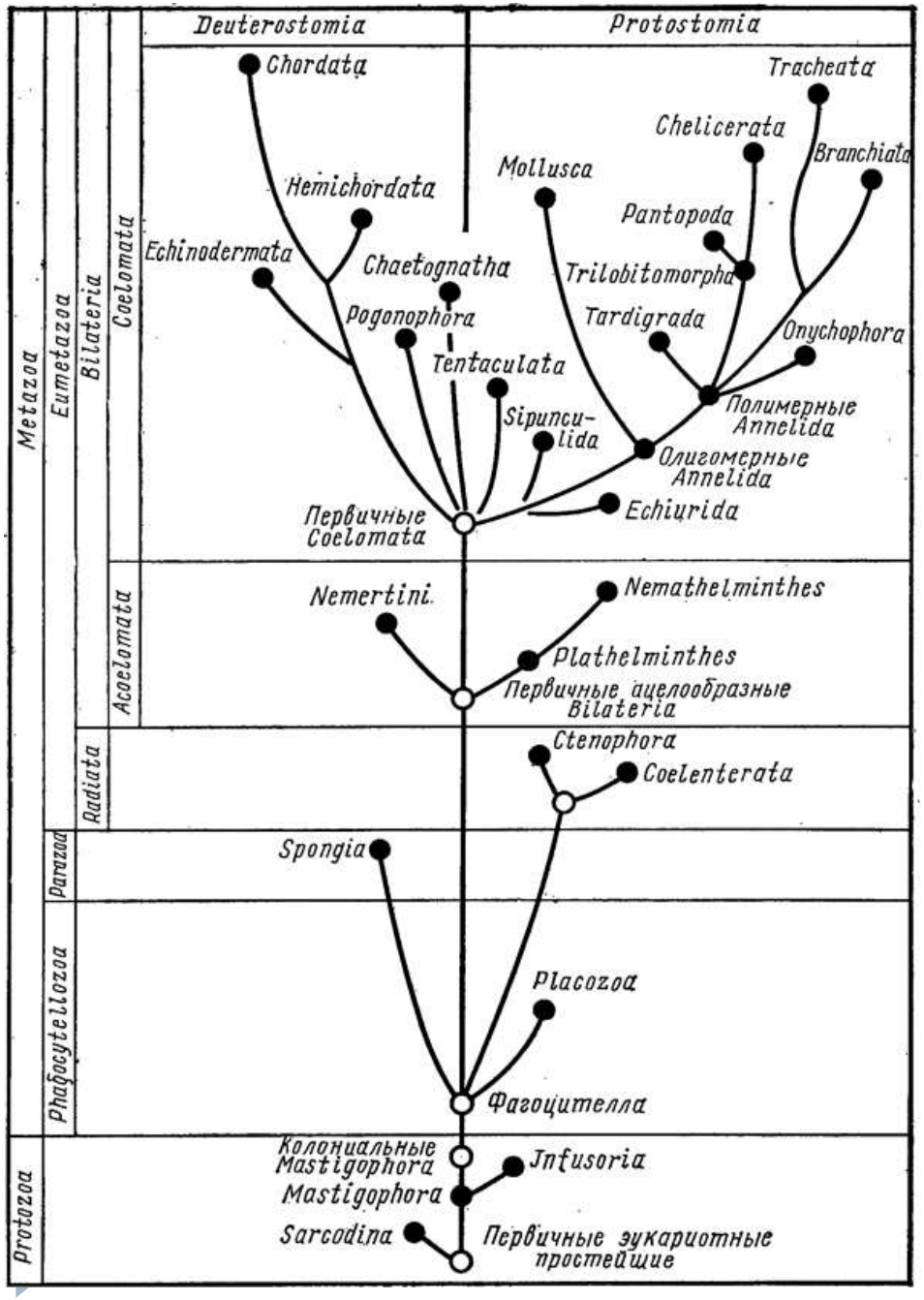
Молекулярная Зоология, весна 2015 лекция 8

Систематика беспозвоночных – современные «молекулярные революции» Xenoturbellida и прочие плоские загадки



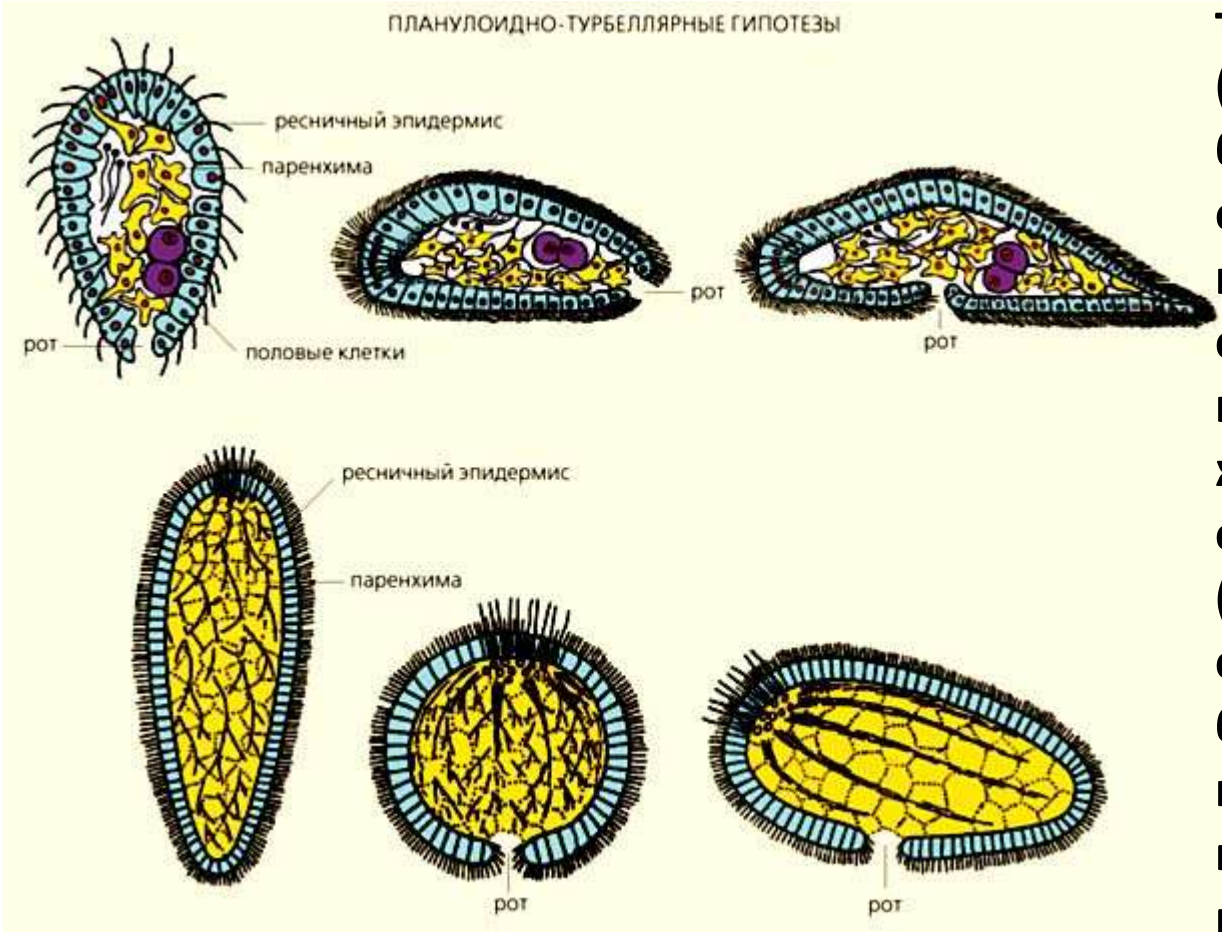
В·А·ДОГЕЛЬ

ЗООЛОГИЯ БЕСПОЗВОНОЧНЫХ

ИЗДАНИЕ СЕДЬМОЕ,
ПЕРЕРАБОТАННОЕ
И ДОПОЛНЕННОЕ

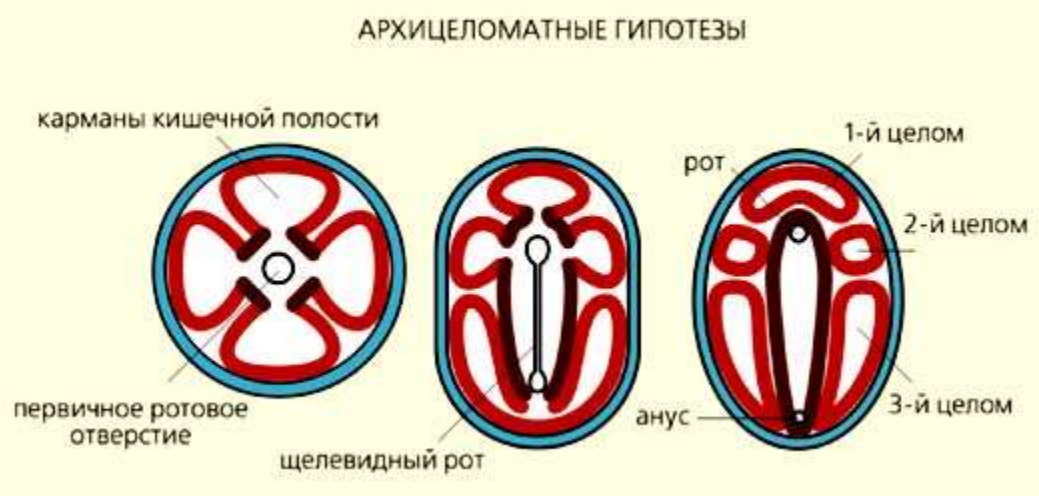
Под общей редакцией
чл.-корр. АН СССР Ю. И. Полянского

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.**

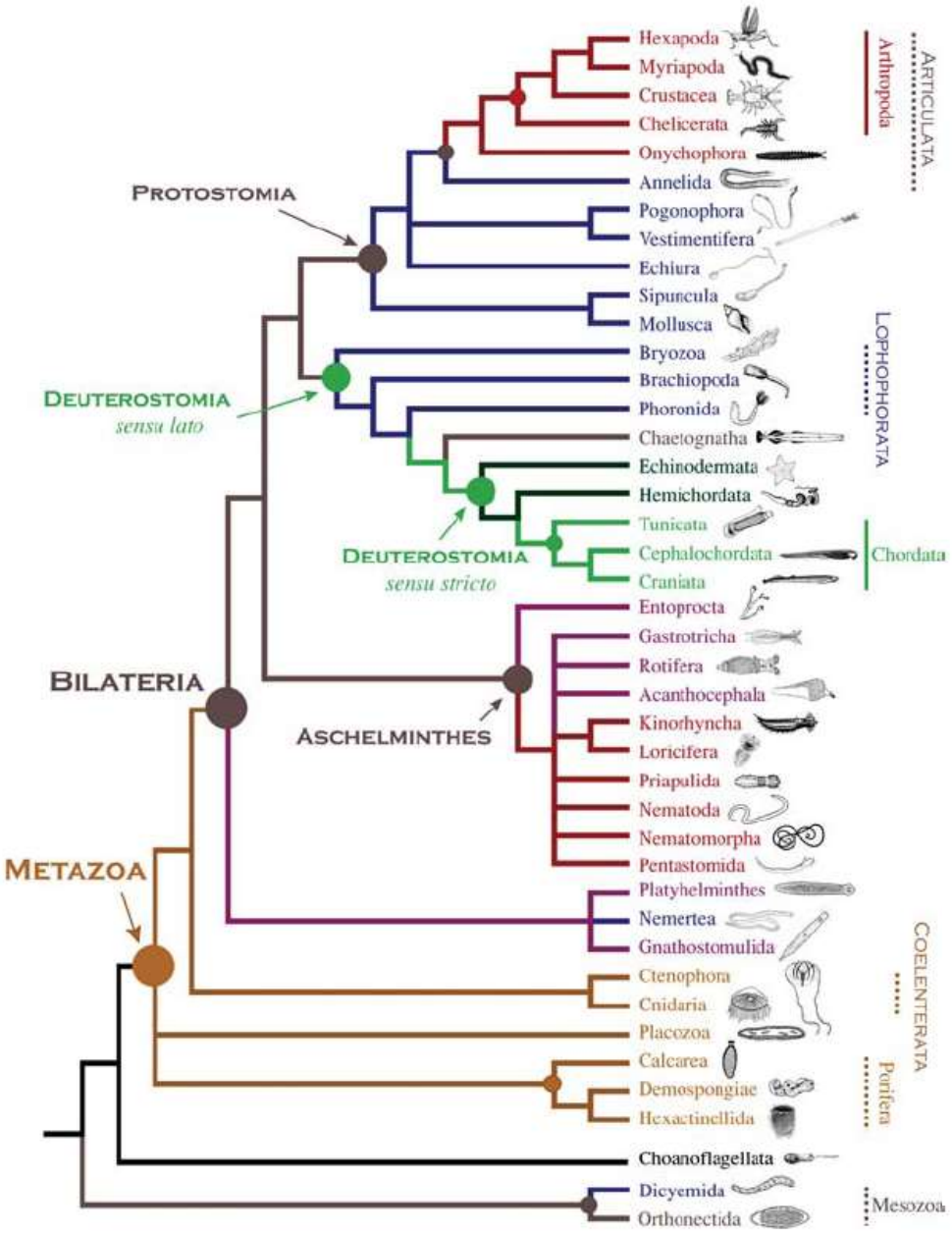
Из: Малахов В.В. Новый взгляд на происхождение билатерий. Природа 2004



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

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

Science 1988 (239) 748-753

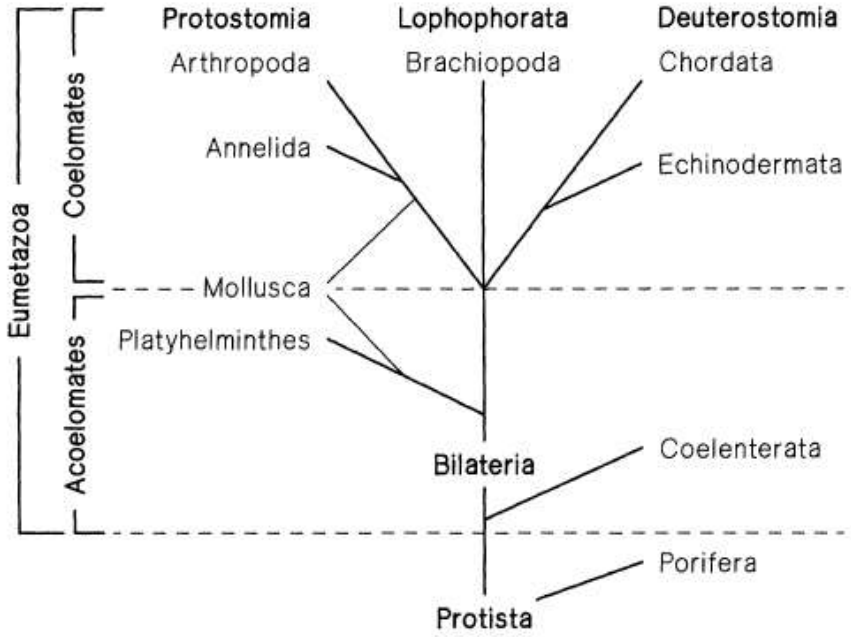


Fig. 1. Phylogenetic tree for the Metazoa, based on the views of Hyman (*5*). This phylogeny is based on morphology of both adults and embryos. Phylum names are shown in lightface lettering.

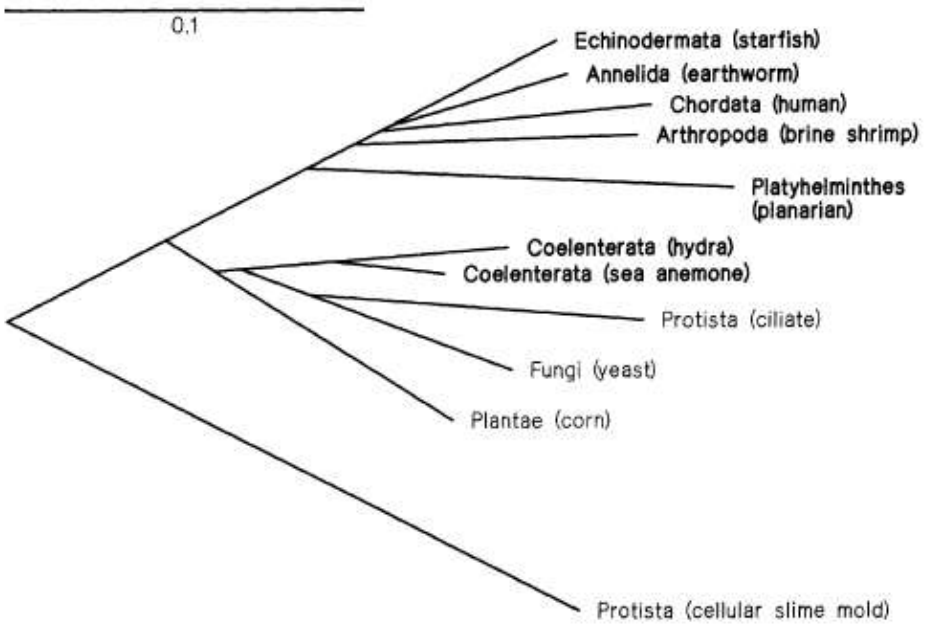


Fig. 2. An evolutionary tree for animals that is based on partial sequences of 18*S* rRNAs. The tree is read from left to right. The root of the tree is provided by the most distantly related organism, the cellular slime mold. The

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

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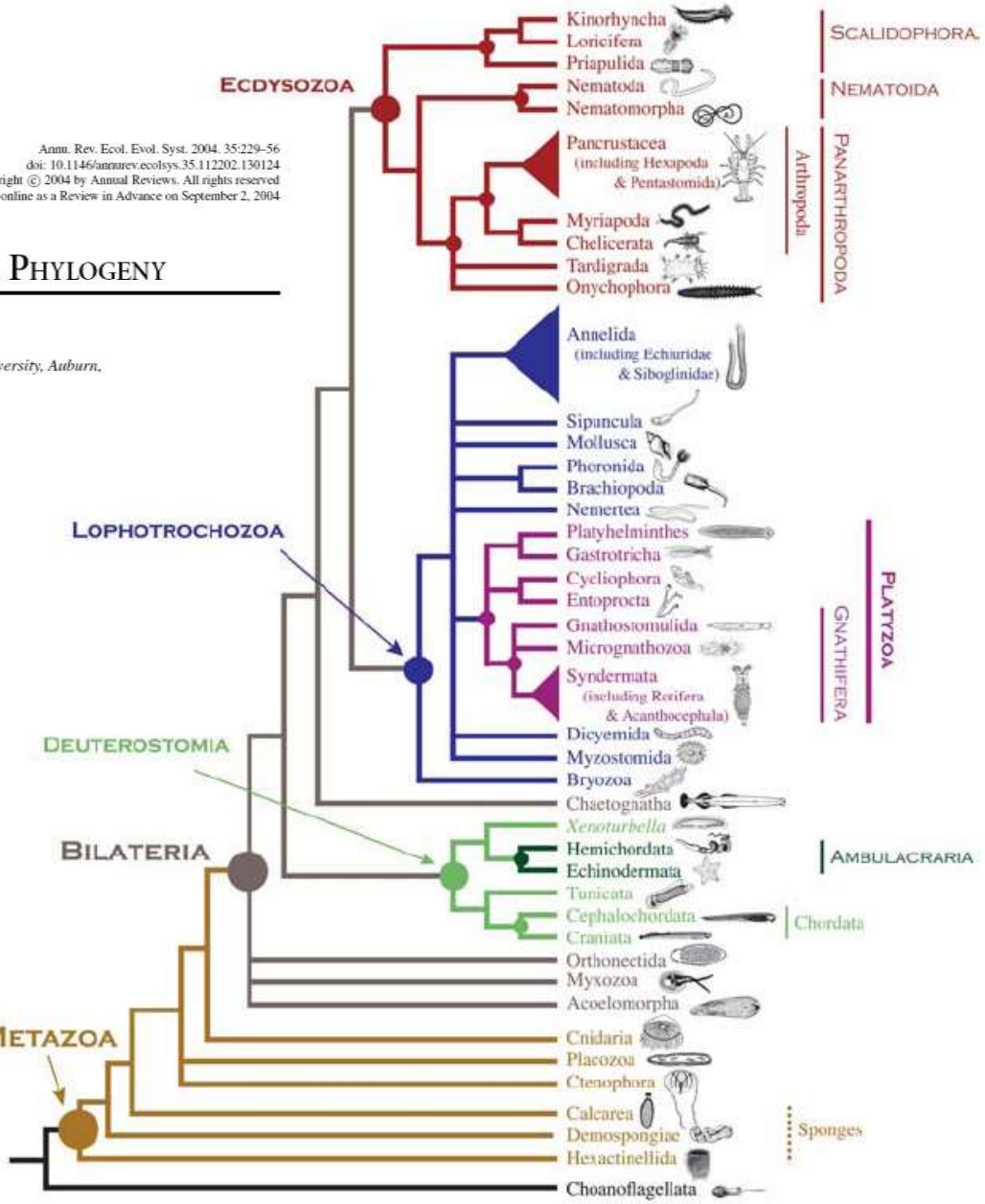

Figure 2 Modern synthesis. The new view of animal phylogeny based largely on molecular data. Details and support for various clades are discussed in the text. This

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.

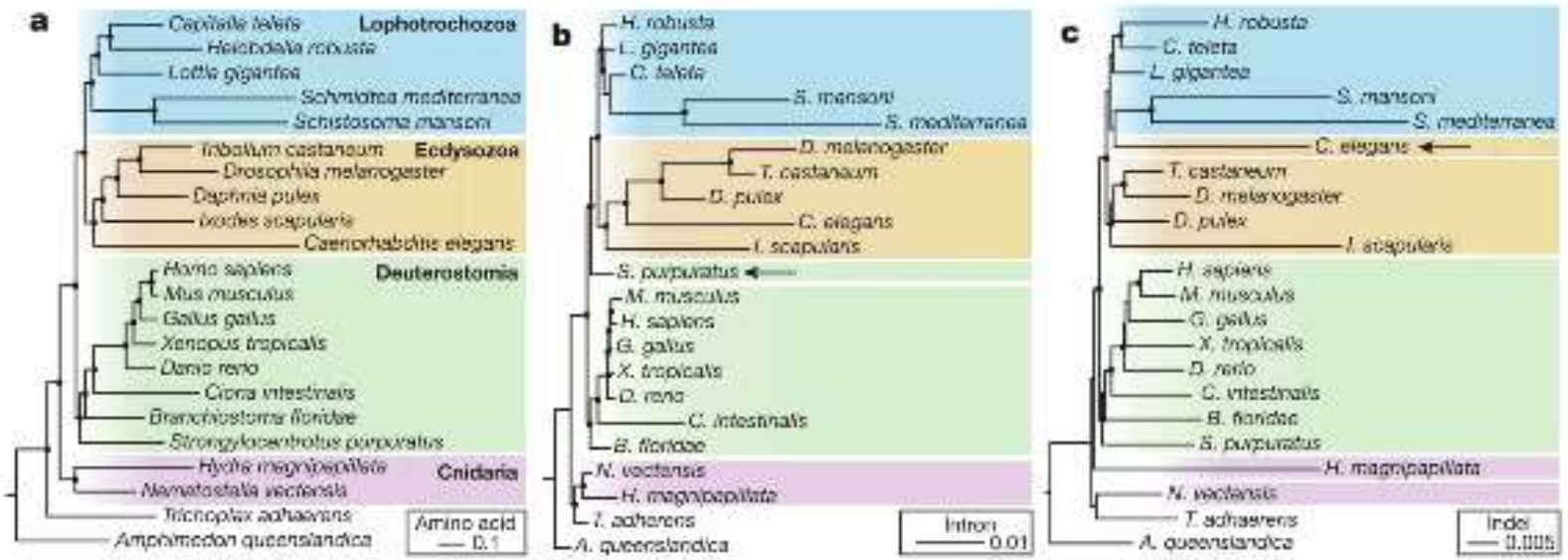

Figure 1. Full-genome evidence resolves metazoan relationships and verifies the monophyly of lophotrochozoans and spiralians

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.

FEBS Letters 584 (2010) 4458–4462

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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.

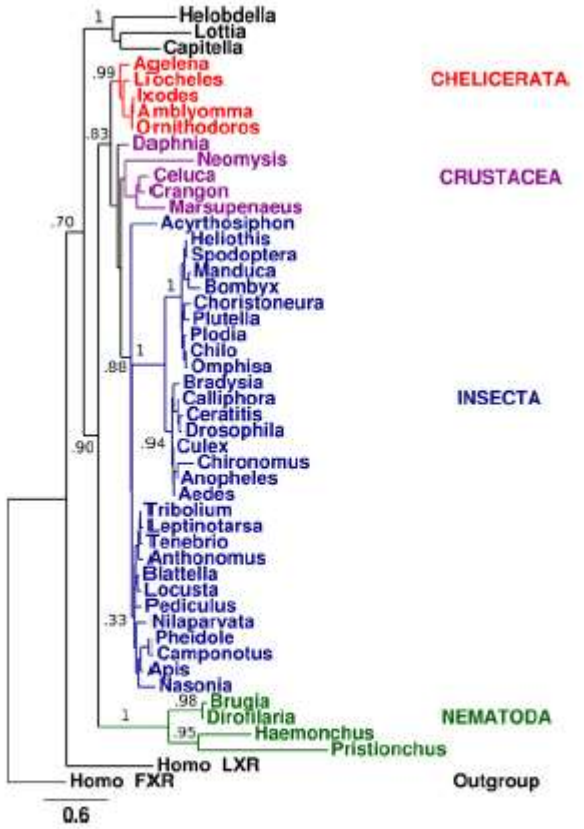


Fig. 3. Phylogenetic tree of ecdysone receptors as constructed using PhyML [13]. Number of bootstrap replicates 100, WAG substitution model with a gamma distribution between sites, four categories, α estimated by the programm. Selected bootstrap values are indicated. Human FXR and LXR were used for rooting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

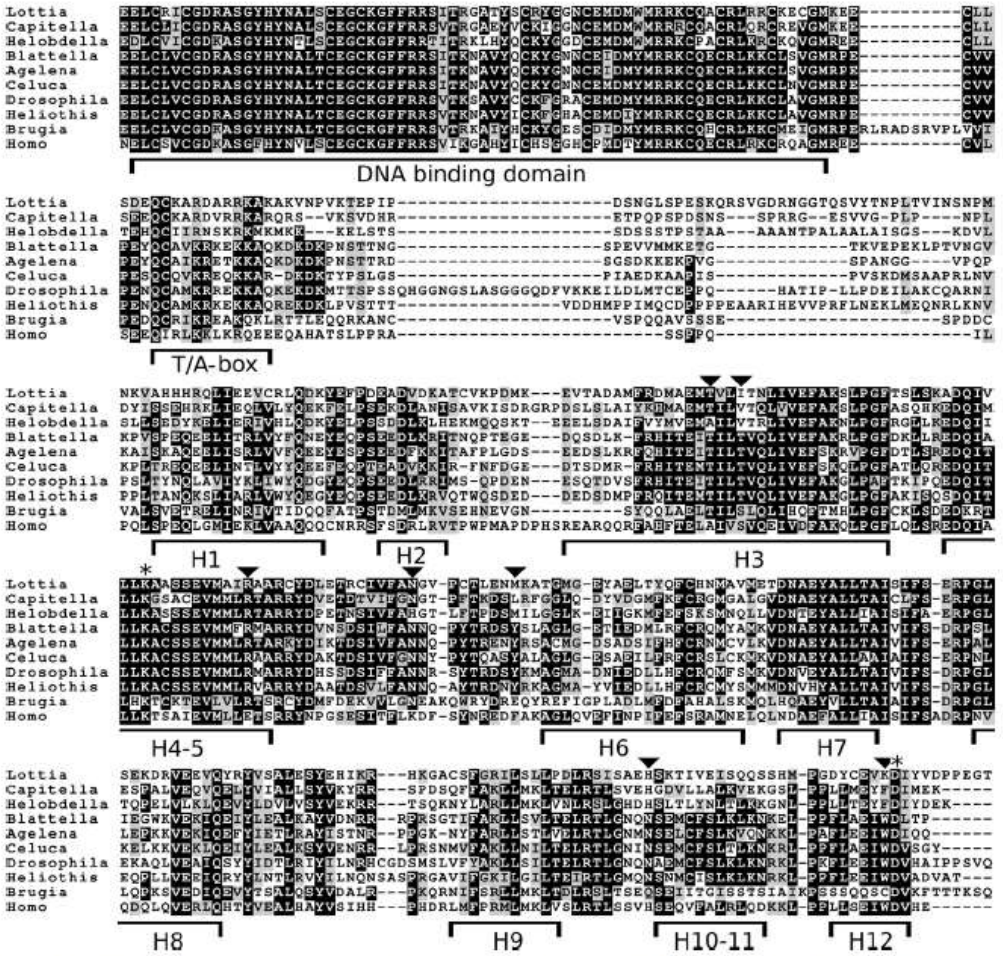
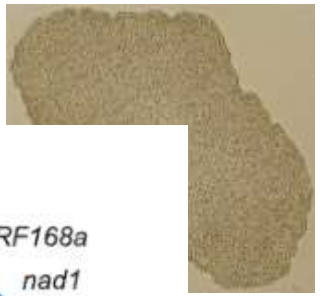
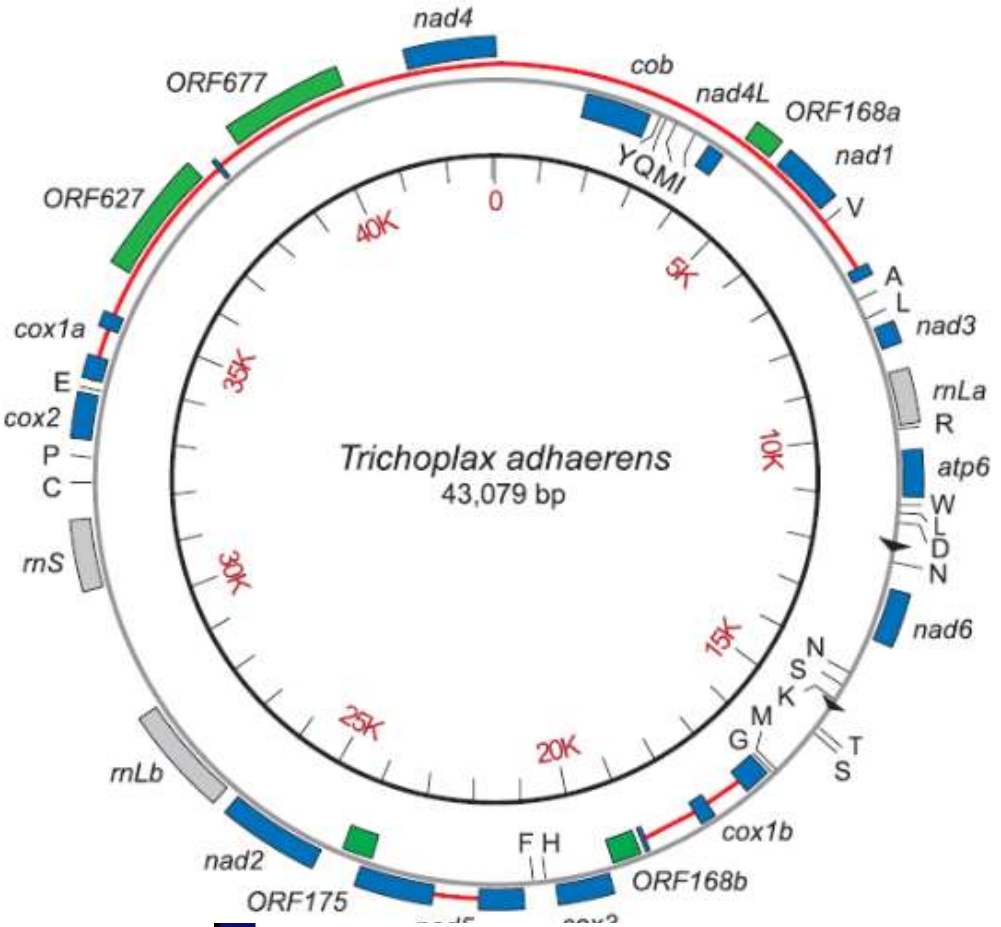


Fig. 1. Protein sequence similarity of the putative ecdysone receptors identified from *L. gigantea*, *C. teleta* and *H. robusta* with ecdysone receptors identified from various arthropods, the nematode *Brugia malayi* as well as human LXR. The DNA binding domains and the helices 1 through 12 (H1–H12) 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.

Трихоплакс – полный мт геном:



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.



PNAS

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)

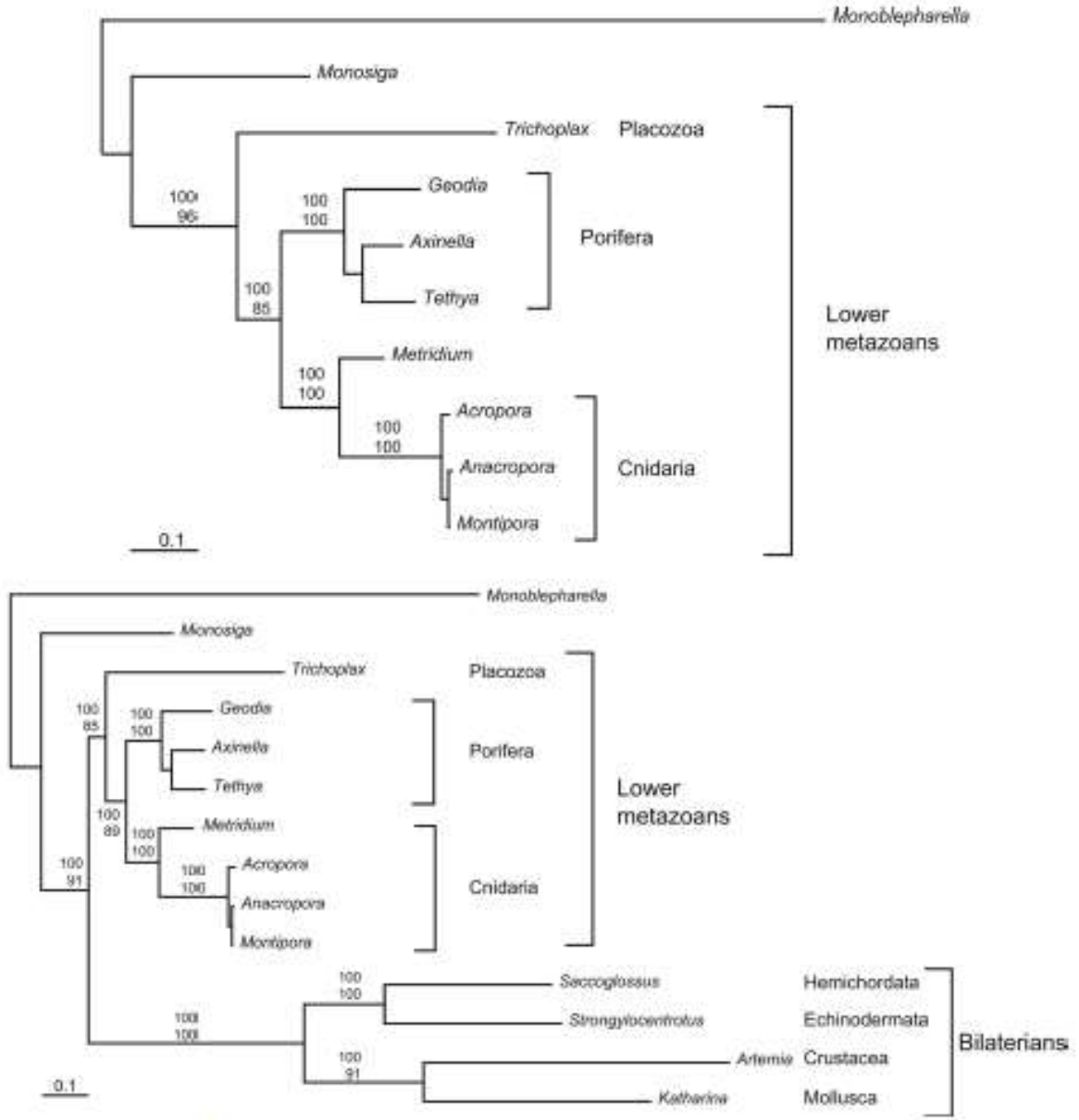


Fig. 2. Phylogenetic analysis of concatenated mitochondrial proteins. The data set consisted of a total of 2,730 amino acid positions concatenated from 12

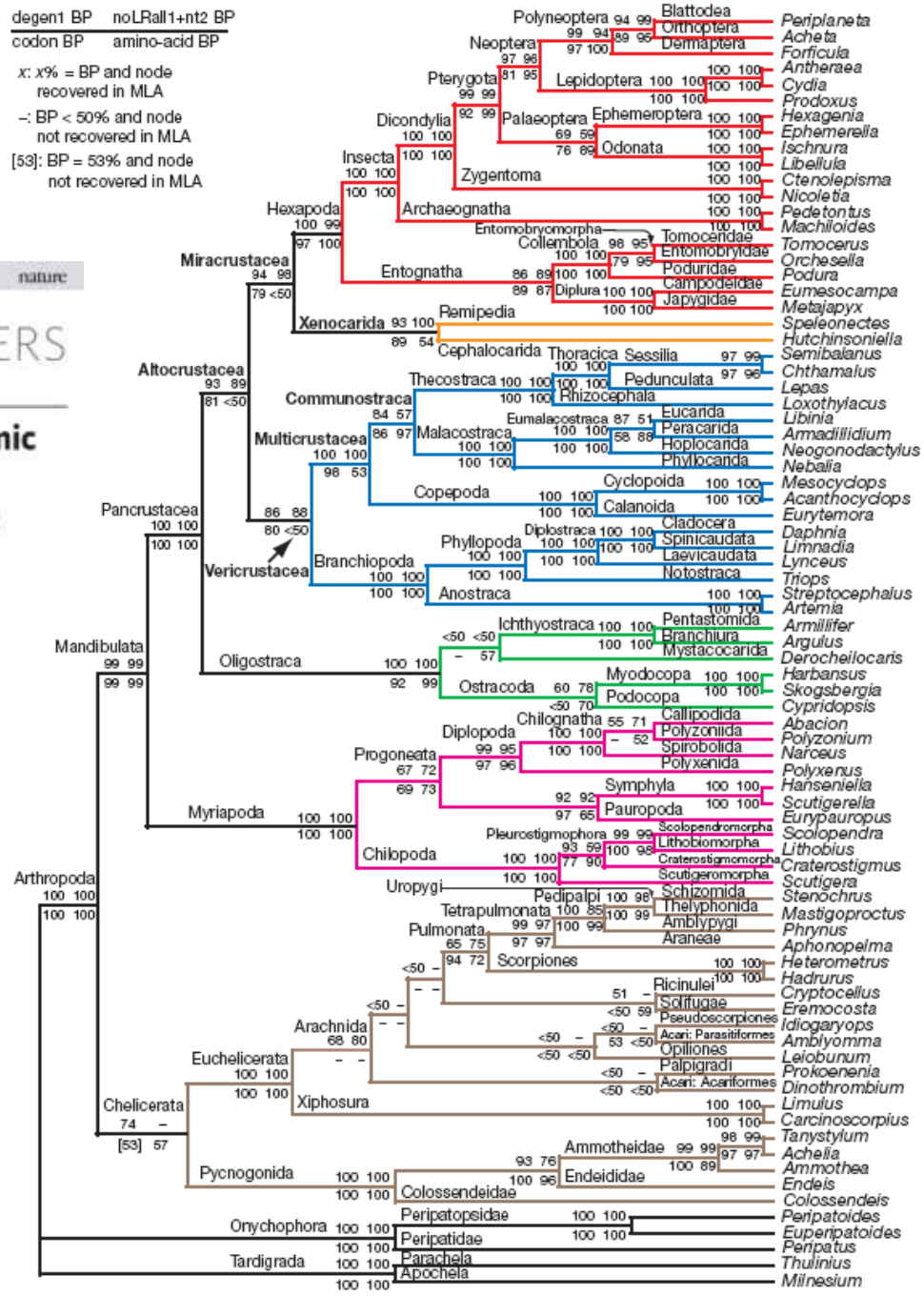
PNAS 2006

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[1], Regina Wetzer[1], Joel W. Martin[1] & Clifford W. Cunningham[1]



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LETTERS

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

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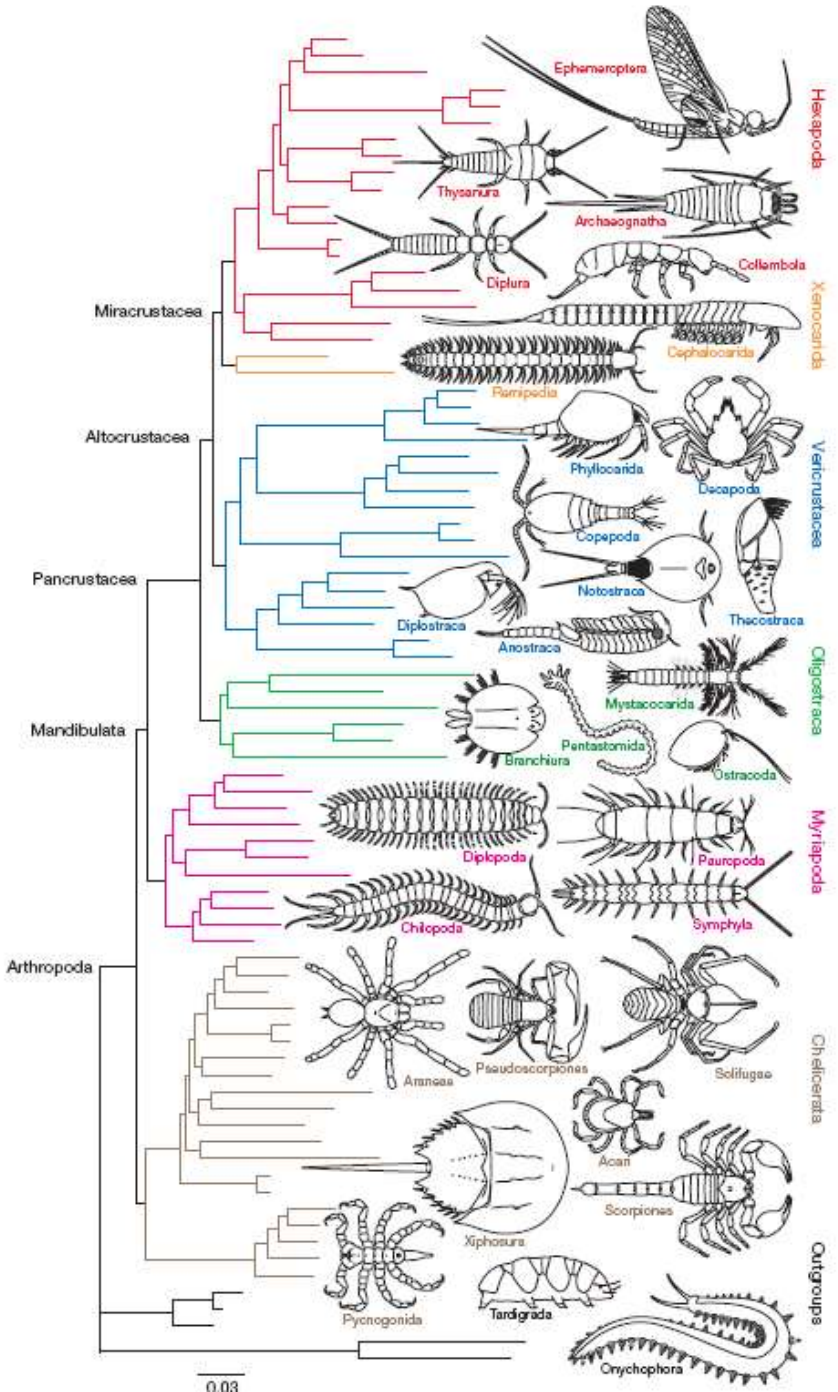
Our results strongly support Pancrustacea (Hexapoda plus Crustacea) but also strongly favour the traditional morphology-based Mandibulata11 (Myriapoda plus Pancrustacea) over the molecule-based Paradoxopoda (Myriapoda plus Chelicerata). In addition to Hexapoda, Pancrustacea includes three major extant 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.



- 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

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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

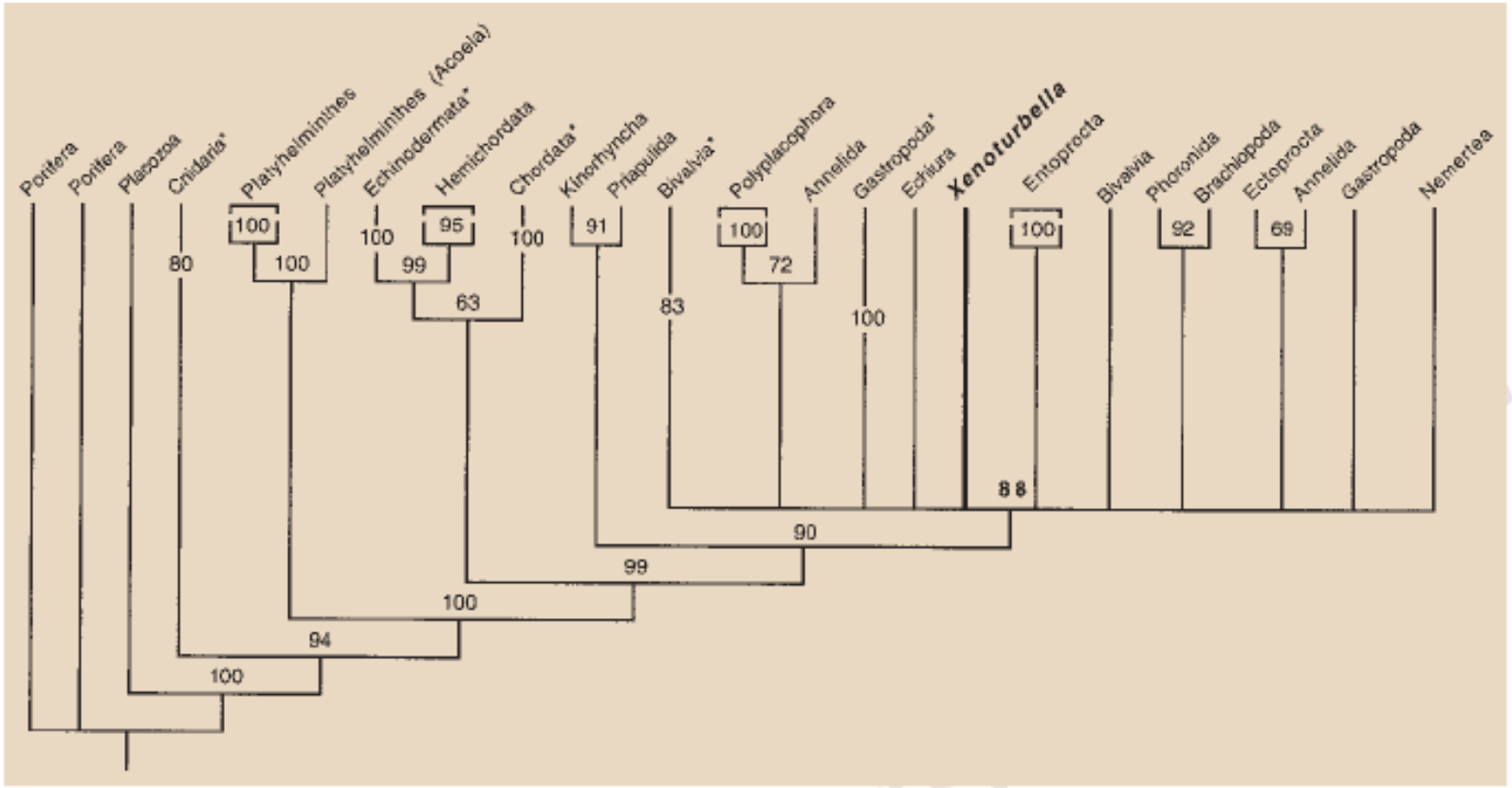

Figure 1 Consensus tree showing groups present in 60% of jack-knife replicates from analysis of 18S rRNA matrix (successive weighting of characters, 10 iterations with 100 replicates each, deletion frequency e^{-1}). Labels indicate jack-knife frequencies. Clades marked with asterisks represent multiple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

Noren & Jondelius, 1997 – COI tree

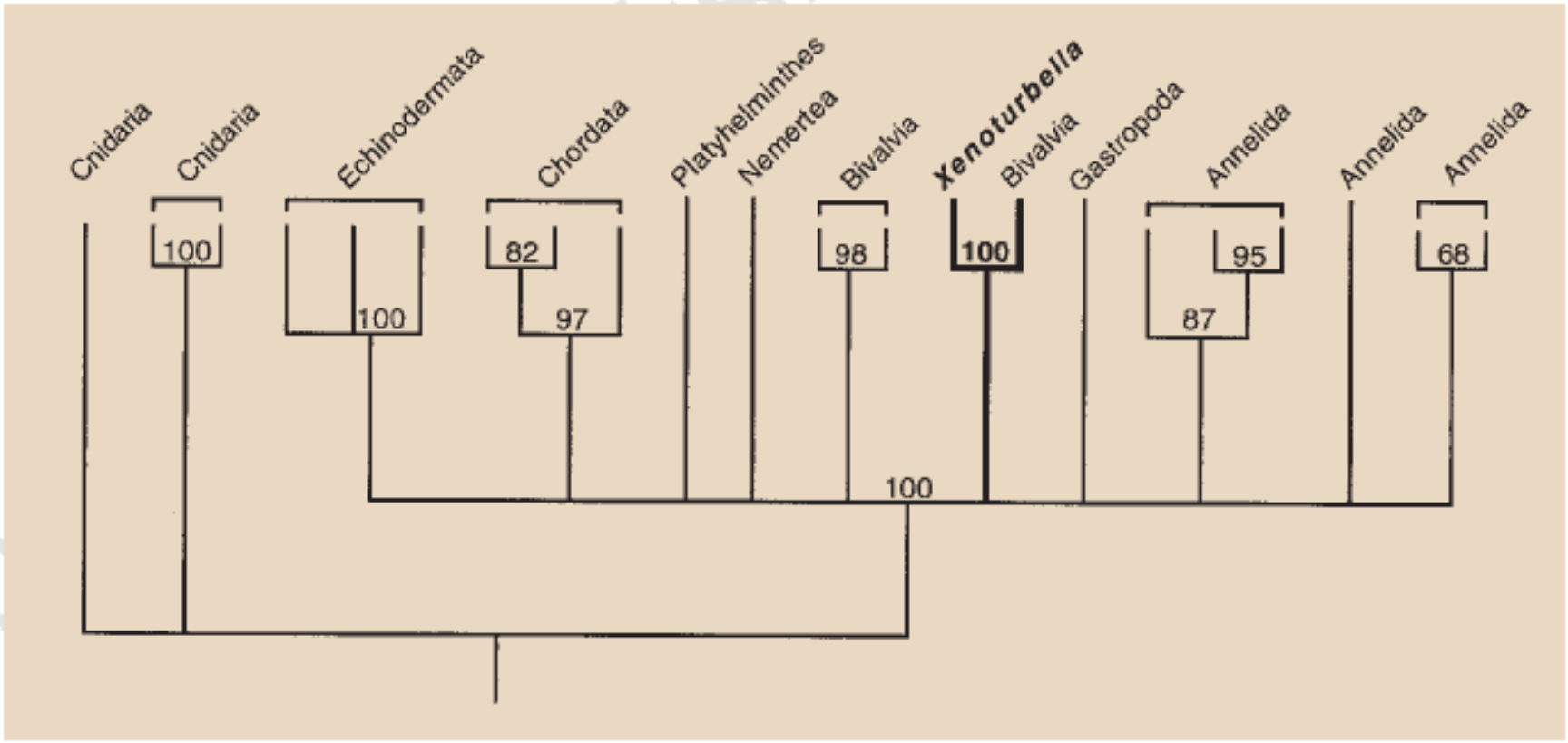

Figure 2 Consensus tree showing groups present in 60% of jack-knife replicates from analysis of COI matrix (3,000 replicates, 5 random additions and branch swapping, deletion frequency e^{-1}). Labels indicate jack-knife frequencies. Full details of tree topology and sequence alignment are available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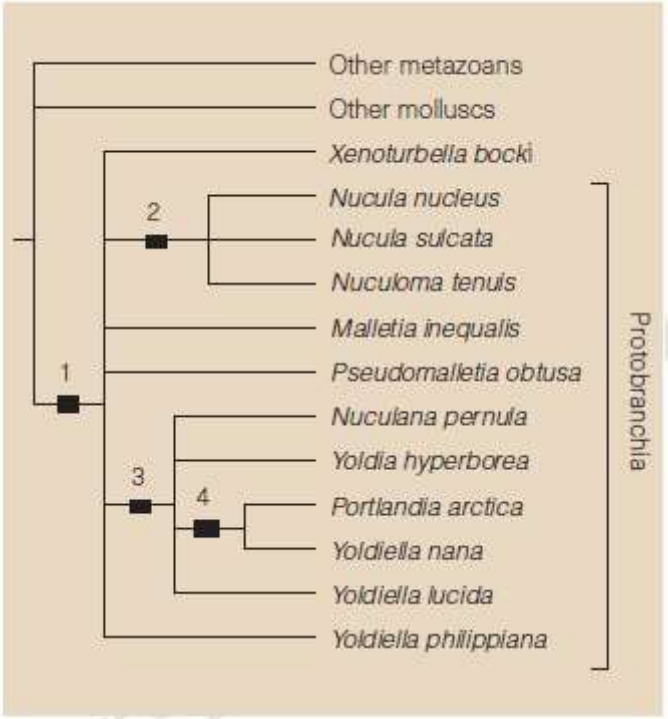

Figure 2 Cladistic analyses of oogenesis indicates that *Xenoturbella bocki* is a sister group or a subgroup of protobranch bivalves. The analysed characters, with their apomorphic states, are: **1,**

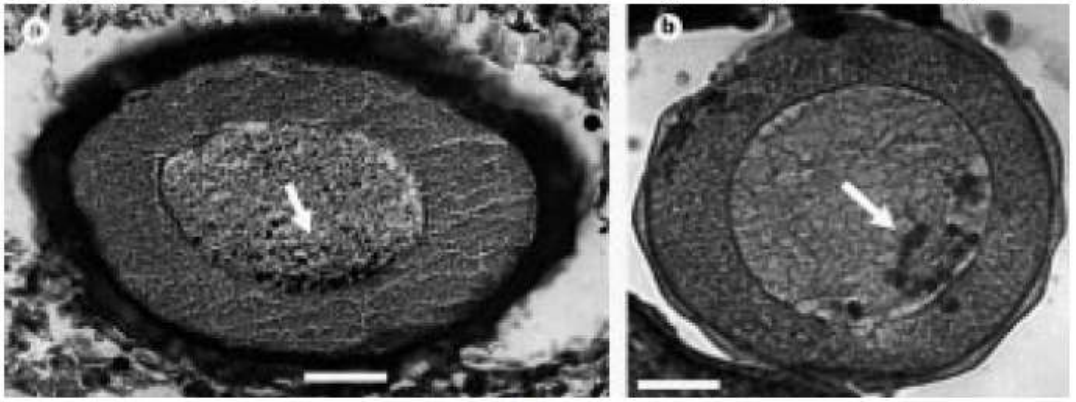

Figure 1 Relationship of *Xenoturbella bocki* to molluscs. Late vitellogenous oocytes of **a,** *Xenoturbella bocki* and **b,** the protobranch mollusc *Nucula nucleus*. Scale bars, 20 μm.

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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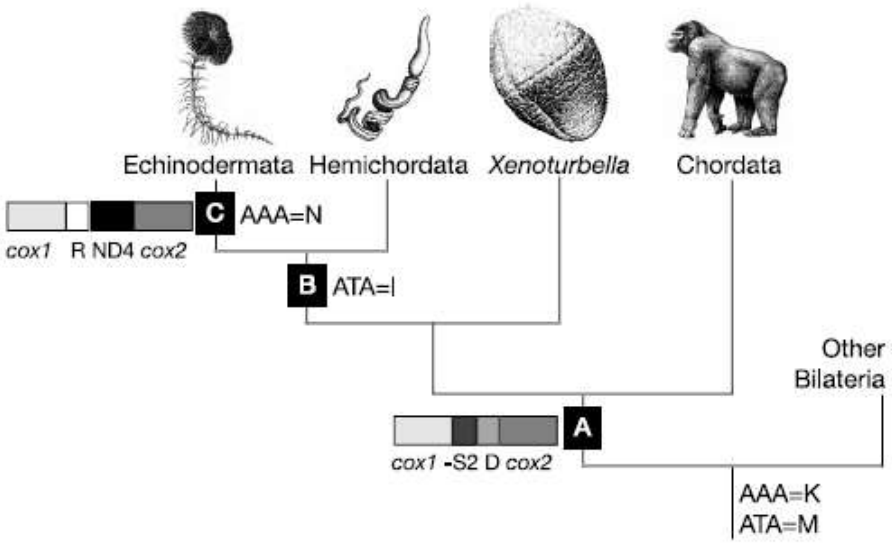
[2]*Zoological Museum (University of Copenhagen), Universitetsparken 15, DK-2100 Copenhagen, Denmark*
[3]*Department of Zoology, The Natural History Museum, Cromwell Road,*



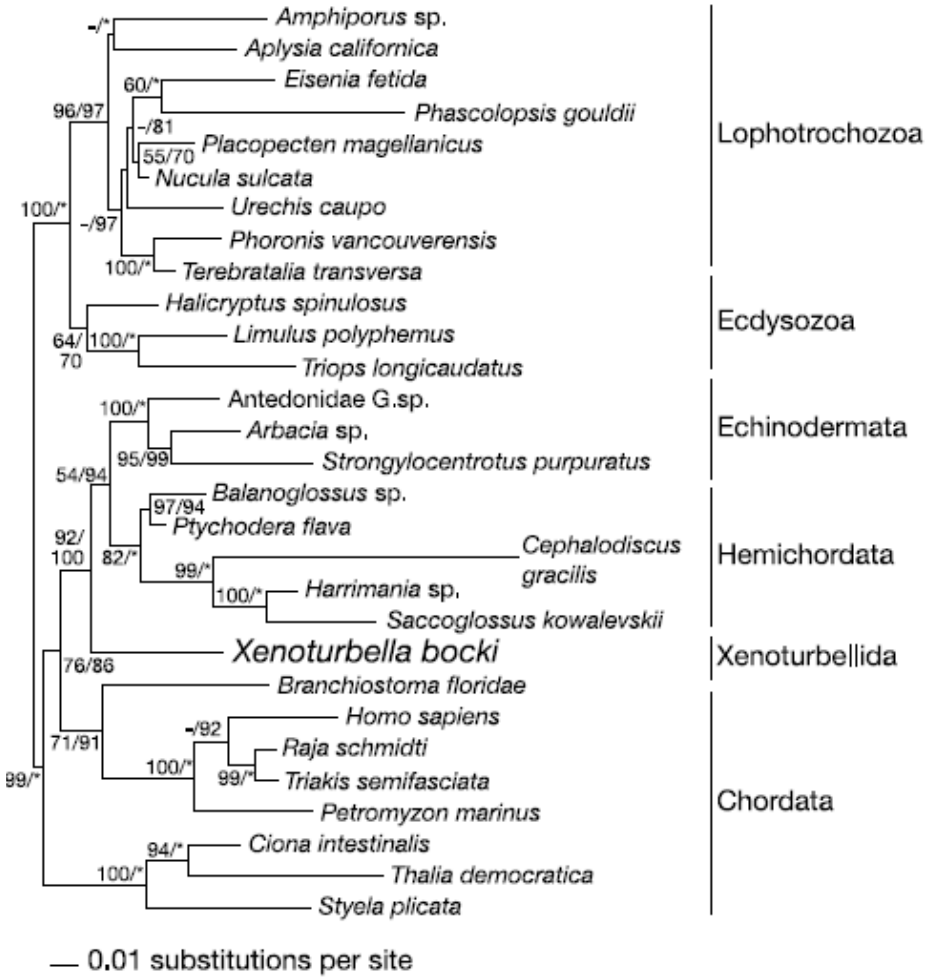


Figure 2 Position of *Xenoturbella* within the deuterostomes as suggested by our analyses of *SSU* and mitochondrial data. The distribution of synapomorphic molecular character

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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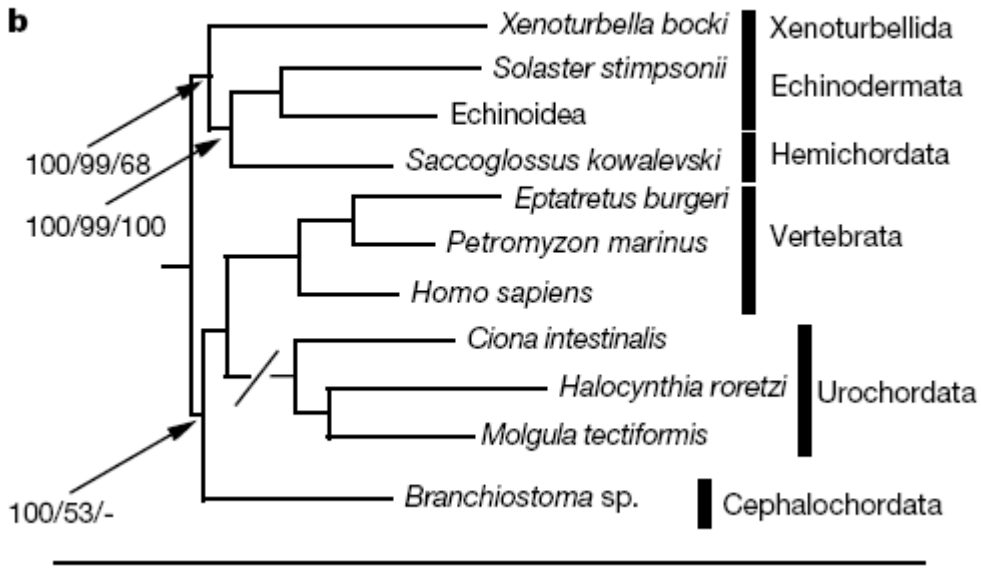

- Figure 1 | Phylogenetic analyses of 170 nuclear proteins and 13 mitochondrial proteins support a monophyletic chordate clade and an independent deuterostome phylum of Xenoturbellida.

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).

- .

Deuterostome phylogeny reveals monophyletic chordates and the new phylum Xenoturbellida

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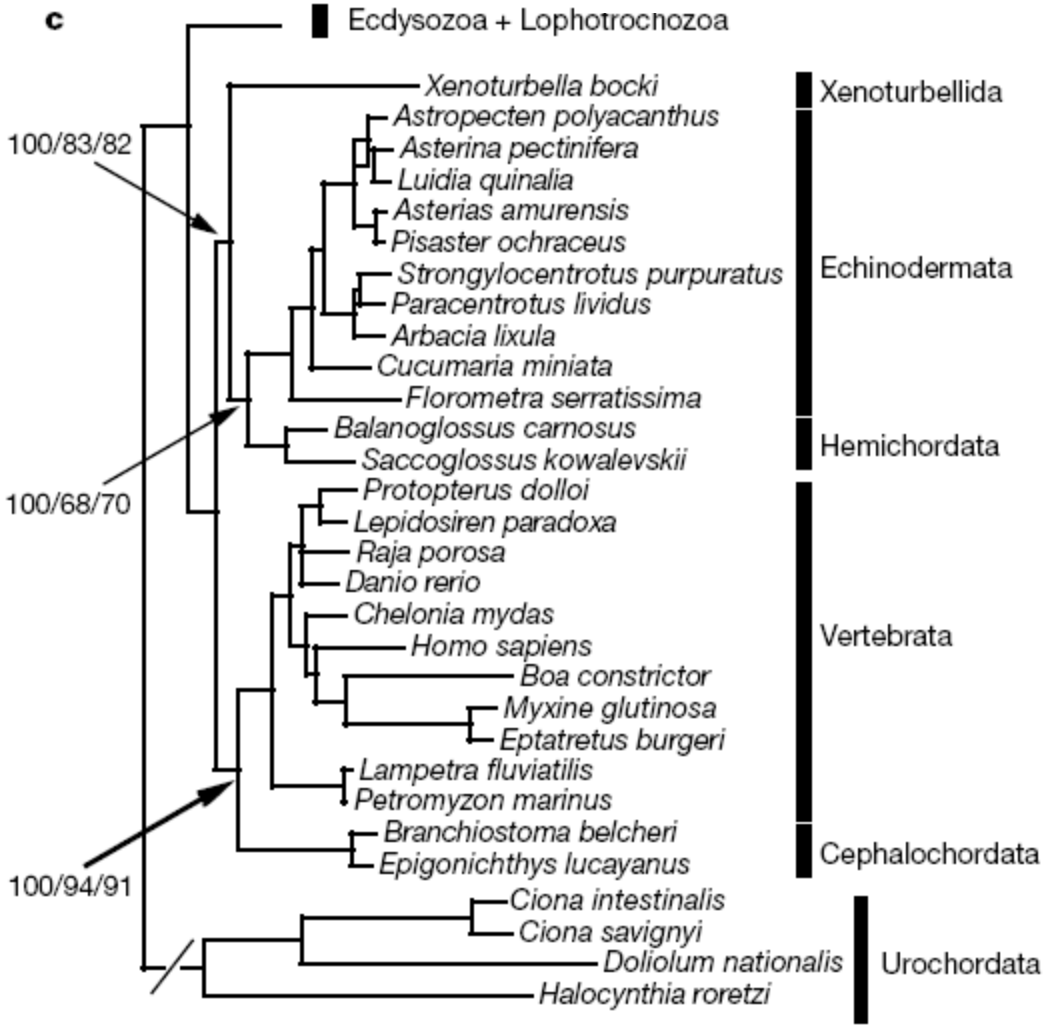


- C. Bayesian analysis of mitochondrial data with the amino acids M, I, N and K recoded as missing data places the cephalochordates with vertebrates; Xenoturbella is the sister group of Ambulacraria.

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

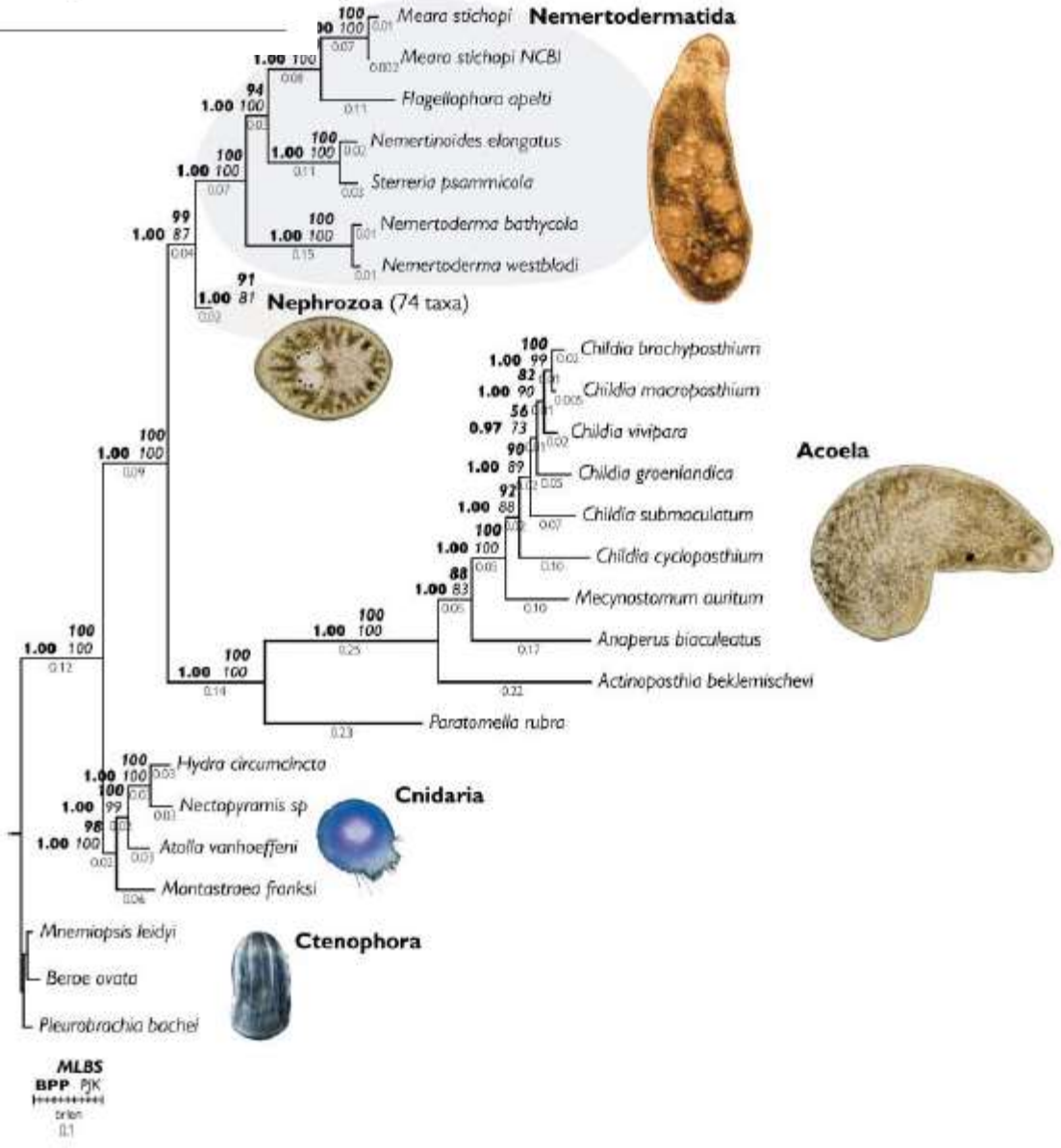
Phylogenetic distribution of microRNAs supports the basal position of acoel flatworms and the polyphyly of Platyhelminthes

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



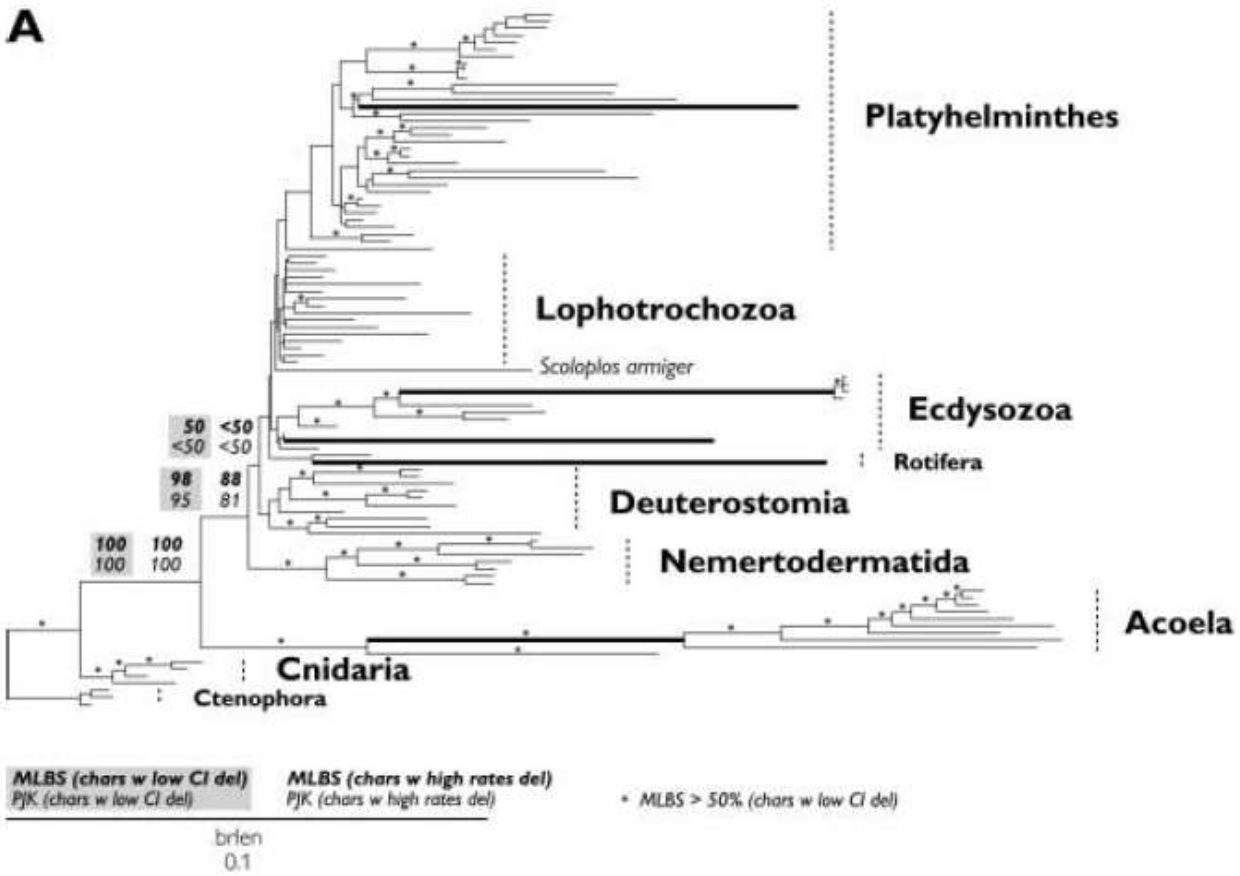


Fig. 5 A, B. The positions of Acoela and Nemertodermatida as separate braches are not artefacts of globally fast evolving characters. Maximum likelihood non-parametric bootstrap values (MLBS; bold italics; 200 pseudoreplicates, GTR + Γ + I model, PHYML) and parsimony jackknife values (PJK; italics; 1000 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

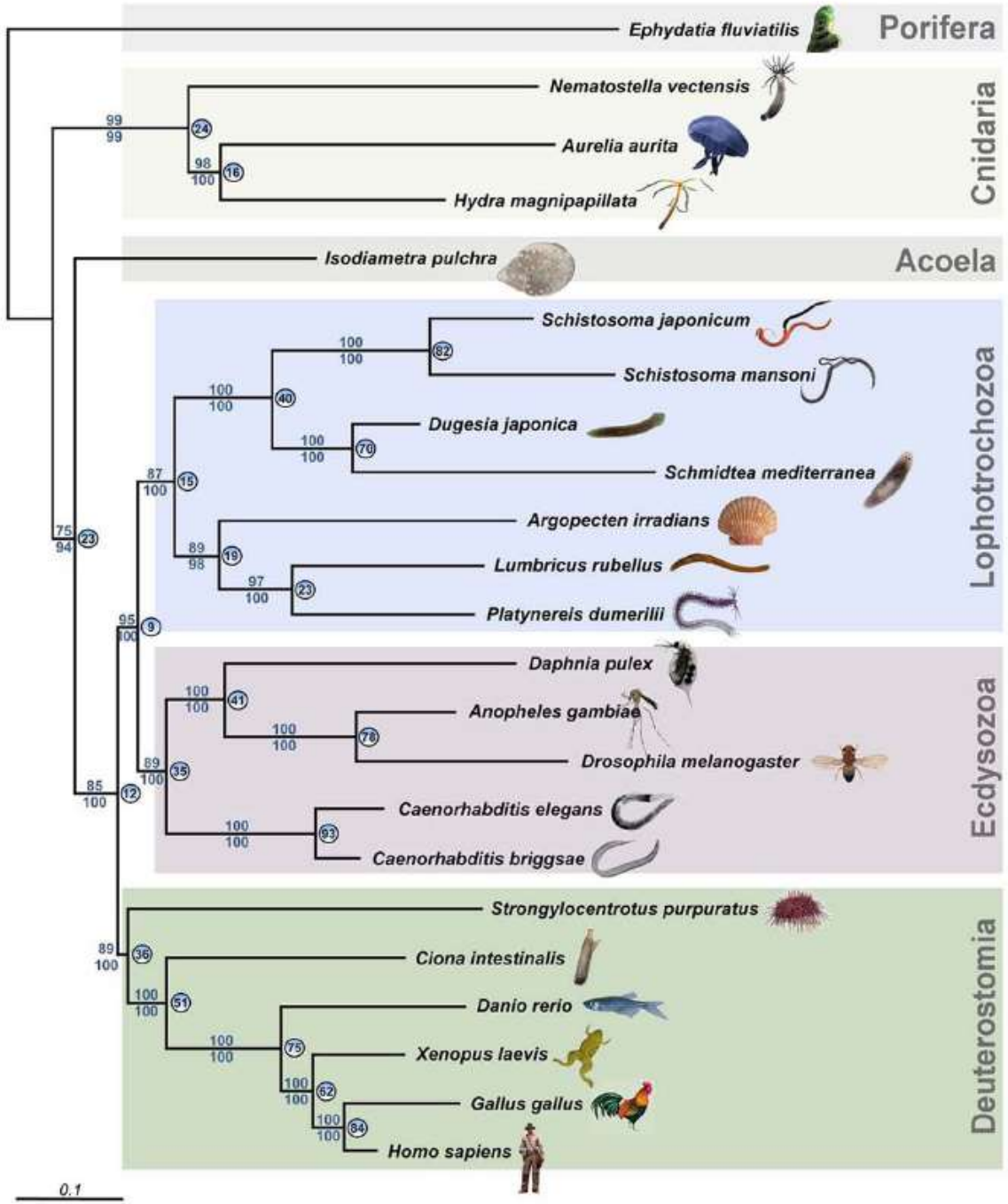
To Be or Not to Be a Flatworm: The Acoel Controversy

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

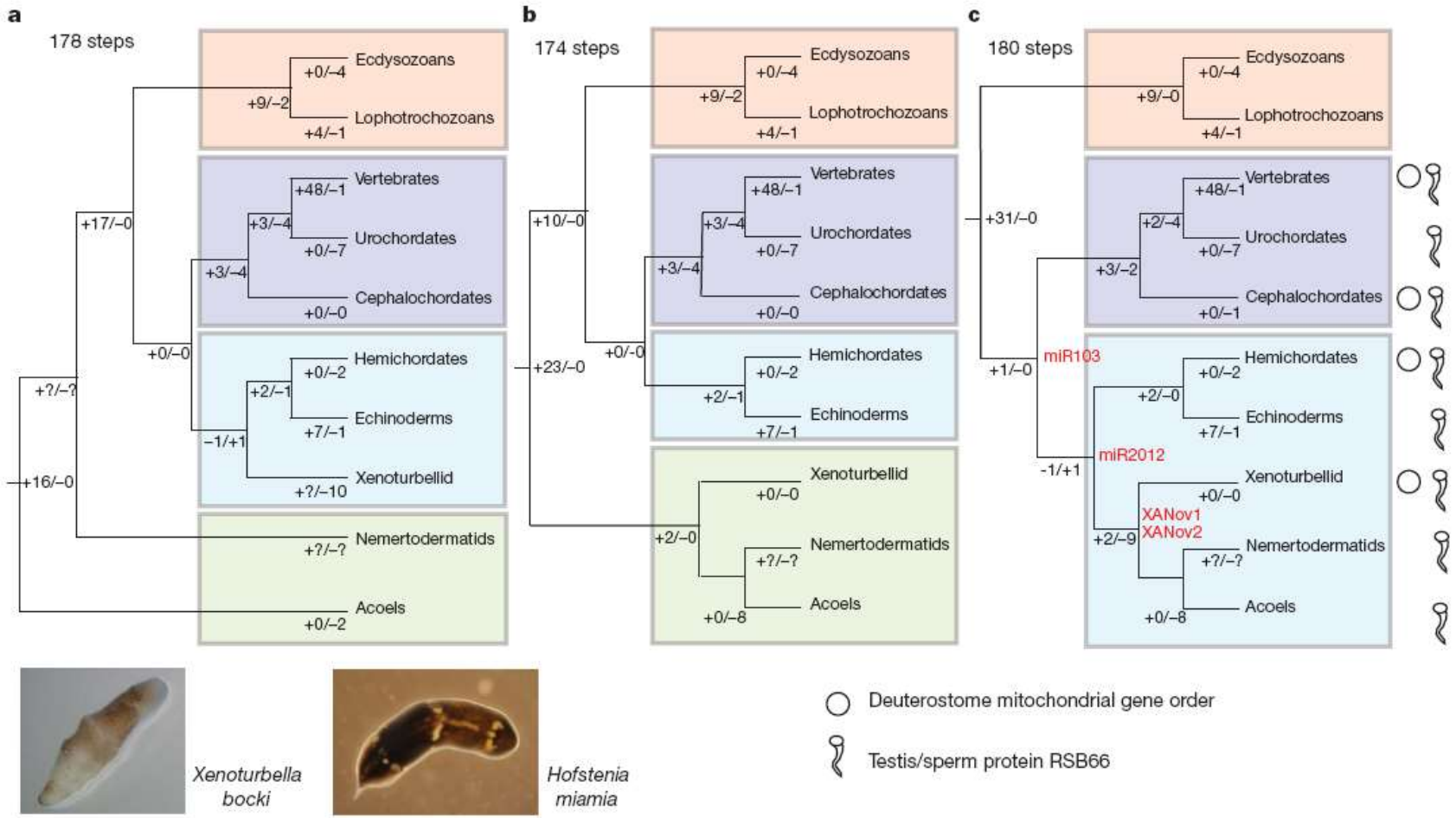
LETTER

doi:10.1038/nature09676

Acoelomorph flatworms are deuterostomes related to *Xenoturbella*

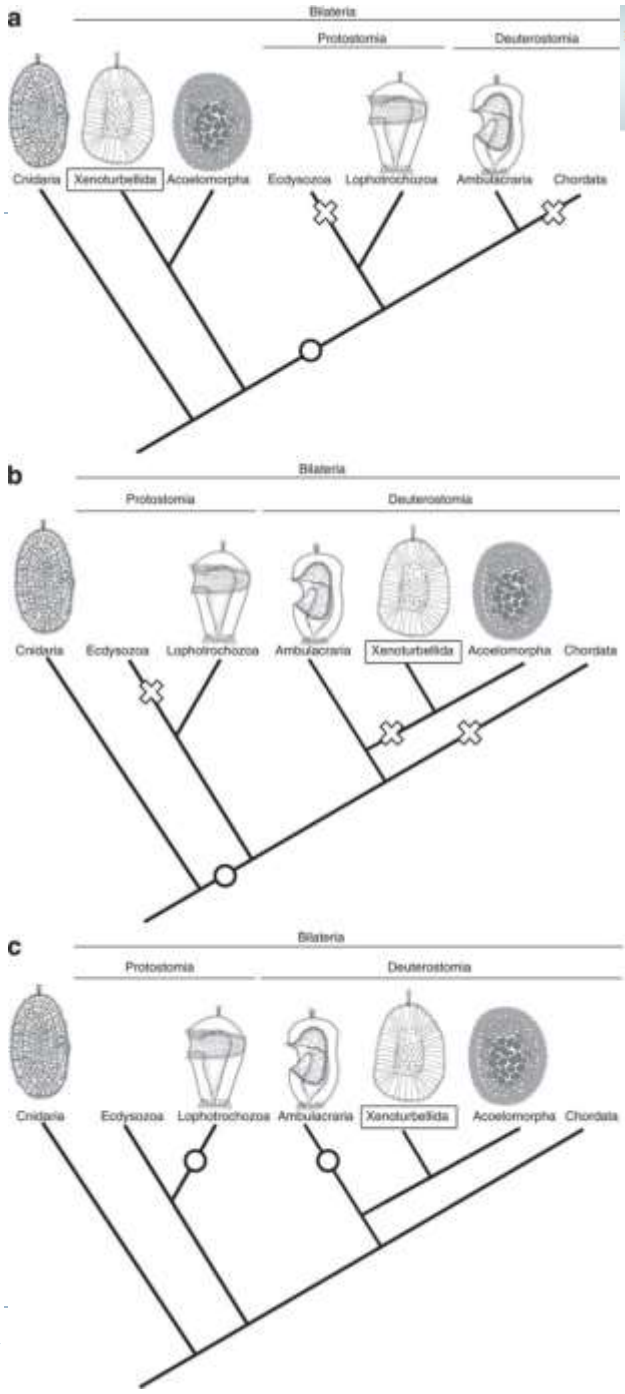
Hervé Philippe[1], Henner Brinkmann[1], Richard R. Copley[2], Leonid L. Moroz[3], Hiroaki Nakano[4]†, Albert J. Poustka[5], Andreas Wallberg[6], Kevin J. Peterson[7] & Maximilian J. Telford[8]

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.



Xenoturbella bocki

Hofstenia miamia



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ARTICLE

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DOI: 10.1038/ncomms2556 OPEN

Xenoturbella bocki exhibits direct development with similarities to Acoelomorpha

Hiroaki Nakano[1,2], Kennet Lundin[3], Sarah J. Bourlat[1,4], Maximilian J. Telford[5], Peter Funch[6], Jens R. Nyengaard[7], Matthias Obst[1] & Michael C. Thorndyke[1,8]

Xenoturbella bocki, a marine animal with a simple body plan, has recently been suggested to be sister group to the Acoelomorpha, together forming the new phylum Xenacoelomorpha. The phylogenetic position of the phylum is still under debate, either as an early branching bilaterian or as a sister group to the Ambulacraria (hemichordates and echinoderms) within the deuterostomes. Although development has been described for several species of Acoelomorpha, little is known about the life cycle of *Xenoturbella*. Here we report the embryonic stages of *Xenoturbella*, and show that it is a direct developer without a feeding larval stage. This mode of development is similar to that of the acoelomorphs, supporting the newly proposed phylum Xenacoelomorpha and suggesting that the last common ancestor of the phylum might have been a direct developer.

Animal Evolution: A Soap Opera of Unremarkable Worms

Recent phylogenies have suggested that acoelomorph flatworms might provide insights into the nature of the ancestor of bilaterian animals. How according to new data acoelomorphs might instead be degenerate deuterostomes closely related to *Xenoturbella*, muddying the waters of e animal evolution.

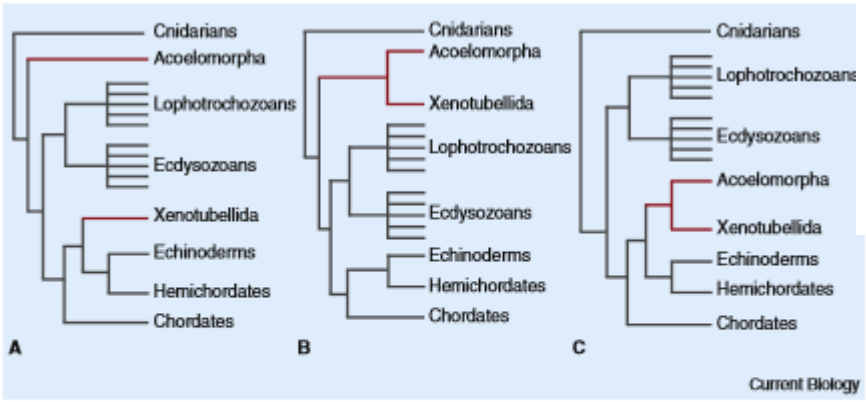

Figure 2. Alternative hypotheses for the phylogenetic position of acoelomorphs and Xenoturbellida within metazoans.

(A) Basal position of Acoelomorpha within bilaterians, but *Xenoturbella* located within the deuterostomes [10]. (B) Grouping of Acoelomorpha with *Xenoturbella* at the base of the bilaterians [6]. (C) New hypothesis of Xenacoelomorpha as sister group to echinoderms and hemichordates within the deuterostomes [2].

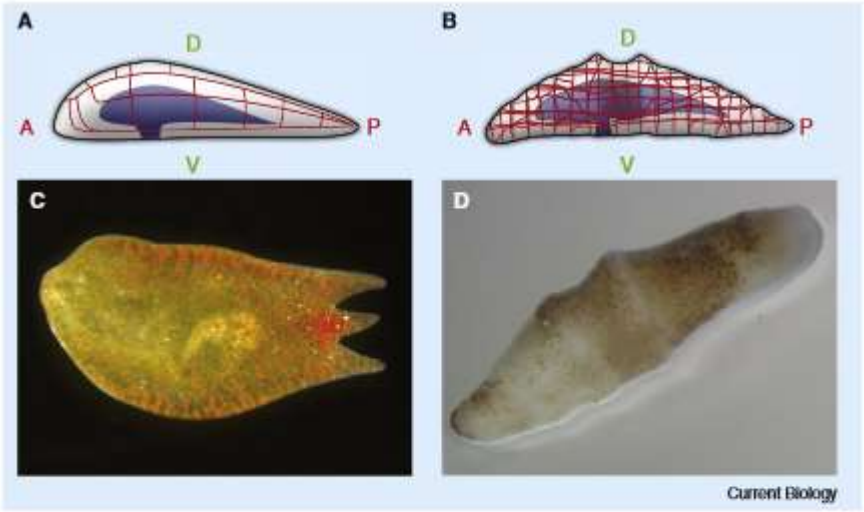

Figure 1. Morphology and basic body plans of acoel flatworms and *Xenoturbella*.

Diagram of a lateral view of the body plan of acoel flatworms (A) and *Xenoturbella* (B). The diffusely organized nervous systems are marked in red and the ventral mouth and blind gut are marked in blue. The dorso/ventral axes are indicated by D/V and the anteroposterior axis by A/P. (C) Photomicrograph of an acoel flatworm, dorsal view, courtesy of James Sikes. (D) Photomicrograph of *Xenoturbella bocki* courtesy of Max Telford.

Current Biology, Volume 21, Issue 4, R151-R153, 22 February 2011

10.1016/j.cub.2010.12.017

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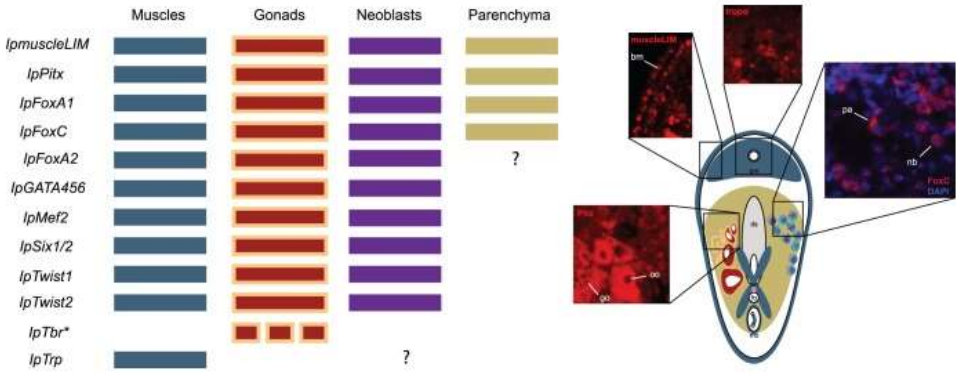
PLoS One. 2013; 8(2): e55499.
Published online 2013 February 6. doi: 10.1371/journal.pone.0055499
PMCID: PMC3566195

Mesodermal Gene Expression in the Acoel *Isodiametra pulchra* Indicates a Low Number of Mesodermal Cell Types and the Endomesodermal Origin of the Gonads

Marta Chiodin,[1] Aina Børve,[2] Eugene Berezikov,[4] Peter Ladurner,[3] Pedro Martinez,[1,5] and Andreas Hejnol[2,*]

Figure 6



Summary of mesodermal gene expression in adult *I. pulchra*.

Conclusions

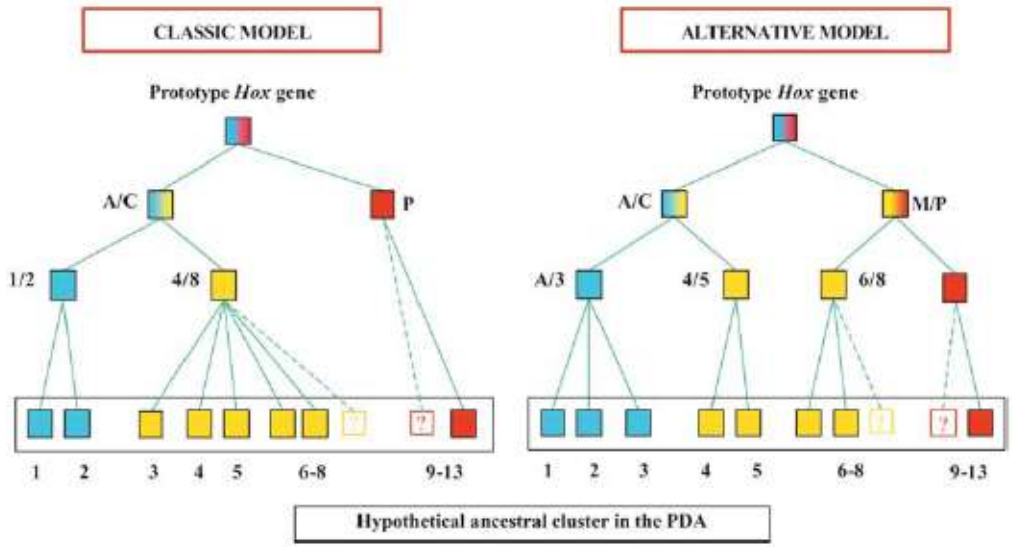
In this study we show that most of the acoel homologs of bilaterian mesodermal transcription factors are also expressed in mesodermal compartments of the acoel, which only consist of muscles, gonads and neoblasts [26]. Our gene expression study suggests that some neoblasts and germ cells may have been derived from endomesodermal precursors and are thus true mesoderm. If the acoelomorphs are nested inside the deuterostomes [22], it is likely the acoelomate condition in acoels arose from a coelomate ancestor. However, we find no traces or anlage of mesodermal tissue that indicates the former presence of a coelom in a coelomate ancestor. Only the gonads could represent the 'vestige' of a secondary coelomic cavity. If the Acoelomorpha are the sister group to the remaining Bilateria [20], [21], mesoderm evolution by 'enterocoely' is less parsimonious. In this scenario, myocytes that form an orthogon of circular and longitudinal musculature are likely the first mesodermal cell type that evolved in Bilateria. Other mesodermal tissues such as coeloms or connective tissue must have evolved independently as secondary separations from the endoderm - similar to the secondary separation of the parenchyma in the acoel lineage. However, a solid phylogenetic framework of animals is needed to trace the path of mesoderm evolution and differentiation.

Dev Genes Evol (2003) 213:142–148
DOI 10.1007/s00427-003-0306-z

SEQUENCE CORNER

Daniel Papillon · Yvan Perez · Laurent Fasano ·
Yannick Le Parco · Xavier Caubit

Hox gene survey in the chaetognath *Spadella cephaloptera*: evolutionary implications



SceMedPost ген - несет у хетогнат признаки и медианных, и постериальных генов Нох. Авторы предполагают что это анцестральный признак.

BMC Evolutionary Biology

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Research article

Open Access

Translational machinery of the chaetognath *Spadella cephaloptera*: a transcriptomic approach to the analysis of cytosolic ribosomal protein genes and their expression

Roxane M Barthélémy[1], Anne Chenuil[2], Samuel Blanquart[3], Jean-Paul Casanova[1] and Eric Faure*[1]

Results: This analysis has allowed us to determine the complete primary structures of 23 out of 32 RPs from the small ribosomal subunit (SSU) and 32 out of 47 RPs from the large ribosomal subunit (LSU). Ten proteins are partially determined and 14 proteins are missing. Phylogenetic analyses of concatenated RPs from six animals (chaetognath, echinoderm, mammalian, insect, mollusc and sponge) and one fungal taxa do not resolve the chaetognath phylogenetic position, although each mega-sequence comprises approximately 5,000 amino acid residues. This is probably due to the extremely biased base composition and to the high evolutionary rates in chaetognaths. However, the analysis of chaetognath RP genes revealed three unique features in the animal Kingdom. First, whereas generally in animals one RP appeared to have a single type of mRNA, two or more genes are generally transcribed for one RP type in chaetognath. Second, cDNAs with complete 5'-ends encoding a given protein sequence can be divided in two sub-groups according to a short region in their 5'-ends: two novel and highly conserved elements have been identified (5'-TAATTGAGTAGTTT-3' and 5'-TATTAAGTACTAC-3') which could correspond to different transcription factor binding sites on paralog RP genes. And, third, the overall number of deduced paralogous RPs is very high compared to those published for other animals.

Conclusion: These results suggest that in chaetognaths the deleterious effects of the presence of paralogous RPs, such as apoptosis or cancer are avoided, and also that in each protein family, some of the members could have tissue-specific and extra-ribosomal functions. These results are congruent with the hypotheses of an allopolyploid origin of this phylum and of a ribosome heterogeneity.

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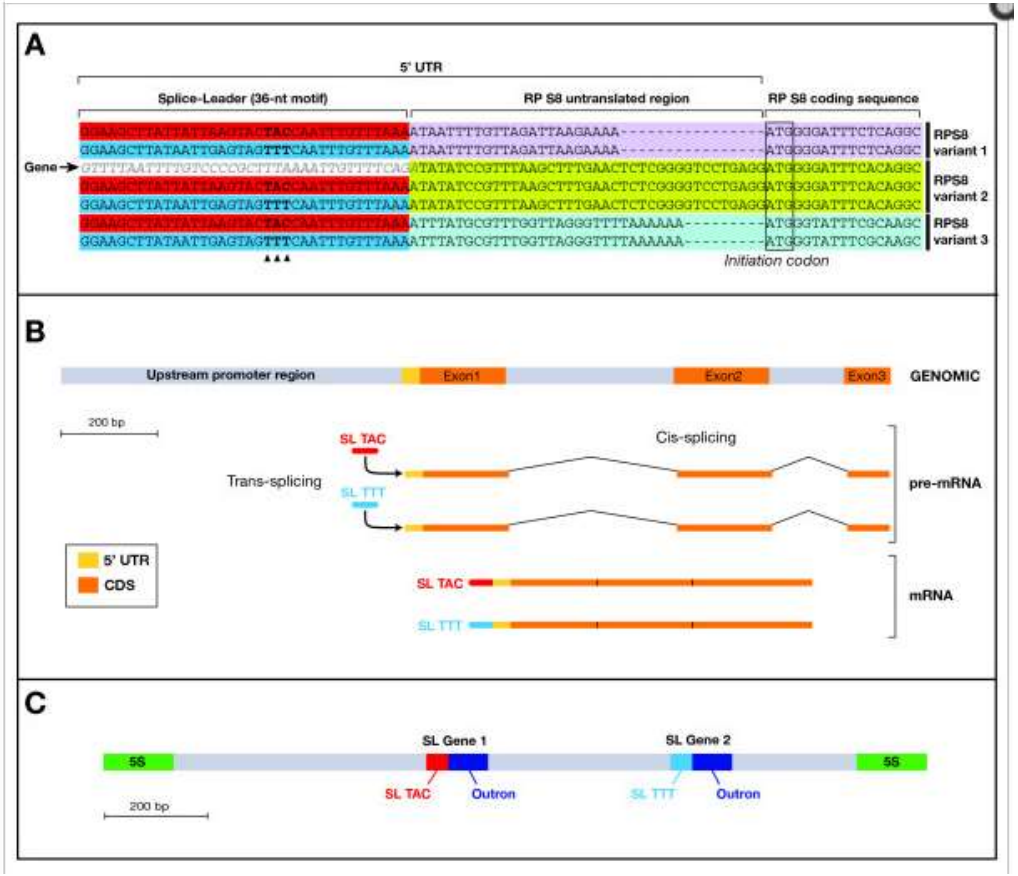
Careful with understudied phyla: The case of chaetognath

Ferdinand Marlétaz and Yannick Le Parco*



Аутсплайсинг – источник «паралогов большинства рибосомальных генов хетогнат, описанных в предыдущей статье