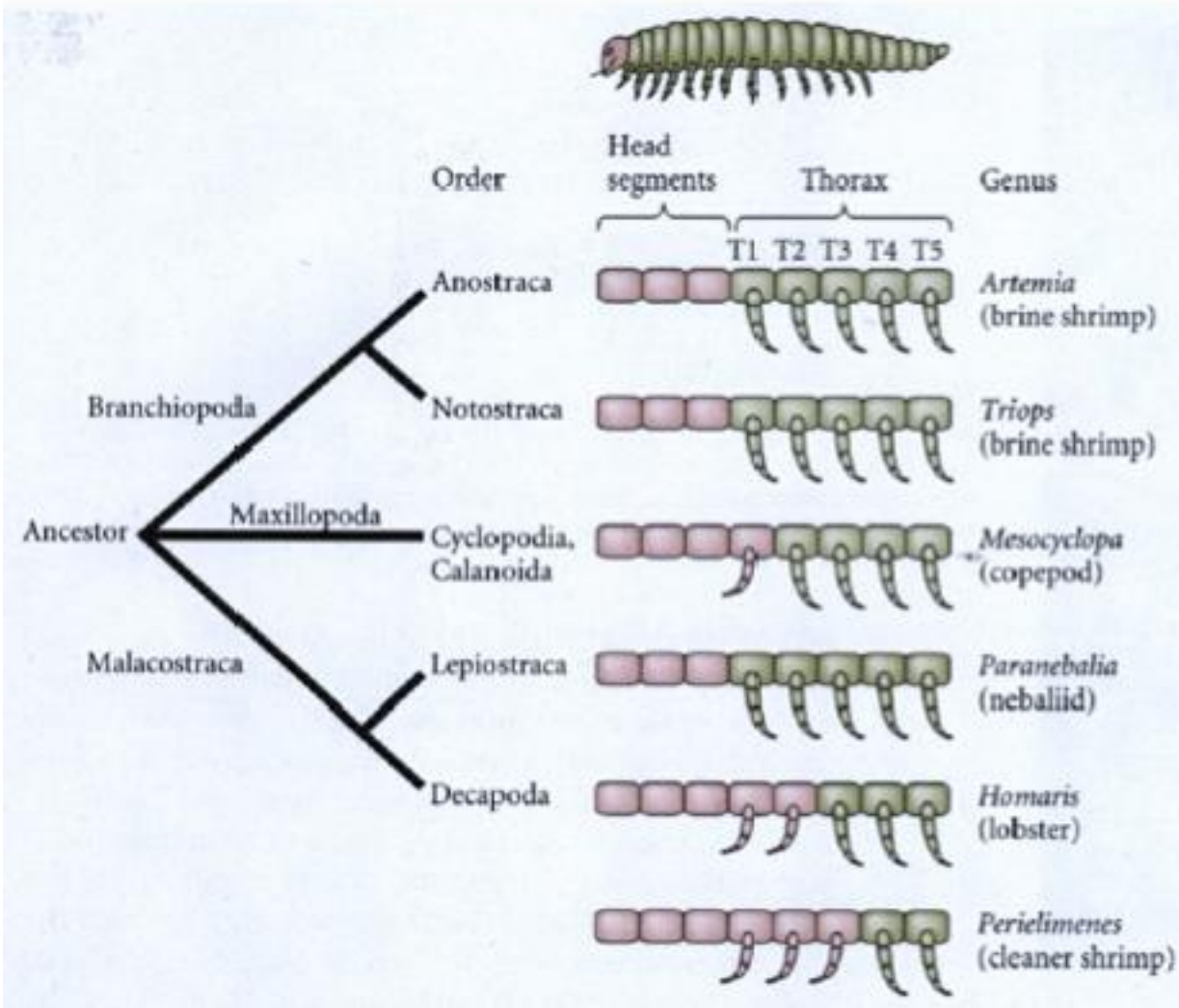
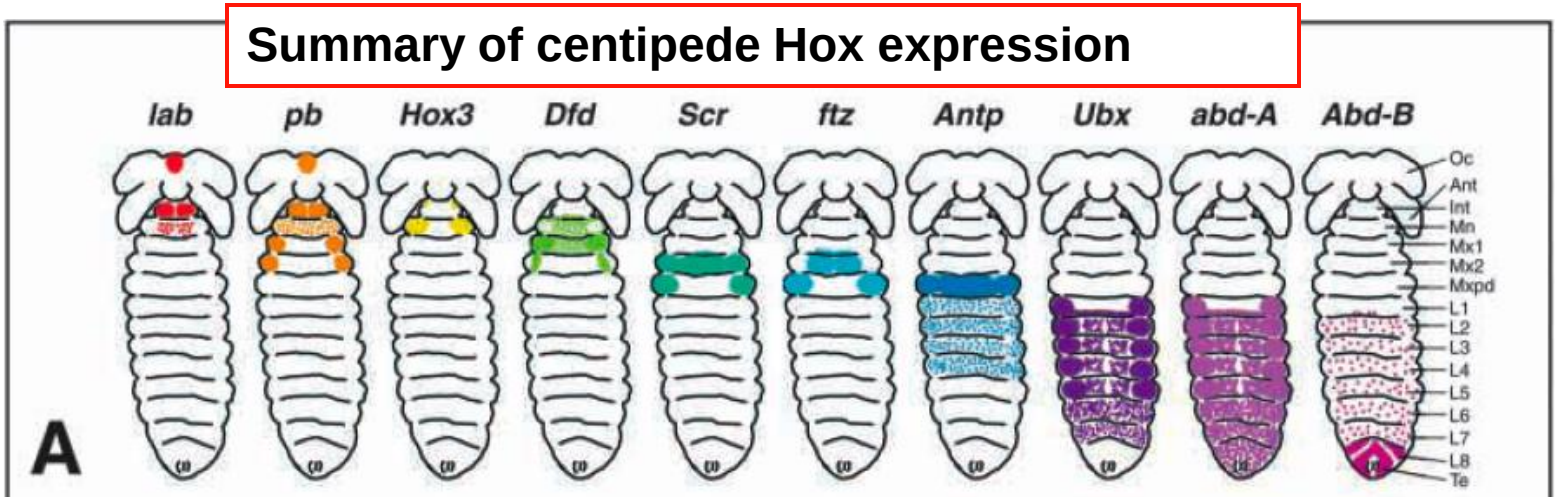
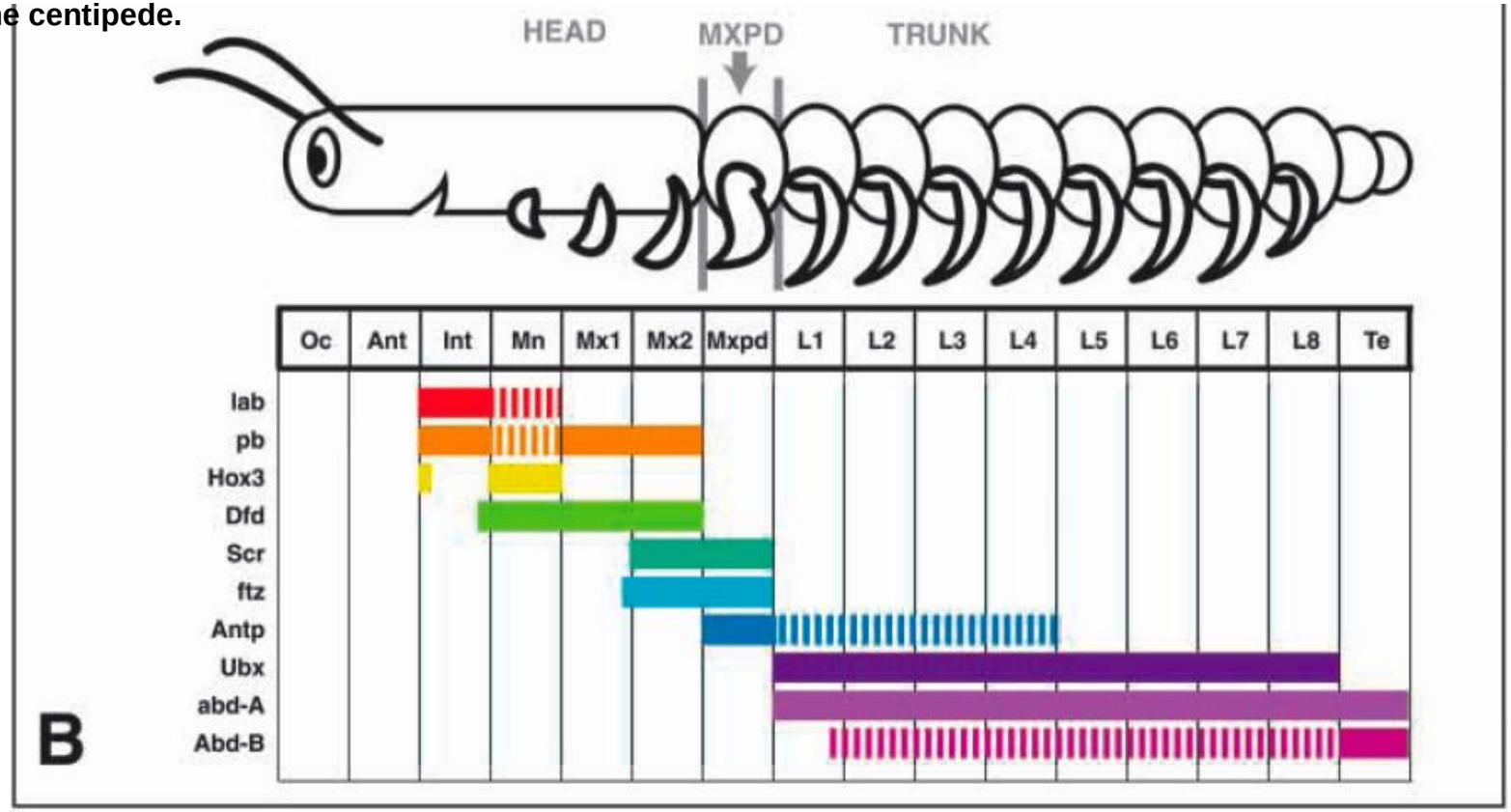


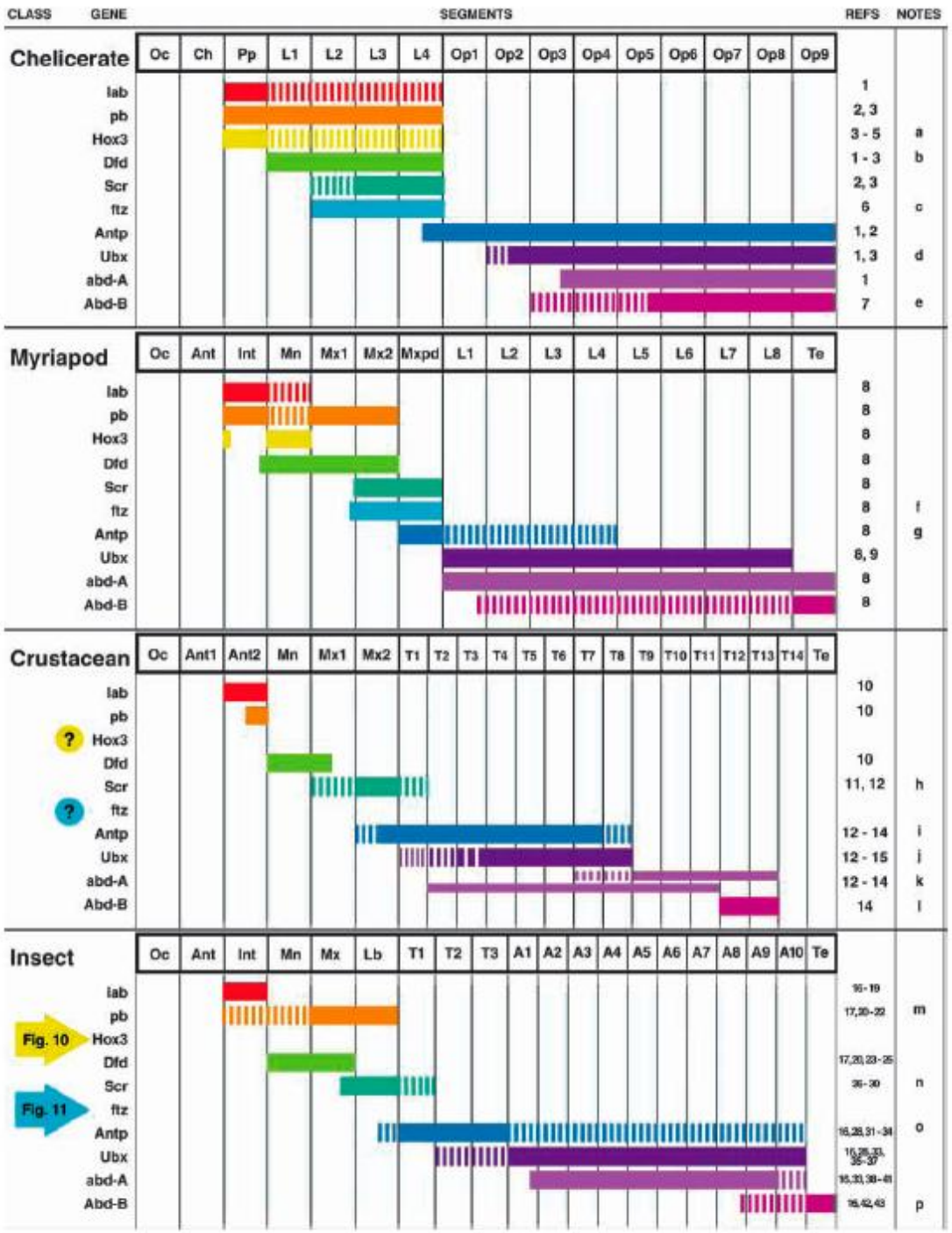
Figure 22.8
Schematic representation of the expression of *Ubx* and *abdA* (green) in the thoracic segments of different types of crustaceans. The generation of maxillipeds occurs in the thoracic segments that do not express either of these homeodomain proteins. (After Averof and Patel 1997.)

Summary of centipede Hox expression



The expression of fushi tarazu suggests that it has both a Hox-like role (as in the mite), as well as a role in segmentation (as in insects). This suggests that this dramatic change in function was achieved via a multifunctional intermediate, as found in the centipede.

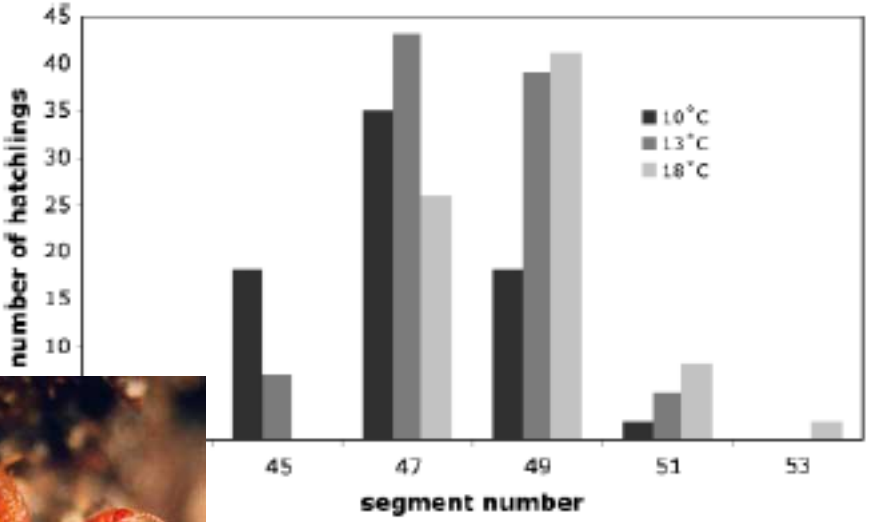


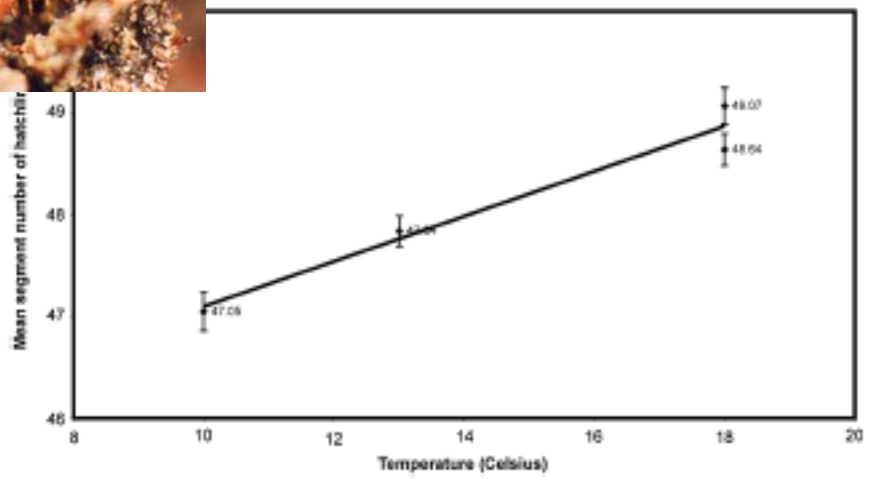


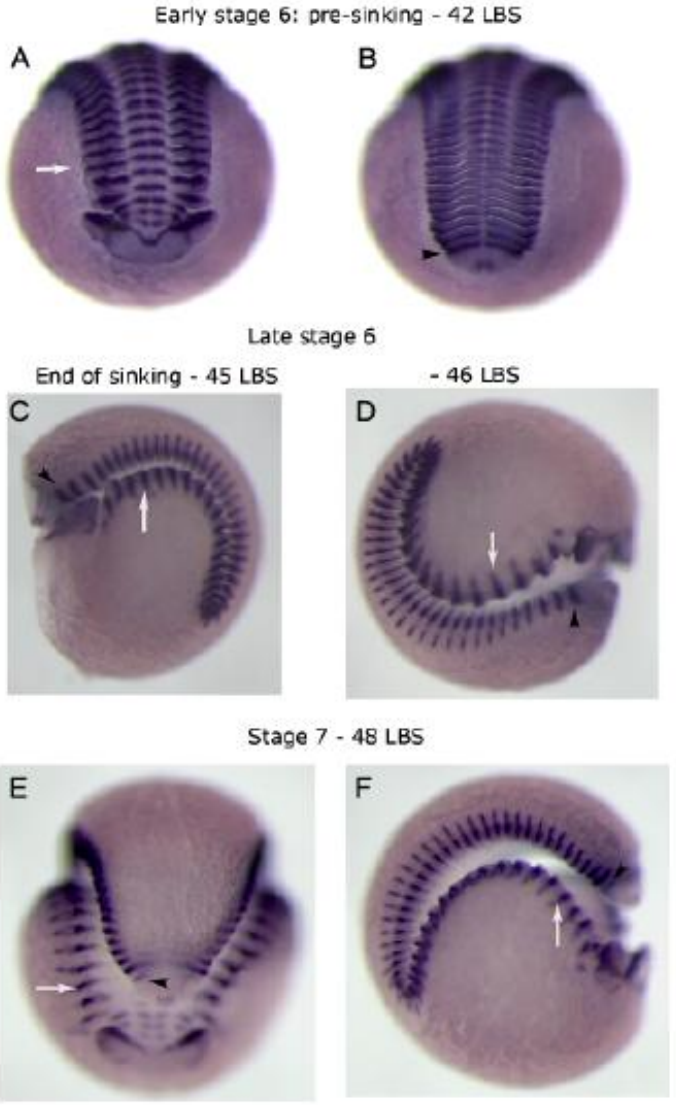
Shifting Hox domains across the arthropods

Hox expression correlates with tagmatic boundaries, consistent with the theory that changes in Hox genes

Temperature dependant plasticity of segment number in a centipede, *Strigamia maritima*







Vedel et al., Evol. Dev. 10, 487, 2008

Engrailed

The Ubx protein in arthropods is highly variable

Sequences shared by Hexapods (Dros. [Dm] & mosquito [Ag]) is yellow

Artemia [Af] & velvet worm [Ak]

This is only observations. What do you do next?

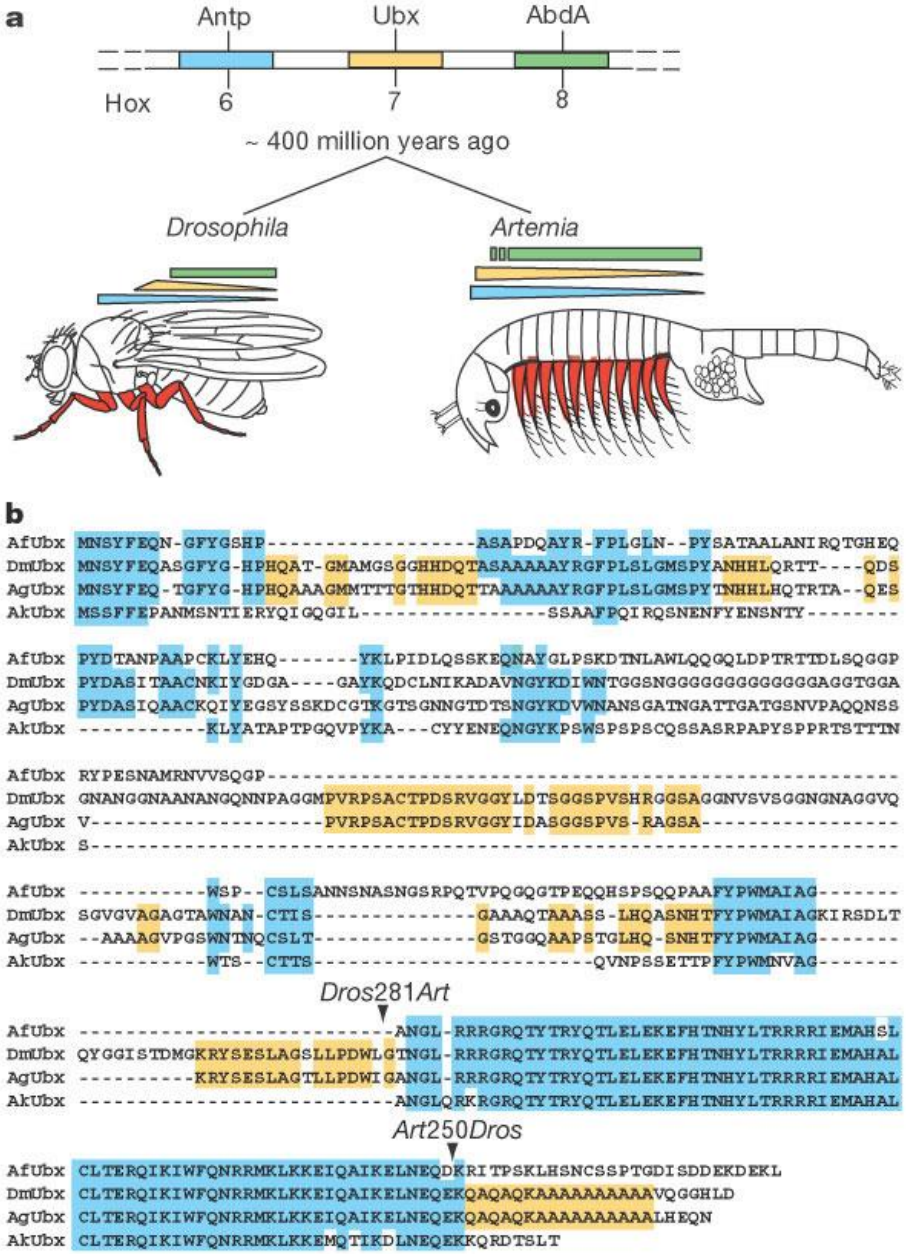
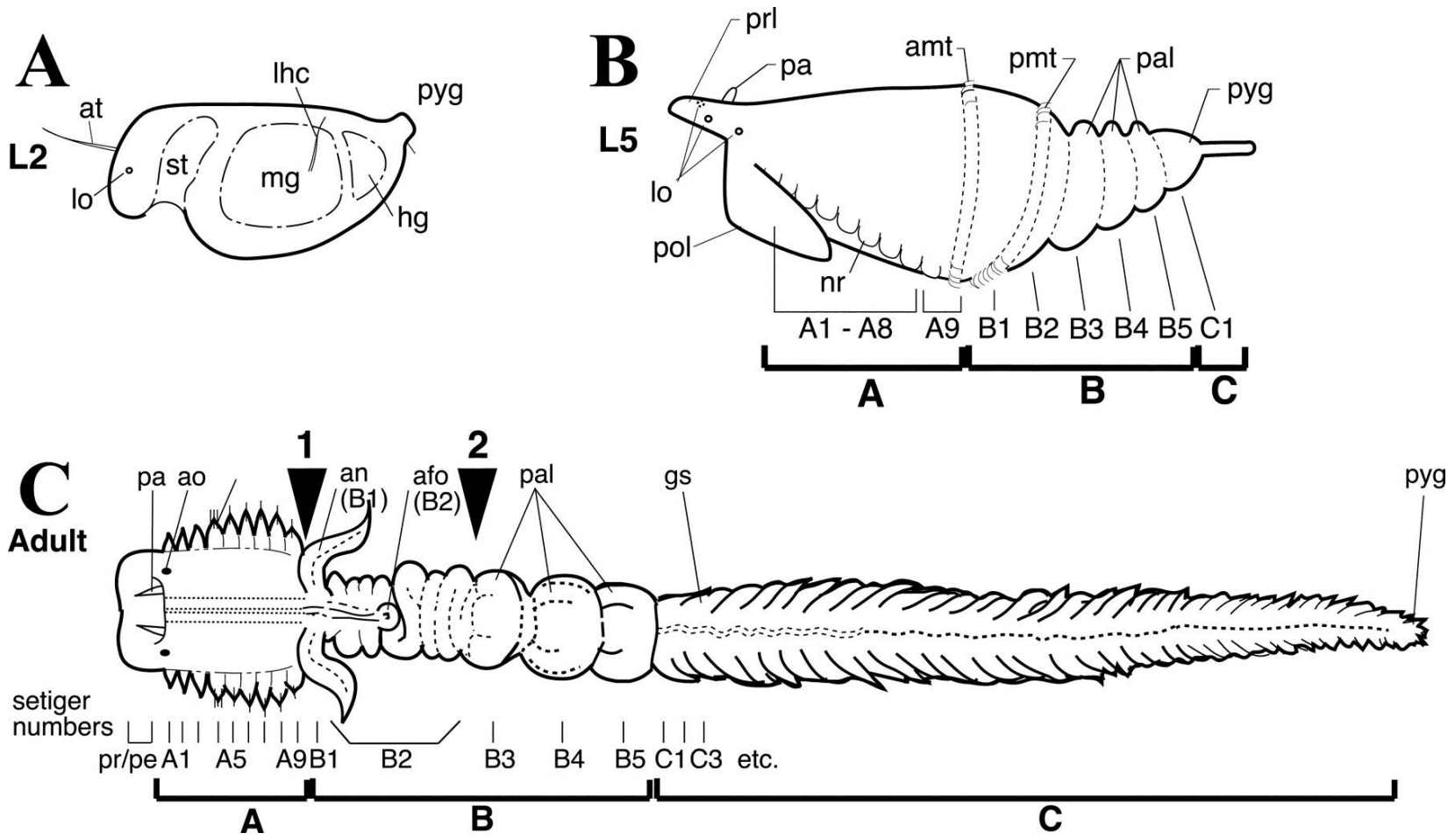


Fig. 1. Diagrams of three stages in Chaetopterus development.



AMER. ZOOL., 41:640–651 (2001)

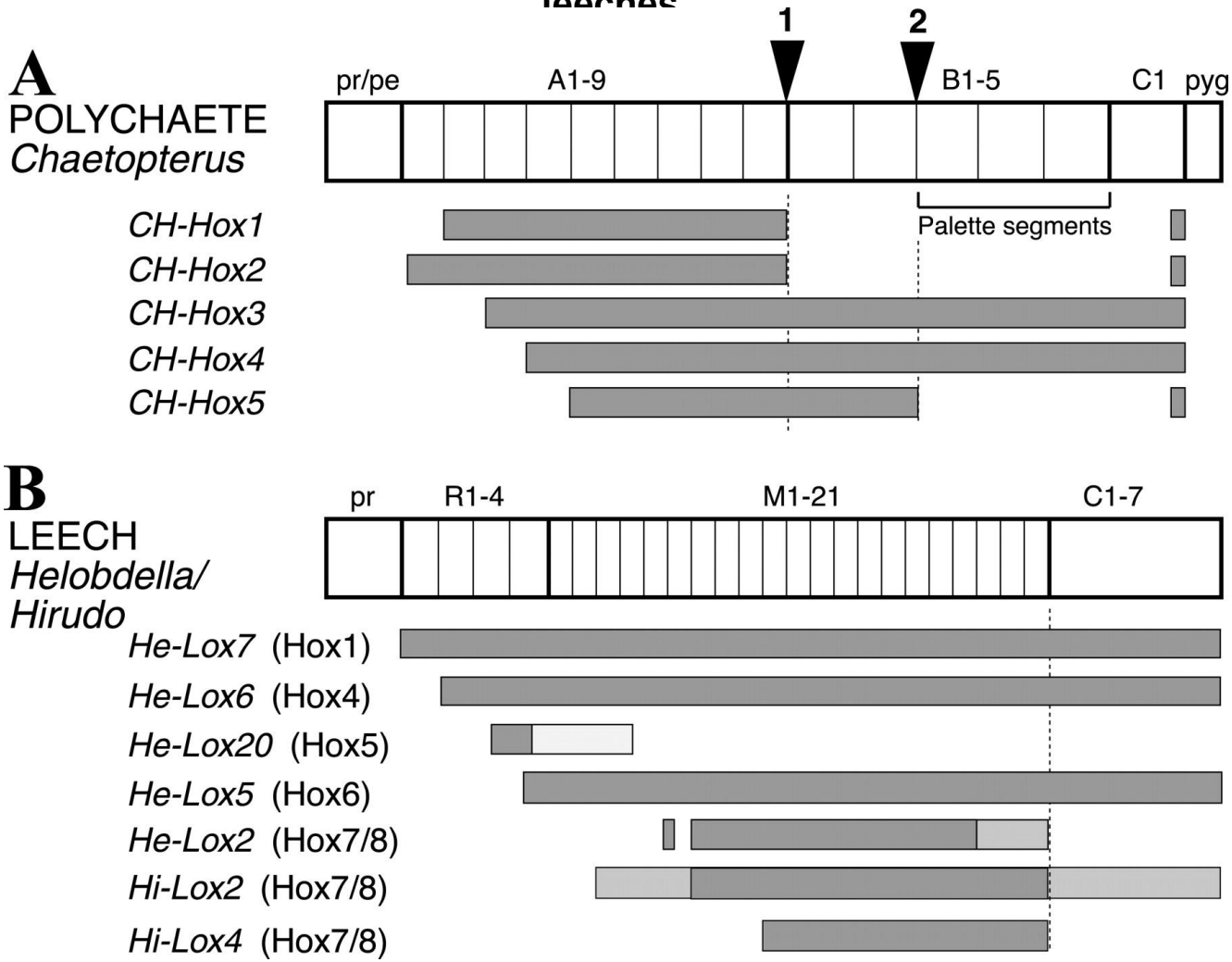
Comparative Analysis of Hox Gene Expression in the Polychaete *Chaetopterus*: Implications for the Evolution of Body Plan Regionalization[1]

STEVEN Q. IRVINE* AND MARK Q. MARTINDALE[2,†]

*Department of Cellular, Molecular and Developmental Biology, Yale University, P.O. Box 208103, New Haven, Connecticut 06520-8103 and
†Kewalo Marine Lab, PBRC/Univ. of Hawaii, 41 Ahui St., Honolulu, HI 96813

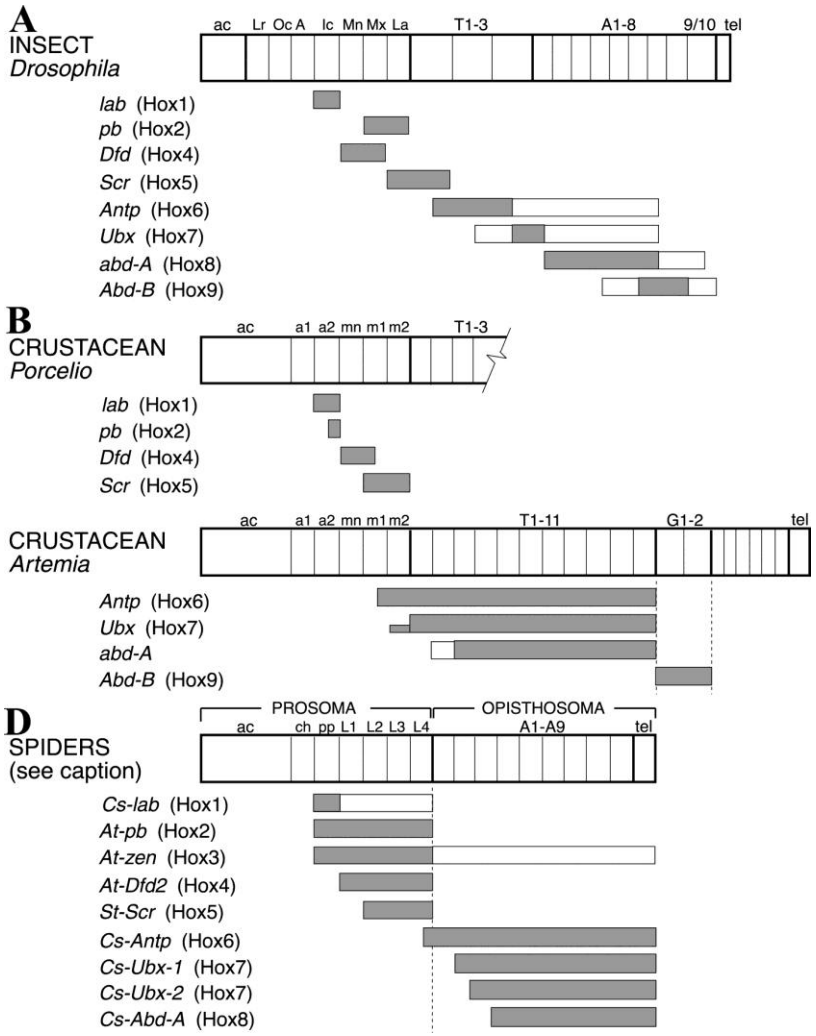
Integrative and Comparative Biology

Fig. 2. A diagram relating the late larval expression domains of the five most anteriorly-expressed Hox genes in Chaetopterus to the reported expression patterns for Hox genes in leeches



Irvine S Q , Martindale M Q Amer. Zool. 2001;41:640-651

Fig. 3. Diagrammatic representation of Hox gene expression patterns at intermediate stages of development reported for representative arthropods, displayed as described for Figure 2.



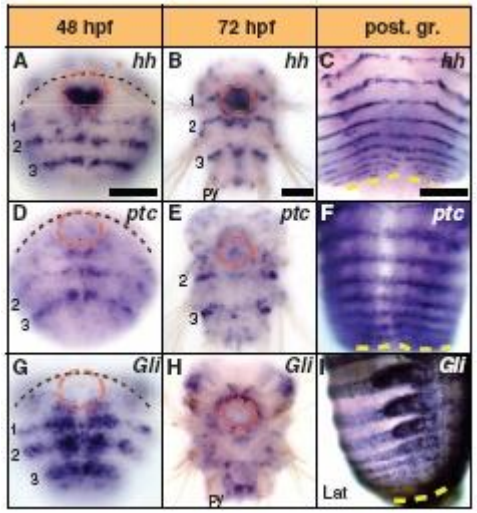
Irvine S Q , Martindale M Q Amer. Zool. 2001;41:640-651

Сегментация у полихет и насекомых – сходство и различия

Hedgehog Signaling Regulates Segment Formation in the Annelid *Platynereis*

Nicolas Dray,[1*†] Kristin Tessmar-Raible,[2,3*] Martine Le Gouar,[1*] Laura Vibert,[1] Foteini Christodoulou,[3] Katharina Schipany,[2] Aurélien Guillou,[4] Juliane Zantke,[2] Heidi Snyman,[3] Julien Béhague,[1,4] Michel Vervoort,[1,4] Detlev Arendt,[3] Guillaume Balavoine[1,4‡]

SCIENCE VOL 329 16 JULY 2010



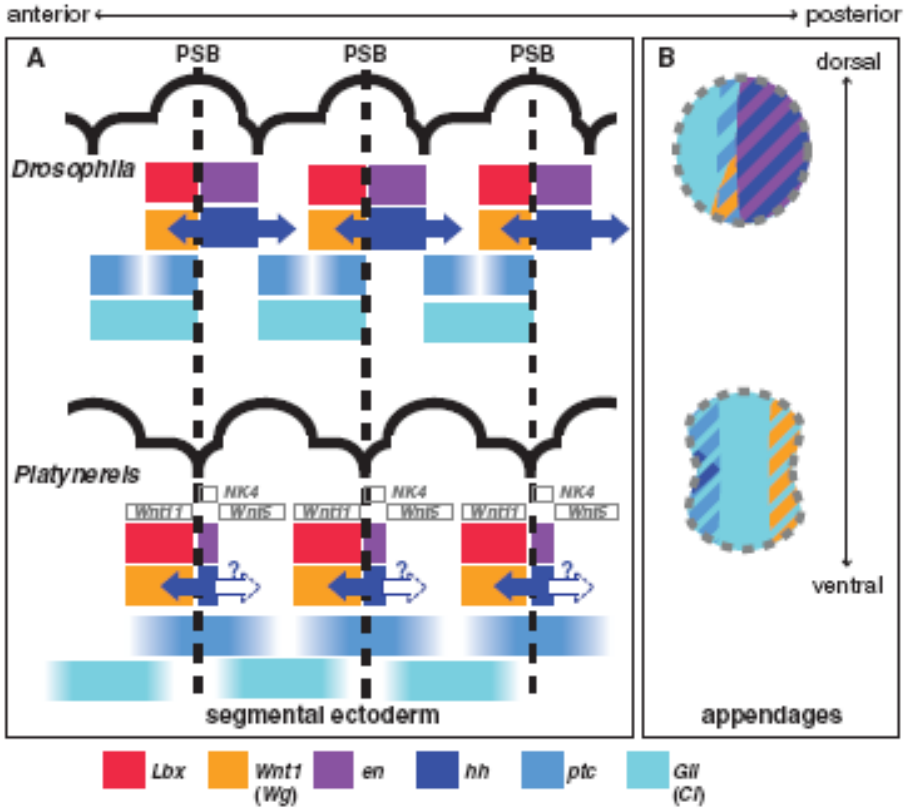


Fig. 3. (**A**) Comparison of the anteroposterior extension of striped expression patterns of proven and presumed segment polarity orthologous genes in *Platynereis* and *Drosophila*. Segment boundaries and limb anlagen positions are represented with a schematic body wall section in black. Orthologous genes are color-coded; segment polarity–like genes specific to *Platynereis* are represented by gray rectangles. The morphogenetic actions of the diffusible Hh proteins are represented with blue arrows. A white arrow with question mark indicates that Hh action on the anterior parts of annelid segments is not proven in this study. Unlike in fly, *Pdu-ptc* is expressed in *en*- and *hh*-positive cells, and *Pdu-Gli* expression does not abut *en*- and *hh*-positive cells in *Platynereis*. (**B**) Comparison of expression patterns of some of these segment polarity–like genes in the early stages of appendage formation. The homology of annelid segments with arthropod parasegments implies that annelid parapodia do not correspond in embryonic position with the arthropod appendages, which suggests that these appendages do not share a common origin in the protostome ancestor. PSB, parasegmental boundary.

BMC Evolutionary Biology

RESEARCH ARTICLE Open Access

A non-tree-based comprehensive study of metazoan Hox and ParaHox genes prompts new insights into their origin and evolution

Morgane Thomas-Chollier[1,2,6*], Valérie Ledent[3], Luc Leyns[2], Michel Vervoort[4,5]

Conclusions: Our analysis suggests that the presence of a single type of Posterior Hox genes (PG9-like) is ancestral to bilaterians, and that new Posterior PGs would have arisen in deuterostomes through independent gene duplications. Four types of Central genes would also be ancestral to bilaterians, with two of them, PG6- and PG7-like that gave rise, in protostomes, to the UbdA- and ftz/Antp/Lox5-type genes, respectively. A fifth type of Central genes (PG8) would have emerged in the vertebrate lineage. Our results also suggest the presence of Anterior (PG1 and PG3), Central and Posterior Hox genes in the cnidarians, supporting an ancestral four-gene Hox cluster. In addition, our data support the relationship of the bilaterian ParaHox genes *Gsx* and *Xlox* with PG3, and *Cdx* with the Central genes. Our study therefore indicates three possible models for the origin of Hox and ParaHox in early metazoans, a two-gene (Anterior/PG3 - Central/Posterior), a three-gene (Anterior/PG1, Anterior/PG3 and Central/Posterior), or a four-gene (Anterior/PG1 - Anterior/PG3 - Central - Posterior) ProtoHox cluster.

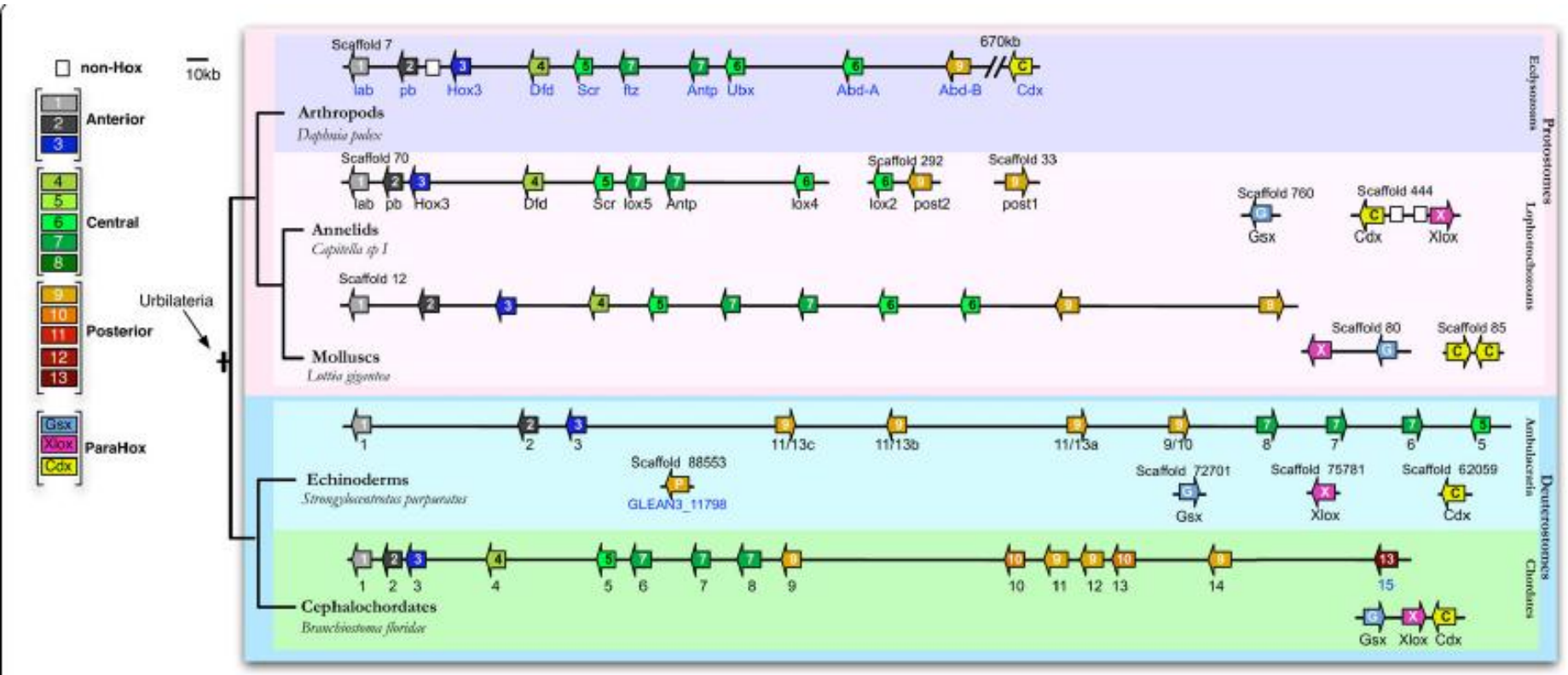


Figure 2 Genomic organization of the Hox genes identified with HoxPred in the genome-scale analyses. Hox and ParaHox genes are

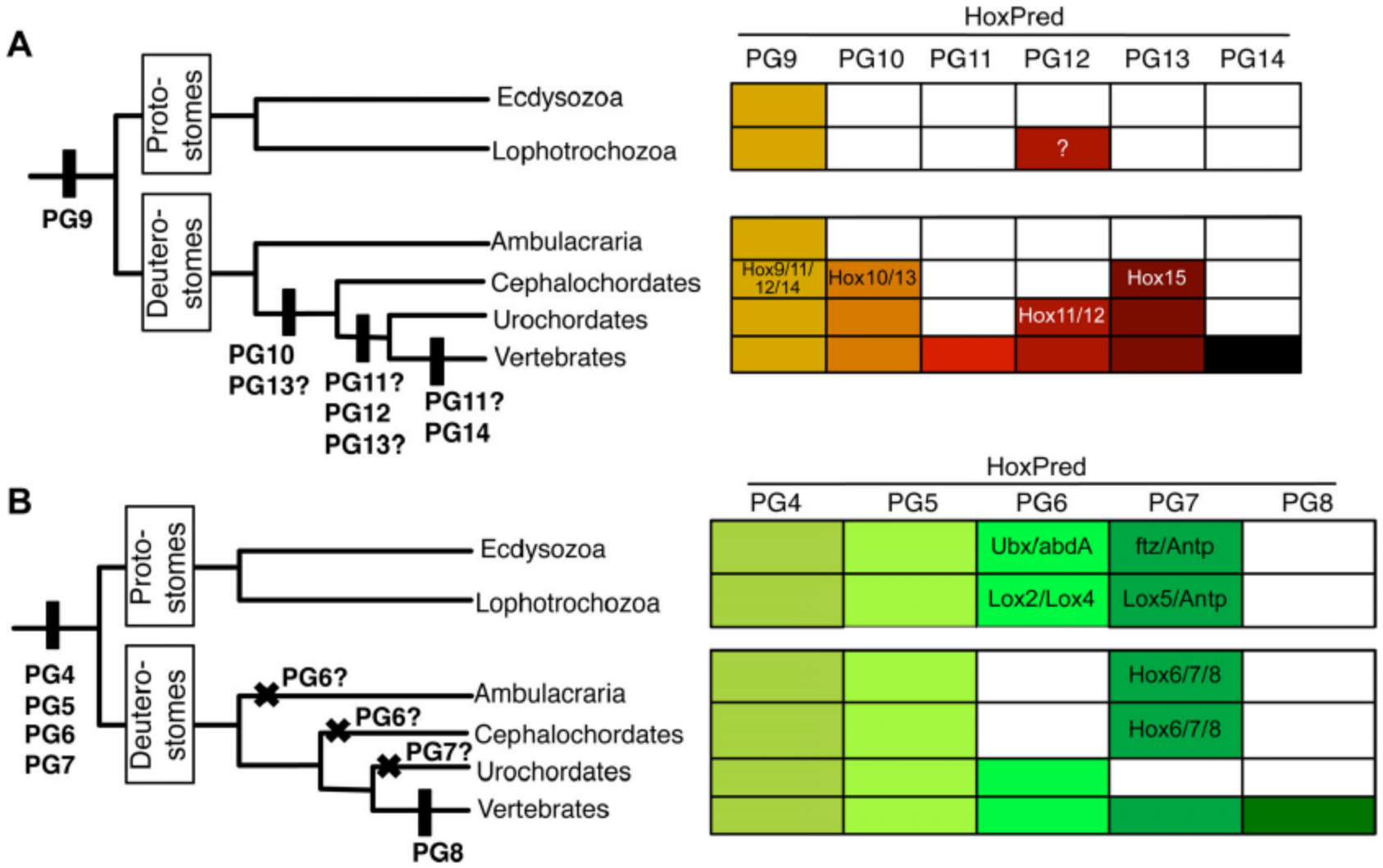
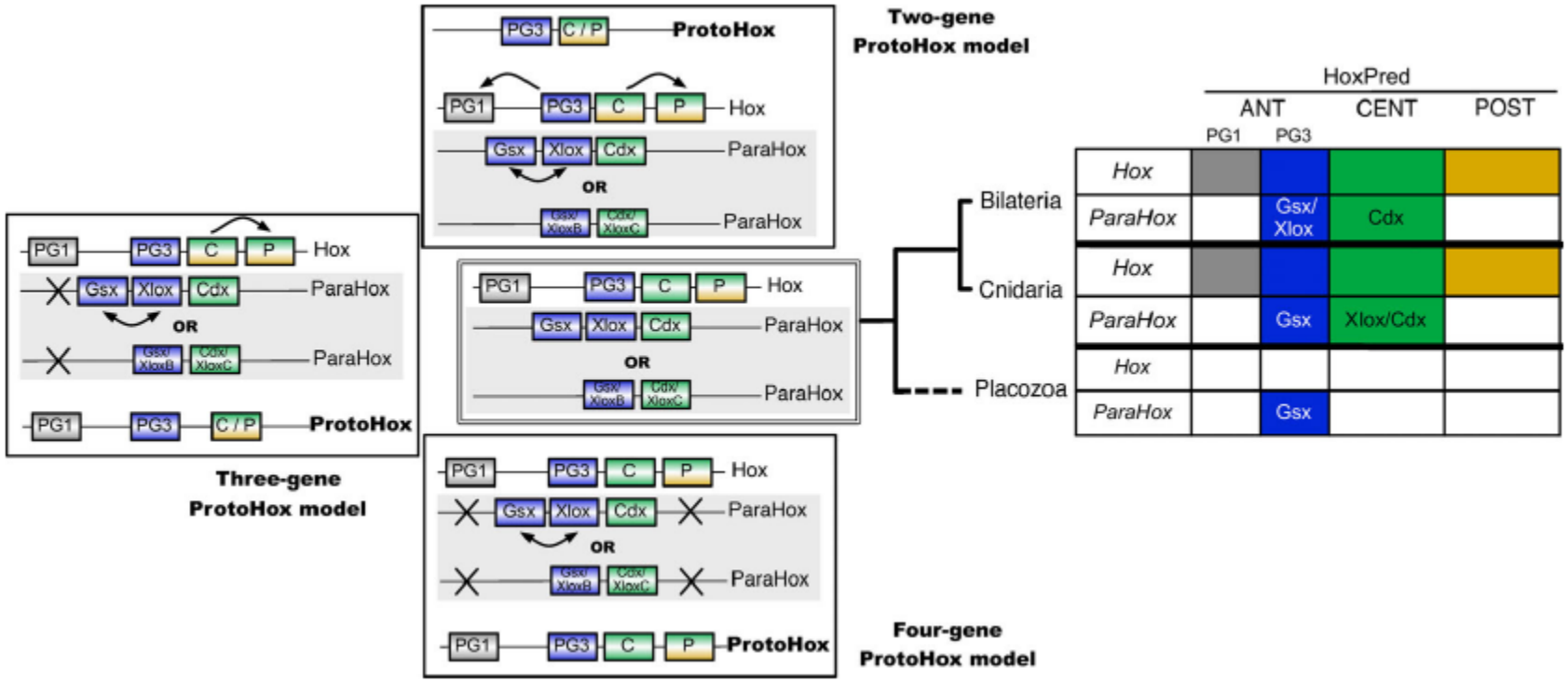


Figure 3 Models for the evolution of Posterior and Central Hox genes in bilaterians. A. Posterior Hox genes. The predicted PGs for each


PG3
C / P
ProtoHox
Two-gene
ProtoHox model
PG1
PG3
C
P
Hox
Gsx
Xlox
Cdx
ParaHox
OR
Gsx/
XloxB
Cdx/
XloxC
ParaHox
Bilateria
Cnidaria
Placozoa
Three-gene
ProtoHox model
Four-gene
ProtoHox model
HoxPred
ANT
CENT
POST
PG1
PG3
Hox
ParaHox
Gsx/
Xlox
Cdx
Xlox/Cdx
Gsx

Ген Dscam - 38016 изоформ ?

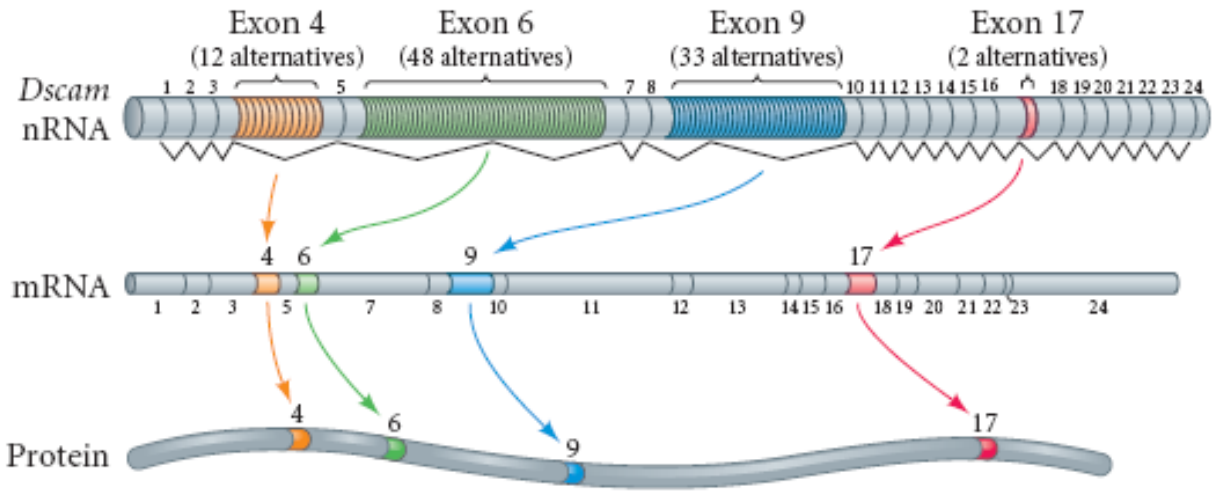
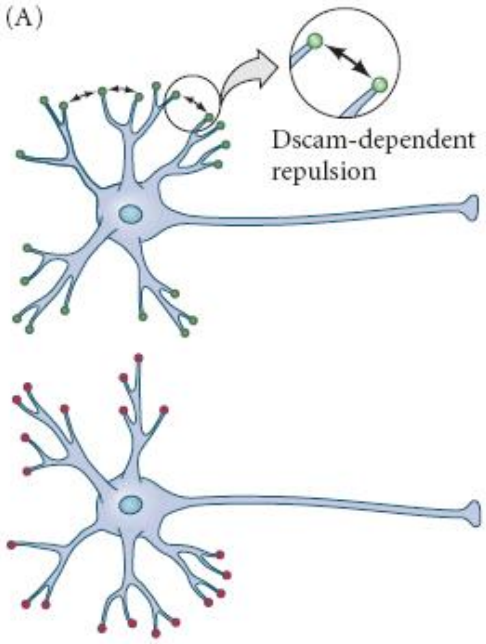
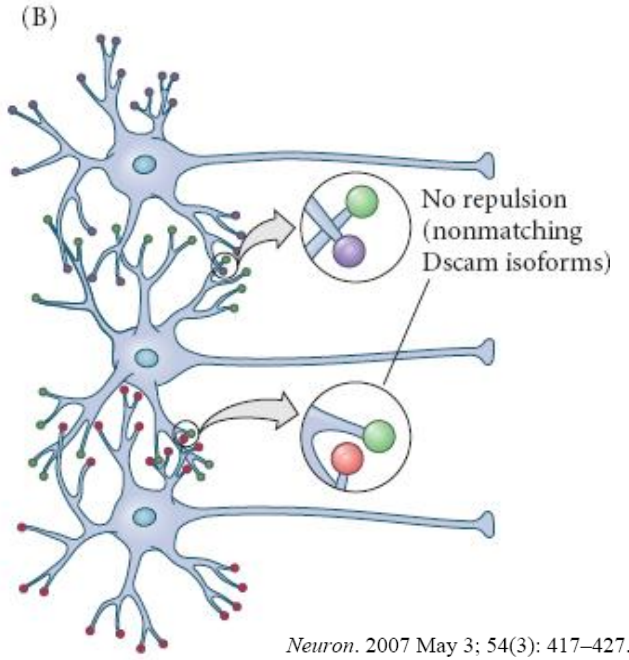


FIGURE 2.28 The *Dscam* gene of *Drosophila* can produce 38,016 different types of proteins by alternative nRNA splicing. The gene contains 24 exons. Exons 4, 6, 9, and 17 are encoded by sets of mutually exclusive possible sequences. Each messenger RNA will contain one of the 12 possible exon 4 sequences, one of the 48 possible exon 6 alternatives, one of the 33 possible exon 9 alternatives, and one of the 2 possible exon 17 sequences. The *Drosophila Dscam* gene is homologous to a DNA sequence on human chromosome 21 that is expressed in the nervous system. Disturbances of this gene in humans may lead to the neurological defects of Down syndrome (Yamakawa et al. 1998; Saito 2000).

Необходим для образования нейронных сетей – каждый нейрон имеет свою изоформу, что предотвращает образование синапсов между дендритами одной клетки?

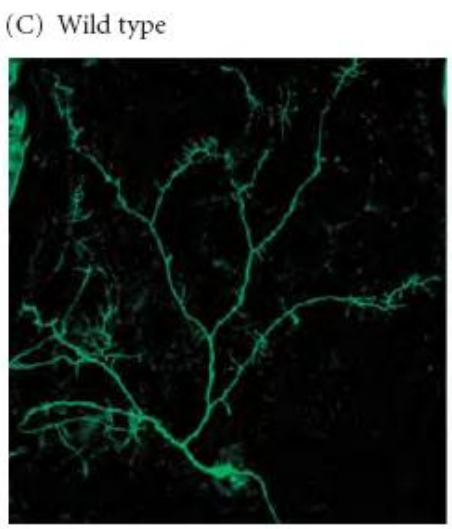
Hattori et al., 2007

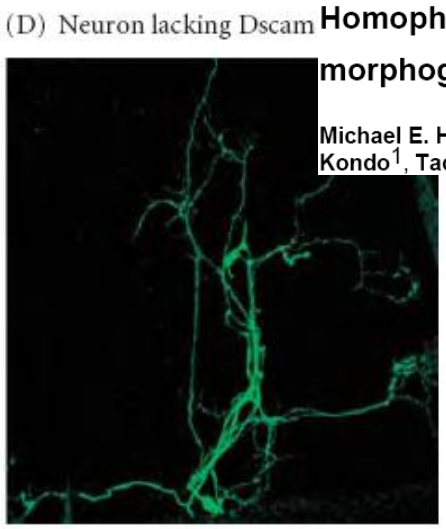




Dietmar Schmucker

Neuron. 2007 May 3; 54(3): 417–427.





Homophilic Dscam interactions control complex dendrite morphogenesis

Michael E. Hughes[1,2], **Rachel Bortnick**[1,2], **Asako Tsubouchi**[3], **Philipp Bäumer**[1], **Masahiro Kondo**[1], **Tadashi Uemura**[3], and **Dietmar Schmucker**

Smith *et al. Malaria Journal* 2011, **10**:156
http://www.malariajournal.com/content/10/1/156

MALARIA JOURNAL

RESEARCH Open Access

Alternative splicing of the *Anopheles gambiae Dscam* gene in diverse *Plasmodium falciparum* infections

Paul H Smith[1*], Jonathan M Mwangi[2], Yaw A Afrane[3], Guiyun Yan[4], Darren J Obbard[1], Lisa C Ranford-Cartwright[2] and Tom J Little[1]

- Альтернативные сплайс-формы *Dscam* участвуют иммунном ответе на инфицирование различными формами плазмодия

MALARIA JOURNAL

Dscam and DSCAM: complex genes in simple animals, complex animals yet simple genes

"we would like to speculate that despite the absence of isoform diversity, vertebrate DSCAM, and DSCAML1 receptors maintained a functional role in complex molecular recognition processes complementing the functions of other CAMs and newly diversified receptors (e.g., Neurexins)."

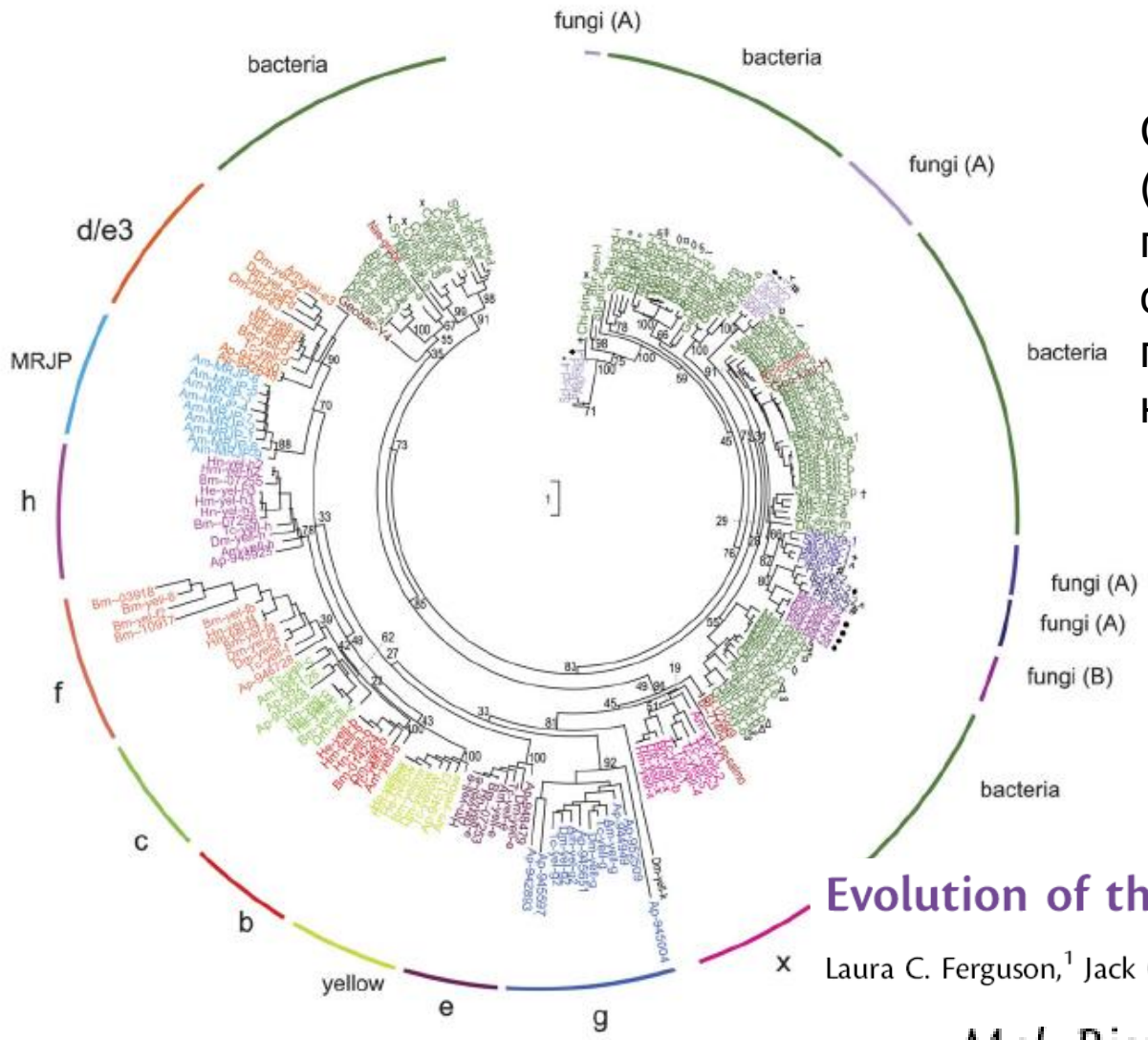
Dscam and DSCAM: complex genes in simple animals, complex animals yet simple genes

Dietmar Schmucker and Brian Chen

Genes Dev. 2009 23: 147-156
Access the most recent version at doi:10.1101/gad.1752909

Загадочный желтый ген у насекомых – параллельный перенос от бактерий?

Ferguson et al. · doi:10.1093/molbev/msq192 MBE



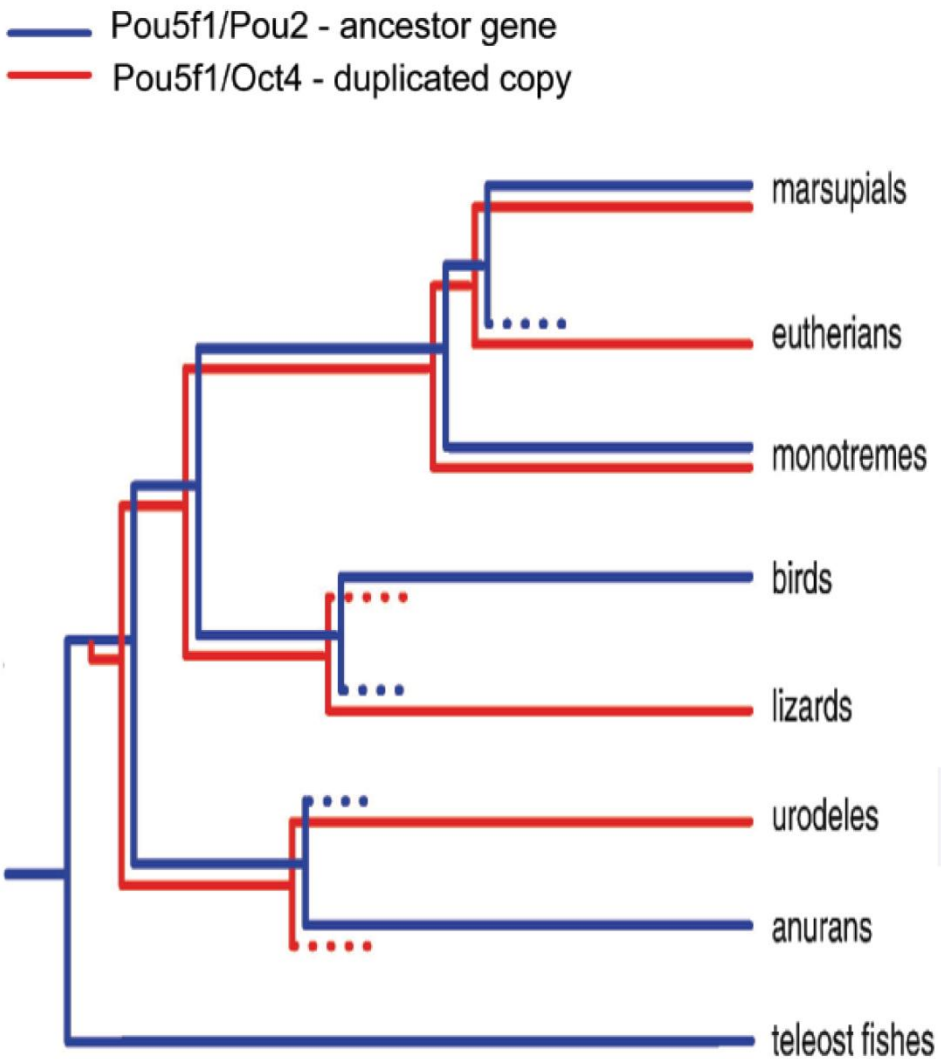
Семейство генов *yellow* (регуляция пигментации, поведение дрозофилы, формирование каст у пчел) известно только у насекомых и бактерий.

Evolution of the Insect *Yellow* Gene Family

Laura C. Ferguson,[1] Jack Green,[1] Alison Surridge,[1] and Chris D. Jiggins*,[1]

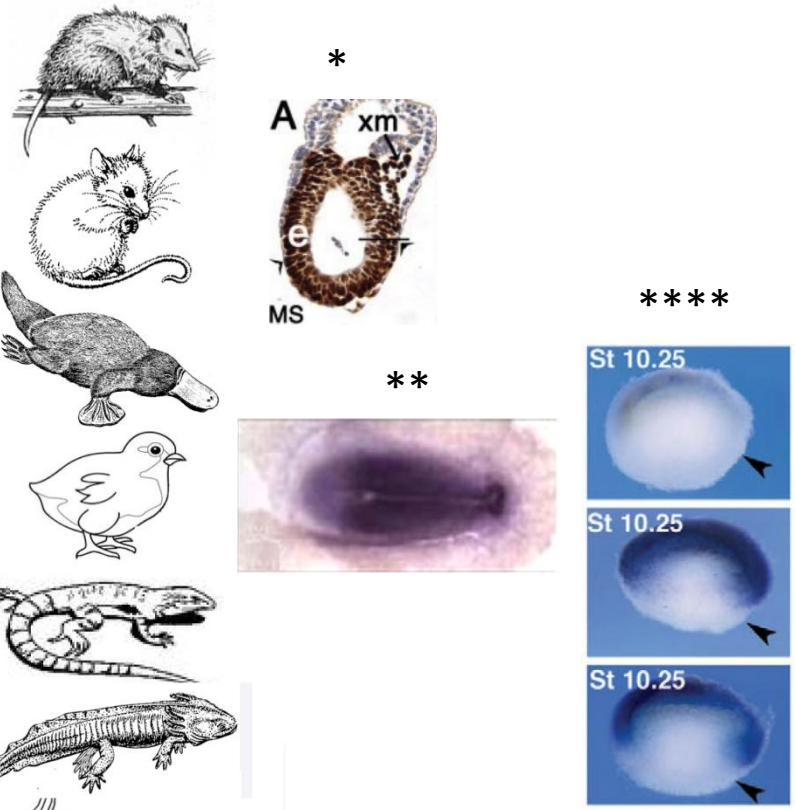
Mol. Biol. Evol. 28(1):257–272. 2011

Evolution of Pou5f1



Frankenberg,, Dev.Biol.,2009

Expression
at gastrula stages



- **Downs KM, Dev.Dyn.2008*
- ***Lavial et al., Development 2007*
- ****Belting et al., Development 2002*
- ***** Morrison,Brickmann 2006*

Роль Pou5 в развитии Danio

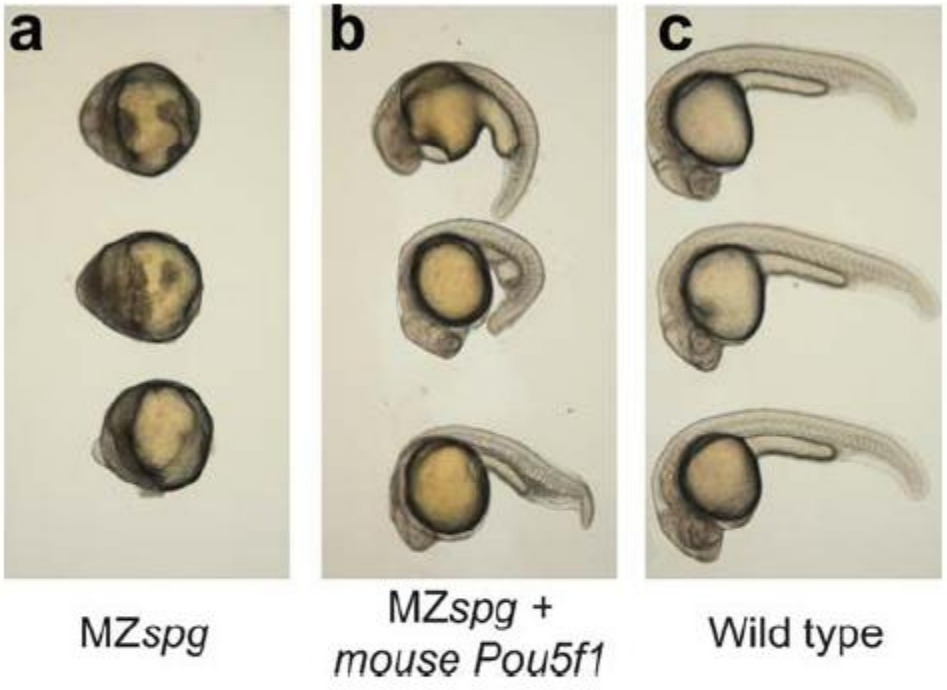


FIG. 2. Mouse Pou5f1 overexpression rescues the phenotype of zebrafish maternal and zygotic Pou5f1 mutant embryos (MZ*spg*). (**a**) Embryonic phenotype (MZ*spg*) at 24 h postfertilization (hpf). Note the absence of body axes and recognizable organs. (**b**) MZ*spg* embryos that were injected with 25 pg mouse *Pou5f1* mRNA at one cell stage at 24 hpf. Note that body axes, head, eyes, and tail formation are restored. (**c**) Wild-type control embryos are 24 hpf.

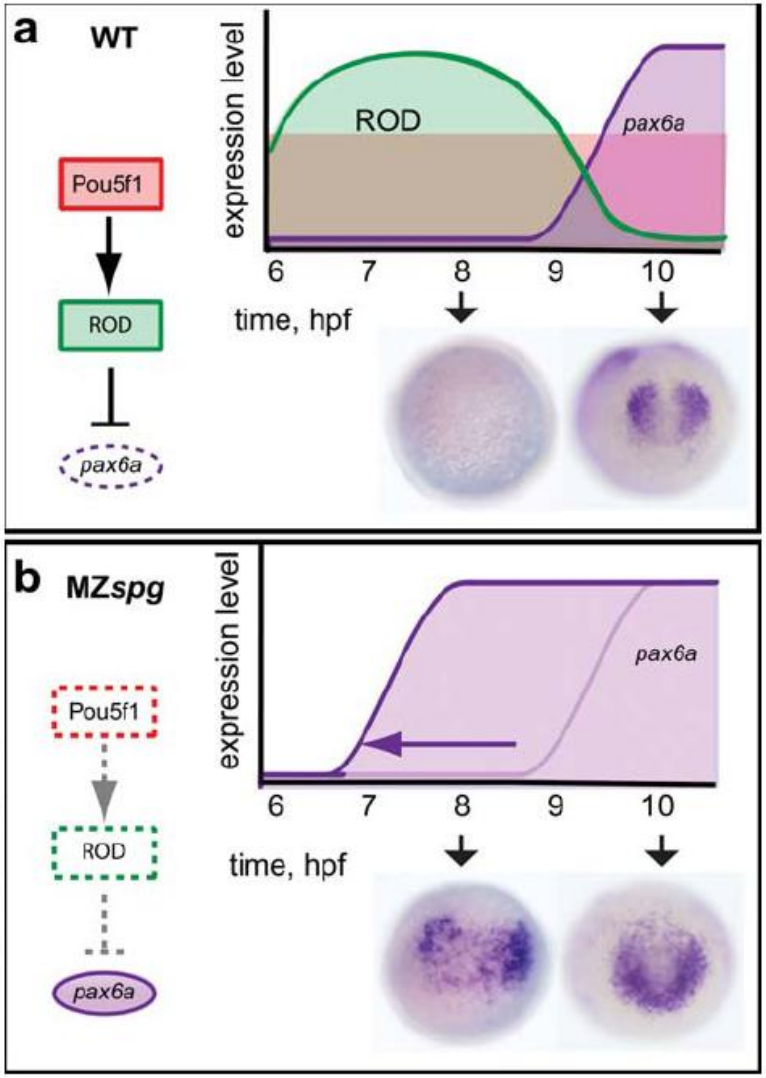
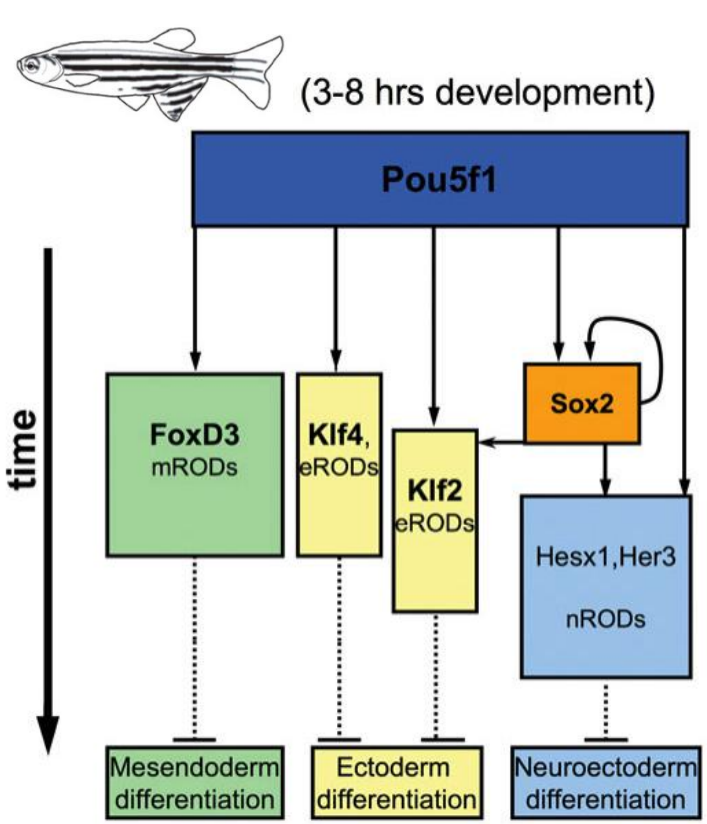
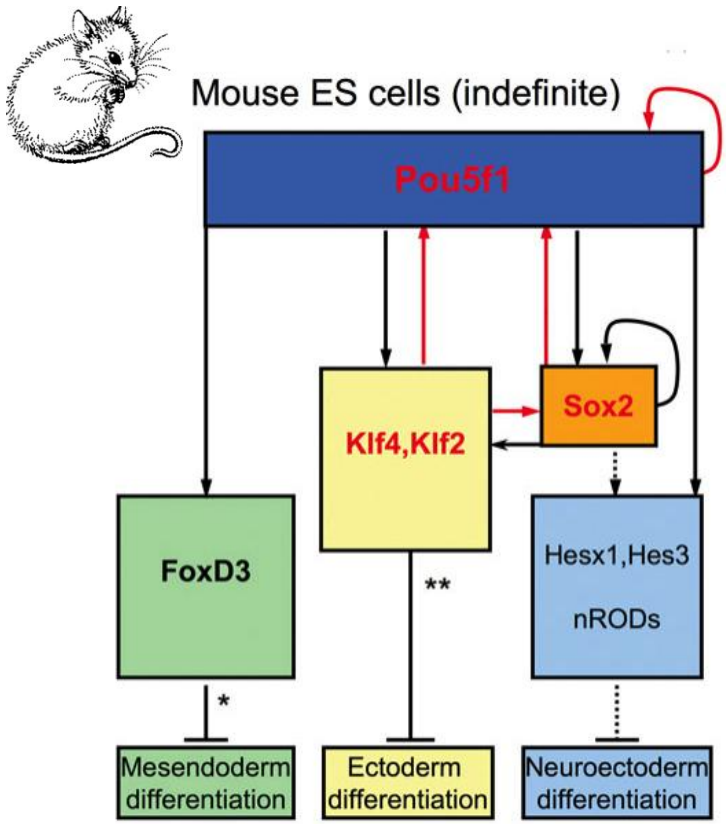


FIG. 3. Pou5f1 activates repressors of differentiation to suppress premature expression of PODs. (**a**) Wild-type embryo (WT).

Onichtchouk et al., 2010;

Pou5f1 activates germlayer-specific repressors to control gene expression in time





Hypothesis: The ES cell regulatory network in mammals evolved from the timing control network common for all in vertebrates

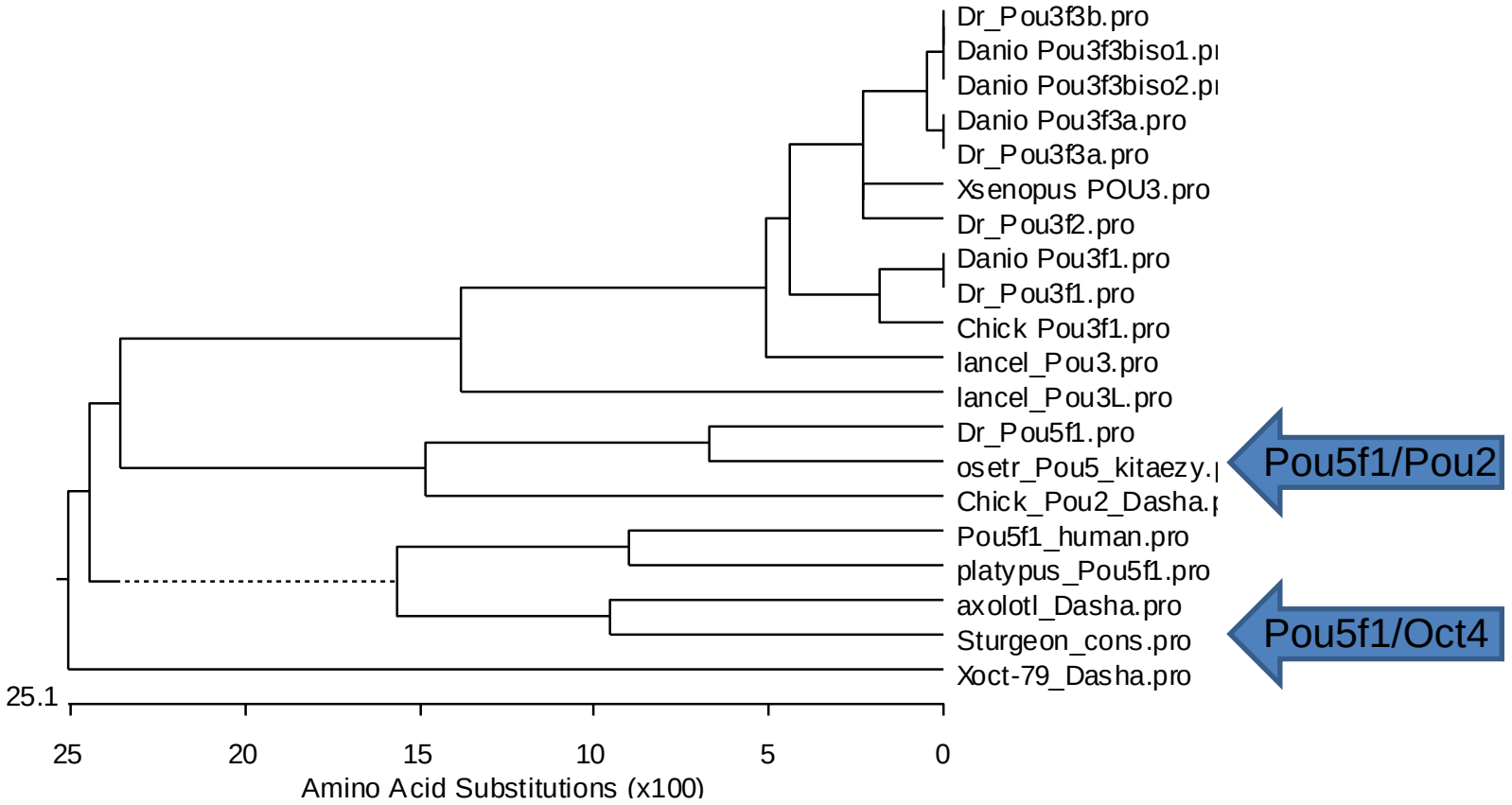
suggestive evidence
direct evidence
evolutionary conserved links
ES self-maintenance (mammals only)

* *Liu Y, Labosky PA (2008) Regulation of embryonic stem cell self-renewal and pluripotency by Foxd3. Stem Cells 26: 2475–2484*

** *Jiang J, (2008) A core Klf circuitry regulates self-renewal of embryonic stem cells. Nat Cell Biol 10: 353–360*

Onichtchouk et al., Molecular Systems Biology, 6:354 Mar 9 2010

Дупликация Pou5 (появление Oct4) – раньше появления осетровых



25 лет Evo-Devo: генетика морфологической эволюции

Leading Edge
Perspective

Cell

Evo-Devo and an Expanding Evolutionary Synthesis: A Genetic Theory of Morphological Evolution

Sean B. Carroll[1,*]
[1]Howard Hughes Medical Institute, Laboratory of Molecular Biology, University of Wisconsin–Madison, Madison, WI 53706, USA
*Correspondence: sbcarrol@wisc.edu
DOI 10.1016/j.cell.2008.06.030

Парадоксы на заре Evo-Devo

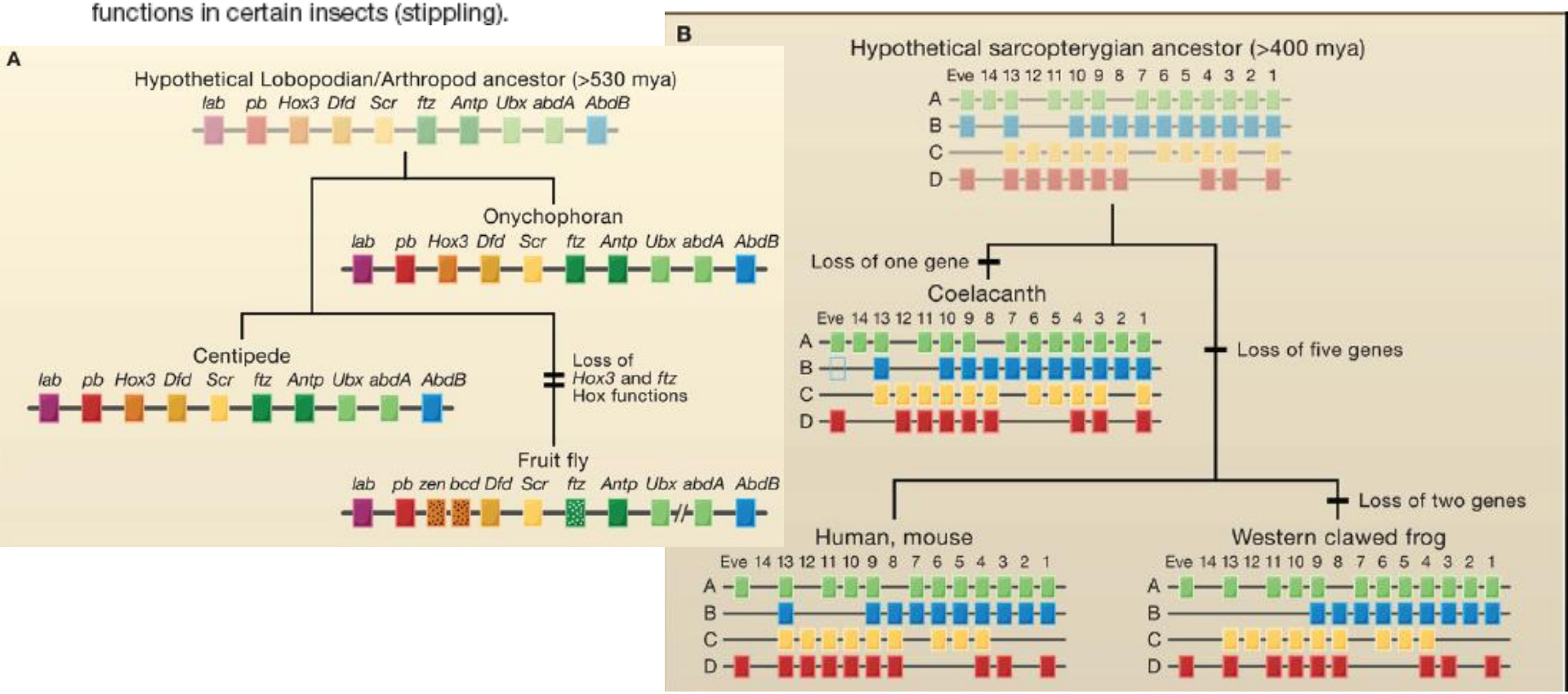
- Белки у филогенетически далеких видов(цитохромы, глобины) сильно отличаются, но функция консервативна. Zuckerkandl and Pauling, 1965 – фенотипы изменяются за счет изменения времени и силы экспрессии.

- Очень близкие геномы (человек-шимпанзе) – разный фенотип. King and Wilson, 1975- “to explain how species which have such substantially similar genes can differ so substantially in anatomy…” - evolution of anatomy occurred more by changing gene regulation than by changing protein sequences.

Гены редко появляются, часто теряются

(A) Based upon the *Hox* gene complements of onychophora and arthropods, a minimum of ten *Hox* genes must have existed in the common ancestor of lobopodians and arthropods. No new *Hox* genes arose in centipedes or insects while the *Hox3* and *ftz* genes were co-opted into new functions in certain insects (stippling).

(B) No new *Hox* genes are known to have evolved since the divergence of tetrapods from a common sarcopterygian ancestor shared with coelacanths. Rather, gene loss has occurred in several lineages.



- 1. Новые формы образуются за счет изменения экспрессии консервативных белков

- 2. Эти изменения за счет cis-регуляторных областей мозаичных плейотропных регуляторных генов и генов, которые ими контролируются