Молекулярная генетика на службе зоологии беспозвоночных

Уровни организации

- Гены (ДНК, Геном)

↓

- Информационная РНК (Экспрессом)

↓

- Белки (Протеомика)

↓

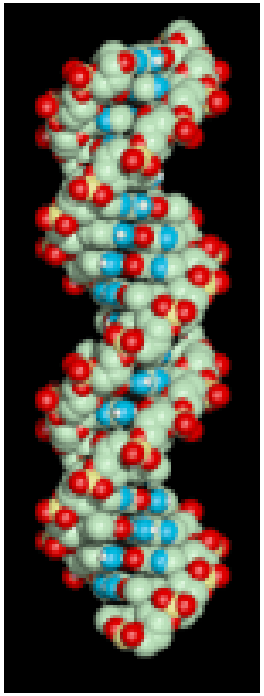
- Белок-белковые и белок-ДНК взаимодействия

↓

- Фенотип (морфология, физиология, гомеостаз, адаптации)

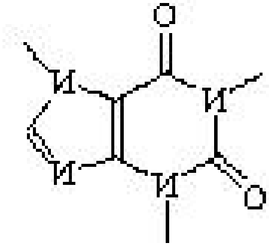
ДНК – самая сложная структура в живых организмах!

VS.

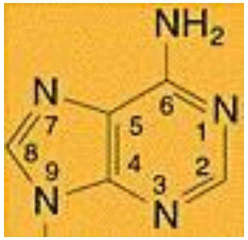


С другой стороны, ДНК по составу мало отличается от бутылки Кока-Колы!

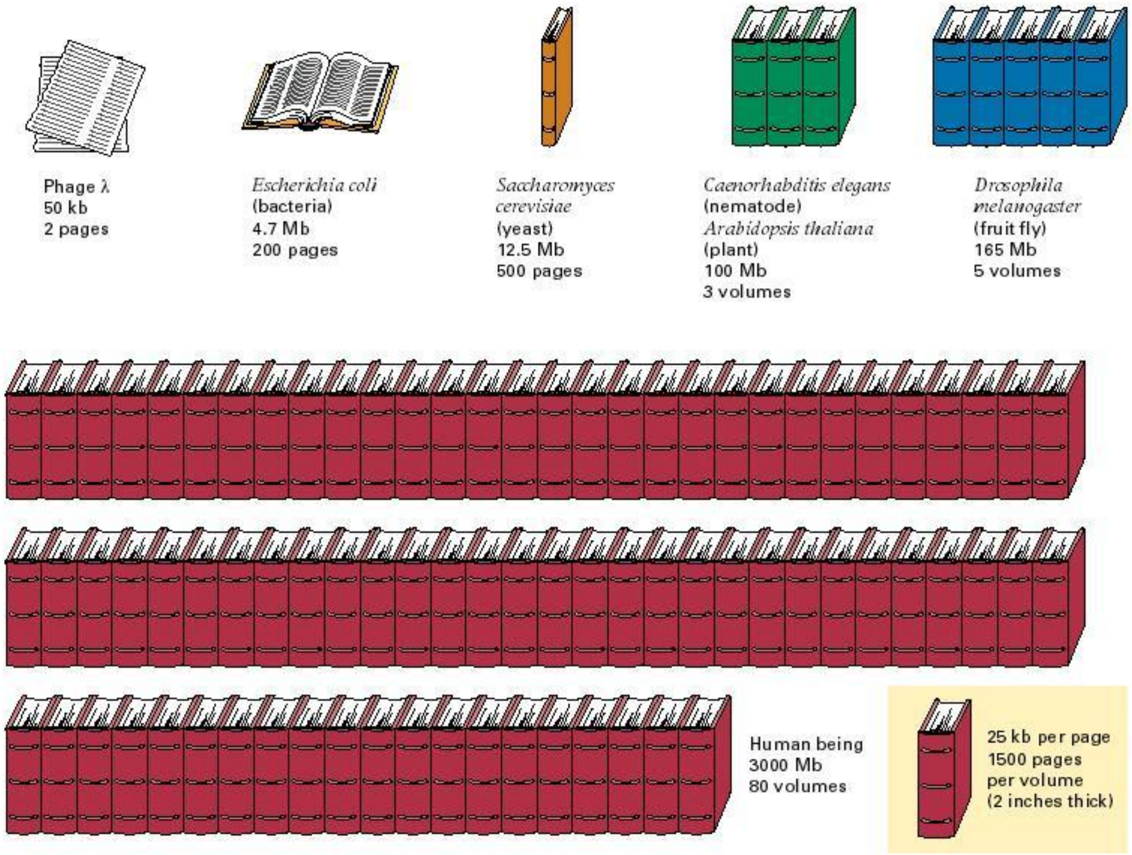
Coke	DNA	Solubility
water	water	-
Sugar (sucrose)	Sugar (dexoyribose)	VERY High
Phosphate (PO_4^- acid)	phosphate	moderate
caffeine	bases (A,T,C,G)	extremely low



caffeine



Adenine

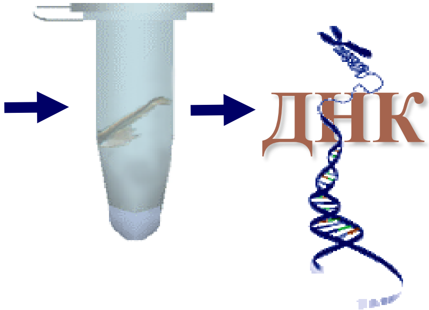


У мужчин на два тома меньше…

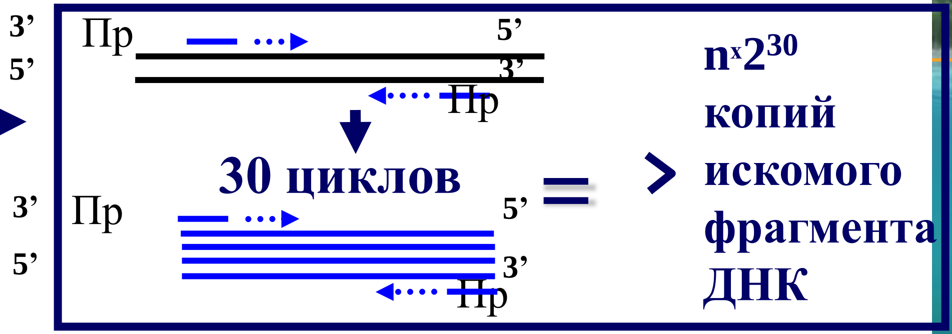
Но многие организмы имеют геном еще больше!

Общая схема изучения нуклеотидных последовательностей

1. Сбор материала



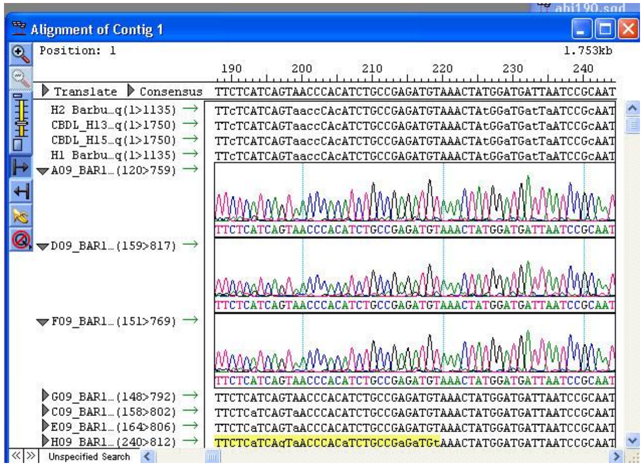
2. Выделение ДНК



30 циклов = > n^x2^{30} копий искомого фрагмента ДНК

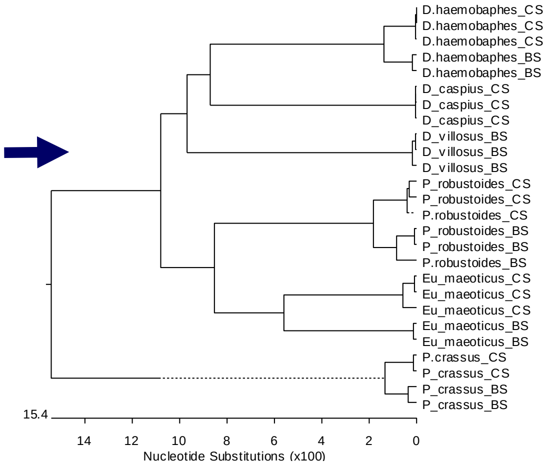
3. ПЦР-амплификация фрагмента мтДНК

4. Сиквенс пцр-фрагмента



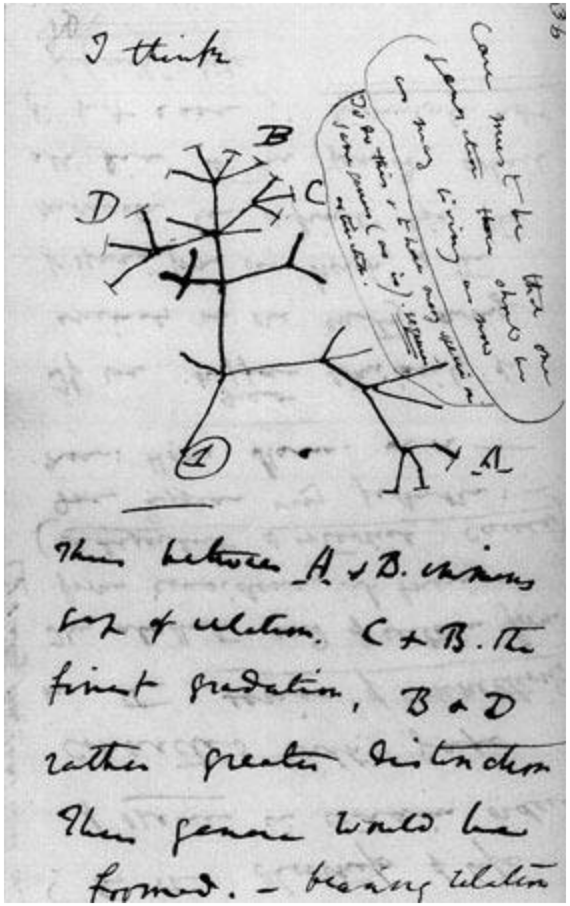
```
Position: 1                                                        1.753kb
                              190       200       210       220       230       240
Translate  Consensus     TTCTCATCAGTAACCCACATCTGCCGAGATGTAAACTATGGATGATTAATCCGCAAT
  H2 Barbu…q(1>1135) →   TTcTCATCAGTaaccCAcATCTGCCGAGATGTAAACTAtGGaTGatTaATCCGcAAT
  CBDL_H13…q(1>1750) →   TTcTCATCAGTaaccCAcATCTGCCGAGATGTAAACTAtGGaTGatTaATCCGcAAT
  CBDL_H15…q(1>1750) →   TTcTCATCAGTaaccCAcATCTGCCGAGATGTAAACTAtGGaTGatTaATCCGcAAT
  H1 Barbu…q(1>1135) →   TTcTCATCAGTaaccCAcATCTGCCGAGATGTAAACTAtGGaTGatTaATCCGcAAT
  A09_BAR1…(120>759) →
                         TTCTCATCAGTAACCCACATCTGCCGAGATGTAAACTATGGATGATTAATCCGCAAT
  D09_BAR1…(159>817) →
                         TTCTCATCAGTAACCCACATCTGCCGAGATGTAAACTATGGATGATTAATCCGCAAT
  F09_BAR1…(151>769) →
                         TTCTCATCAGTAACCCACATCTGCCGAGATGTAAACTATGGATGATTAATCCGCAAT
  G09_BAR1…(148>792) →   TTCTCATCAGTAACCCACATCTGCCGAGATGTAAACTATGGATGATTAATCCGCAAT
  C09_BAR1…(158>802) →   TTCTCaTCAGTaACCCACATCTGCCGAGATGTAAACTATGGATGATTAATCCGCAAT
  E09_BAR1…(164>806) →   TTCTCaTCAGTaACCCACATCTGCCGAGATGTAAACTATGGATGATTAATCCGCAAT
  H09_BAR1…(240>812) →   TTCTCaTCAqTaACCCACaTCTGCCGaGaTGtAAACTATGGATGATTAATCCGCAAT
```

5. Стыковка и множественное выравнивание последовательностей



6. Филогенетическая реконструкция

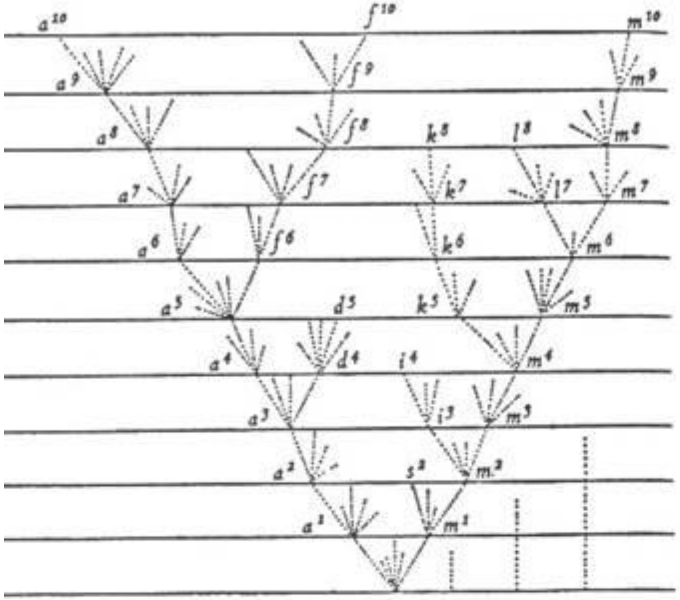
Дерева- виды и гены

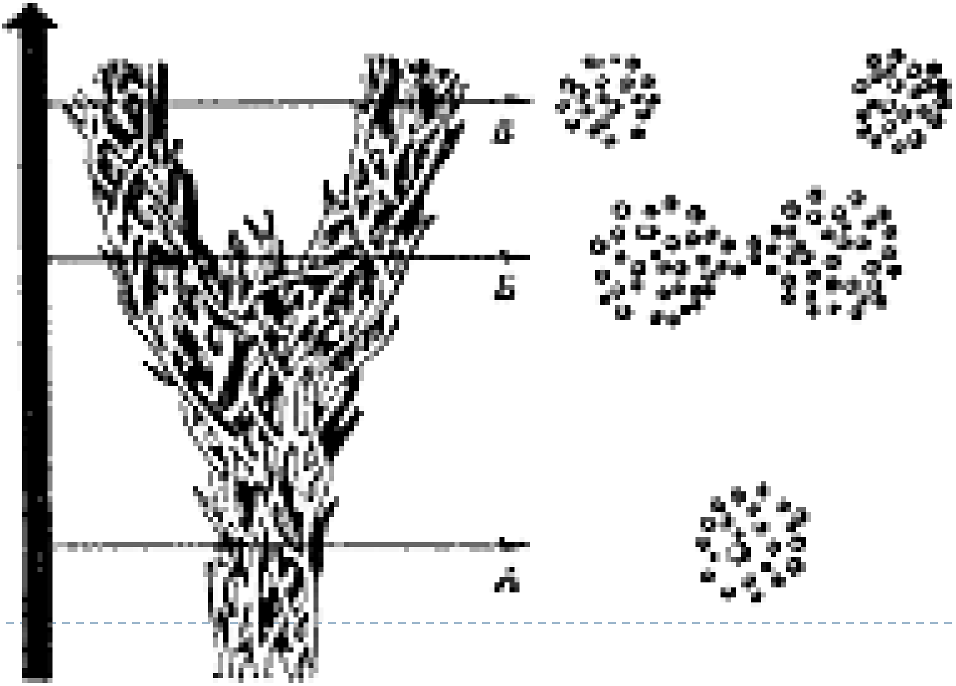

36

I think

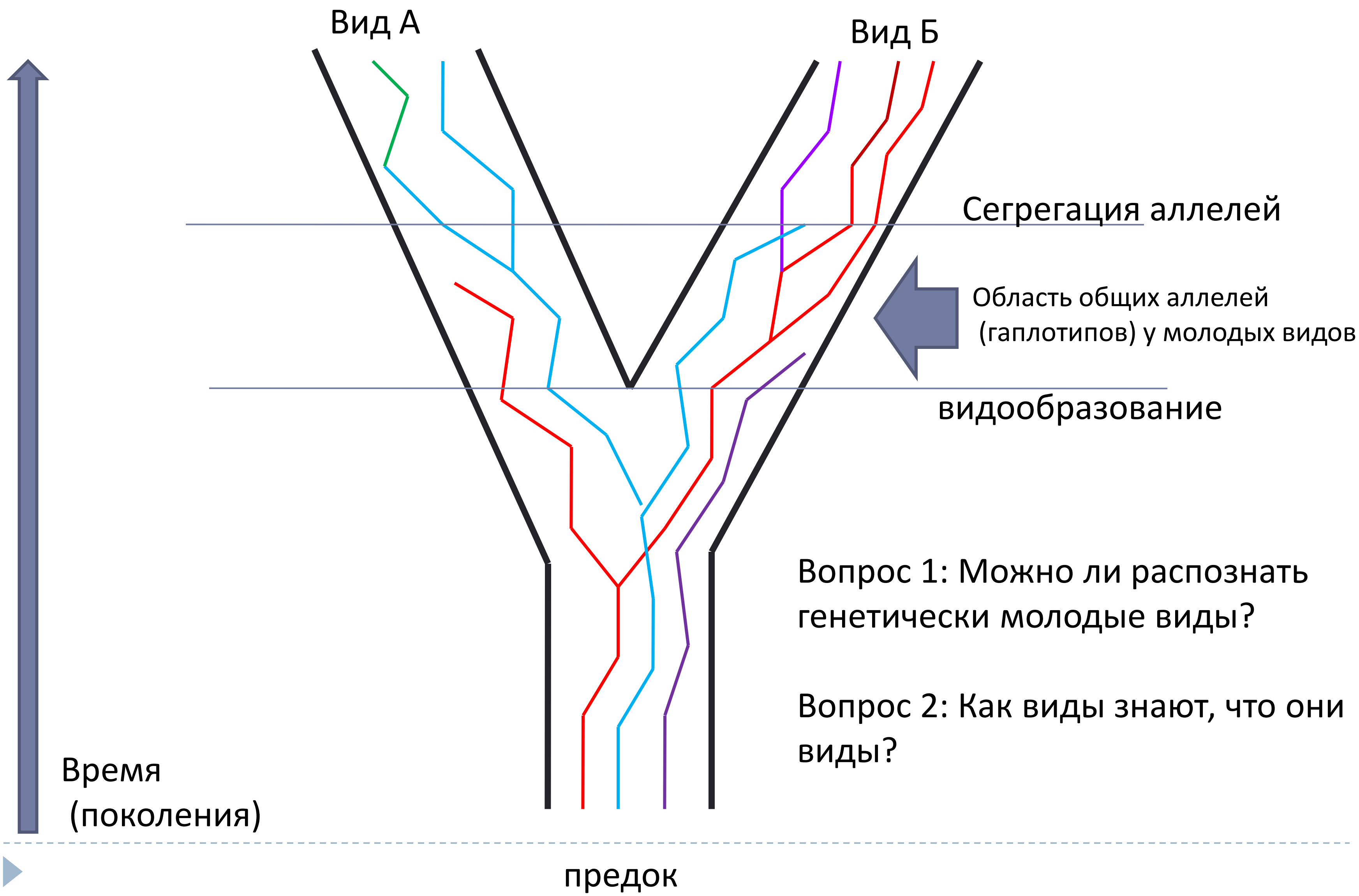
Case must be that one generation then should be as many living as now. To do this & to have many species in same genus (as is) requires extinction.

Thus between A & B. immense gap of relation. C & B. the finest gradation, B & D rather greater distinction. Thus genera would be formed. — bearing relation





Генеалогия генов и видообразование



Вид А

Вид Б

Сегрегация аллелей

Область общих аллелей
(гаплотипов) у молодых видов

видообразование

Время
(поколения)

предок

Вопрос 1: Можно ли распознать генетически молодые виды?

Вопрос 2: Как виды знают, что они виды?

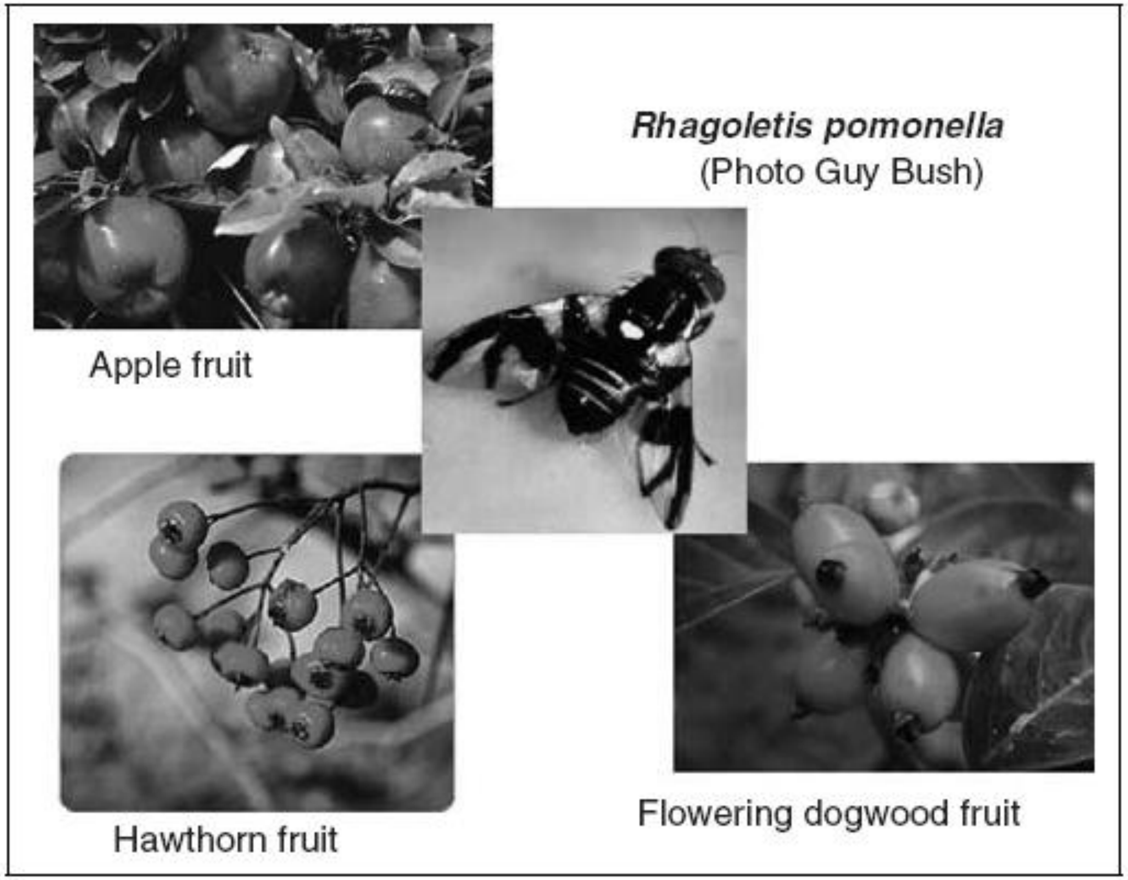
Определение (концепция) вида должно решать следующие задачи

- I. Помочь в классификации
- 2. описывать дискретные природные явления (группы организмов)
- 3. Помочь понять как эти «дискретные явления» возникли в природе
- 4. Отражать эволюционную историю
- 5. Быть применимо к максимальному числу организмов

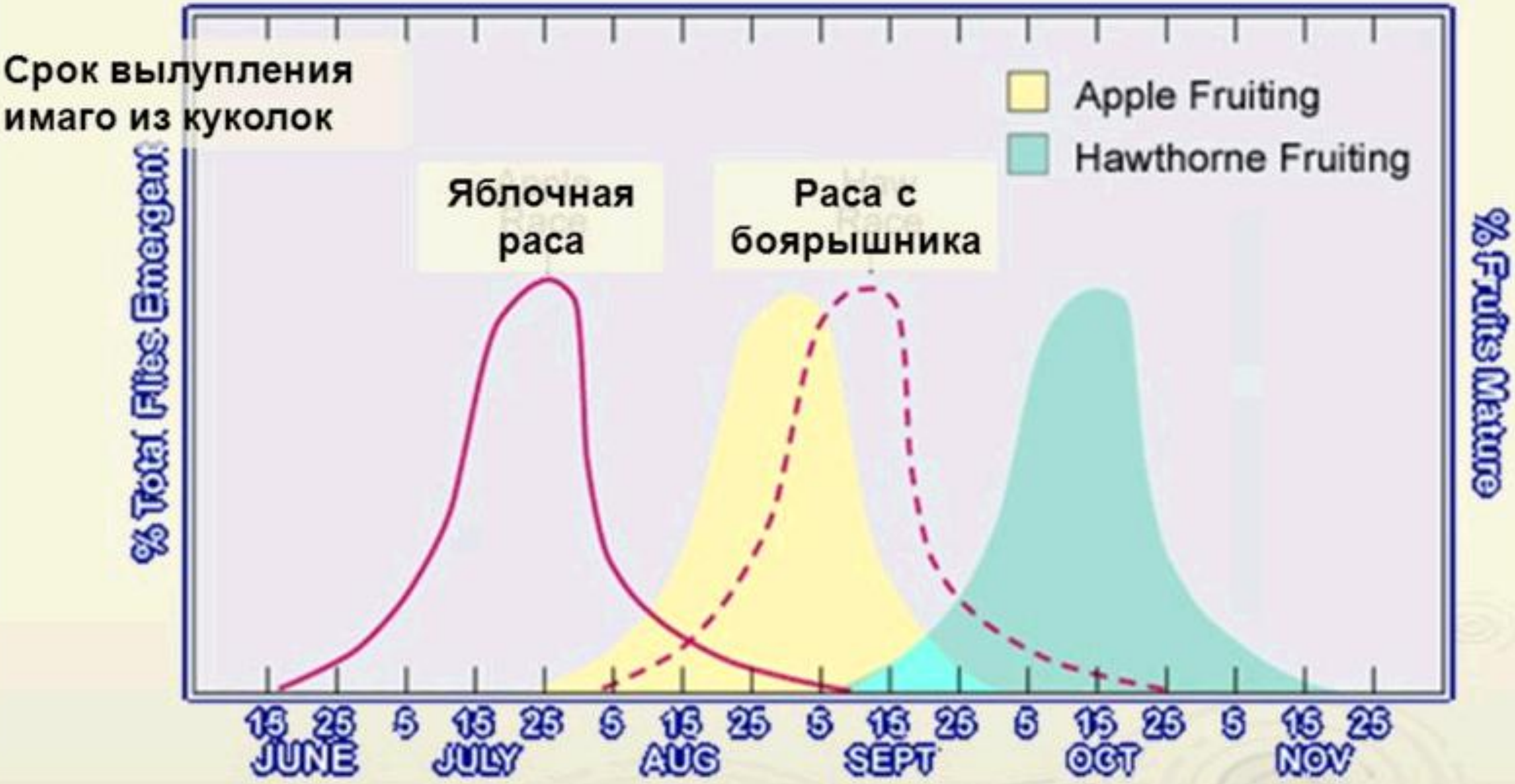
- Ни одна концепция вида не решает **ВСЕ** поставленные задачи

Боярышниковая моль Rhagoletis pomonella

- Классический пример видообразования, приуроченного к специализации на объекте питания (изначально боярышник, затем яблоня, в последнее время -шиповник) и ассортативному скрещиванию.



Экологическая изоляция, возникшая как пищевая и по месту обитания, постепенно стала и временной – в связи с разными сроками плодоношения у растений-хозяев.



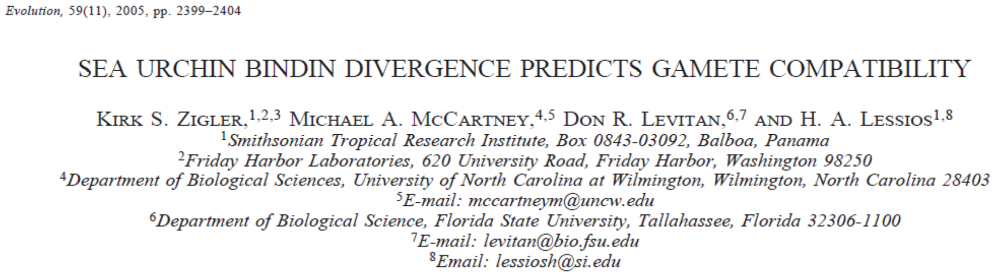
Bush, G.L. 1969. Sympatric host race formation and speciation in frugivorous flies of the genus *Rhagoletis* (Diptera: Tephritidae). *Evolution* **23:** 237-251.

Байндин морских ежей

Белок bindin покрывает акросому спермия морского ежа и способствует связыванию с вителлиновой оболочкой яйцеклетки (Metz et al. 1994)

У разных видов большое количество аминокислотных замен – признак движущего отбора

Полная репродуктивная изоляция – при 8-10 аминокислотных заменах в bindin (и предположительно, в bindin-рецепторе яйца.



Evolution, 59(11), 2005, pp. 2399–2404

SEA URCHIN BINDIN DIVERGENCE PREDICTS GAMETE COMPATIBILITY

KIRK S. ZIGLER,[1,2,3] MICHAEL A. MCCARTNEY,[4,5] DON R. LEVITAN,[6,7] AND H. A. LESSIOS[1,8]
[1]*Smithsonian Tropical Research Institute, Box 0843-03092, Balboa, Panama*
[2]*Friday Harbor Laboratories, 620 University Road, Friday Harbor, Washington 98250*
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[5]*E-mail: mccartneym@uncw.edu*
[6]*Department of Biological Science, Florida State University, Tallahassee, Florida 32306-1100*
[7]*E-mail: levitan@bio.fsu.edu*
[8]*Email: lessiosh@si.edu*

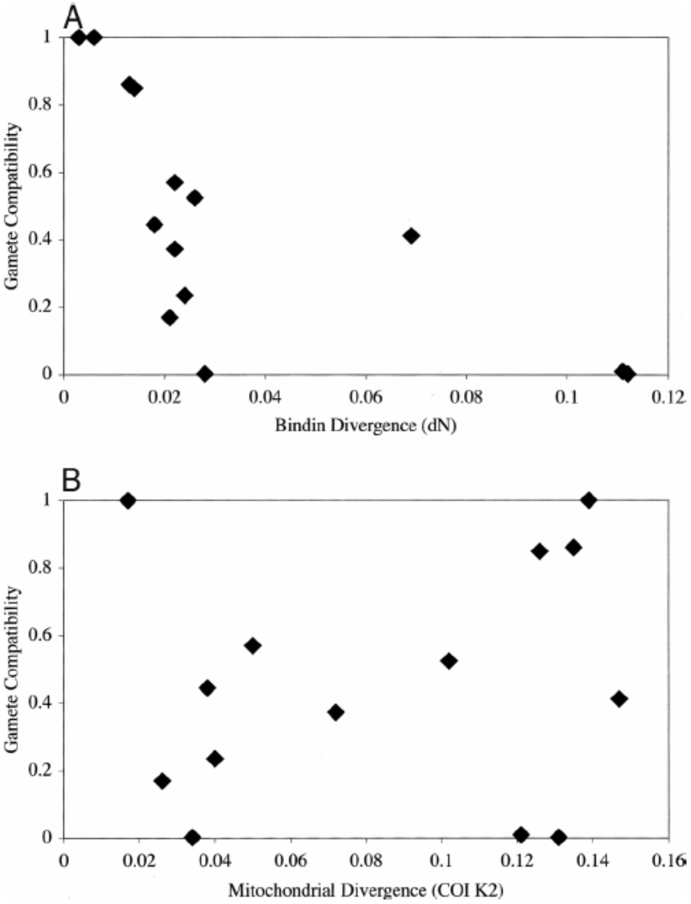
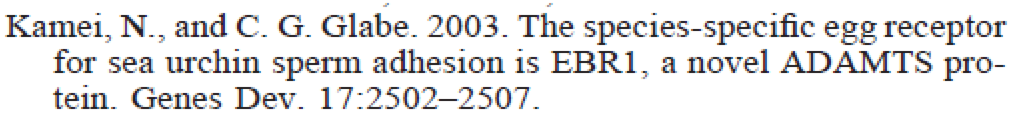


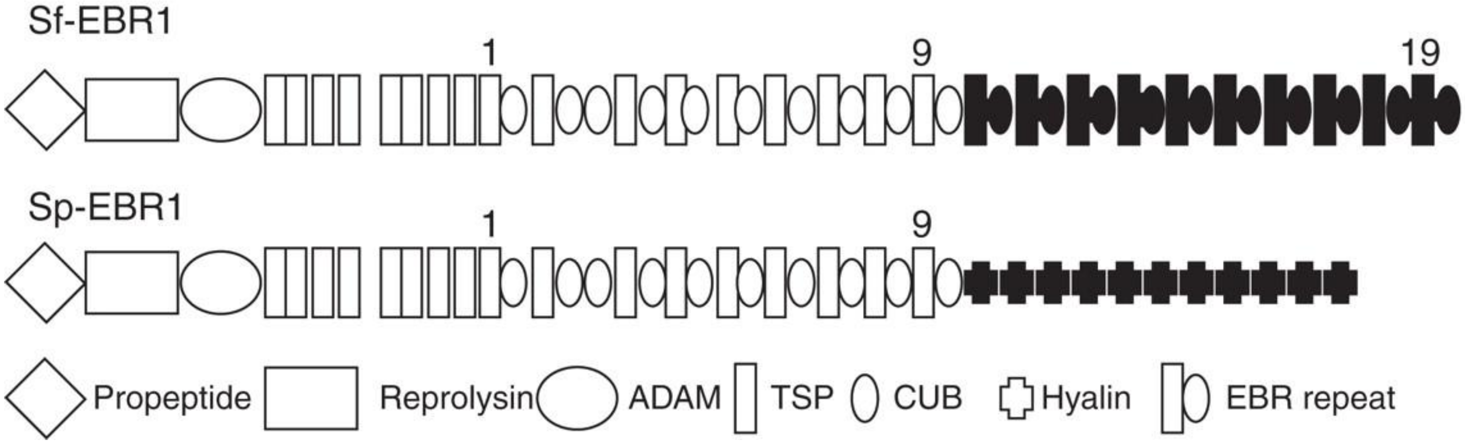
FIG. 1. Correlation between gametic compatibility and (A) divergence of bindin at nonsynonymous sites and (B) COI divergence for 14 interspecific (uncorrected for phylogenetic and statistical interdependence) comparisons. Nonsynonymous bindin divergence (d_N) was calculated in MEGA (ver. 2.1; Kumar et al. 2001) by the Pamilo and Bianchi (1993) and Li (1993) method. Mitochondrial cytochrome oxidase I (COI) divergence was calculated by the Kimura (1980) two-parameter (K_2) method.

Рецептор на яйце, комплиментарный байндину:



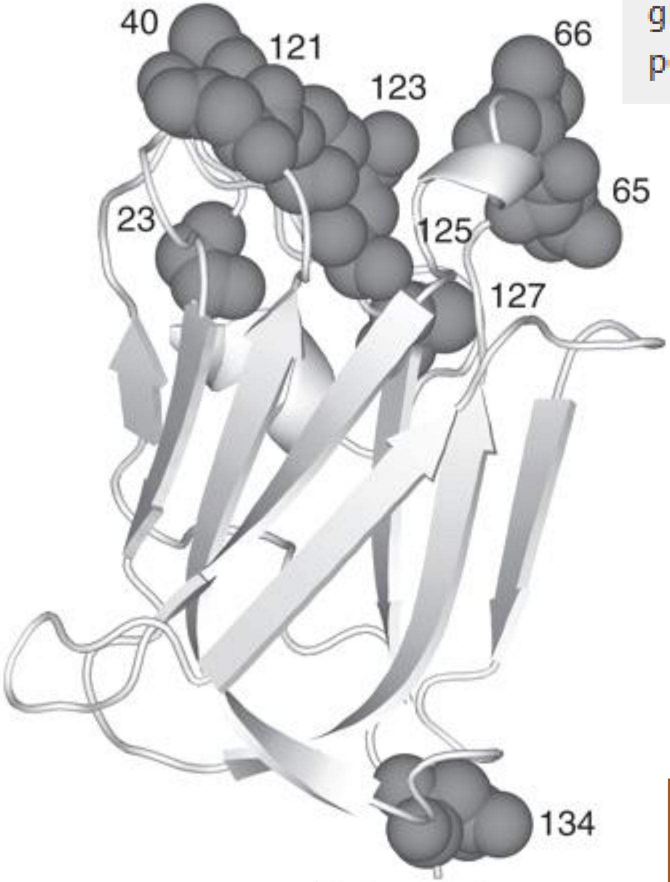
Kamei, N., and C. G. Glabe. 2003. The species-specific egg receptor for sea urchin sperm adhesion is EBR1, a novel ADAMTS protein. Genes Dev. 17:2502–2507.

The protein domains of the sea urchin egg bindin receptor, EBR1, from Strongylocentrotus franciscanus and S. purpuratus.



Victor D. Vacquier, and Willie J. Swanson Cold Spring Harb Perspect Biol 2011;3:a002931

The oyster bindin fucose lectin repeat threads onto the known fucose lectin crystal structure. Dark residues are eight sites under positive selection that surround the fucose-binding groove, indicating the importance of adaptive evolution in binding fucose. Number 138 is the ninth positively selected site, which is not in the fucose binding groove. (Figure adapted from Moy et al. [2008] and reprinted, with permission, from the National Academy of Sciences © 2008.)



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Selection in the Rapid Evolution of Gamete Recognition Proteins in Marine Invertebrates

Victor D. Vacquier[1] and Willie J. Swanson[2]

Ключевая роль протеогликанов в распознавании сперматозоидом «своей» яйцеклетки

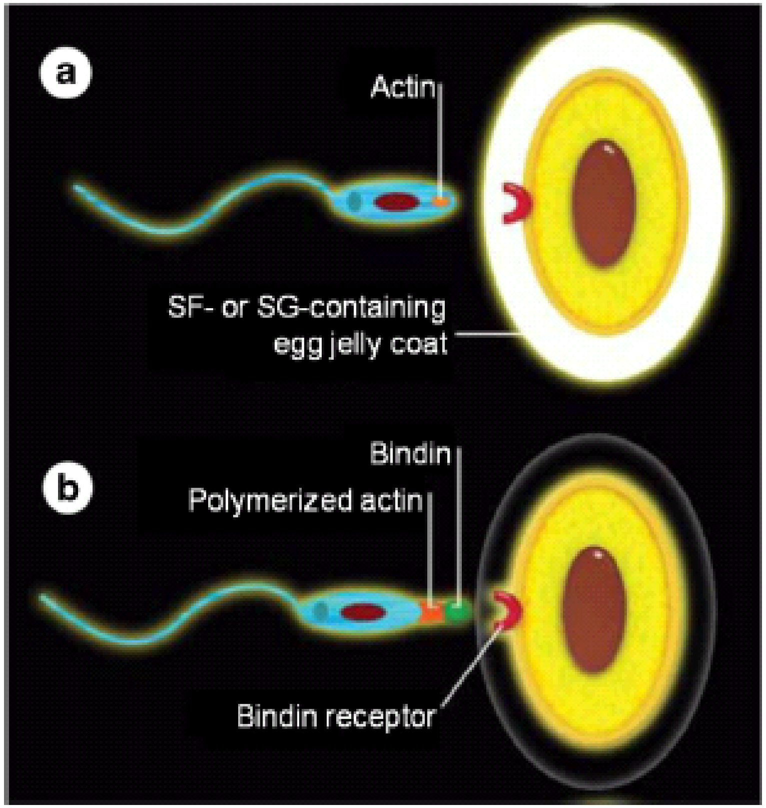
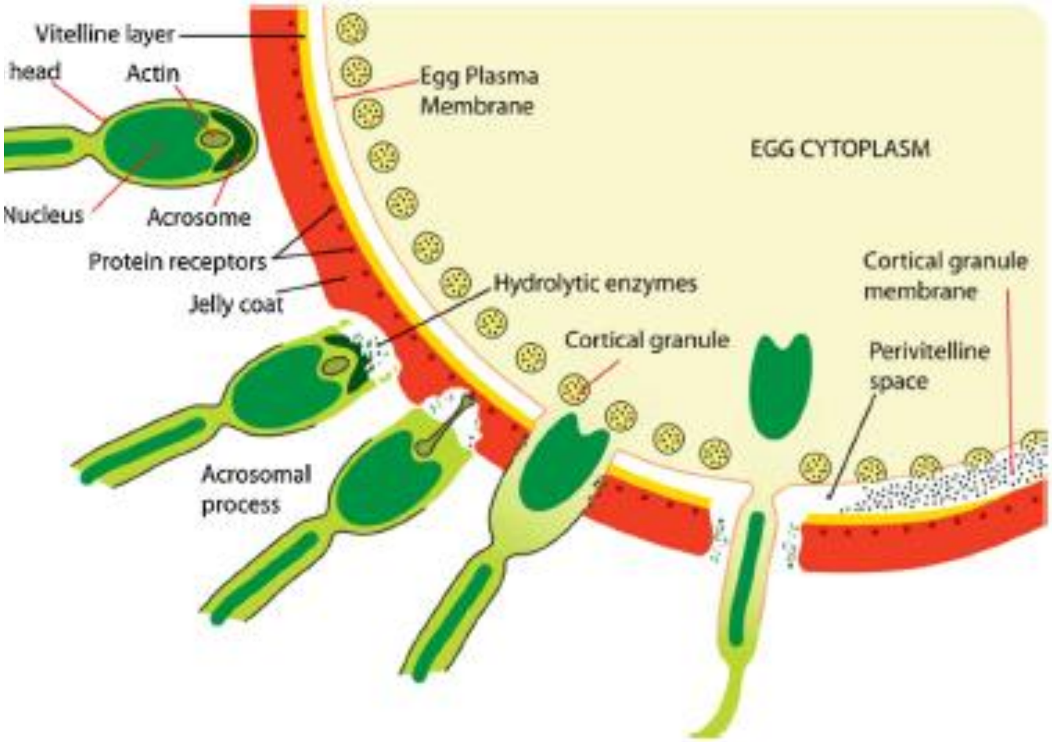


Fig. 2 Schematic representation of the two hierarchical regulatory events in egg-sperm recognition of sea urchin fertilization: the first one (**a**), a carbohydrate-based mechanism, is primarily driven by the sea urchin egg jelly sulfated glycans, sulfated fucan (SF) or sulfated galactan (SG), which play the role as inducers of the AR; the second one (**b**), a protein-based mechanism, driven by the bindin protein found at the tip of the sea urchin-reacted sperm, plays the role to ultimately enable cell membrane fusion of both gametes involved in the fertilization process



Glycoconj J (2015) 32:9–15
DOI 10.1007/s10719-015-9573-y

MINI-REVIEW

Sulfated glycans in sea urchin fertilization

Vitor H. Pomin

Олигосахариды желеобразной оболочки яйца различных близких видов морских ежей

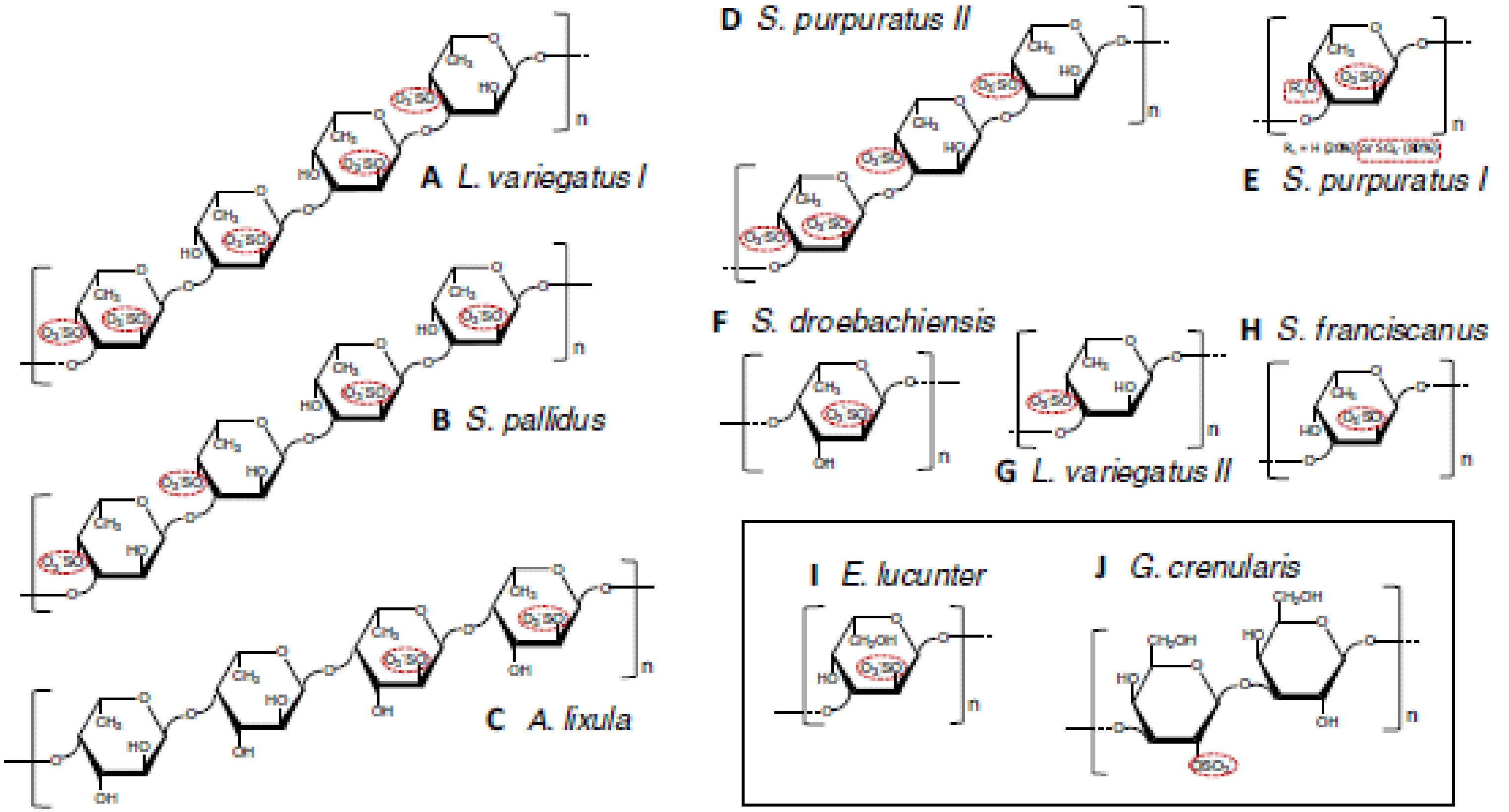
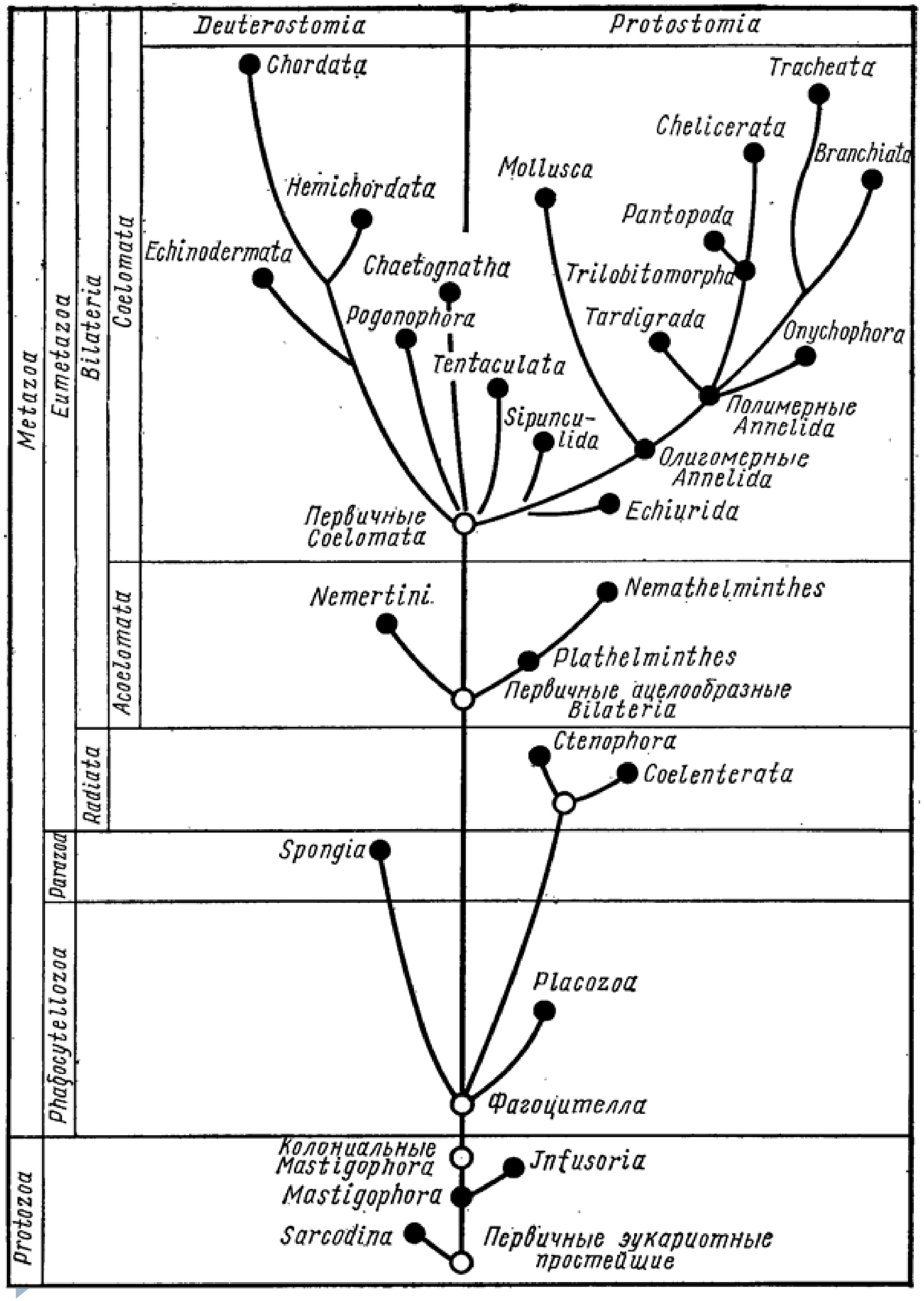
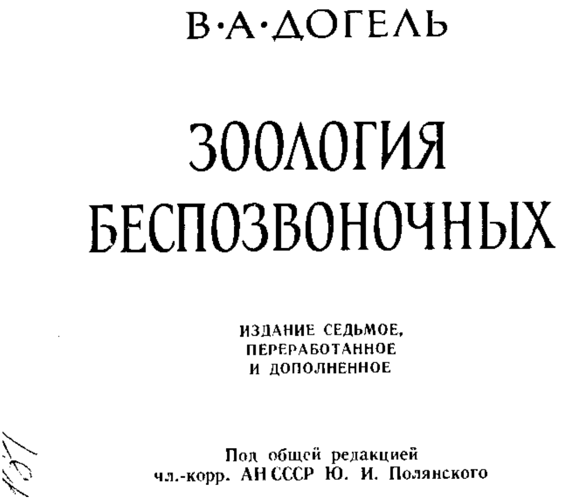


Fig. 3 Representation of the repetitive oligosaccharide units of sea urchin egg jelly sulfated fucans (**a**-**h**) and sulfated galactans (**i** and **j**, inside the *box*). Sulfation patterns are highlighted in *red*

Springer





В·А·ДОГЕЛЬ

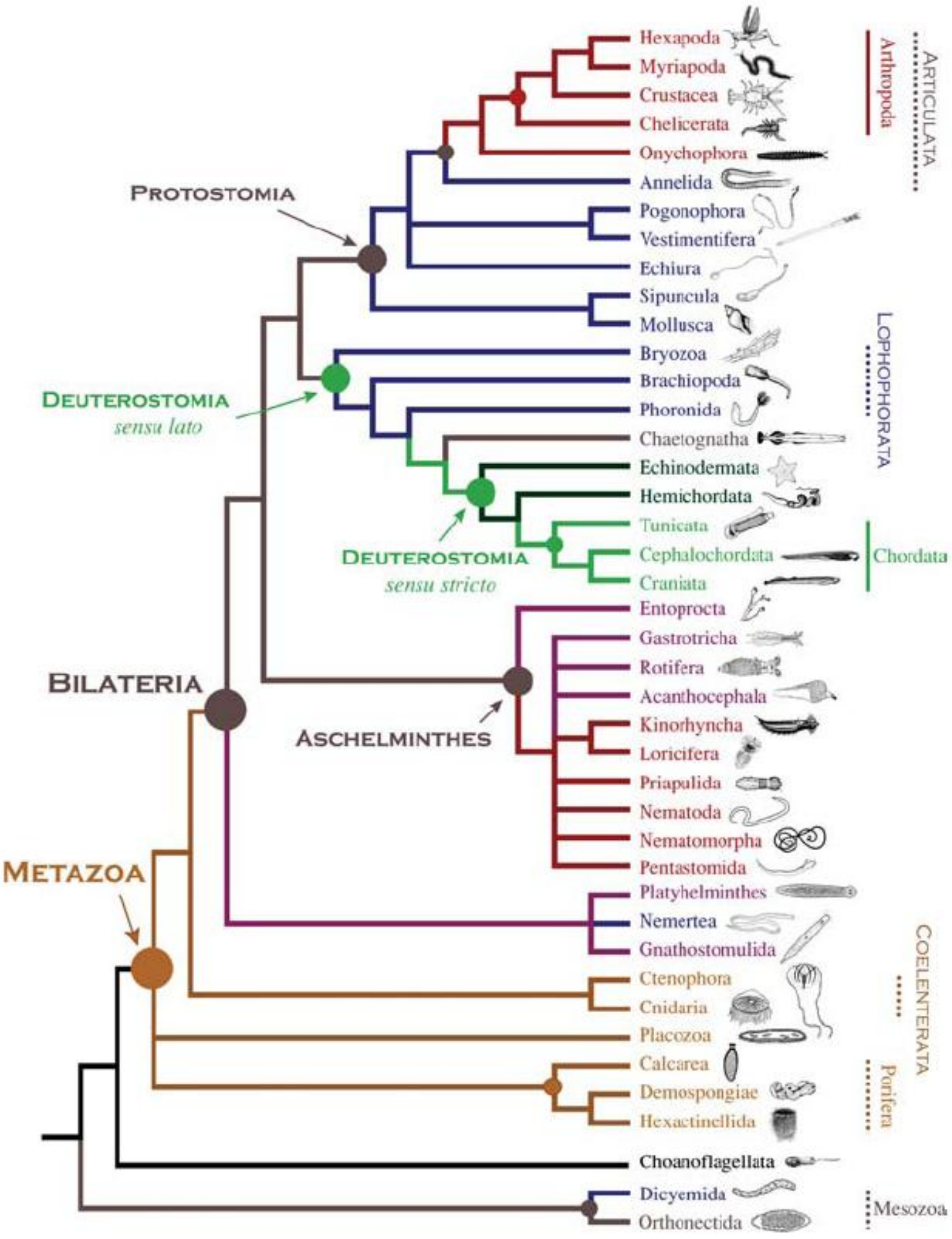
ЗООЛОГИЯ
БЕСПОЗВОНОЧНЫХ

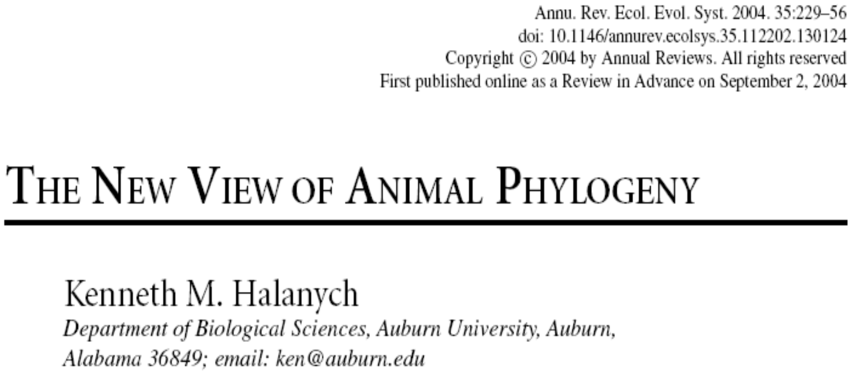
ИЗДАНИЕ СЕДЬМОЕ,
ПЕРЕРАБОТАННОЕ
И ДОПОЛНЕННОЕ

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.

Систематика беспозвоночных до начала эры «молекулярных революций»





Annu. Rev. Ecol. Evol. Syst. 2004. 35:229–56
doi: 10.1146/annurev.ecolsys.35.112202.130124

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 по данным сиквенса 18s РНК.
- Также впервые был применен адекватный набор методов анализа сиквенсов

Science 1988 (239) 748-753

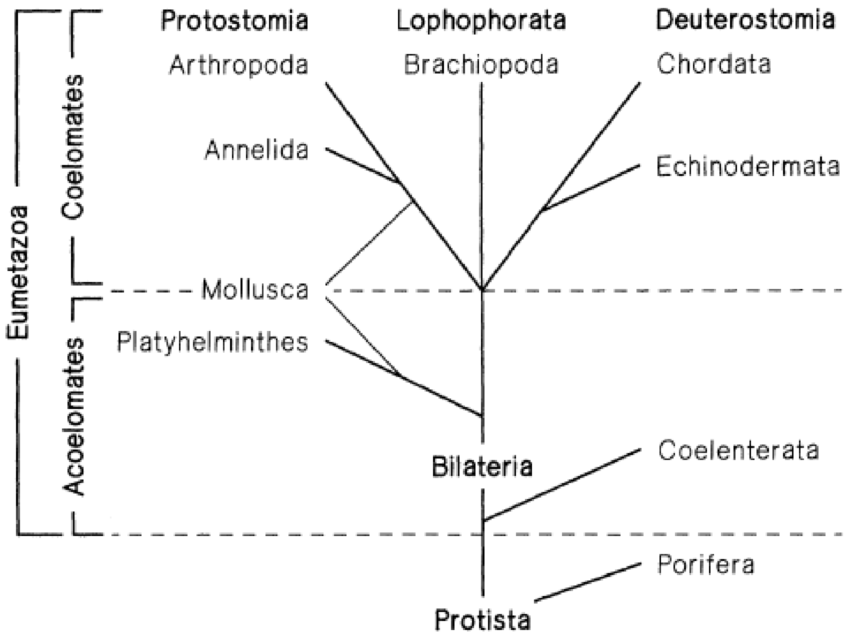


Fig. 1. Phylogenetic tree for the Metazoa, based on the views of Hyman (*5*). This phylogeny is based on morphology of both adults and embryos. Phylum names are shown in lightface lettering.

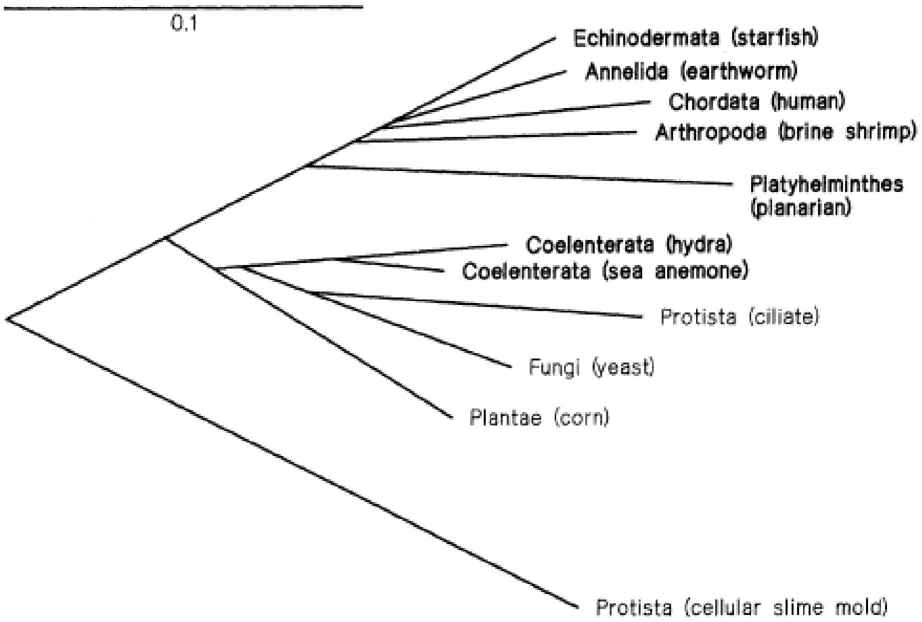
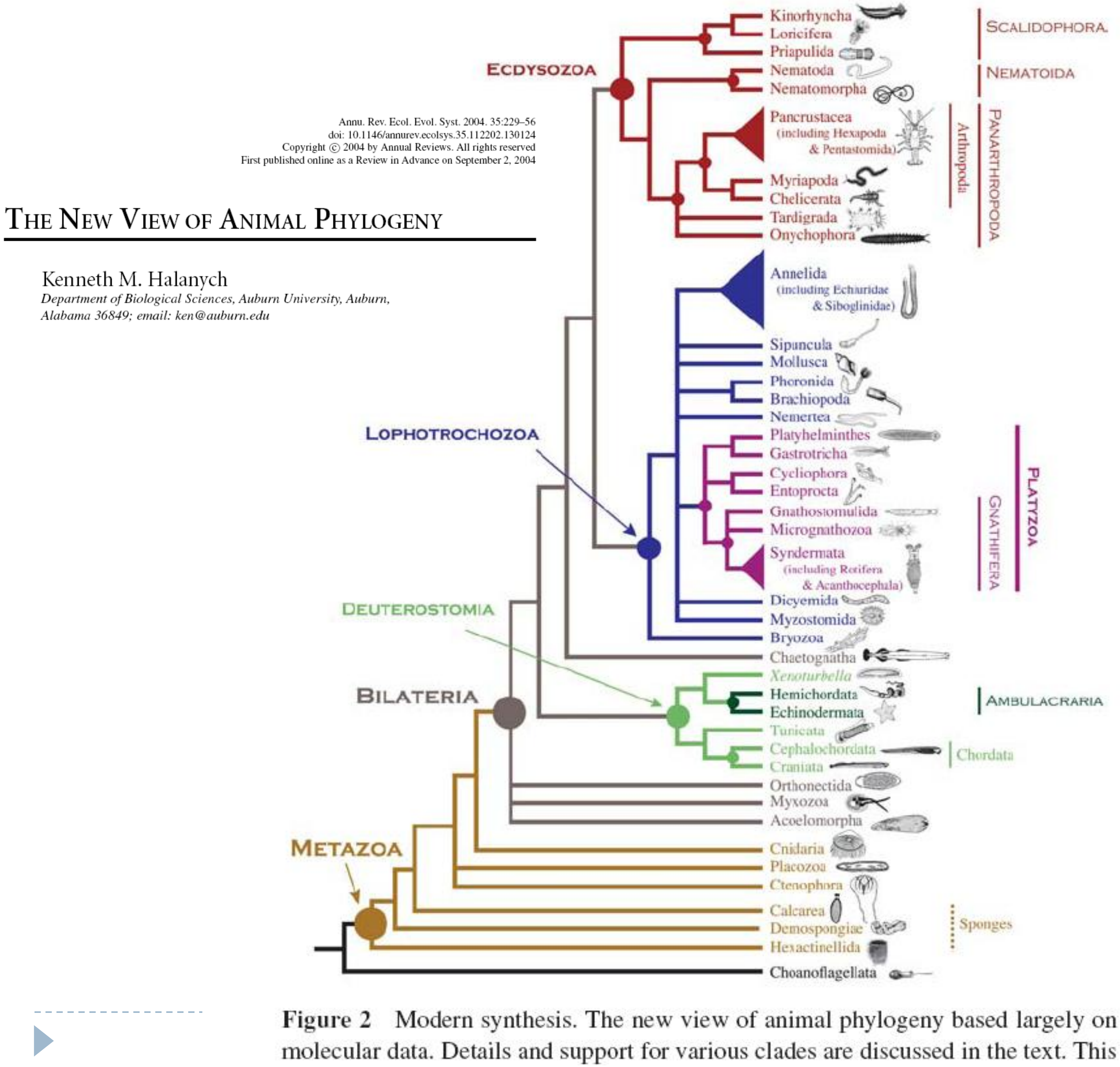


Fig. 2. An evolutionary tree for animals that is based on partial sequences of 18*S* rRNAs. The tree is read from left to right. The root of the tree is provided by the most distantly related organism, the cellular slime mold. The

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

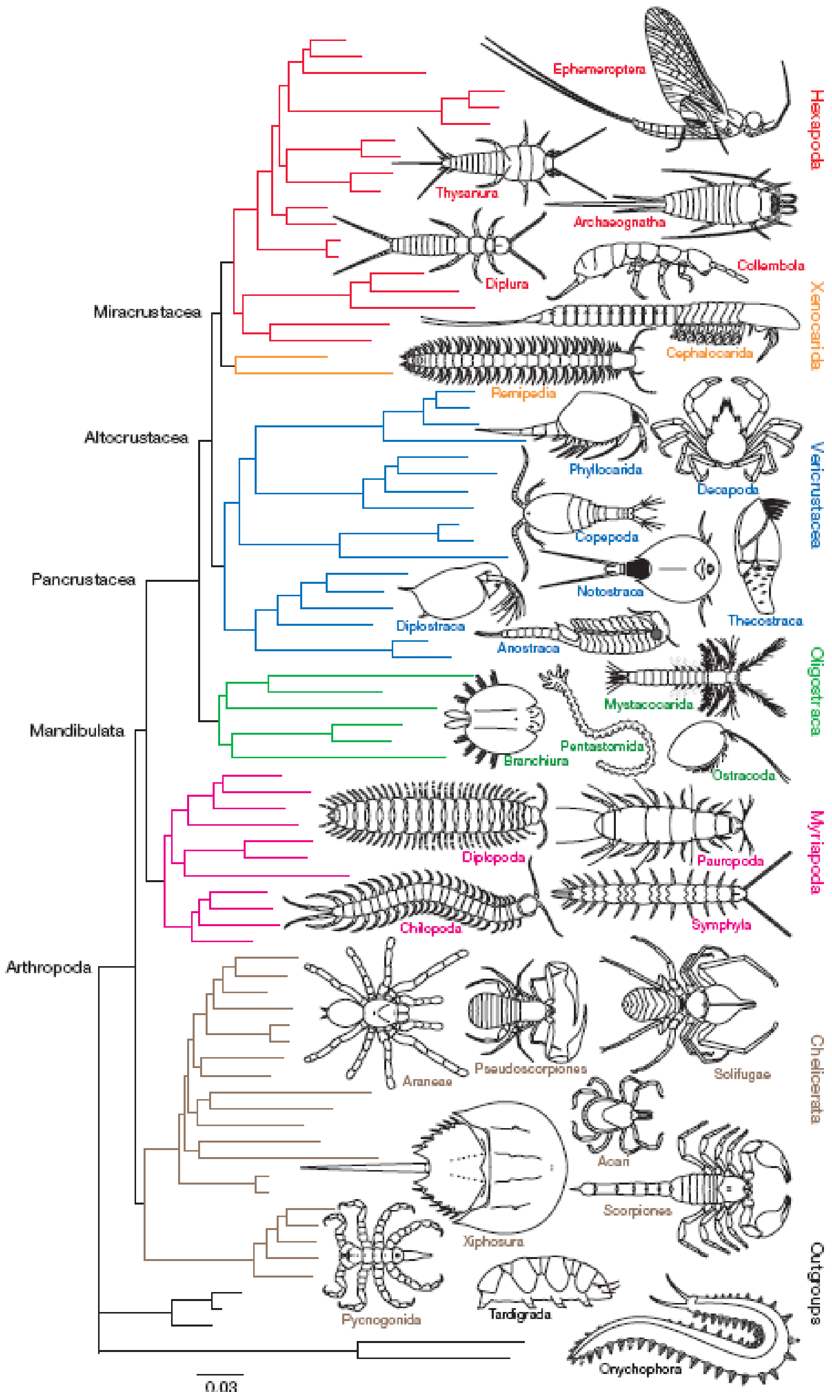


Annu. Rev. Ecol. Evol. Syst. 2004. 35:229–56
doi: 10.1146/annurev.ecolsys.35.112202.130124

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



- 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]

Nature. 2013 January 24; 493(7433): 526–531. doi:10.1038/nature11696.

Insights into bilaterian evolution from three spiralian genomes

Oleg Simakov[1,2], **Ferdinand Marletaz**[1,†], **Sung-Jin Cho**[2], **Eric Edsinger-Gonzales**[2], **Paul Havlak**[3], **Uffe Hellsten**[4], **Dian-Han Kuo**[2,†], **Tomas Larsson**[1], **Jie Lv**[3], **Detlev Arendt**[1], **Robert Savage**[5], **Kazutoyo Osoegawa**[6], **Pieter de Jong**[6], **Jane Grimwood**[4,7], **Jarrod A. Chapman**[4], **Harris Shapiro**[4], **Andrea Aerts**[4], **Robert P. Otillar**[4], **Astrid Y. Terry**[4], **Jeffrey L. Boore**[4,†], **Igor V. Grigoriev**[4], **David R. Lindberg**[8], **Elaine C. Seaver**[9,†], **David A. Weisblat**[2], **Nicholas H. Putnam**[3,10], and **Daniel S. Rokhsar**[2,4,11]

Abstract

Current genomic perspectives on animal diversity neglect two prominent phyla, the molluscs and annelids, that together account for nearly one-third of known marine species and are important both ecologically and as experimental systems in classical embryology[1–3]. Here we describe the draft genomes of the owl limpet (*Lottia gigantea*), a marine polychaete (*Capitella teleta*) and a freshwater leech (*Helobdella robusta*), and compare them with other animal genomes to investigate the origin and diversification of bilaterians from a genomic perspective. We find that the genome organization, gene structure and functional content of these species are more similar to those of some invertebrate deuterostome genomes (for example, amphioxus and sea urchin) than those of other protostomes that have been sequenced to date (flies, nematodes and flatworms). The conservation of these genomic features enables us to expand the inventory of genes present in the last common bilaterian ancestor, establish the tripartite diversification of bilaterians using multiple genomic characteristics and identify ancient conserved long- and short-range genetic linkages across metazoans. Superimposed on this broadly conserved pan-bilaterian background we find examples of lineage-specific genome evolution, including varying rates of rearrangement, intron gain and loss, expansions and contractions of gene families, and the evolution of clade-specific genes that produce the unique content of each genome.

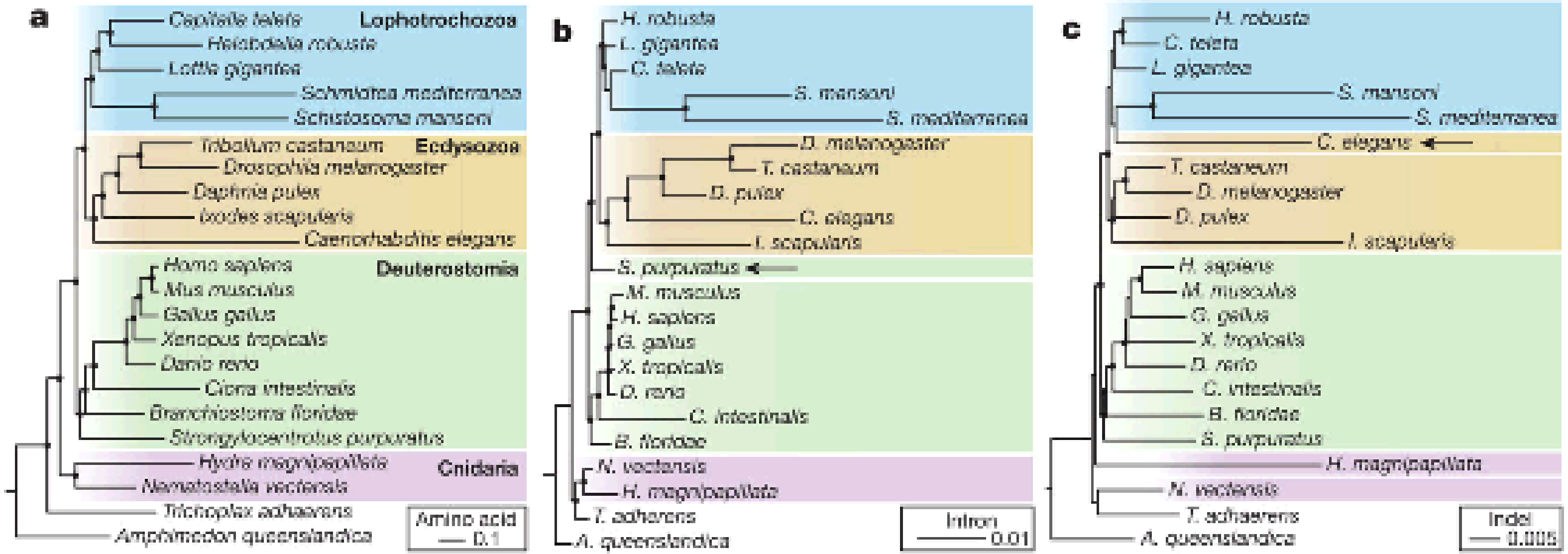
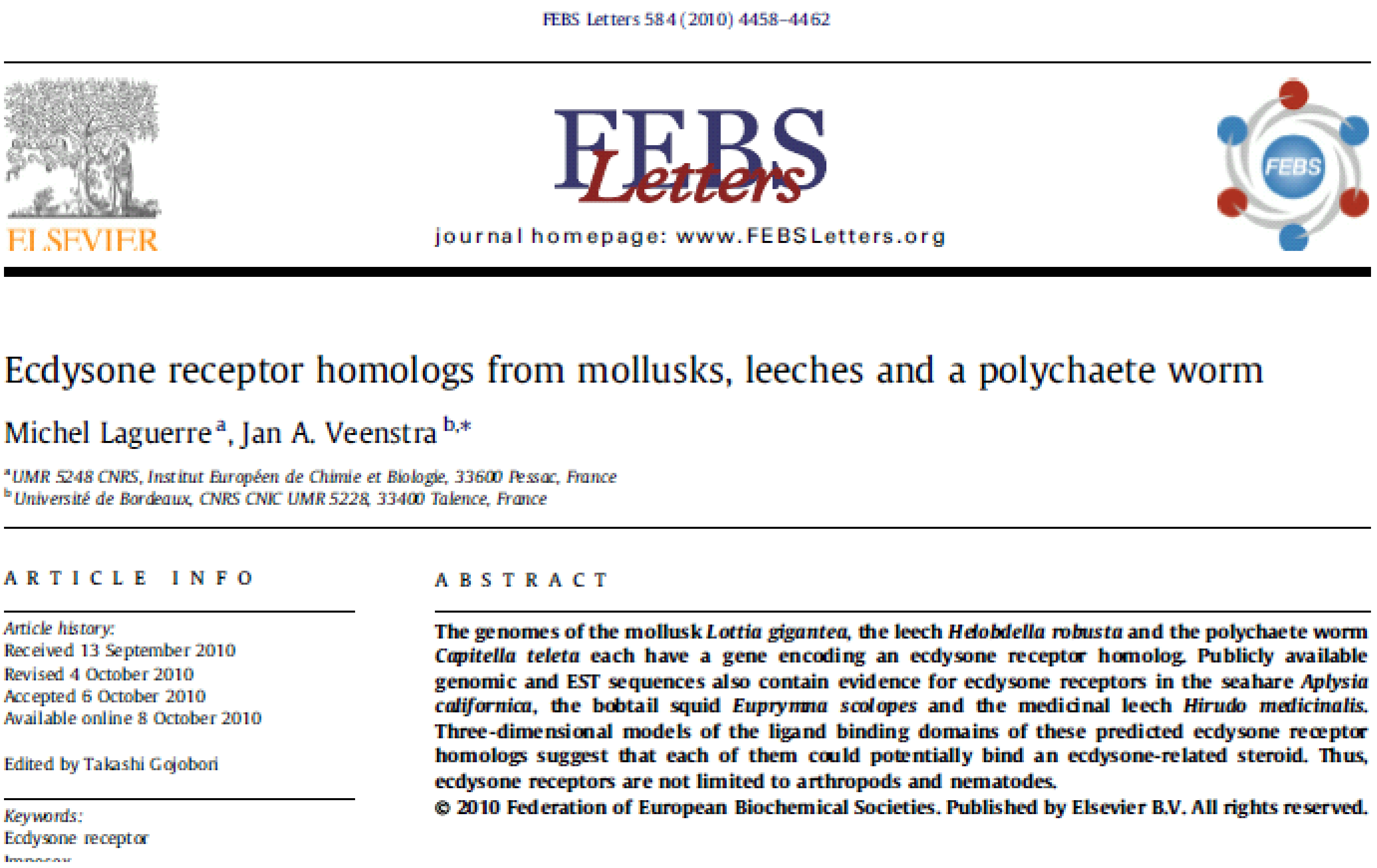


Figure 1. Full-genome evidence resolves metazoan relationships and verifies the monophyly of lophotrochozoans and spiralians

a, A protein tree inferred from 299,129 amino acid positions gathered from 827 slow-evolving orthologues using RAxML and modelling heterogeneity of substitution processes using a LG + Γ4 model with each gene partitioned. Strong support is obtained for the monophyly of lophotrochozoans. **b**, Intron tree obtained from a matrix of 5,377 introns analysed using MrBayes and an asymmetric binary model (probability of gain: 0.01). **c**, Indel tree reconstructed from a matrix of 1,928 indel sites using a regular binary model. Circles at nodes indicate a bootstrap support of >0.90 (**a**) or a posterior probability of >0.95 (**b** and **c**). In **b** and **c**, arrows indicate species that do not follow the protein family tree topology.



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Ecdysone receptor homologs from mollusks, leeches and a polychaete worm

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ABSTRACT

The genomes of the mollusk *Lottia gigantea*, the leech *Helobdella robusta* and the polychaete worm *Capitella teleta* each have a gene encoding an ecdysone receptor homolog. Publicly available genomic and EST sequences also contain evidence for ecdysone receptors in the seahare *Aplysia californica*, the bobtail squid *Euprymna scolopes* and the medicinal leech *Hirudo medicinalis*. Three-dimensional models of the ligand binding domains of these predicted ecdysone receptor homologs suggest that each of them could potentially bind an ecdysone-related steroid. Thus, ecdysone receptors are not limited to arthropods and nematodes.

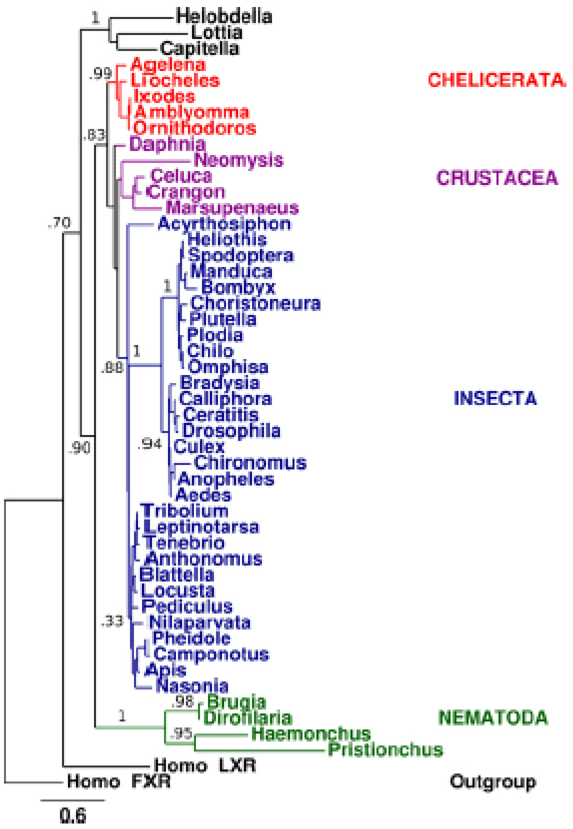


Fig. 3. Phylogenetic tree of ecdysone receptors as constructed using PhyML [13]. Number of bootstrap replicates 100, WAG substitution model with a gamma distribution between sites, four categories, α estimated by the programm. Selected bootstrap values are indicated. Human FXR and LXR were used for rooting the tree.

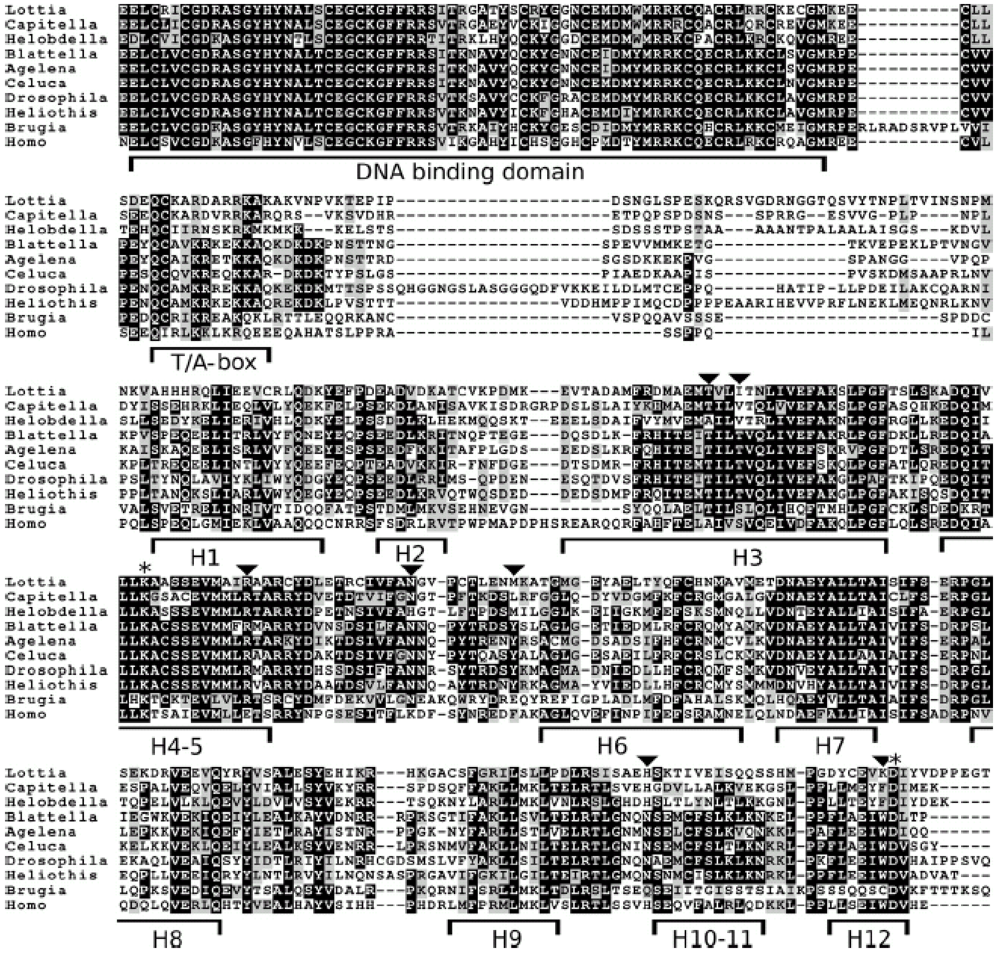


Fig. 1. Protein sequence similarity of the putative ecdysone receptors identified from *L. gigantea*, *C. teleta* and *H. robusta* with ecdysone receptors identified from various arthropods, the nematode *Brugia malayi* as well as human LXR. The DNA binding domains and the helices 1 through 12 (H1–H12) of the ligand binding domain have been indicated, as has the T/A-box. The amino acid residues from Table 1 have been indicated with a triangle in the *Lottia* sequence. Some residues are well conserved between the typical arthropod ecdysone receptors and the putative ecdysone receptors identified here, e.g., the residues forming the salt bridge between helices 4 and 12, indicated by asterisks, others, such as for example the tryptophane in helix 12, are not.

История зверька Xenoturbella

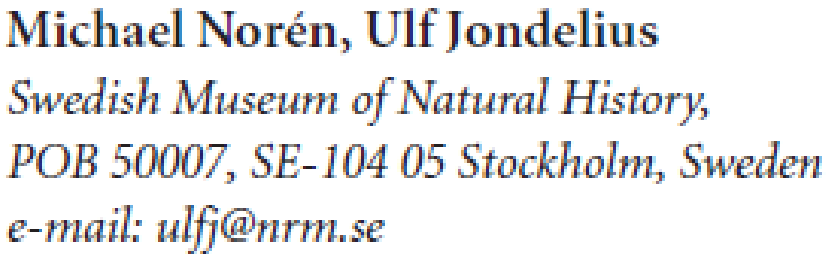
- Описаны из фьордов Швеции в 1949 г. по сборам 1915 года

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

- Отнесены к бескишечным турбелляриям (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



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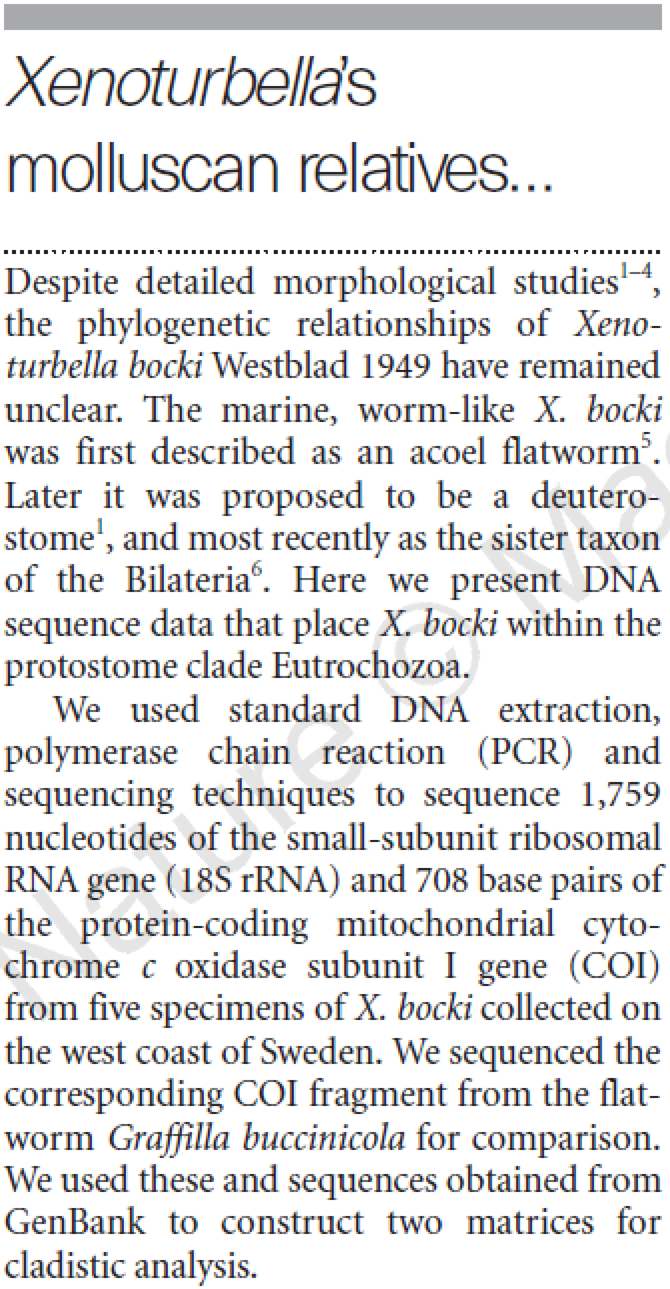

Xenoturbella's molluscan relatives...

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.

Noren & Jondelius, 1997 – 18s tree

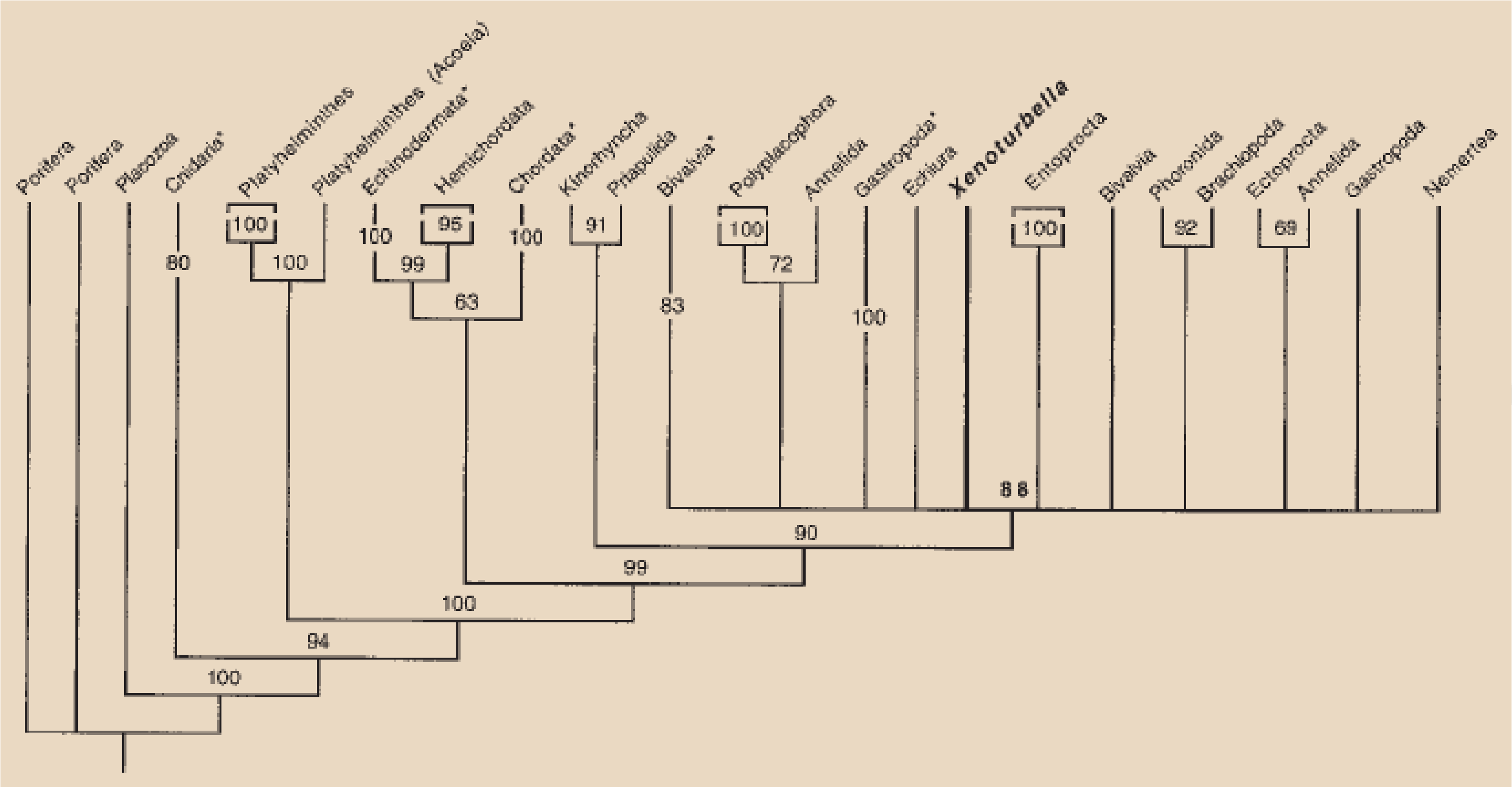

Figure 1 Consensus tree showing groups present in 60% of jack-knife replicates from analysis of 18S rRNA matrix (successive weighting of characters, 10 iterations with 100 replicates each, deletion frequency e^{-1}). Labels indicate jack-knife frequencies. Clades marked with asterisks represent multiple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

Noren & Jondelius, 1997 – COI tree

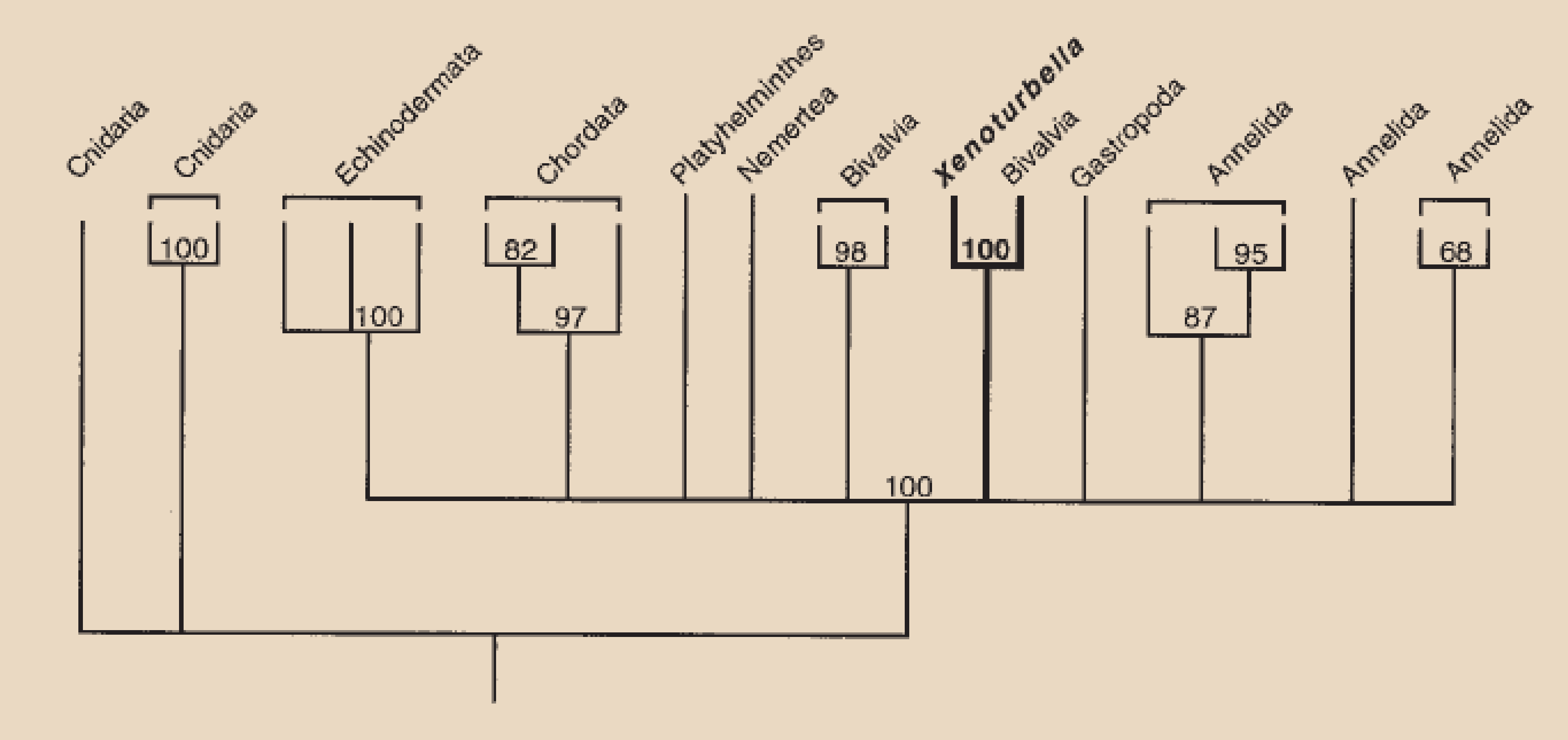

Figure 2 Consensus tree showing groups present in 60% of jack-knife replicates from analysis of COI matrix (3,000 replicates, 5 random additions and branch swapping, deletion frequency e^{-1}). Labels indicate jack-knife frequencies. Full details of tree topology and sequence alignment are available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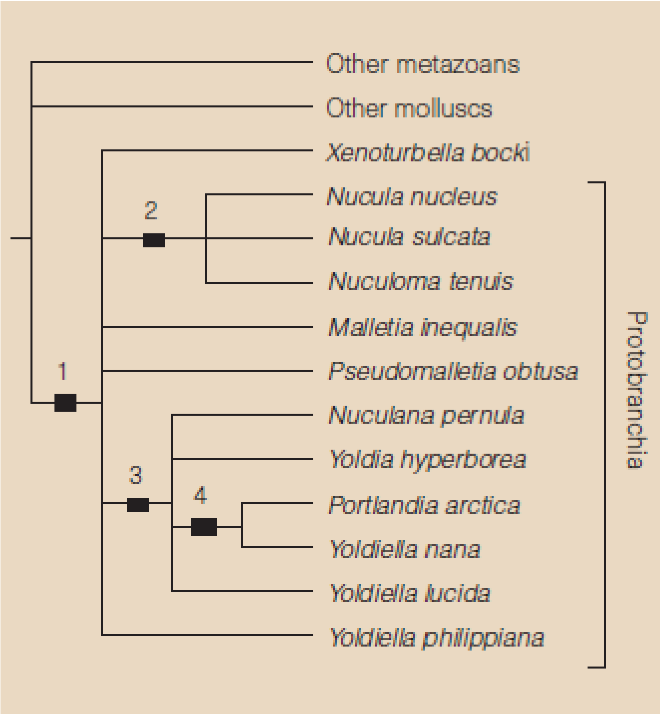

Figure 2 Cladistic analyses of oogenesis indicates that *Xenoturbella bocki* is a sister group or a subgroup of protobranch bivalves. The analysed characters, with their apomorphic states, are: **1**,

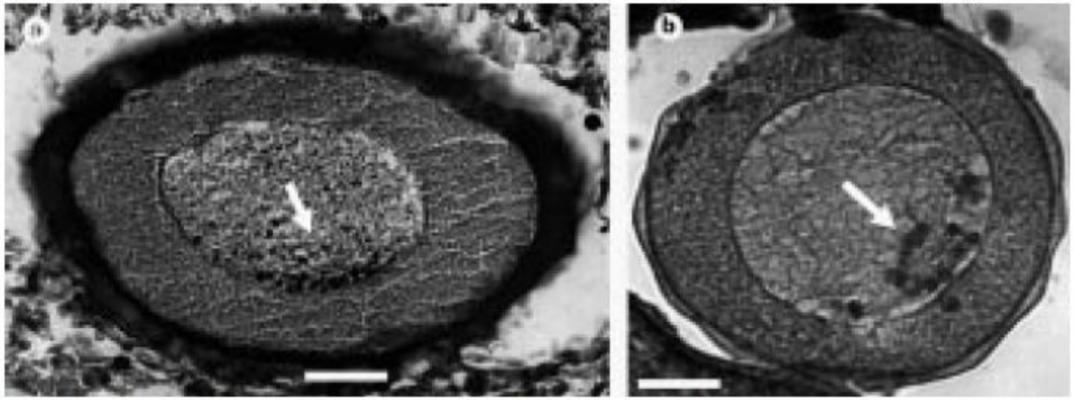

Figure 1 Relationship of *Xenoturbella bocki* to molluscs. Late vitellogenous oocytes of **a**, *Xenoturbella bocki* and **b**, the protobranch mollusc *Nucula nucleus*. Scale bars, 20 µm.

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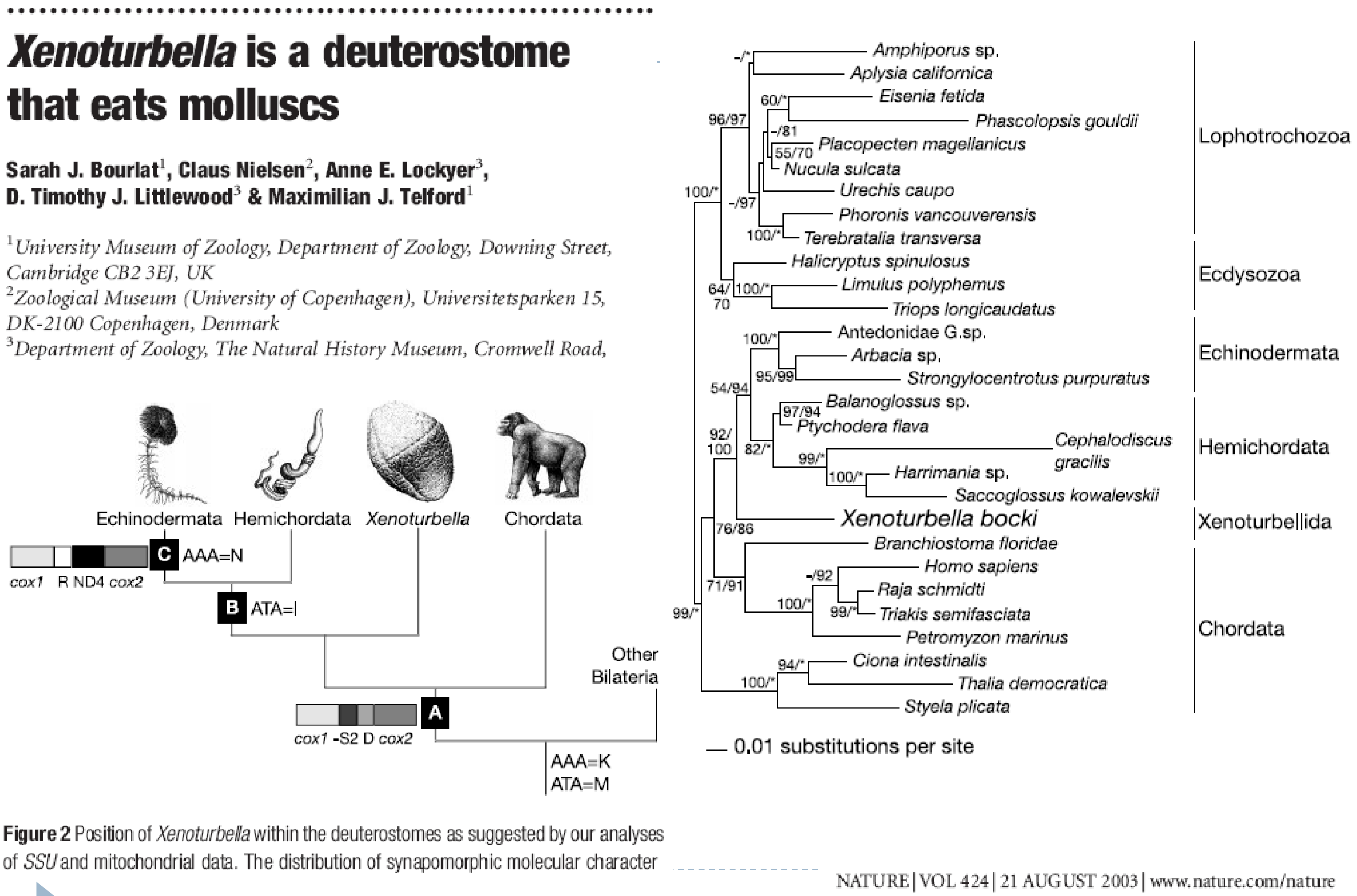

Xenoturbella is a deuterostome that eats molluscs

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

[1] *University Museum of Zoology, Department of Zoology, Downing Street, Cambridge CB2 3EJ, UK*
[2] *Zoological Museum (University of Copenhagen), Universitetsparken 15, DK-2100 Copenhagen, Denmark*
[3] *Department of Zoology, The Natural History Museum, Cromwell Road,*

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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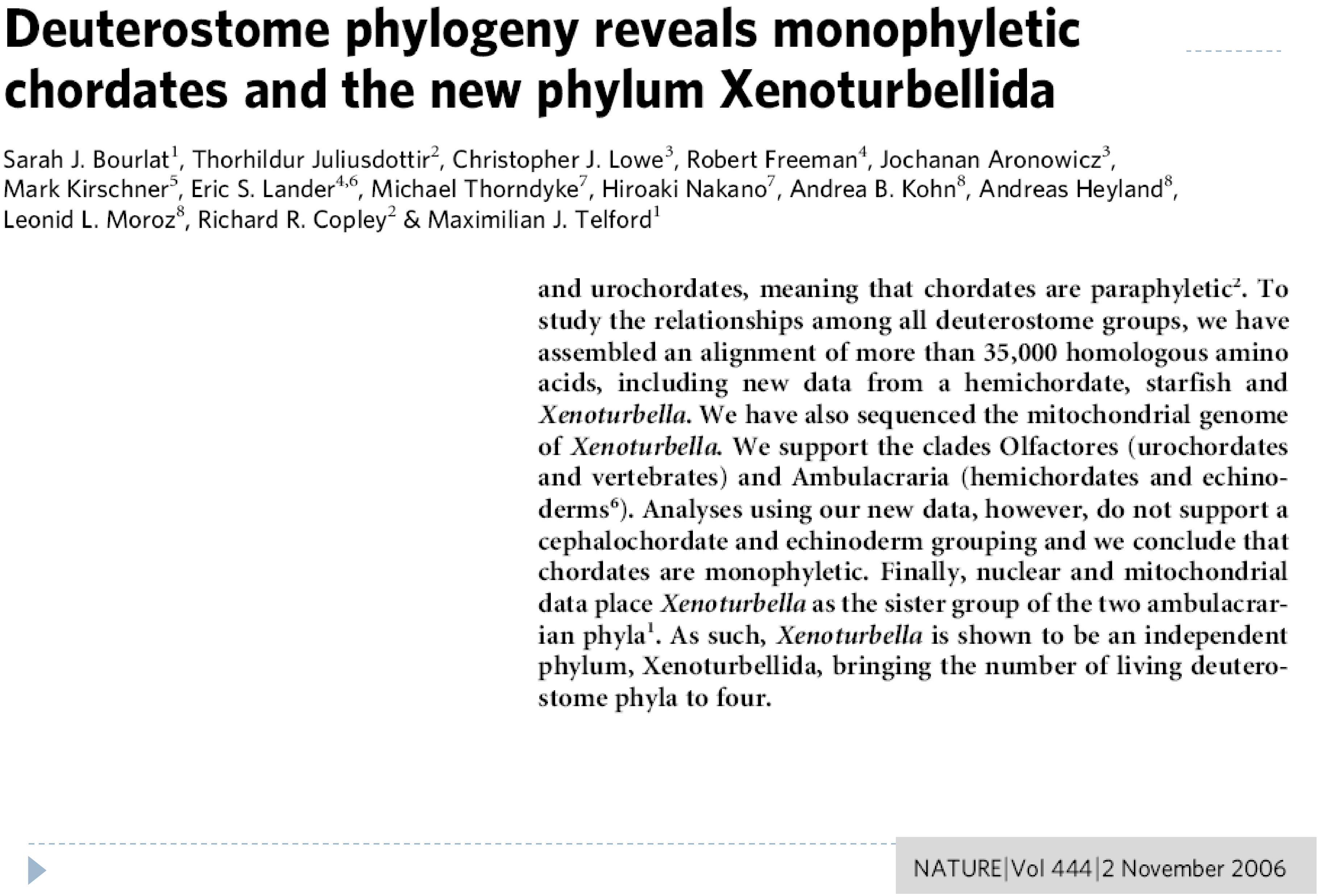

Deuterostome phylogeny reveals monophyletic chordates and the new phylum Xenoturbellida

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.

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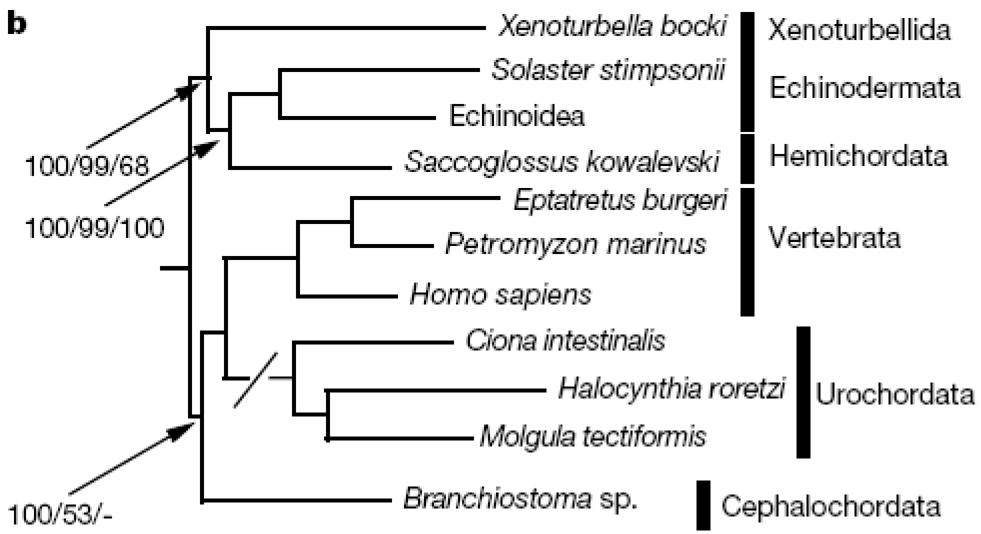

- Figure 1 | Phylogenetic analyses of 170 nuclear proteins and 13 mitochondrial proteins support a monophyletic chordate clade and an independent deuterostome phylum of Xenoturbellida.

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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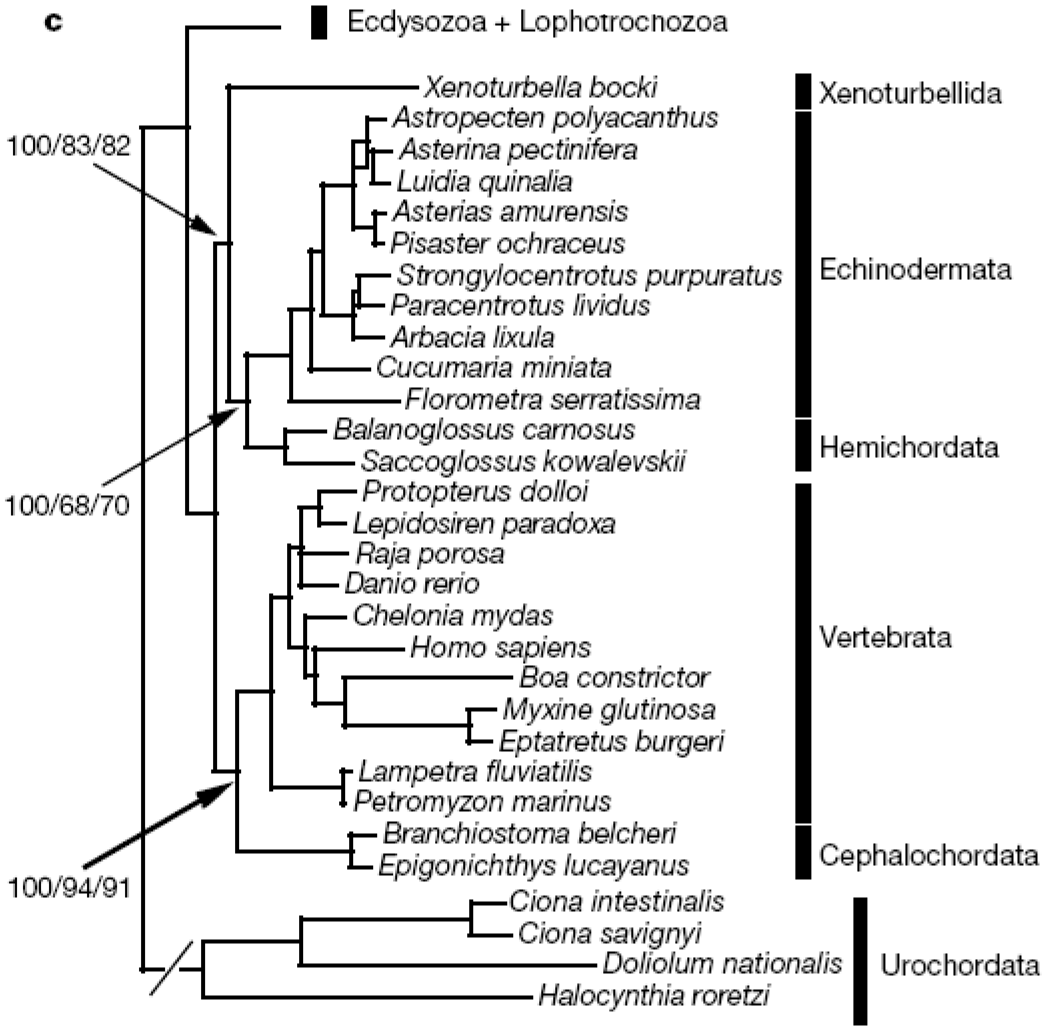

- C. Bayesian analysis of mitochondrial data with the amino acids M, I, N and K recoded as missing data places the cephalochordates with vertebrates; Xenoturbella is the sister group of Ambulacraria.