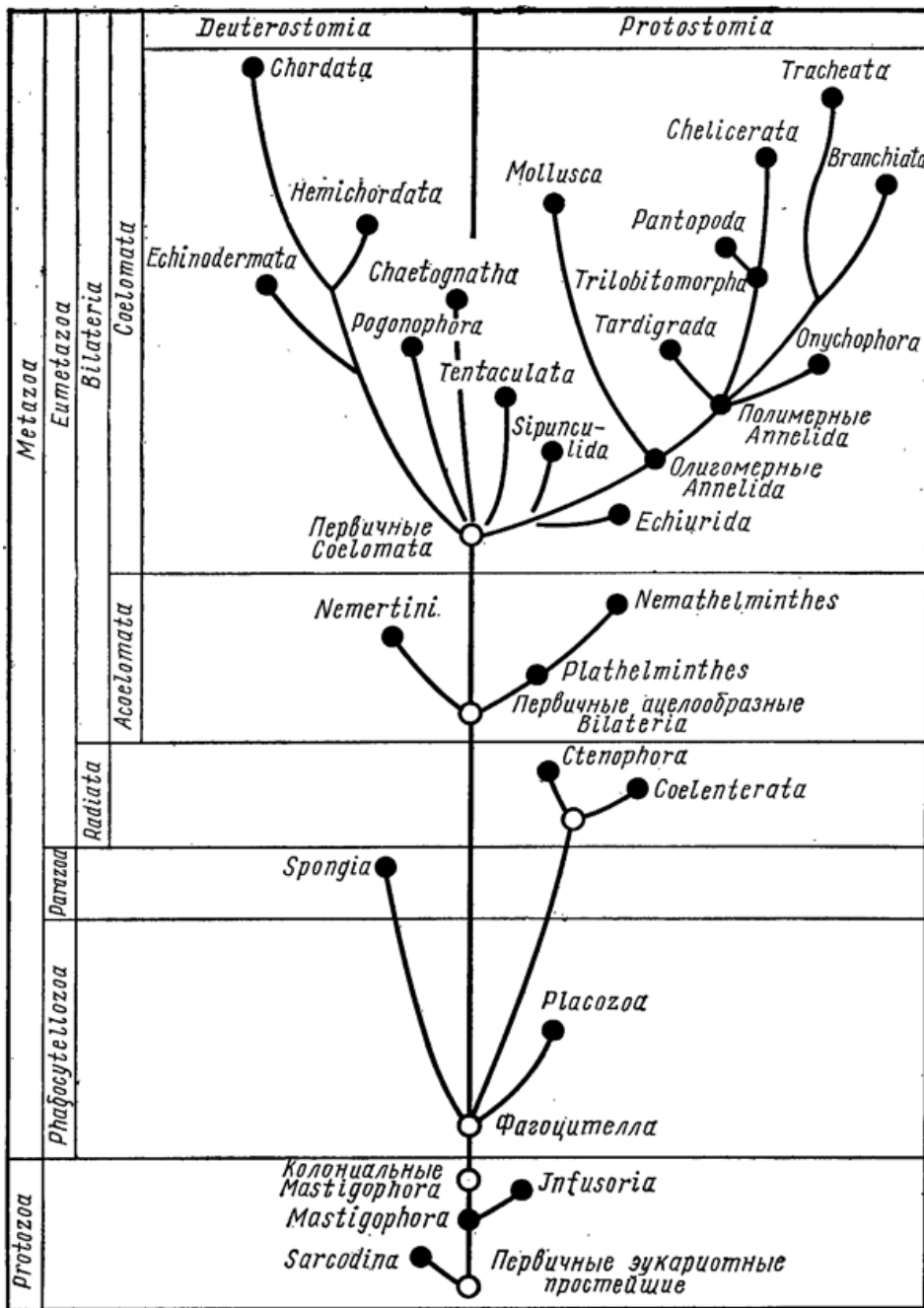


Молекулярная Зоология, весна 2011

лекция 8

**Систематика беспозвоночных –
современные «молекулярные революции»
Часть 2. «Все не так»**



В.А.ДОГЕЛЬ

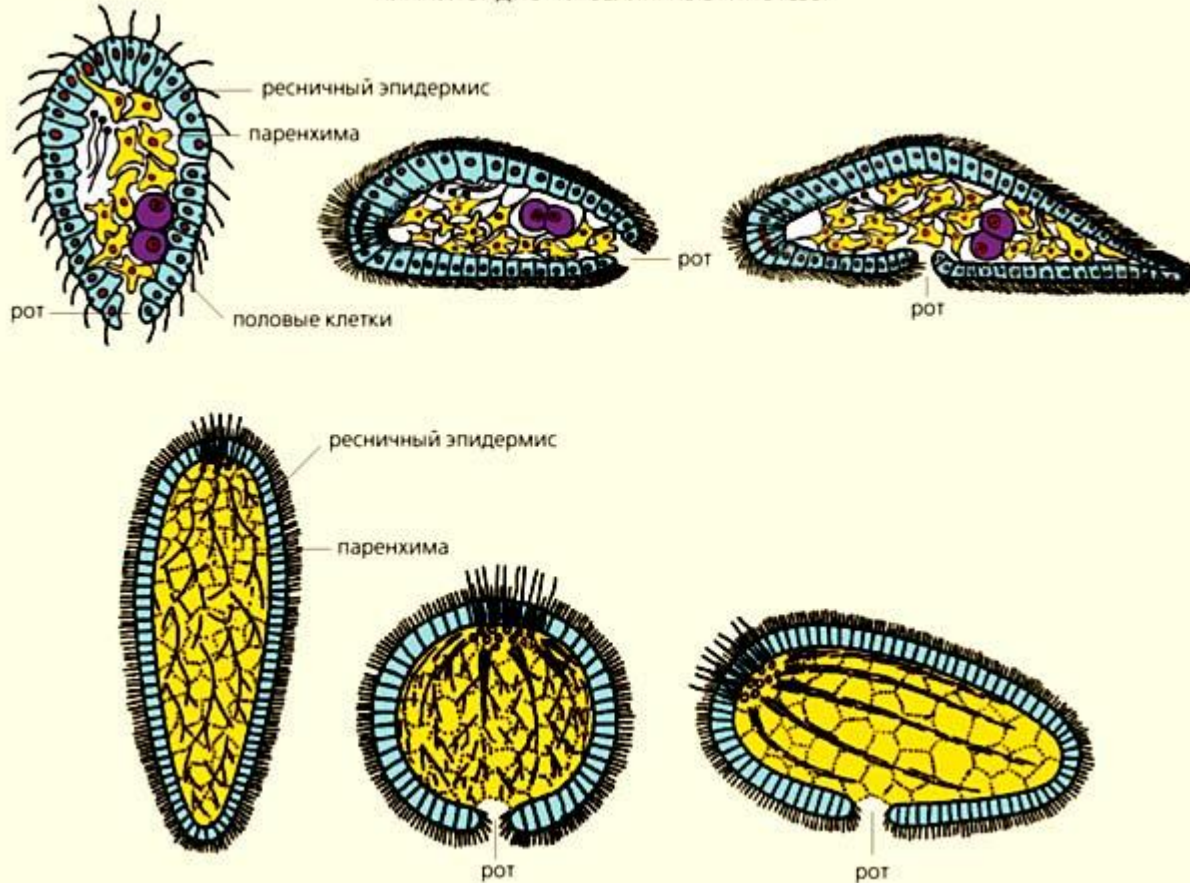
ЗООЛОГИЯ БЕСПОЗВОНОЧНЫХ

ИЗДАНИЕ СЕДЬМОЕ,
ПЕРЕРАБОТАННОЕ
И ДОПОЛНЕННОЕ

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

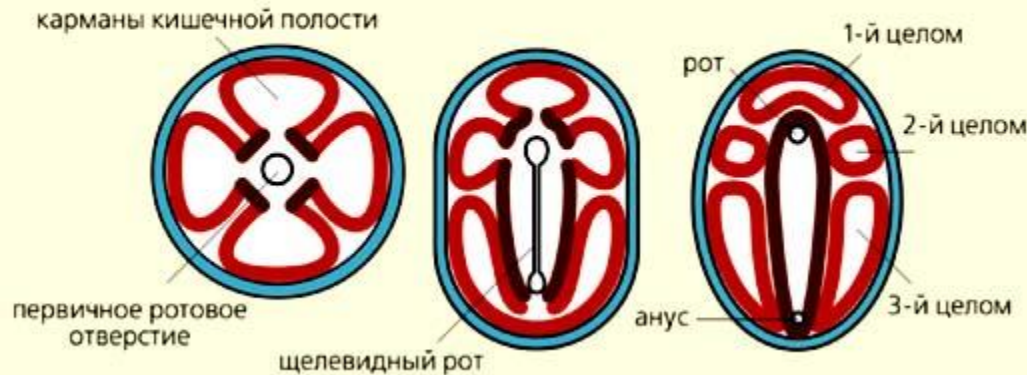
Согласно классическим представлениям, все билатерии, имеющие целом (вторичную полость тела), происходят от общего предка и противопоставляются «доцеломическим» билатериям, таким как плоские и круглые черви. Целоматы подразделяются на первичноротых (кольчатые черви, моллюски, членистоногие и др.) и вторичноротых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

ПЛАНУЛОИДНО-ТУРБЕЛЛЯРНЫЕ ГИПОТЕЗЫ



- ▶ 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.

АРХИЦЕЛОМАТНЫЕ ГИПОТЕЗЫ



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

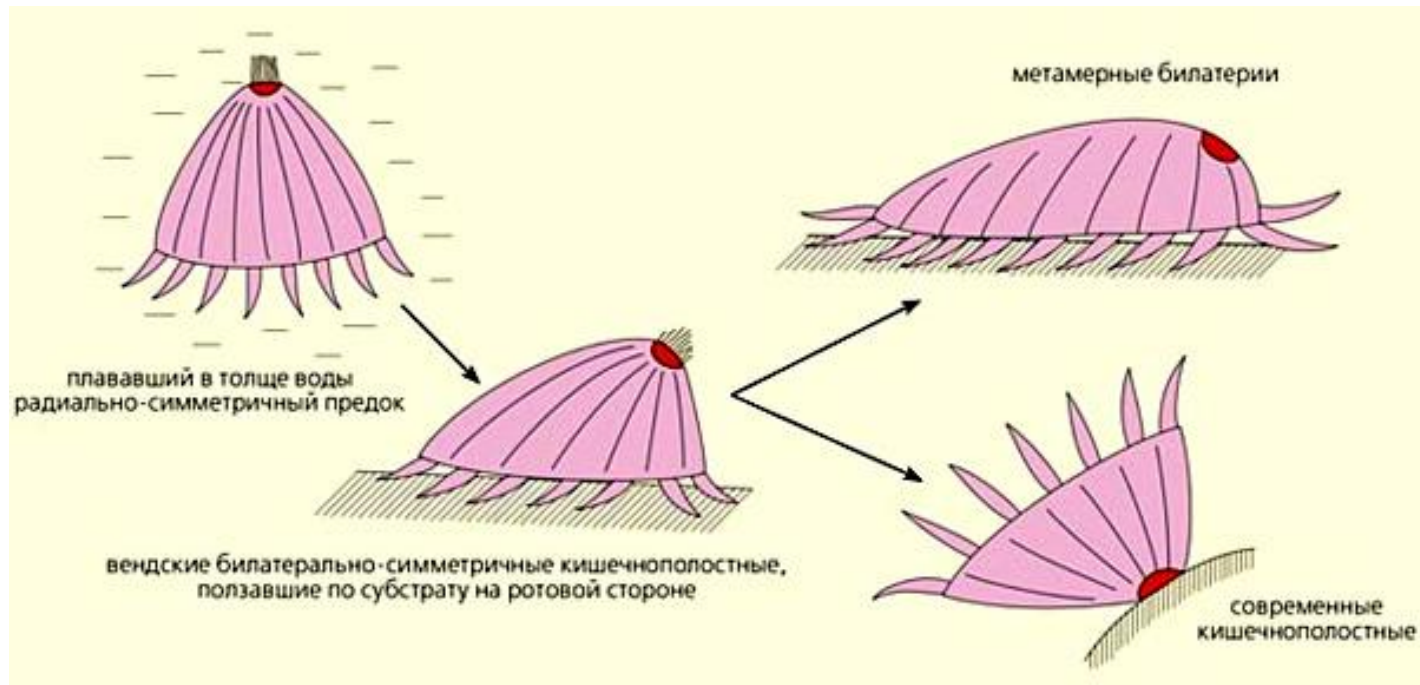
Метамерные животные произошли (Sedgwick, 1884) от многолучевых кораллов (вид сверху и сбоку [Beneden E. van. 1881], а также со стороны ротовой поверхности

МЕТАМЕРНЫЕ ГИПОТЕЗЫ

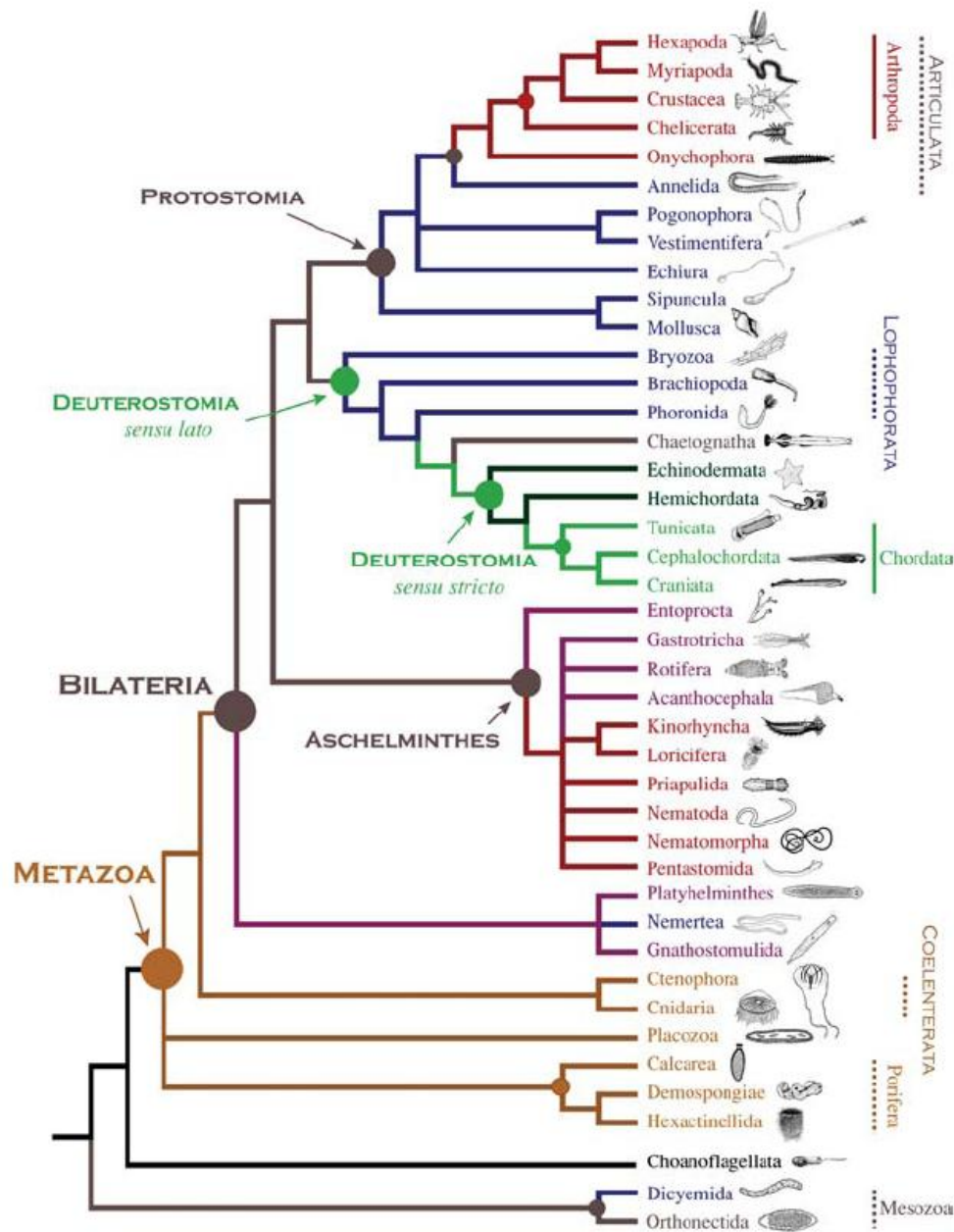


Из: Малахов В.В. Новый взгляд на происхождение билатерий. Природа 2004

Происхождение билатерально-симметричных животных. Красным цветом выделен аборальный нервный центр.



Систематика беспозвоночных до начала эры «молекулярных революций»



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A 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

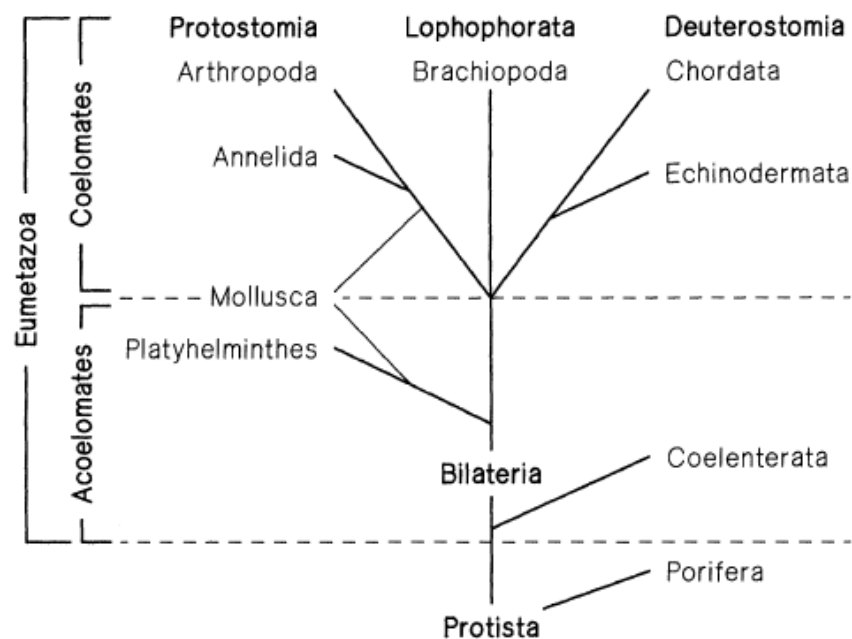


Fig. 1. Phylogenetic tree for the Metazoa, based on the views of Hyman (5). This phylogeny is based on morphology of both adults and embryos. Phylum names are shown in lightface lettering.

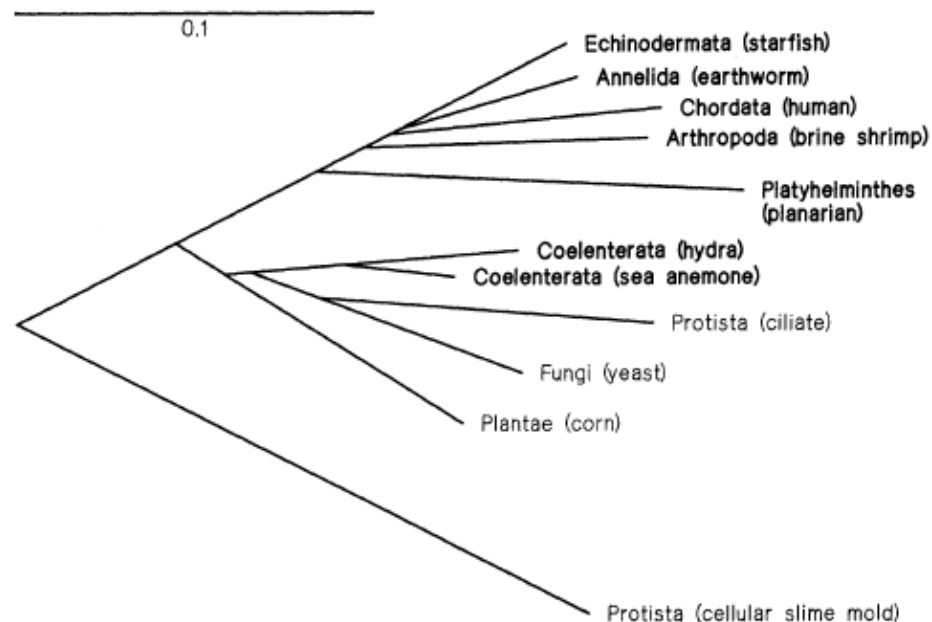


Fig. 2. An evolutionary tree for animals that is based on partial sequences of 18S rRNAs. The tree is read from left to right. The root of the tree is provided by the most distantly related organism, the cellular slime mold. The

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

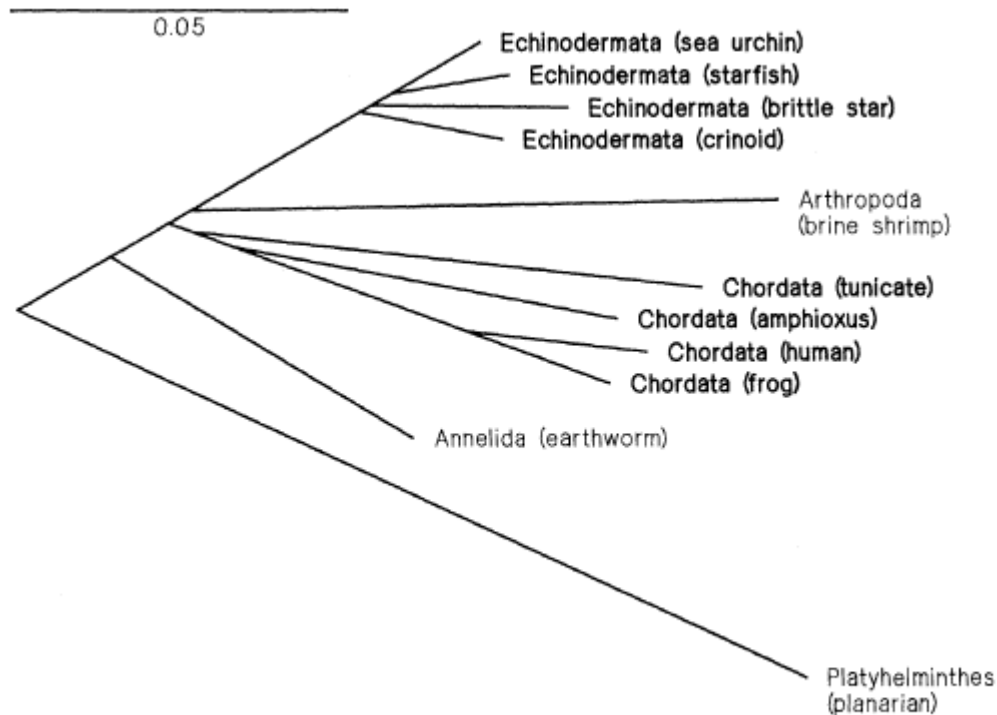


Fig. 3. An expansion of the chordate and echinoderm portions (boldface) of the 18S rRNA evolutionary tree for animals. The planarian is included as an

- ▶ Проверка гипотезы что хордовые произошли от иглокожих. Ответ: Хордовые – сестринская группа по отношению к иглокожим (в группе вторичноротых)

Артроподы

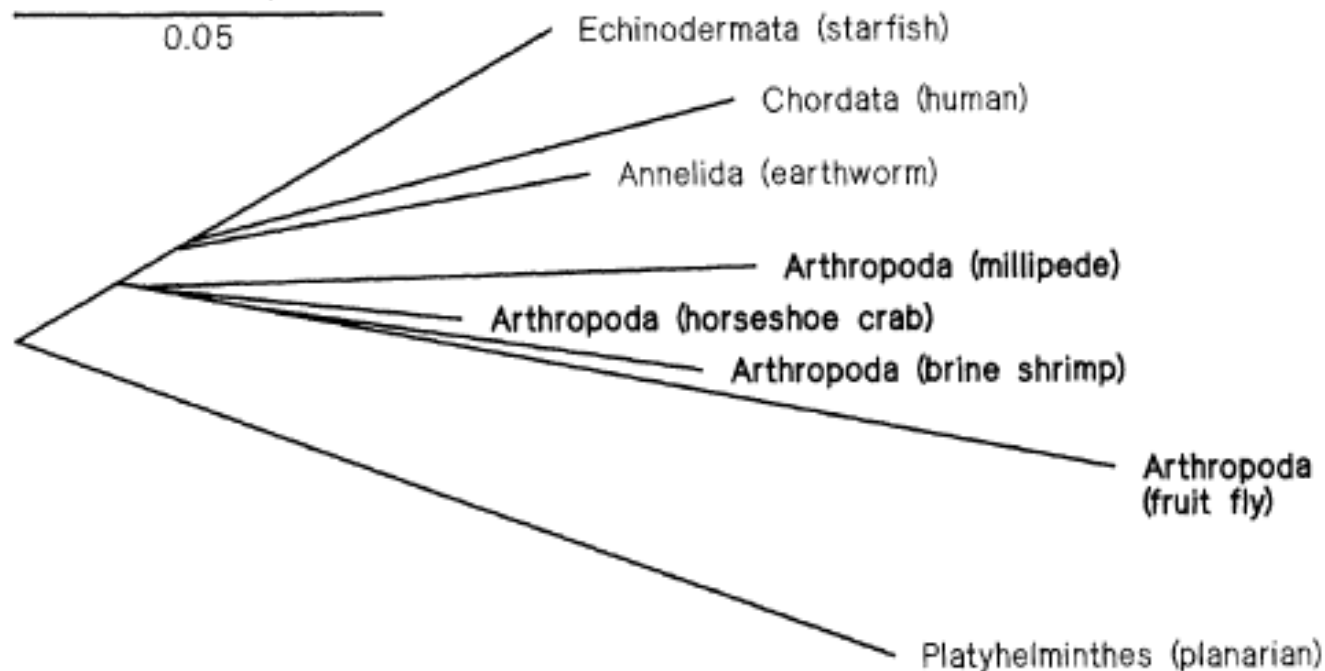


Fig. 4. An expansion of the arthropod portion (boldface) of the 18S rRNA tree for animals. The planarian is included as an outgroup. An echinoderm, a chordate, and an annelid represent the other eucoelomate groups. Organisms

Дерево целомных первичноротых (Field et al., 1988)

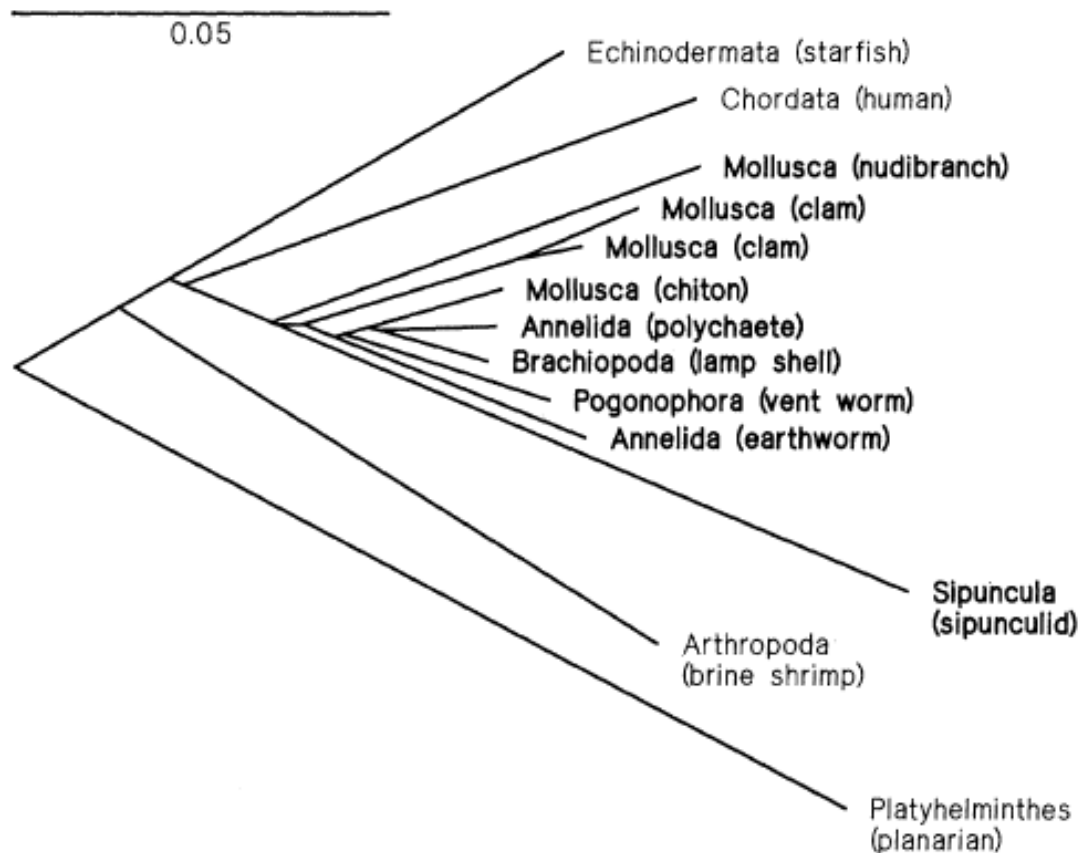


Fig. 5. An expansion of the eucoelomate protostome portion (boldface) of the 18S rRNA evolutionary tree for animals. The planarian is included as an outgroup. A chordate, an echinoderm, and an arthropod represent the other eucoelomate groups. Organisms shown: starfish, *Asterias forbesi*; human,

THE NEW VIEW OF ANIMAL PHYLOGENY

Kenneth M. Halanych

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

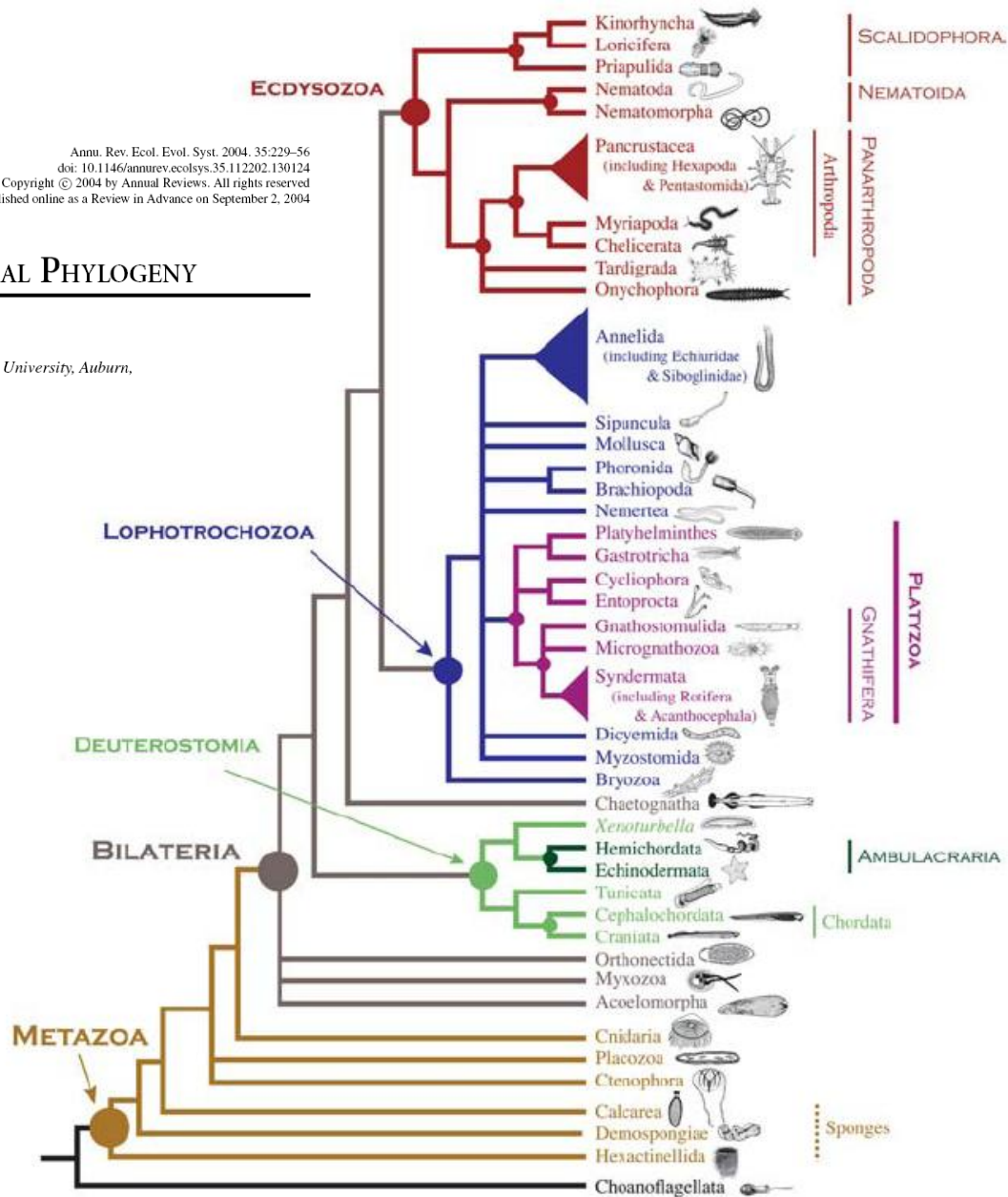


Figure 2 Modern synthesis. The new view of animal phylogeny based largely on molecular data. Details and support for various clades are discussed in the text. This

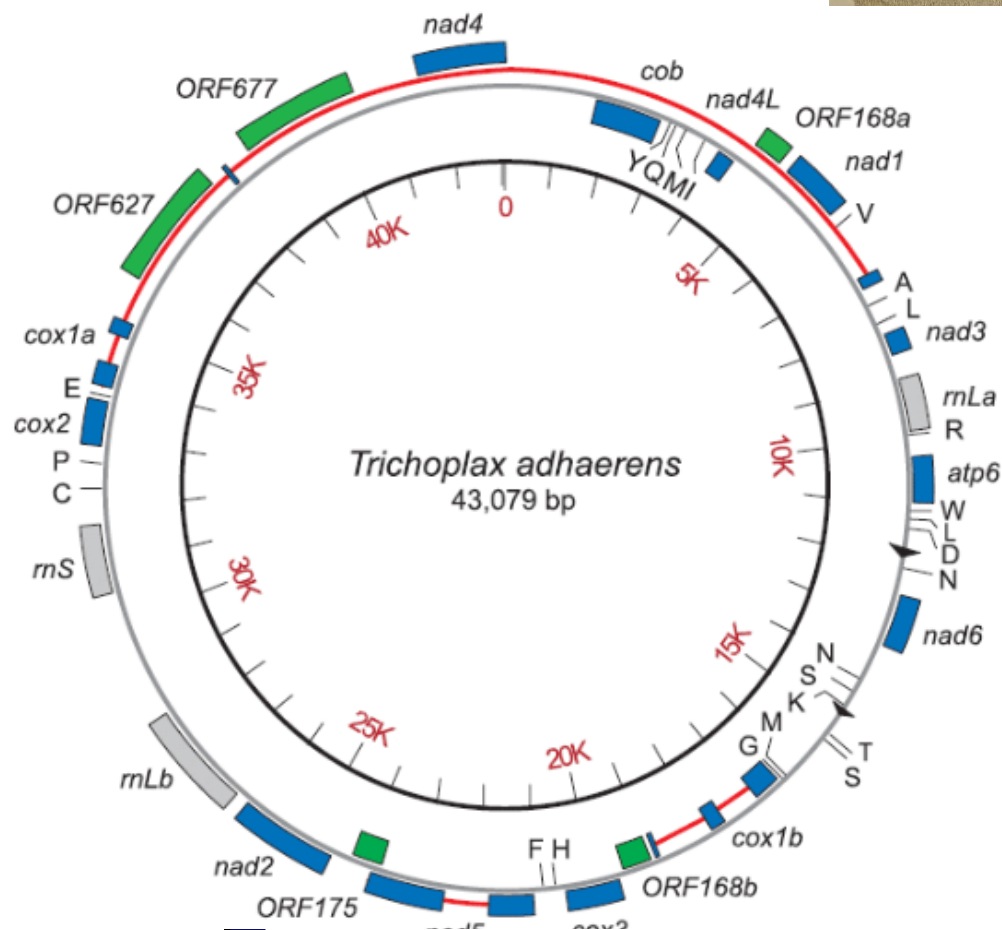
10 провокационных гипотез (по Калянычу)

- ▶ 1. Placozoans branched off from the main animal lineage before sponges.
 - ▶ 2. Mesoderm first arose in ctenophores.
 - ▶ 3. Acoelomorphs are secondarily simplified animals.
 - ▶ 4. Chaetognatha is the sister to the Lophotrochozoa/Ecdysozoa clade.
 - ▶ 5. Spiral cleavers do not form a monophyletic clade exclusive of other cleavage patterns.
 - ▶ 6. Genetic mechanisms controlling annelid segmentation are different than in arthropods.
 - ▶ 7. The Brachiopoda/Phoronida clade is sister to Mollusca.
 - ▶ 8. Panarthropoda evolved from a small infaunal organism.
 - ▶ 9. Platyzoa is a derived subclade of Lophotrochozoa.
 - ▶ 10. The hidden history of early bilaterian evolution was less than 50 My.
-



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 кишечнорастворных, 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.



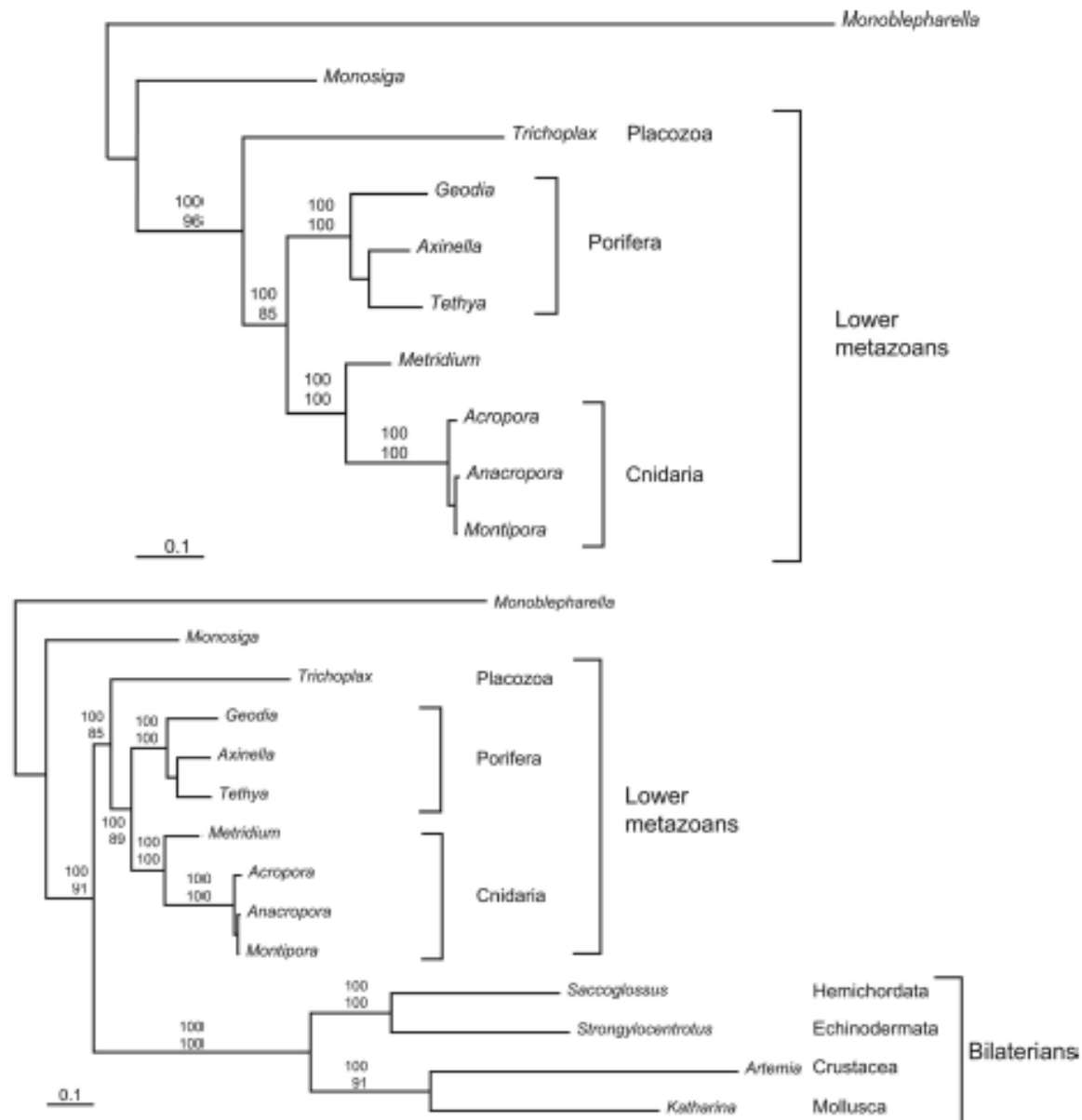


Fig. 2. Phylogenetic analysis of concatenated mitochondrial proteins. The data set consisted of a total of 2,730 amino acid positions concatenated from 12

LETTERS

Broad phylogenomic sampling improves resolution of the animal tree of life

Casey W. Dunn^{1†}, Andreas Hejnol¹, David Q. Matus¹, Kevin Pang¹, William E. Browne¹, Stephen A. Smith², Elaine Seaver¹, Greg W. Rouse³, Matthias Obst⁴, Gregory D. Edgecombe⁵, Martin V. Sørensen⁶, Steven H. D. Haddock⁷, Andreas Schmidt-Rhaesa⁸, Akiko Okusu⁹, Reinhardt Møbjerg Kristensen¹⁰, Ward C. Wheeler¹¹, Mark Q. Martindale¹ & Gonzalo Giribet^{12,13}

- ▶ Вариант молекулярного эволюционного древа животных (2008 год) , основанный на рекордном количестве генов (150) и групп животных. В анализе использовано 77 видов, относящихся к 21 типу животных, причем для 11 из этих типов геномные данные до сих пор отсутствовали. Многие части (узлы) получившегося древа действительно оказались значительно более устойчивыми, чем в более ранних исследованиях такого рода.



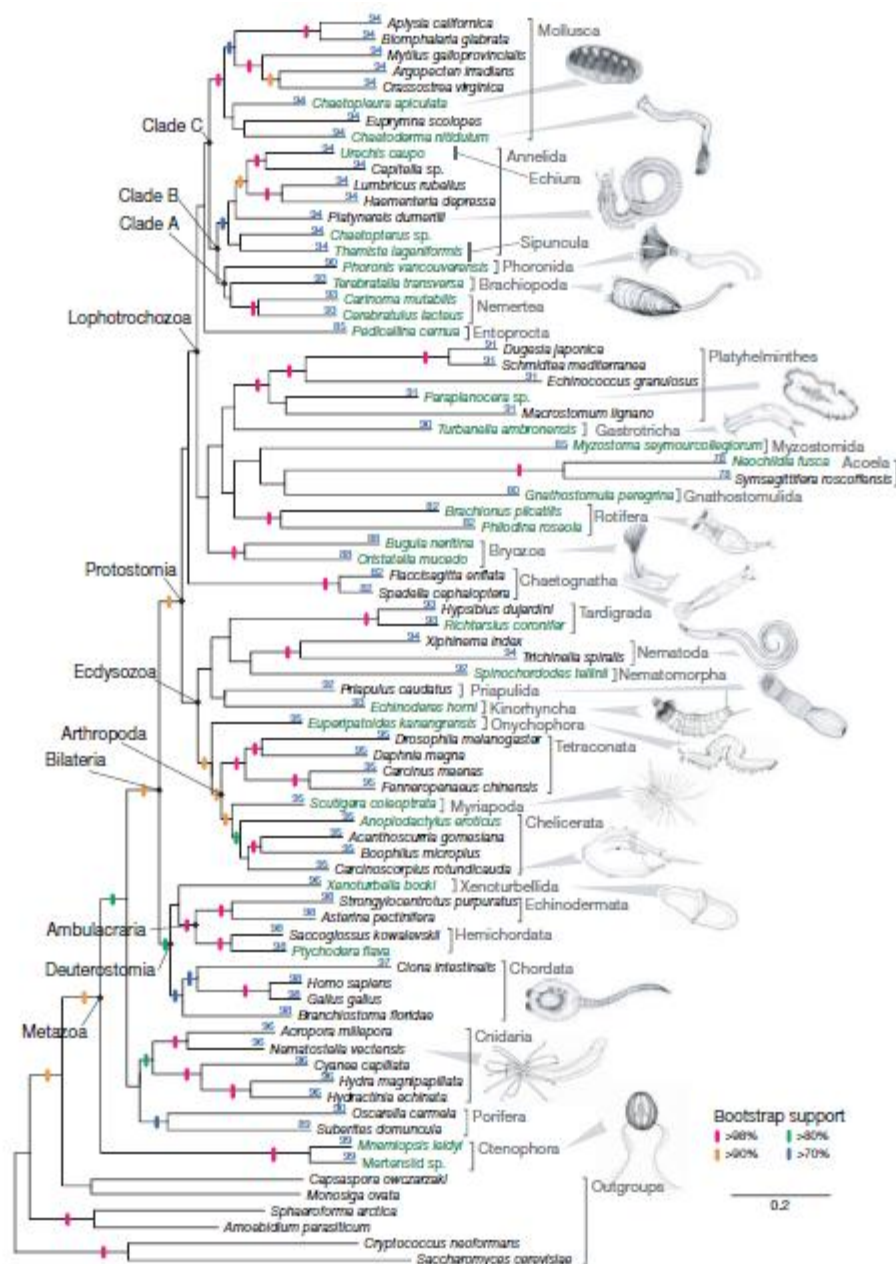
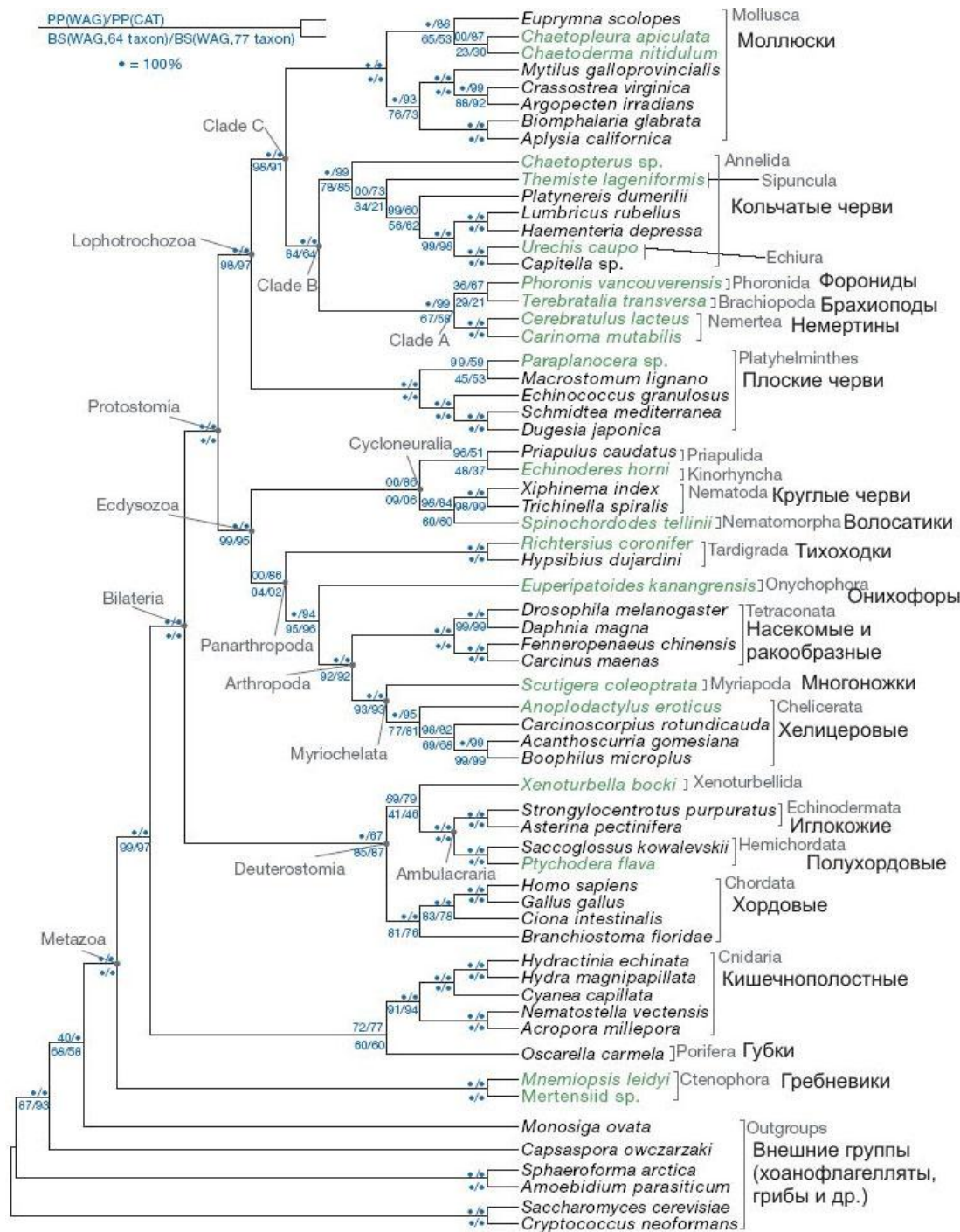


Figure 1 | Phylogram of the 77-taxon RaxML maximum likelihood analysis conducted under the WAG model. The figured topology and branch lengths are for the sampled tree with the highest likelihood (1,000 searches, log

likelihood = -796,399.2). Support values are derived from 1,000 bootstrap replicates. Leaf stabilities are shown in blue above each branch. Taxa for which we collected new data are shown in green.

PP(WAG)/PP(CAT)
BS(WAG,64 taxon)/BS(WAG,77 taxon)
* = 100%

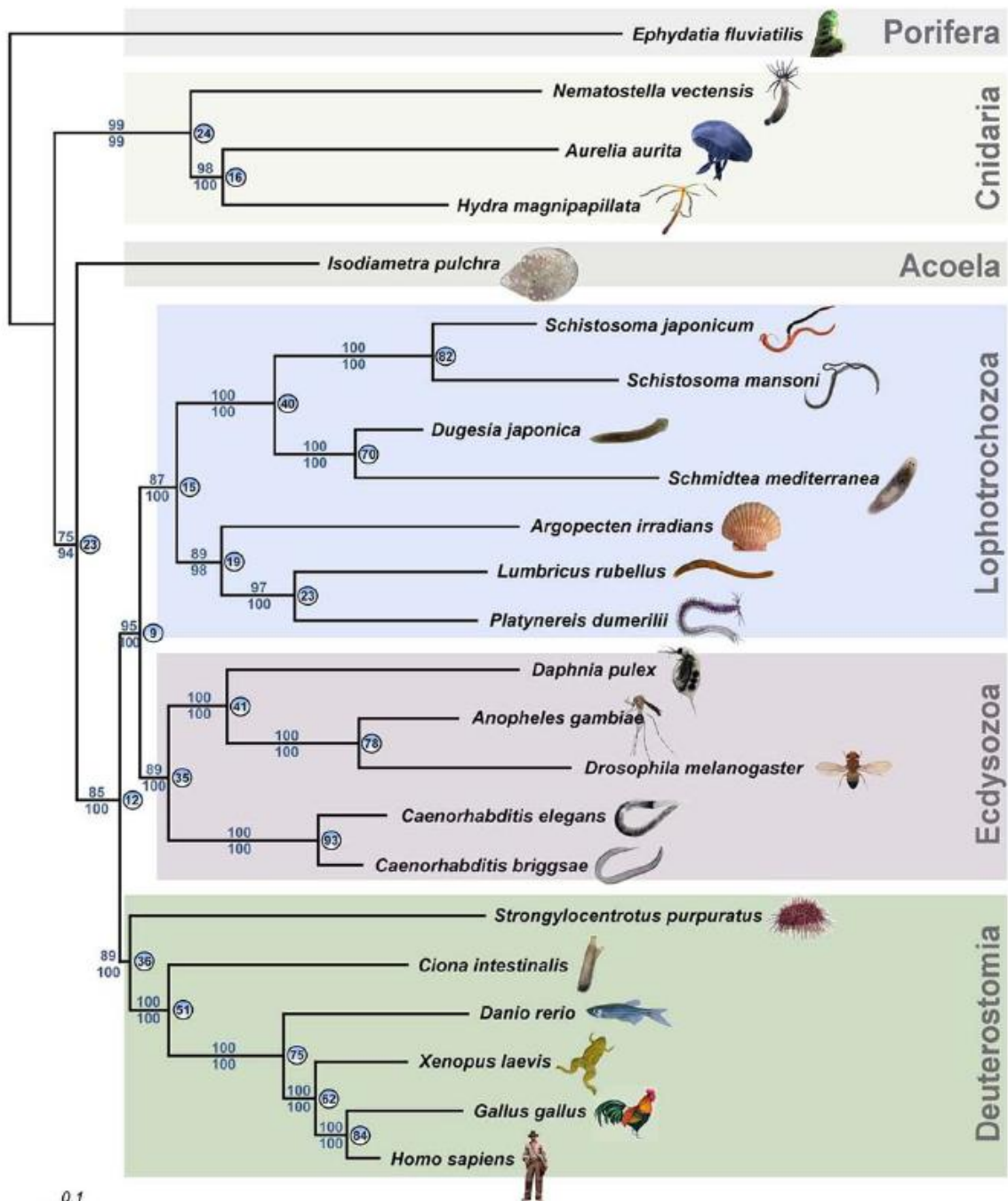


To Be or Not to Be a Flatworm: The Acoel Controversy

Bernhard Egger¹*, Dirk Steinke²*, Hiroshi Tarui³*, Katrien De Mulder⁴*, Detlev Arendt⁵, Gaëtan Borgonie⁴, Noriko Funayama⁸, Robert Gschwentner¹, Volker Hartenstein⁶, Bert Hobmayer¹, Matthew Hooge⁷, Martina Hroudá⁸, Sachiko Ishida⁹, Chiyoko Kobayashi^{3,10}, Georg Kualess¹, Osamu Nishimura³, Daniela Pfister¹, Reinhard Rieger¹, Willi Salvenmoser¹, Julian Smith, III¹¹, Ulrich Technau¹², Seth Tyler⁷*, Kiyokazu Agata⁸*, Walter Salzburger¹³*, Peter Ladurner¹*

Abstract

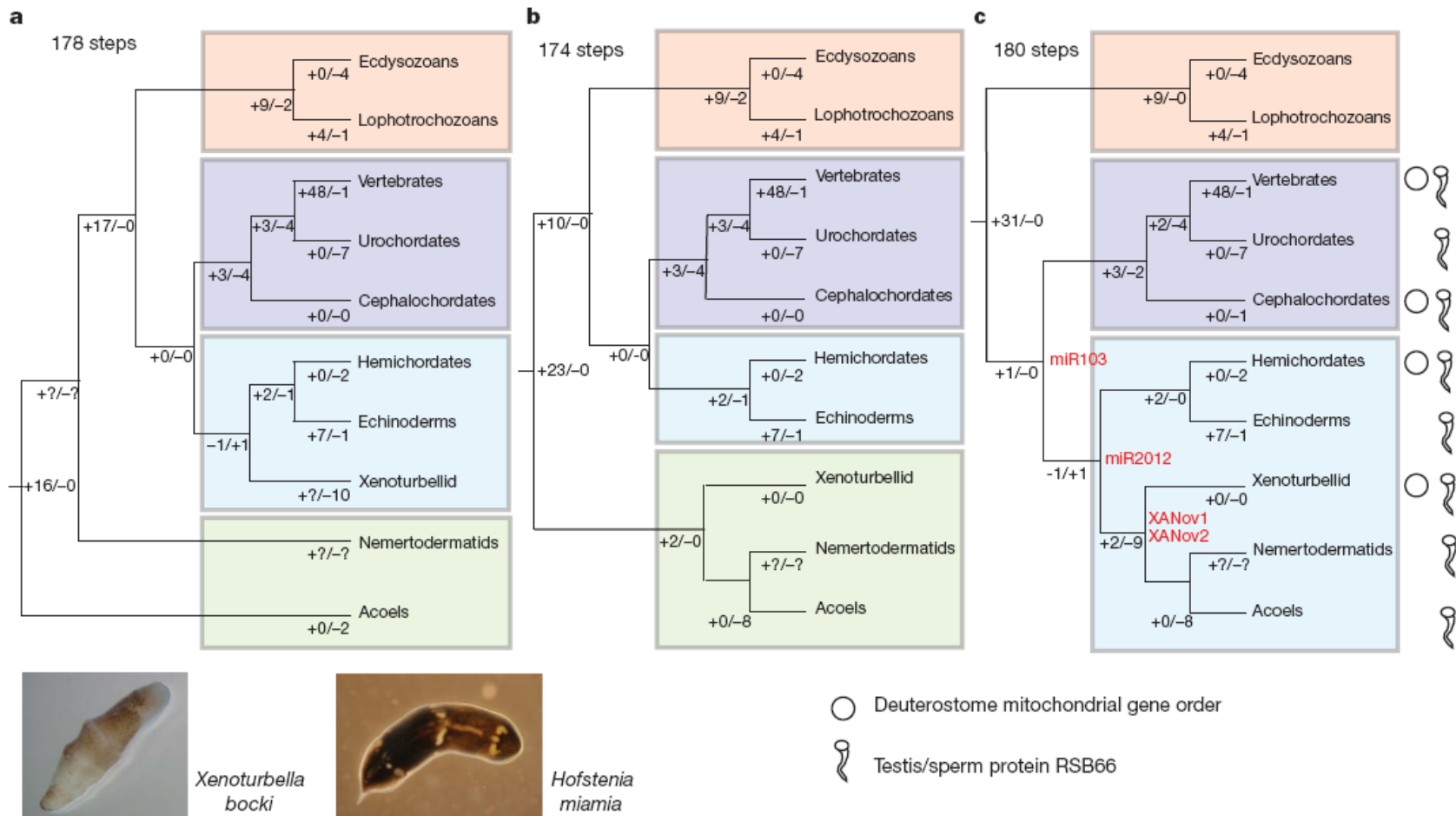
Since first described, acoels were considered members of the flatworms (Platyhelminthes). However, no clear synapomorphies among the three large flatworm taxa - the Catenulida, the Acoelomorpha and the Rhabditophora - have been characterized to date. Molecular phylogenies, on the other hand, commonly 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.



Acoelomorph flatworms are deuterostomes related to *Xenoturbella*

Hervé Philippe¹, Henner Brinkmann¹, Richard R. Copley², Leonid L. Moroz³, Hiroaki Nakano^{4†}, Albert J. Poustka⁵, Andreas Wallberg⁶, Kevin J. Peterson⁷ & Maximilian J. Telford⁸

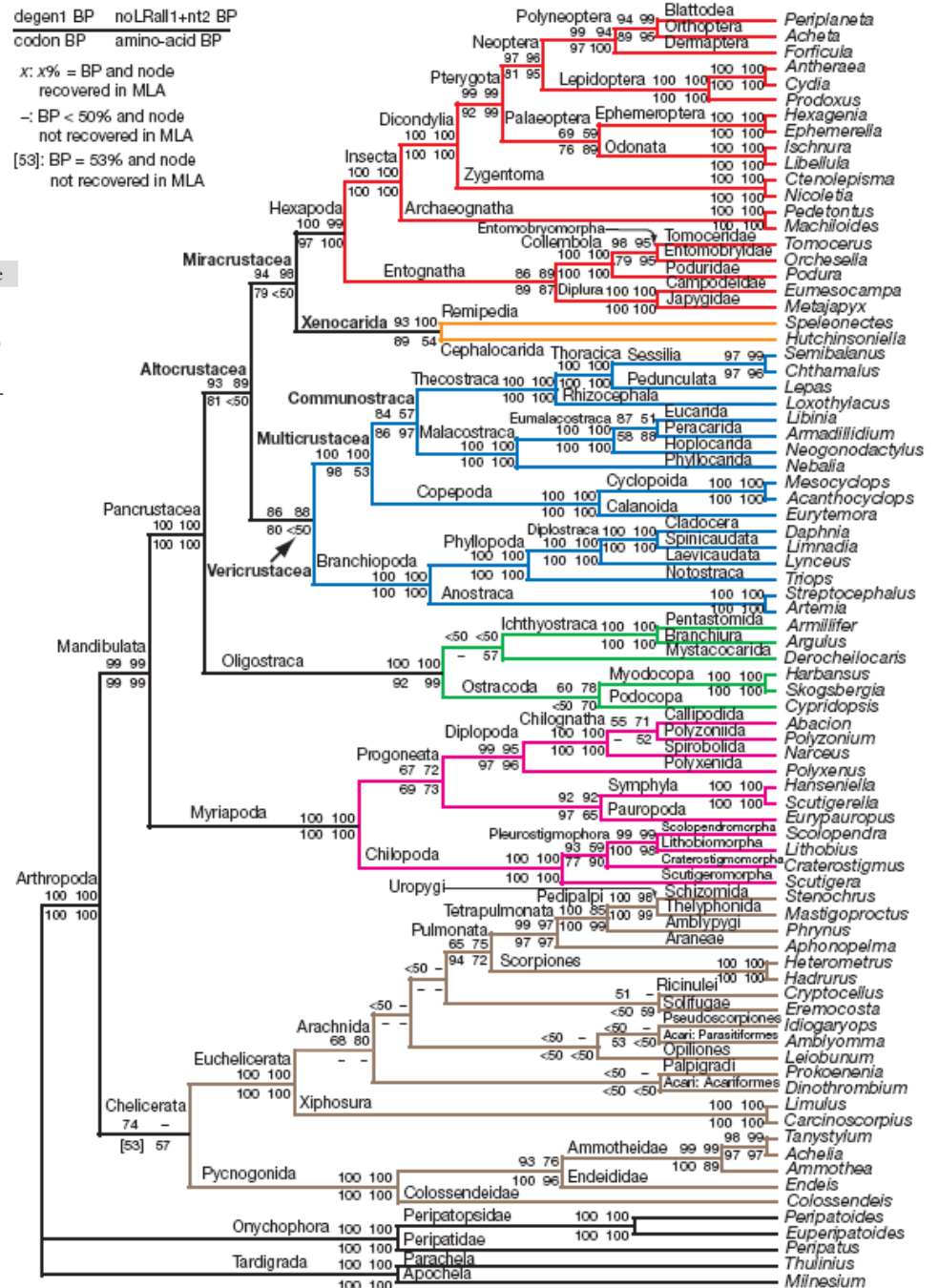
Xenoturbellida and Acoelomorpha are marine worms with contentious ancestry. Both were originally associated with the flatworms (Platyhelminthes), but molecular data have revised their phylogenetic positions, generally linking *Xenoturbellida* to the deuterostomes^{1,2} and positioning the Acoelomorpha 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 Bilateria⁷. 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 complements⁸ 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.



LETTERS

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

Jerome C. Regier¹, Jeffrey W. Shultz^{1,2,3}, Andreas Zwick¹, April Hussey¹, Bernard Ball⁴, Regina Wetzter⁵, Joel W. Martin² & Clifford W. Cunningham¹

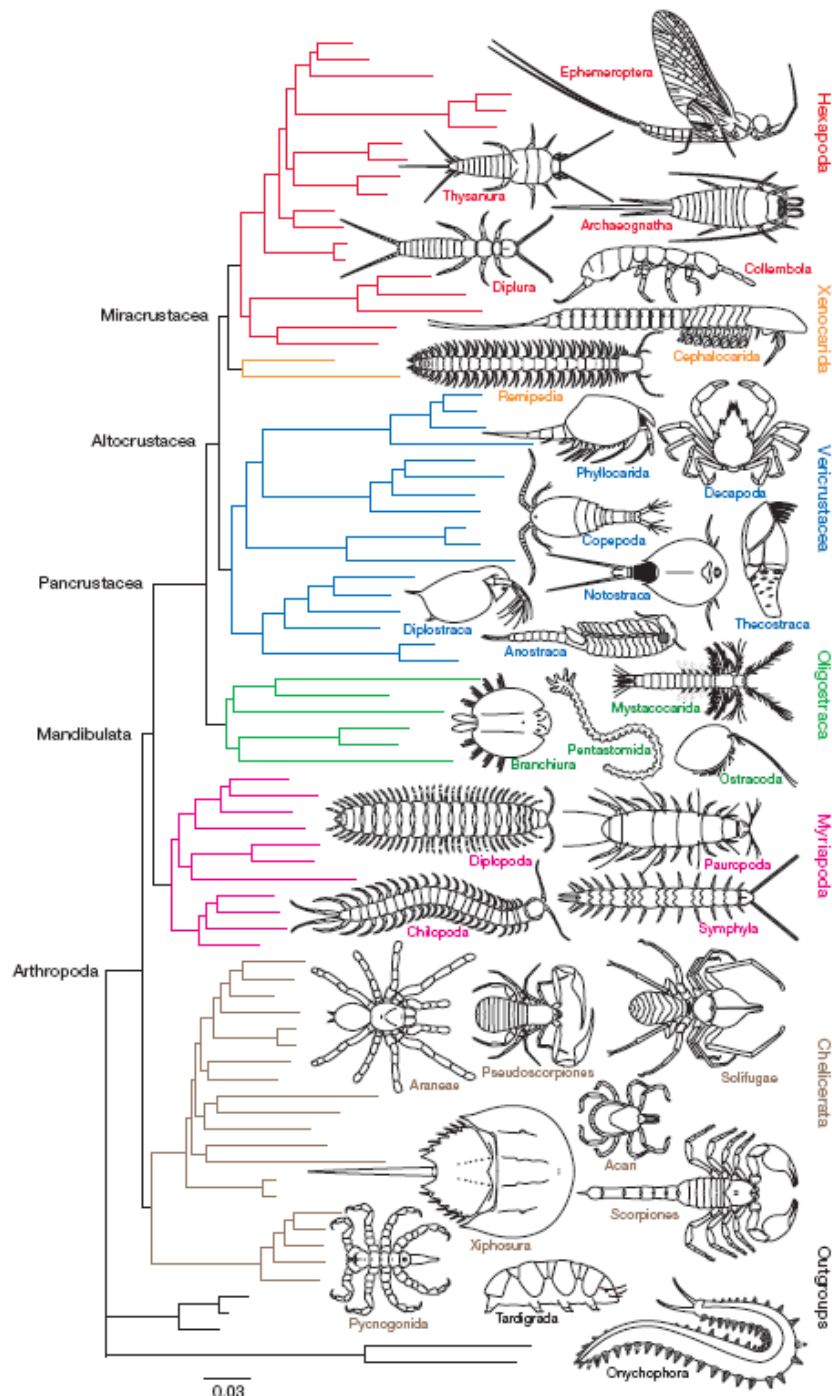


LETTERS

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

Jerome C. Regier¹, Jeffrey W. Shultz^{1,2,3}, Andreas Zwick¹, April Hussey¹, Bernard Ball⁴, Regina Wetzter⁵, Joel W. Martin⁵ & Clifford W. Cunningham⁴

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 the Hexapoda, a result confirming that ‘crustaceans’ are not monophyletic.



- ▶ 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

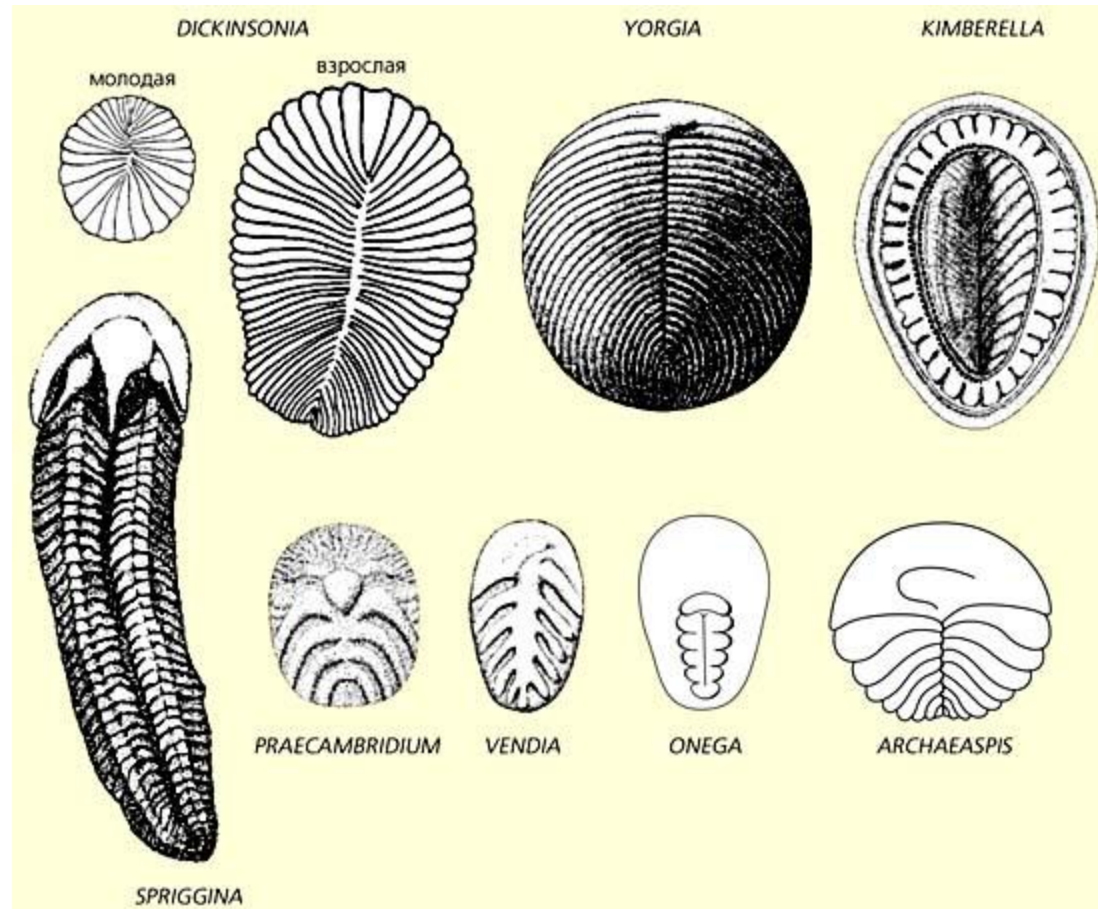
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LETTERS

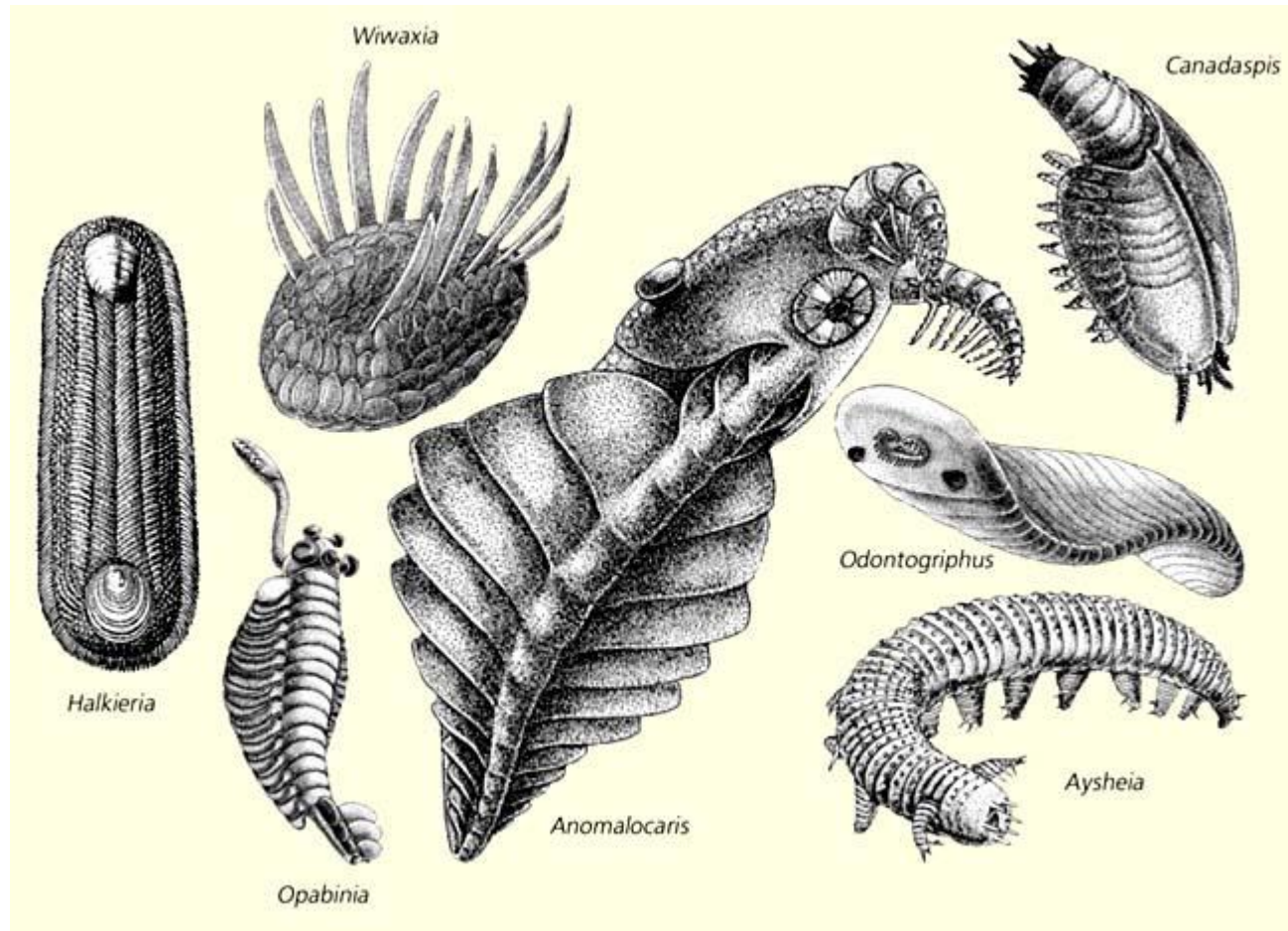
Arthropod relationships revealed by phylogenomic analysis of nuclear protein-coding sequences

Jerome C. Regier¹, Jeffrey W. Shultz^{1,2,3}, Andreas Zwick¹, April Hussey¹, Bernard Ball⁴, Regina Wetzter⁵, Joel W. Martin⁵ & Clifford W. Cunningham⁴

Так кем были вендские билатерии?



И кем – первые кембрийские билатерально-симметричные организмы?



► И какими НОХ-генами регулировался их онтогенез ?

