①

Zhang Z, Strotz LC, Topper TP, Chen F, Chen Y, Liang Y, Zhang Z, Skovsted CB, Brock GA (2020)

An Encrusting Kleptoparasite-Host Interaction From the Early Cambrian

Nat Communications 11: 2625

Abstract

Parasite-host systems are pervasive in nature but are extremely difficult to convincingly identify in the fossil record. Here we report quantitative evidence of parasitism in the form of a unique, enduring life association between tube-dwelling organisms encrusted to densely clustered shells of a monospecific organophosphatic brachiopod assemblage from the lower Cambrian (Stage 4) of South China. Brachiopods with encrusting tubes have decreased biomass (indicating reduced fitness) compared to individuals without tubes. The encrusting tubes orient tightly in vectors matching the laminar feeding currents of the host, suggesting kleptoparasitism. With no convincing parasite-host interactions known from the Ediacaran, this widespread sessile association reveals intimate parasite-host animal systems arose in early Cambrian benthic communities and their emergence may have played a key role in driving the evolutionary and ecological innovations associated with the Cambrian radiation.

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②

Bartolomaeus T, Ax P (1992)

Protonephridia and Metanephridia - their relation within the Bilateria

Journal of Zoological Systematics and Evolutionary Research 30: 21-45

Abstract

Two different kinds of nephridia occur within the Bilateria, protonephridia closed up by a terminal cell and metanephridia opening into the coelomic cavity. Both initially filter and subsequently modify intercellular fluids. Whereas metanephridia are strictly correlated to a coelom, proto-nephria occur in acoelomate as well as in coelomate organisms. Protonephridia of different bilaterian taxa correspond to each other in several structural features. Therefore, it is hypothesized that protonephridia are homologous organs throughout the Bilateria. They must have evolved once as one pair of monociliated organs orinatinng from the ectoderm and consistin of one terminal, one duct and one nephropore cell In the ground pattern of the Bilateria the cilium of the terminal cell has only one rootlet and is surrounded by resumably eight strengthened and elongated microvilli. Cilium and microvilli extend into the hollow cyinder of the terminal cell, which is oriented distally and is attached to the adjacent duct cell by desmosomes. [...].

③

Sato A, Bishop JDD, Holland PWH (2008)

Developmental biology of pterobranch hemichordates: History and perspectives

Genesis 46: 587-591

Abstract

Hemichordates, like echinoderms and chordates, are deuterostomes, and study of their developmental biology could shed light on chordate origins. To date, molecular developmental studies in hemichordates have been confined to the enteropneusts or acorn worms. Here, we introduce the developmental biology of the other group of hemichordate, the pterobranchs. Pterobranchs generally live in cold, deep waters; this has hampered studies of this group. However, about 40 years ago, the colonial pterobranchs Rhabdopleura compacta and R. normani were discovered from shallow water, which has facilitated their study. Using Rhabdopleura compacta from south-west England, we have initiated molecular developmental studies in pterobranchs. Here, we outline methods for collecting adults, larvae, and embryos and demonstrate culturing of larvae under laboratory conditions. Given that the larval and adult forms differ from enteropneusts, we suggest that molecular developmental studies of pterobranchs may offer new insights into chordate origins. © 2008 Wiley-Liss, Inc.

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④

Adoutte A, Balavoine G, Lartillot N, Lespinet O, Prud'homme B, De Rosa R (2000)

The new animal phylogeny: Reliability and implications

Proc Nat Acad Sci USA 97: 4453-4456

Abstract

A deep reorganization of the metazoan phylogenetic tree is presently taking place as a result of the input of molecular data. Far from being an exercise confined to a small circle of aficionados, the changing views on the pattern of animal interrelationships has profound consequences for understanding the underlying processes of animal diversification. As has repeatedly been stressed, we shall never be able to reason on the evolution of development and the way it has shaped animal diversity unless we have a reliable history of the path taken by this diversification. Here, we highlight the salient recent results based on genetic data, especially the displacement of taxa long thought to represent successive grades of complexity at the base of the metazoan tree, to much higher positions inside the tree. This leaves us with no evolutionary "intermediates" and forces us to rethink the genesis of bilaterian complexity. The reappraisal of animal evolution rests on several congruent approaches ranging from primary gene sequence analysis to qualitative molecular signatures within appropriate genes. Each of them, however, has its methodological difficulties; we shall, therefore, also try to briefly pinpoint the issues of contention and discuss the strength of the present view.

⑤

Perez Y, Müller CHG, Harzsch S (2014)
The chaetognatha: An anarchistic taxon between protostomia and deuterostomia
Deep Metazoan Phylogeny: The Backbone of the Tree of Life, 49-78

Abstract

The phylogenetic position of the chaetognaths within the Bilateria is heavily debated but this taxon so far has resisted all serious attempts to pin down its phylogenetic affinities. Despite the ever increasing number of molecular phylogenetic studies and an emerging consensus for protostome affinities, we must conclude that still the position of the Chaetognatha is among the most enigmatic issues of metazoan phylogeny.Here, we review the current molecular phylogenetic studies and discuss morphological features that play important roles in the discussion of chaetognath affinities including the integument, musculature and neuromuscular innervation, sensory systems, the nervous system and aspects of embryology. The chaetognath genome is likely the product of a unique evolutionary history and witnesses a long isolation of this group. Furthermore, morphological characters provide evidence for the long evolutionary distance that separates the Chaetognatha from its closest (unknown) metazoan relative and suggest that this taxon in many aspects seems to have explored its own evolutionary pathways in generating tissue and organ diversity. Both the genome and morphological characters include many autapomorphies of this group in addition to a character mix of protostome and deuterostome features. However, despite intense analyses of their genome and tissue ultrastructure, so far we do not know of any convincing synapomorphies that clearly would suggest a sister-group relationship to another metazoan taxon. These facts are most parsimoniously interpreted such that Chaetognatha are likely an early offshoot of the protostome lineage but so far it is not possible to precisely say whether they are basal lophotrochozoans, basal ecdysozoans or sister-group to all others protostomes. All together, we currently tend to suggest a new basal rooting of the Bilateria, which considers the Chaetognatha as the sister-group to the Lophotrochozoa and Ecdysozoa (soft polytomy). This assemblage may be called Hyponeuria to indicate the ventralization of the nervous system as one of the most important steps in metazoan evolution.

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⑥

Parfrey LW, Lahr DJG (2013)
Multicellularity arose several times in the evolution of eukaryotes
BioEssays 35: 339-347

Abstract

The cellular slime mold Dictyostelium has cell-cell connections similar in structure, function, and underlying molecular mechanisms to animal epithelial cells. These similarities form the basis for the proposal that multicellularity is ancestral to the clade containing animals, fungi, and Amoebozoa (including Dictyostelium): Amorphea (formerly "unikonts"). This hypothesis is intriguing and if true could precipitate a paradigm shift. However, phylogenetic analyses of two key genes reveal patterns inconsistent with a single origin of multicellularity. A single origin in Amorphea would also require loss of multicellularity in each of the many unicellular lineages within this clade. Further, there are numerous other origins of multicellularity within eukaryotes, including three within Amorphea, that are not characterized by these structural and mechanistic similarities. Instead, convergent evolution resulting from similar selective pressures for forming multicellular structures with motile and differentiated cells is the most likely explanation for the observed similarities between animal and dictyostelid cell-cell connections.

⑦

Kapp H (2000)
The unique embryology of chaetognatha
Zool Anz 239: 263-266

Abstract

Chaetognaths are doubtlessly coelomate Bilateria, but after doubting the relationship of Chaetognatha and Deuterostomia there is no phylogenetic basis for considering the embryology of chaetognaths as a kind of enterocoely, on the contrary it differs considerably from an enterocoely. The pattern of the embryonic development and especially of the stages determining the further formations or the body organisation are outlined. This developmental pattern is characterised by a blastocoel which soon after gastrulation disappears - hence the mesoderm cannot grow between ectoderm and entoderm - and by an entoderm which is so closely connected to the mesoderm that it does not even persist as a primitive gut: A part of the entoderm develops into epithelial folds being anlagen of coelom walls as well as gut anlagen: The other part of the entoderm differentiates directly to coelom wall anlagen. All the embryonic organs grow in the cavity enclosed by the original entoderm. I propose to term this unique mode of embryonic development heterocoely and place it beside enterocoely and metamerism.

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⑧

Moller PC, Philpott CW (1973)
The circulatory system of Amphioxus (Branchiostoma floridae) I. Morphology of the major vessels of the pharyngeal area
Journal of Morphology 139: 389-406

Abstract

In order to clarify the morphology of the circulatory system of amphioxus the blood vessels were investigated using modern techniques of light and electron microscopy. The pattern of circulation in amphioxus is forward ventrally and backwards dorsally. In addition, circulating corpuscles, usually associated with the blood of higher chordates, are absent. The circulatory system of amphioxus consists of well defined contractile vessels and vascular spaces or sinuses within a connective tissue matrix. The contractile vessels have a discontinuous endothelial lining resting on a basal lamina and are enclosed by a simple layer of contractile myoepithelial cells. Discontinuous endothelial linings occur throughout the vascular tree, including major and minor afferent and efferent vessels and blood sinuses. This is in contrast to higher animals where the endothelium forms a more or less continuous lining along the inner surface of the boundary layer. It is suggested that the endothelial cells of amphioxus, like the endothelial cells in capillaries of higher chordates, most likely play a role in the physiology of the circulatory system by removing residues of filtration from the basal lamina, thereby facilitating an exchange of materials to and from the surrounding tissues.

⑨

Gasmi S, Nève G, Pech N, Tekaya S, Gilles A, Perez Y (2014)
Evolutionary history of Chaetognatha inferred from molecular and morphological data: A case study for body plan simplification
Frontiers in Zoology 11: 84

Abstract

Chaetognatha are a phylum of marine carnivorous animals which includes more than 130 extant species. The internal systematics of this group have been intensively debated since it was discovered in the 18(th) century. While they can be traced back to the earlier Cambrian, they are an extraordinarily homogeneous phylum at the morphological level - a fascinating characteristic that puzzled many a scientist who has tried to clarify their taxonomy. Recent studies which have attempted to reconstruct a phylogeny using molecular data have relied on single gene analyses and a somewhat restricted taxon sampling. Here, we present the first large scale phylogenetic study of Chaetognatha based on a combined analysis of nearly the complete ribosomal RNA (rRNA) genes. We use this analysis to infer the evolution of some morphological characters. This work includes 36 extant species, mainly obtained from Tara Oceans Expedition 2009/2012, that represent 16 genera and 6 of the 9 extant families.

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⑩

Telford MJ, Holland PW (1993)
The phylogenetic affinities of the chaetognaths: a molecular analysis.
Mol Biol Evol 10: 660-676

Abstract

The chaetognaths, or arrowworms, constitute a small and enigmatic phylum of marine invertebrates whose phylogenetic affinities have long been uncertain. A popular hypothesis is that the chaetognaths are the sister group of the major deuterostome phyla: chordates, hemichordates, and echinoderms. Here we attempt to determine the affinities of the chaetognaths by using molecular sequence data. We describe the isolation and nucleotide sequence determination of 18S ribosomal DNA from one species of chaetognath and one acanthocephalan. Extensive phylogenetic analyses employing a suite of phylogenetic reconstruction methods (maximum parsimony, maximum likelihood, evolutionary parsimony, and two distance methods) suggest that the hypothesized relationship between chaetognaths and the deuterostomes is incorrect. In contrast, we propose that the lineage leading to the chaetognaths arose prior to the advent of the coelomate metazoa.

11

Marlétaz F, Peijnenburg KTCA, Goto T, Satoh N, Rokhsar DS (2019)

A New Spiralian Phylogeny Places the Enigmatic Arrow Worms among Gnathiferans

Current Biology 29: 312-318

Abstract

Chaetognaths (arrow worms) are an enigmatic group of marine animals whose phylogenetic position remains elusive, in part because they display a mix of developmental and morphological characters associated with other groups [1, 2]. In particular, it remains unclear whether they are a sister group to protostomes [1, 2], one of the principal animal superclades, or whether they bear a closer relationship with some spiralian phyla [3, 4]. Addressing the phylogenetic position of chaetognaths and refining our understanding of relationships among spiralians are essential to fully comprehend character changes during bilaterian evolution [5]. To tackle these questions, we generated new transcriptomes for ten chaetognath species, compiling an extensive phylogenomic dataset that maximizes data occupancy and taxonomic representation. We employed inference methods that consider rate and compositional heterogeneity across taxa to avoid limitations of earlier analyses [6]. In this way, we greatly improved the resolution of the protostome tree of life. We find that chaetognaths cluster together with rotifers, gnathostomulids, and micrognathozoans within an expanded Gnathifera clade and that this clade is the sister group to other spiralians [7, 8]. Our analysis shows that several previously proposed groupings are likely due to systematic error, and we propose a revised organization of Lophotrochozoa with three main clades: Tetraneuralia (mollusks and entoprocts), Lophophorata (brachiopods, phoronids, and ectoprocts), and a third unnamed clade gathering annelids, nemerteans, and platyhelminthes. Consideration of classical morphological, developmental, and genomic characters in light of this topology indicates secondary loss as a fundamental trend in spiralian evolution.

12

Hervé P, Brinkmann H, Martinez P, Riutort M, Baguñà J (2007)

Acoel flatworms are not Platyhelminthes: Evidence from phylogenomics

PLoS ONE 8: e717

Abstract

Acoel flatworms are small marine worms traditionally considered to belong to the phylum Platyhelminthes. However, molecular phylogenetic analyses suggest that acoels are not members of Platyhelminthes, but are rather extant members of the earliest diverging Bilateria. This result has been called into question, under suspicions of a long branch attraction (LBA) artefact. Here we re-examine this problem through a phylogenomic approach using 68 different protein-coding genes from the acoel Convoluta pulchra and 51 metazoan species belonging to 15 different phyla. We employ a mixture model, named CAT, previously found to overcome LBA artefacts where classical models fail. Our results unequivocally show that acoels are not part of the classically defined Platyhelminthes, making the latter polyphyletic. Moreover, they indicate a deuterostome affinity for acoels, potentially as a sister group to all deuterostomes, to Xenoturbellida, to Ambulacraria, or even to chordates. However, the weak support found for most deuterostome nodes, together with the very fast evolutionary rate of the acoel Convoluta pulchra, call for more data from slowly evolving acoels (or from its sister-group, the Nemertodermatida) to solve this challenging phylogenetic problem.

13

Standen EM, Du TY, Larsson HCE (2014)

Developmental plasticity and the origin of tetrapods.

Nature 513: 54-58

Abstract

The origin of tetrapods from their fish antecedents, approximately 400 million years ago, was coupled with the origin of terrestrial locomotion and the evolution of supporting limbs. Polypterus is a member of the basal-most group of ray-finned fish (actinopterygians) and has many plesiomorphic morphologies that are comparable to elpistostegid fishes, which are stem tetrapods. Polypterus therefore serves as an extant analogue of stem tetrapods, allowing us to examine how developmental plasticity affects the 'terrestrialization' of fish. We measured the developmental plasticity of anatomical and biomechanical responses in Polypterus reared on land. Here we show the remarkable correspondence between the environmentally induced phenotypes of terrestrialized Polypterus and the ancient anatomical changes in stem tetrapods, and we provide insight into stem tetrapod behavioural evolution. Our results raise the possibility that environmentally induced developmental plasticity facilitated the origin of the terrestrial traits that led to tetrapods.

14

Srivastava M, Begovic E, Chapman J, Putnam NH, Hellsten U, Kawashima T, Kuo A, Mitros T, Salamov A, Carpenter ML, Signorovitch AY, Moreno MA, Kamm K, Grimwood J, Schmutz J, Shapiro H, Grigoriev IV, Buss LW, Schierwater B, Dellaporta SL, Rokhsar DS (2008)

The Trichoplax genome and the nature of placozoans

Nature 454: 955-960

Abstract

As arguably the simplest free-living animals, placozoans may represent a primitive metazoan form, yet their biology is poorly understood. Here we report the sequencing and analysis of the approximately 98 million base pair nuclear genome of the placozoan Trichoplax adhaerens. Whole-genome phylogenetic analysis suggests that placozoans belong to a 'eumetazoan' clade that includes cnidarians and bilaterians, with sponges as the earliest diverging animals. The compact genome shows conserved gene content, gene structure and synteny in relation to the human and other complex eumetazoan genomes. Despite the apparent cellular and organismal simplicity of Trichoplax, its genome encodes a rich array of transcription factor and signalling pathway genes that are typically associated with diverse cell types and developmental processes in eumetazoans, motivating further searches for cryptic cellular complexity and/or as yet unobserved life history stages.

(15)

Green SA, Simoes-Costa M, Bronner ME (2015)
Evolution of vertebrates as viewed from the crest
Nature 520: 474-482

Abstract

The origin of vertebrates was accompanied by the advent of a novel cell type: the neural crest. Emerging from the central nervous system, these cells migrate to diverse locations and differentiate into numerous derivatives. By coupling morphological and gene regulatory information from vertebrates and other chordates, we describe how addition of the neural-crest-specification program may have enabled cells at the neural plate border to acquire multipotency and migratory ability. Analysis of the topology of the neural crest gene regulatory network can serve as a useful template for understanding vertebrate evolution, including elaboration of neural crest derivatives.

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(16)

Leininger S, Adamski M, Bergum B, Guder C, Liu J, Laplante M, Bråte J, Hoffmann F, Fortunato S, Jordal S, Rapp HT, Adamska M (2014)
Developmental gene expression provides clues to relationships between sponge and eumetazoan body plans
Nature Communications 5: 3905

Abstract

Elucidation of macroevolutionary transitions between diverse animal body plans remains a major challenge in evolutionary biology. We address the sponge-eumetazoan transition by analyzing expression of a broad range of eumetazoan developmental regulatory genes in Sycon ciliatum (Calcispongiae). Here we show that many members of surprisingly numerous Wnt and Tgfβ gene families are expressed higher or uniquely in the adult apical end and the larval posterior end. Genes involved in formation of the eumetazoan endomesoderm, such as β-catenin, Brachyury and Gata, as well as germline markers Vasa and PI10, are expressed during formation and maintenance of choanoderm, the feeding epithelium of sponges. Similarity in developmental gene expression between sponges and eumetazoans, especially cnidarians, is consistent with Haeckel's view that body plans of sponges and cnidarians are homologous. These results provide a framework for further studies aimed at deciphering ancestral developmental regulatory networks and their modifications during animal body plans evolution.

(17)

Egger B, Steinke D, Tarui H, De Mulder K, Arendt D, Borgonie G, Funayama N, Gschwentner R, Hartenstein V, Hobmayer B, Hooge M, Hrouda M, Ishida S, Kobayashi C, Kuales G, Nishimura O, Pfister D, Rieger R, Salvenmoser W, Smith J, Technau Ul, Tyler S, Agata K, Salzburger W, Ladurner P (2009)
To be or not to be a flatworm: The Acoel controversy
PLoS ONE 4: e5502

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.

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(18)

Chiodin M, Børve A, Berezikoy E, Ladurner P, Martinez P, Hejnol A (2013)
Mesodermal Gene Expression in the Acoel Isodiametra pulchra Indicates a Low Number of Mesodermal Cell Types and the Endomesodermal Origin of the Gonads
PLoS ONE 8: e55499

Abstract

Acoelomorphs are bilaterally symmetric small marine worms that lack a coelom and possess a digestive system with a single opening. Two alternative phylogenetic positions of this group within the animal tree are currently debated. In one view, Acoelomorpha is the sister group to all remaining Bilateria and as such, is a morphologically simple stepping stone in bilaterian evolution. In the other, the group is a lineage within the Deuterostomia, and therefore, has derived a simple morphology from a more complex ancestor. Acoels and the closely related Nemertodermatida and Xenoturbellida, which together form the Acoelomorpha, possess a very limited number of cell types. To further investigate the diversity and origin of mesodermal cell types we describe the expression pattern of 12 orthologs of bilaterian mesodermal markers including Six1/2, Twist, FoxC, GATA4/5/6, in the acoel Isodiametra pulchra. All the genes are expressed in stem cells (neoblasts), gonads, and at least subsets of the acoel musculature. Most are expressed in endomesodermal compartments of I. pulchra developing embryos similar to what has been described in cnidarians. Our molecular evidence indicates a very limited number of mesodermal cell types and suggests an endomesodermal origin of the gonads and the stem cell system. We discuss our results in light of the two prevailing phylogenetic positions of Acoelomorpha.

19

Eitel M, Osigus HJ, DeSalle R, Schierwater, B (2013)
Global Diversity of the Placozoa
PLoS ONE 8: e57131

Abstract

The enigmatic animal phylum Placozoa holds a key position in the metazoan Tree of Life. A simple bauplan makes it appear to be the most basal metazoan known and genetic evidence also points to a position close to the last common metazoan ancestor. Trichoplax adhaerens is the only formally described species in the phylum to date, making the Placozoa the only monotypic phylum in the animal kingdom. However, recent molecular genetic as well as morphological studies have identified a high level of diversity, and hence a potential high level of taxonomic diversity, within this phylum. Different taxa, possibly at different taxonomic levels, are awaiting description. In this review we firstly summarize knowledge on the morphology, phylogenetic position and ecology of the Placozoa. Secondly, we give an overview of placozoan morphological and genetic diversity and finally present an updated distribution of placozoan populations. We conclude that there is great potential and need to erect new taxa and to establish a firm system for this taxonomic tabula rasa.

20

Smith FW, Boothby TC, Giovannini I, Rebecchi L, Jockusch EL, Goldstein B (2016)
The Compact Body Plan of Tardigrades Evolved by the Loss of a Large Body Region
Current Biology 26: 224-229

Abstract

The superphylum Panarthropoda (Arthropoda, Onychophora, and Tardigrada) exhibits a remarkable diversity of segment morphologies, enabling these animals to occupy diverse ecological niches. The molecular identities of these segments are specified by Hox genes and other axis patterning genes during development [1, 2]. Comparisons of molecular segment identities between arthropod and onychophoran species have yielded important insights into the origins and diversification of their body plans [3-9]. However, the relationship of the segments of tardigrades to those of arthropods and onychophorans has remained enigmatic [10, 11], limiting our understanding of early panarthropod body plan diversification. Here, we reveal molecular identities for all of the segments of a tardigrade. Based on our analysis, we conclude that tardigrades have lost a large intermediate region of the body axis - a region corresponding to the entire thorax and most of the abdomen of insects - and that they have lost the Hox genes that originally specified this region. Our data suggest that nearly the entire tardigrade body axis is homologous to just the head region of arthropods. Based on our results, we reconstruct a last common ancestor of Panarthropoda that had a relatively elongate body plan like most arthropods and onychophorans, rather than a compact, tardigrade-like body plan. These results demonstrate that the body plan of an animal phylum can originate by the loss of a large part of the body.

21

Koonin, EV (2015)

Archaeal ancestors of eukaryotes: Not so elusive any more

BMC Biology 13: 84

Abstract

The origin of eukaryotes is one of the hardest problems in evolutionary biology and sometimes raises the ominous specter of irreducible complexity. Reconstruction of the gene repertoire of the last eukaryotic common ancestor (LECA) has revealed a highly complex organism with a variety of advanced features but no detectable evolutionary intermediates to explain their origin. Recently, however, genome analysis of diverse archaea led to the discovery of apparent ancestral versions of several signature eukaryotic systems, such as the actin cytoskeleton and the ubiquitin network, that are scattered among archaea. These findings inspired the hypothesis that the archaeal ancestor of eukaryotes was an unusually complex form with an elaborate intracellular organization. The latest striking discovery made by deep metagenomic sequencing vindicates this hypothesis by showing that in phylogenetic trees eukaryotes fall within a newly identified archaeal group, the Lokiarchaeota, which combine several eukaryotic signatures previously identified in different archaea. The discovery of complex archaea that are the closest living relatives of eukaryotes is most compatible with the symbiogenetic scenario for eukaryogenesis.

22

Lu TM, Kanda M, Satoh N, Furuya H (2017)

The phylogenetic position of dicyemid mesozoans offers insights into spiralian evolution

Zoological Letters 3: 6

Abstract

Background: Obtaining phylogenomic data for enigmatic taxa is essential to achieve a better understanding of animal evolution. Dicyemids have long fascinated biologists because of their highly simplified body organization, but their life-cycles remain poorly known. Based on the discovery of the dicyemid DoxC gene, which encodes a spiralian peptide, it has been proposed that dicyemids are members of the Spiralia. Other studies have suggested that dicyemids may have closer affinities to mollusks and annelids. However, the phylogenetic position of dicyemids has remained a matter of debate, leading to an ambiguous picture of spiralian evolution. Results: In the present study, newly sequenced transcriptomic data from Dicyema japonicum were complemented with published transcriptomic data or predicted gene models from 29 spiralian, ecdysozoan, and deuterostome species, generating a dataset (Dataset 1) for phylogenomic analyses, which contains 348 orthologs and 58,124 amino acids. In addition to this dataset, to eliminate systematic errors, two additional sub-datasets were created by removing compositionally heterogeneous or rapidly evolving sites and orthologs from Dataset 1, which may cause compositional heterogeneity and long-branch attraction artifacts. Maximum likelihood and Bayesian inference analyses both placed Dicyema japonicum (Dicyemida) in a clade with Intoshia linei (Orthonectida) with strong statistical support. Furthermore, maximum likelihood analyses placed the Dicyemida + Orthonectida clade within the Gastrotricha, while in Bayesian inference analyses, this clade is sister group to the clade of Gastrotricha + Platyhelminthes. Conclusions: Whichever the case, in all analyses, Dicyemida, Orthonectida, Gastrotricha, and Platyhelminthes constitute a monophyletic group that is a sister group to the clade of Mollusca + Annelida. Based on present phylogenomic analyses, dicyemids display close affinity to orthonectids, and they may share a common ancestor with gastrotrichs and platyhelminths, rather than with mollusks and annelids. Regarding spiralian phylogeny, the Gnathifera forms the sister group to the Rouphozoa and Lophotrochozoa, as has been suggested by previous studies; thus our analysis supports the traditional acoeloid–planuloid hypothesis of a nearly microscopic, non-coelomate common ancestor of spiralians.

23

Danovaro R, Dell'Anno A, Pusceddu A, Gambi C, Heiner I, Møbjerg Kristensen R (2010)

The first metazoa living in permanently anoxic conditions

BMC Biology 8: 30

Abstract

Several unicellular organisms (prokaryotes and protozoa) can live under permanently anoxic conditions. Although a few metazoans can survive temporarily in the absence of oxygen, it is believed that multi-cellular organisms cannot spend their entire life cycle without free oxygen. Deep seas include some of the most extreme ecosystems on Earth, such as the deep hypersaline anoxic basins of the Mediterranean Sea. These are permanently anoxic systems inhabited by a huge and partly unexplored microbial biodiversity.

During the last ten years three oceanographic expeditions were conducted to search for the presence of living fauna in the sediments of the deep anoxic hypersaline L'Atalante basin (Mediterranean Sea). We report here that the sediments of the L'Atalante basin are inhabited by three species of the animal phylum Loricifera (Spinoloricus nov. sp., Rugiloricus nov. sp. and Pliciloricus nov. sp.) new to science. Using radioactive tracers, biochemical analyses, quantitative X-ray microanalysis and infrared spectroscopy, scanning and transmission electron microscopy observations on ultra-sections, we provide evidence that these organisms are metabolically active and show specific adaptations to the extreme conditions of the deep basin, such as the lack of mitochondria, and a large number of hydrogenosome-like organelles, associated with endosymbiotic prokaryotes.

24

Schiffer PH, Robertson HE, Telford MJ (2018)

Orthonectids Are Highly Degenerate Annelid Worms

Current Biology 28: 1970-1974

Abstract

The animal groups of Orthonectida and Dicyemida are tiny, extremely simple, vermiform endoparasites of various marine animals and have been linked in the Mesozoa (Figure 1). The Orthonectida (Figures 1A and 1B) have a few hundred cells, including a nervous system of just ten cells [2], and the Dicyemida (Figure 1C) are even simpler, with ~40 cells [3]. They are classic "Problematica" [4]—the name Mesozoa suggests an evolutionary position intermediate between Protozoa and Metazoa (animals) [5] and implies that their simplicity is a primitive state, but molecular data have shown they are members of Lophotrochozoa within Bilateria [6–9], which means that they derive from a more complex ancestor. Their precise affinities remain uncertain, however, and it is disputed whether they even constitute a clade. Ascertaining their affinities is complicated by the very fast evolution observed in their genes, potentially leading to the common systematic error of long-branch attraction (LBA) [10]. Here, we use mitochondrial and nuclear gene sequence data and show that both dicyemids and orthonectids are members of the Lophotrochozoa. Carefully addressing the effects of unequal rates of evolution, we show that the Mesozoa is polyphyletic. While the precise position of dicyemids remains unresolved within Lophotrochozoa, we identify orthonectids as members of the phylum Annelida. This result reveals one of the most extreme cases of body-plan simplification in the animal kingdom; our finding makes sense of an annelid-like cuticle in orthonectids [2] and suggests that the circular muscle cells repeated along their body [11] may be segmental in origin. Schiffer et al. examine the phylogenetic positions of orthonectid and dicyemid worms—tiny parasites, previously grouped in phylum Mesozoa. Analyses of mitochondrial genomes and nuclear genes confirm that both dicyemids and orthonectids are lophotrochozoans but that they are not closely related. Orthonectids are extremely simplified annelid worms.

25

Lu TM, Kanda M, Satoh N, Furuya H (2017)

The phylogenetic position of dicyemid mesozoans offers insights into spiralian evolution

Zoological Letters 3: 6

Abstract

Obtaining phylogenomic data for enigmatic taxa is essential to achieve a better understanding of animal evolution. Dicyemids have long fascinated biologists because of their highly simplified body organization, but their life-cycles remain poorly known. Based on the discovery of the dicyemid DoxC gene, which encodes a spiralian peptide, it has been proposed that dicyemids are members of the Spiralia. Other studies have suggested that dicyemids may have closer affinities to mollusks and annelids. However, the phylogenetic position of dicyemids has remained a matter of debate, leading to an ambiguous picture of spiralian evolution. In the present study, newly sequenced transcriptomic data from Dicyema japonicum were complemented with published transcriptomic data or predicted gene models from 29 spiralian, ecdysozoan, and deuterostome species, generating a dataset (Dataset 1) for phylogenomic analyses, which contains 348 orthologs and 58,124 amino acids. In addition to this dataset, to eliminate systematic errors, two additional sub-datasets were created by removing compositionally heterogeneous or rapidly evolving sites and orthologs from Dataset 1, which may cause compositional heterogeneity and long-branch attraction artifacts. Maximum likelihood and Bayesian inference analyses both placed Dicyema japonicum (Dicyemida) in a clade with Intoshia linei (Orthonectida) with strong statistical support. Furthermore, maximum likelihood analyses placed the Dicyemida + Orthonectida clade within the Gastrotricha, while in Bayesian inference analyses, this clade is sister group to the clade of Gastrotricha + Platyhelminthes.

26

Catalano SR (2013)

First descriptions of dicyemid mesozoans (dicyemida: Dicyemidae) from Australian octopus (octopodidae) and cuttlefish (sepiidae), including a new record of Dicyemennea in Australian waters

Folia Parasitologica 60: 306-320

Abstract

Three new species of dicyemid mesozoans are described for the first time from Australian octopus and cuttlefish species. Dicyemennea floscephalum sp. n. is described from Octopus berrima Stranks et Norman (southern keeled octopus) collected from Spencer Gulf and Gulf St. Vincent, South Australia, Australia and represents the first description of a species of Dicyemennea Whitman, 1883 from Australian waters. Dicyema papuceum sp. n. and D. furuyi sp. n. are described from Sepia papuensis Hoyle (Papuan cuttlefish) collected from Shark Bay, Western Australia, Australia. Dicyemennea floscephalum sp. n. is a medium to large species that reaches approximately 4.9 mm in length. The vermiform stages are characterised by having 23-28 peripheral cells, and a disc-shaped, flower-like calotte in larger individuals. An anterior abortive axial cell is absent in vermiform embryos and verruciform cells were not observed in nematogens and rhombogens. Infusoriform embryos comprise 37 cells; one nucleus is present in each urn cell. Dicyema papuceum sp. n. is a small species that reaches approximately 1.1 mm in length. The vermiform stages are characterised by having 30-33 peripheral cells and a relatively small, cap-shaped calotte. An anterior abortive axial cell is absent in vermiform embryos and verruciform cells were occasionally observed in nematogens. Infusoriform embryos comprise 37 cells; two nuclei are present in each urn cell. Dicyema furuyi sp. n. is a large species that reaches approximately 5.3 mm in length. The vermiform stages are characterised by having 22-24 peripheral cells and an elongate calotte. An anterior abortive axial cell is absent in vermiform embryos and verruciform cells were not observed in nematogens and rhombogens. Infusoriform embryos comprise 37 cells; one nucleus is present in each urn cell. Three secondary nematogens were also observed in the right renal appendages of two host individuals, confirming the occurrence of this form.

27

Furuya H, Tsuneki K (2003)

Biology of dicyemid mesozoans.

Zool Sci 20: 519-532

Abstract

We reviewed recent advances of some aspects on the biology of dicyemid mesozoans. To date 42 species of dicyemids have been found in 19 species of cephalopod molluscs from Japanese waters. The body of dicyemids consists of 10-40 cells and is organized in a very simple fashion. There are three basic types of cell junction, septate junction, adherens junction, and gap junction. The presence of these junctions suggests not only cell-to-cell attachment, but also cell-to-cell communication. In the development of dicyemids, early stages and cell lineages are identical in vermiform embryos of four genera, Conocyema, Dicyema, Microcyema, and Pseudicyema. Species-specific differences appear during later stages of embryogenesis. In the process of postembryonic growth in some species, the shape of the calotte changes from conical to cap-shaped and discoidal. This calotte morphology appears to result from adaptation to the structure of host renal tissues and help to facilitate niche separation of coexisting species. In most dicyemids distinctly small numbers of sperms are produced in a hermaphroditic gonad (infusorigen). The number of eggs and sperms are roughly equal. An inverse proportional relationship exists between the number of infusorigens and that of gametes, suggesting a trade-off between them. Recent phylogenetic studies suggest dicyemids are a member of the Lophotrochozoa.

28

Hanelt B, Van chyndel. D, Adema CM, Lewis LA, Loker ES (1996)

The phylogenetic position of Rhopalura ophiocomae (Orthonectida) based on 18S ribosomal DNA sequence analysis

Mol Biol Evol 13: 1187-1191

Abstract

The Orthonectida is a small, poorly known phylum of parasites of marine invertebrates. Their phylogenetic placement is obscure; they have been considered to be multicellular protozoans, primitive animals at a "mesozoan" grade of organization, or secondarily simplified flatworm-like organisms. The best known species in the phylum, Rhopalura ophiocomae, was collected on San Juan Island, Wash. and a complete 18S rDNA sequence was obtained. Using the models of minimum evolution and parsimony, phylogenetic analyses were undertaken and the results lend support to the following hypotheses about orthonectids: (1) orthonectids are more closely aligned with triploblastic metazoan taxa than with the protist or diploblastic metazoan taxa considered in this analysis; (2) orthonectids are not derived members of the phylum Platyhelminthes; and (3) orthonectids and rhombozoans are not each other's closest relatives, thus casting further doubt on the validity of the phylum Mesozoa previously used to encompass both groups.

29

Maslakova SA (2010)

The invention of the pilidium larva in an otherwise perfectly good spiralian phylum Nemertea

Integrative and Comparative Biology m50: 734-743

Abstract

One of the most remarkable larval types among spiralians, and invertebrates in general, is the planktotrophic pilidium. The pilidium is found in a single clade of nemerteans, called the Pilidiophora, and appears to be an innovation of this group. All other nemerteans have either planktotrophic or lecithotrophic juvenile-like planuliform larvae or have direct development. The invention of the pilidium larva is associated with the formation of an extensive blastocoel that supports the delicate larval frame and elaborate ciliary band. Perhaps the most striking characteristic of the pilidium is the way the juvenile worm develops inside the larva from a series of isolated rudiments, called the imaginal discs. The paired cephalic discs, cerebral organ discs, and trunk discs originate as invaginations of larval epidermis and subsequently grow and fuse around the larval gut to form the juvenile. The fully formed juvenile ruptures the larval body and, more often than not, devours the larva during catastrophic metamorphosis. This review is an attempt to examine the pilidium in the context of recent data on development of non-pilidiophoran nemerteans, and speculate about the evolution of pilidial larval development. The author emphasizes the difference between the planuliform larvae of Palaeonemerteans and Hoplonemerteans, and suggest a new name for the hoplonemertean larvae--the decidula.

30

Martín-Durán JM, Vellutini BC, Hejnol A (2015)

Evolution and development of the adelphophagic, intracapsular Schmidt's larva of the nemertean Lineus ruber

EvoDevo 6: 28

Abstract

The life cycle of many animals includes a larval stage, which has diversified into an astonishing variety of ecological strategies. The Nemertea is a group of spiralians that exhibits a broad diversity of larval forms, including the iconic pilidium. A pelagic planktotrophic pilidium is the ancestral form in the Pilidiophora, but several lineages exhibit deviations of this condition, mostly as a transition to pelagic lecithotrophy. The most extreme case occurs, however, in the Pilidiophoran Lineus ruber, which exhibits an adelphophagic intracapsular pilidium, the so-called Schmidt's larva. We combined confocal laser scanning microscopy and gene expression studies to characterize the development and metamorphosis of the Schmidt's larva of L. ruber. The larva forms after gastrulation, and comprises a thin epidermis, a proboscis rudiment and two pairs of imaginal discs from which the juvenile will develop. The cells internalized during gastrulation form a blind gut and the blastopore gives rise to the mouth of the larva and juvenile. The Schmidt's larva eats other siblings that occupy the same egg capsule, accumulating nutrients for the juvenile. A gradual metamorphosis involves the differentiation of the juvenile cell types from the imaginal discs and the shedding of the larval epidermis. The expression of evolutionarily conserved anterior (foxQ2, six3/6, gsc, otx), endomesodermal (foxA, GATA456-a, twi-a) and posterior (evx, cdx) markers demonstrate that the juvenile retains the molecular patterning of the Schmidt's larva. After metamorphosis, the juveniles stay over 20days within the egg masses, until they are fully mature and hatch.

31

Plachetzki DC, Fong CR, Oakley TH (2012)

Cnidocyte discharge is regulated by light and opsin-mediated phototransduction

BMC Biology 10: 17

Abstract

Cnidocytes, the eponymous cell type of the Cnidaria, facilitate both sensory and secretory functions and are among the most complex animal cell types known. In addition to their structural complexity, cnidocytes display complex sensory attributes, integrating both chemical and mechanical cues from the environment into their discharge behavior. Despite more than a century of work aimed at understanding the sensory biology of cnidocytes, the specific sensory receptor genes that regulate their function remain unknown. Here we report that light also regulates cnidocyte function. We show that non-cnidocyte neurons located in battery complexes of the freshwater polyp Hydra magnipapillata specifically express opsin, cyclic nucleotide gated (CNG) ion channel and arrestin, which are all known components of bilaterian phototransduction cascades. We infer from behavioral trials that different light intensities elicit significant effects on cnidocyte discharge propensity. Harpoon-like stenotele cnidocytes show a pronounced diminution of discharge behavior under bright light conditions as compared to dim light. Further, we show that suppression of firing by bright light is ablated by cis-diltiazem, a specific inhibitor of CNG ion channels.

32

Ryan JF, Pang K, Schnitzler CE, Nguyen AD, Moreland RT, Simmons DK, Koch BJ, Francis WR, Havlak P, Smith SA, Putnam NH, Haddock SHD, Dunn CW, Wolfsberg TG, Mullikin CJ, Martindale MQ, Baxevanis AD (2013)

The genome of the ctenophore Mnemiopsis leidyi and its implications for cell type evolution

Science 342: 1336-1343

Abstract

An understanding of ctenophore biology is critical for reconstructing events that occurred early in animal evolution. Toward this goal, we have sequenced, assembled, and annotated the genome of the ctenophore Mnemiopsis leidyi. Our phylogenomic analyses of both amino acid positions and gene content suggest that ctenophores rather than sponges are the sister lineage to all other animals. Mnemiopsis lacks many of the genes found in bilaterian mesodermal cell types, suggesting that these cell types evolved independently. The set of neural genes in Mnemiopsis is similar to that of sponges, indicating that sponges may have lost a nervous system. These results present a newly supported view of early animal evolution that accounts for major losses and/or gains of sophisticated cell types, including nerve and muscle cells.

33

Moroz LL, Kocot KM, Citarella MR, Dosung S, Norekian TP, Povolotskaya IS, Grigorenko AP, Dailey C, Berezikov E, Buckley KM, Ptitsyn A, Reshetov D, Mukherjee K, Moroz TP, Bobkova Y, Yu F, Kapitonov VV, Jurka J, Bobkov YV, Swore JJ, Girardo DO, Fdor, A, Gusev, Fanford R, Bruders R, Kttler E, Mills CE, Rast JP, Derelle R, Solovyev VV, Kondrashov FA, Swalla BJ, Sweedler JV, Rogaev EI, Halanych KM, Kohn AB (2014)
The ctenophore genome and the evolutionary origins of neural systems
Nature 510: 109-114

Abstract

The origins of neural systems remain unresolved. In contrast to other basal metazoans, ctenophores (comb jellies) have both complex nervous and mesoderm-derived muscular systems. These holoplanktonic predators also have sophisticated ciliated locomotion, behaviour and distinct development. Here we present the draft genome of Pleurobrachia bachei, Pacific sea gooseberry, together with ten other ctenophore transcriptomes, and show that they are remarkably distinct from other animal genomes in their content of neurogenic, immune and developmental genes. Our integrative analyses place Ctenophora as the earliest lineage within Metazoa. This hypothesis is supported by comparative analysis of multiple gene families, including the apparent absence of HOX genes, canonical microRNA machinery, and reduced immune complement in ctenophores. Although two distinct nervous systems are well recognized in ctenophores, many bilaterian neuron-specific genes and genes of 'classical' neurotransmitter pathways either are absent or, if present, are not expressed in neurons. Our metabolomic and physiological data are consistent with the hypothesis that ctenophore neural systems, and possibly muscle specification, evolved independently from those in other animals.

34

Vandepas LE, Warren KJ, Amemiya CT, Browne WE (2017)
Establishing and maintaining primary cell cultures derived from the ctenophore Mnemiopsis leidyi
J Exp Biol 220: 1197-1201

Abstract

We have developed an efficient method for the preparation and maintenance of primary cell cultures isolated from adult Mnemiopsis leidyi, a lobate ctenophore. Our primary cell cultures are derived from tissue explants or enzymatically dissociated cells, and maintained in a complex undefined ctenophore mesogleal serum. These methods can be used to isolate, maintain and visually monitor ctenophore cells to assess proliferation, cellular morphology and cell differentiation in future studies. Exemplar cell types that can be easily isolated from primary cultures include proliferative ectodermal and endodermal cells, motile amebocyte-like cells, and giant smooth muscle cells that exhibit inducible contractile properties. We have also derived 'tissue envelopes' containing sections of endodermal canal surrounded by mesoglea and ectoderm that can be used to monitor targeted cell types in an in vivo context. Access to efficient and reliably generated primary cell cultures will facilitate the analysis of ctenophore development, physiology and morphology from a cell biological perspective.

35

Nanglu K, Caron JB (2018)

A New Burgess Shale Polychaete and the Origin of the Annelid Head Revisited

Current Biology 28: 319-326

Abstract

Annelida is one of the most speciose (~17,000 species) and ecologically successful phyla. Key to this success is their flexible body plan with metameric trunk segments and bipartite heads consisting of a prostomium bearing sensory structures and a peristomium containing the mouth. The flexibility of this body plan has traditionally proven problematic for reconstructing the evolutionary relationships within the Annelida. Although recent phylogenies have focused on resolving the interrelationships of the crown group [1–3], many questions remain regarding the early evolution of the annelid body plan itself, including the origin of the head [4]. Here we describe an abundant and exceptionally well-preserved polychaete with traces of putative neural and vascular tissues for the first time in a fossilized annelid. Up to three centimeters in length, Kootenayscolex barbarensis gen. et sp. nov. is described based on more than 500 specimens from Marble Canyon [5] and several specimens from the original Burgess Shale site (both in British Columbia, Canada). K. barbarensis possesses biramous parapodia along the trunk, bearing similar elongate and thin notochaetae and neurochaetae. A pair of large palps and one median antenna project from the anteriormost dorsal margin of the prostomium. The mouth-bearing peristomium bears neuropodial chaetae, a condition that is also inferred in Canadia and Burgessochaeta from the Burgess Shale, suggesting a chaetigorous origin for the peristomial portion of the head and a secondary loss of peristomial parapodia and chaetae in modern polychaetes.

36

Feuda R, Dohrmann M, Pett W, Philippe H, Rota-Stabelli O, Lartillot N, Wörheide G, Pisani D (2017)

Improved Modeling of Compositional Heterogeneity Supports Sponges as Sister to All Other Animals

Current Biology 27: 3864-3870

Abstract

The relationships at the root of the animal tree have proven difficult to resolve, with the current debate focusing on whether sponges (phylum Porifera) or comb jellies (phylum Ctenophora) are the sister group of all other animals [1–5]. The choice of evolutionary models seems to be at the core of the problem because Porifera tends to emerge as the sister group of all other animals ("Porifera-sister") when site-specific amino acid differences are modeled (e.g., [6, 7]), whereas Ctenophora emerges as the sister group of all other animals ("Ctenophora-sister") when they are ignored (e.g., [8–11]). We show that two key phylogenomic datasets that previously supported Ctenophora-sister [10, 12] display strong heterogeneity in amino acid composition across sites and taxa and that no routinely used evolutionary model can adequately describe both forms of heterogeneity. We show that data-recoding methods [13–15] reduce compositional heterogeneity in these datasets and that models accommodating site-specific amino acid preferences can better describe the recoded datasets. Increased model adequacy is associated with significant topological changes in support of Porifera-sister. Because adequate modeling of the evolutionary process that generated the data is fundamental to recovering an accurate phylogeny [16–20], our results strongly support sponges as the sister group of all other animals and provide further evidence that Ctenophora-sister represents a tree reconstruction artifact.

37

Cavalier-Smith T (2016)

Kingdoms Protozoa and Chromista and the eozoan root of the eukaryotic tree

Biology Letters 6: 342-345

Abstract

I discuss eukaryotic deep phylogeny and reclassify the basal eukaryotic kingdom Protozoa and derived kingdom Chromista in the light of multigene trees. I transfer the formerly protozoan Heliozoa and infrakingdoms Alveolata and Rhizaria into Chromista, which is sister to kingdom Plantae and arguably originated by synergistic double internal enslavement of green algal and red algal cells. I establish new subkingdoms (Harosa; Hacrobia) for the expanded Chromista. The protozoan phylum Euglenozoa differs immensely from other eukaryotes in its nuclear genome organization (trans-spliced multicistronic transcripts), mitochondrial DNA organization, cytochrome c-type biogenesis, cell structure and arguably primitive mitochondrial protein-import and nuclear DNA prereplication machineries. The bacteria-like absence of mitochondrial outer-membrane channel Tom40 and DNA replication origin-recognition complexes from trypanosomatid Euglenozoa roots the eukaryotic tree between Euglenozoa and all other eukaryotes (neokaryotes), or within Euglenozoa. Given their unique properties, I segregate Euglenozoa from infrakingdom Excavata (now comprising only phyla Percolozoa, Loukozoa, Metamonada), grouping infrakingdoms Euglenozoa and Excavata as the ancestral protozoan subkingdom Eozoa. I place phylum Apusozoa within the derived protozoan subkingdom Sarcomastigota. Clarifying early eukaryote evolution requires intensive study of properties distinguishing Euglenozoa from neokaryotes and Eozoa from neozoa (eukaryotes except Eozoa; ancestrally defined by haem lyase).

38

Valbonesi A, Ortenzi C, Luporini P (1992)

The Species Problem in a Ciliate with a High Multiple Mating Type System, Euplotes crassus

The Journal of Protozoology 39: 45-54

Abstract

One hundred twenty non-autogamous wild-type strains of Euplotes crassus, collected over seven years, mainly from the Mediterranean coasts, were investigated for their mating interactions. The strains were mixed pair-wise and data from mating reactions were evaluated and organized by means of a specially constructed computer program. The program identified 38 strains with distinctive mating patterns which could be clustered in nine clumps, all of which were connected either directly or indirectly. Thus, all these strains appeared to be components of the same gene pool, even though direct genetic exchange between strains was not possible in every combination. Subsequently, the 38 strains were subjected to cytometric analysis and scored for zymic variations resulting from electrophoretic patterns of five enzyme systems (acid phosphatases. amylases, malic dehydrogenase, malic enzyme, and tetrazolium oxidases) of proved diagnostic value in the identification of Euplotes species. No significant discontinuities correlated with mating patterns was apparent from these analyses. It was concluded that the E. crassus strains analyzed are not properly divided in sibling species and it was consistently suggested to avoid a genetic partitioning of ciliate species endowed with high multiple mating type systems, in which the sets of wild strains brought under investigation with difficulty represent the natural dimensions of the species.

Key words. Isozymes, mating-type interactions, multivariate analysis.

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Hanschen ER, Marriage TN, Ferris PJ, Hamaji T, Toyoda A, Fujiyama A, Neme R, Noguchi H, Minakuchi Y. Suzuki M, Kawai-Toyooka H, Smith DR, Sparks H, Anderson J, Bakarić R, Luria V, Karger A, Kirschner MW, Durand PM, Michod RE, Nozaki H, Olson BJSC (2016)

The Gonium pectorale genome demonstrates co-option of cell cycle regulation during the evolution of multicellularity

Nature Communications 7: 11370

Abstract

The transition to multicellularity has occurred numerous times in all domains of life, yet its initial steps are poorly understood. The volvocine green algae are a tractable system for understanding the genetic basis of multicellularity including the initial formation of cooperative cell groups. Here we report the genome sequence of the undifferentiated colonial alga, Gonium pectorale, where group formation evolved by co-option of the retinoblastoma cell cycle regulatory pathway. Significantly, expression of the Gonium retinoblastoma cell cycle regulator in unicellular Chlamydomonas causes it to become colonial. The presence of these changes in undifferentiated Gonium indicates extensive group-level adaptation during the initial step in the evolution of multicellularity. These results emphasize an early and formative step in the evolution of multicellularity, the evolution of cell cycle regulation, one that may shed light on the evolutionary history of other multicellular innovations and evolutionary transitions.

40

Kirk DL (2005)

A twelve-step program for evolving multicellularity and a division of labor

BioEssays 27: 299-310

Abstract

The volvocine algae provide an unrivalled opportunity to explore details of an evolutionary pathway leading from a unicellular ancestor to multicellular organisms with a division of labor between different cell types. Members of this monophyletic group of green flagellates range in complexity from unicellular Chlamydomonas through a series of extant organisms of intermediate size and complexity to Volvox, a genus of spherical organisms that have thousands of cells and a germ-soma division of labor. It is estimated that these organisms all shared a common ancestor about 50 +/- 20 MYA. Here we outline twelve important ways in which the developmental repertoire of an ancestral unicell similar to modern C. reinhardtii was modified to produce first a small colonial organism like Gonium that was capable of swimming directionally, then a sequence of larger organisms (such as Pandorina, Eudorina and Pleodorina) in which there was an increasing tendency to differentiate two cell types, and eventually Volvox carteri with its complete germ-soma division of labor.

41

Mah JL, Christensen-Dalsgaard KK, Leys SP (2014)

Choanoflagellate and choanocyte collar-flagellar systems and the assumption of homology

Evolution and Development 16: 25-37

Abstract

The similarities between the choanoflagellates and the choanocytes of sponges have been discussed for more than a century yet few studies allow a direct comparison of the two. We reviewed current knowledge of the collar and flagellum and compared their structure and function in the choanoflagellate Monosiga brevicollis and the sponge Spongilla lacustris. Collar microvilli were of similar length and number, but the shape of the collar differed between the two cells. In Monosiga, collars were flared and microvilli were joined by a single band of glycocalyx mid-way along their length; in Spongilla, collars formed a tube and microvilli were joined by a mesh of glycocalyx. Monosiga flagella beat at least four times faster than those in Spongilla. Flagellar vanes were found in both cell types. In both cells, the flagella and so probably also the vanes maintained moving points of contact with the microvilli, which suggested that collars and flagella were integrated systems rather than independent units. There were fundamental differences in how the collar and flagella interacted, however. In Spongilla, the flagellum bent upon contact with the collar; the flagellar amplitude was fitted to the collar diameter. In Monosiga, the flagellar amplitude was unaffected by the collar; instead the collar diameter appeared fitted to the flagellum. These differences suggest that though choanocytes and choanoflagellates are similar, homology cannot be taken for granted. Similarities in collar-flagellum systems separated by 600 million years of evolution, whether maintained or convergent, suggest that these form important adaptations for optimizing fluid flow through micro-scale filters.

42

Döring C, Gosda J, TessmarRaible, K, Hausen H; Arendt D, Purschke G (2013)

Evolution of clitellate phaosomes from rhabdomeric photoreceptor cells of polychaetes - a study in the leech Helobdella robusta (Annelida, Sedentaria, Clitellata)

Frontiers in Zoology 10: 52

Abstract

In Annelida two types of photoreceptor cells (PRCs) are regarded as generally present, rhabdomeric and ciliary PRCs. In certain taxa, however, an additional type of PRC may occur, the so called phaosomal PRC. Whereas the former two types of PRCs are always organized as an epithelium with their sensory processes projecting into an extracellular cavity formed by the PRCs and (pigmented) supportive cells, phaosomes are seemingly intracellular vacuoles housing the sensory processes. Phaosomal PRCs are the only type of PRC found in one major annelid group, Clitellata. Several hypotheses have been put forward explaining the evolutionary origin of the clitellate phaosomes. To elucidate the evolution of clitellate PRC and eyes the leech Helobdella robusta, for which a sequenced genome is available, was chosen. TEM observations showed that extraocular and ocular PRCs are structurally identical. Bioinformatic analyses revealed predictions for four opsin genes, three of which could be amplified. All belong to the rhabdomeric opsin family and phylogenetic analyses showed them in a derived position within annelid opsins. Gene expression studies showed two of them expressed in the eye and in the extraocular PRCs. Polychaete eye-typic key enzymes for ommochromme and pterin shading pigments synthesis are not expressed in leech eyes.

43

Röhlich P, Aros B, Virágh S (1970)

Fine structure of photoreceptor cells in the earthworm, Lumbricus terrestris

Zeitschrift für Zellforschung und Mikroskopische Anatomie 104: 345-357

Abstract

Photoreceptor cells in the epidermis and nerve branches of the prostomium and in the cerebral ganglion of Lumbricus terrestris were investigated with the electron microscope. The photoreceptor cell is similar to the visual cell of Hirudo by having a central intracellular cavity (phaosome) filled with microvilli. Besides microvilli, several sensory cilia can also be found in the phaosome but they are structurally independent of the microvilli. A gradual branching of the phaosome cavity into smaller cavities makes its sectional profile extremely labyrinthic. Flattened smooth-surfaced cisternae in stacks of 2 to 5 are frequently observed around the phaosome. Characteristic constituents of the cytoplasm are vesicles and vacuoles filled with a substance of varying density. The photoreceptor cell is covered by glial cells or by their processes which at many places deeply invaginate the cell surface (trophospongium).

44

Monahan-Earley R, Dvorak AM, Aird WC (2017)

Evolutionary origins of the blood vascular system and endothelium

Journal of Thrombosis and Haemostasis 11: 46-66

Abstract

Every biological trait requires both a proximate and evolutionary explanation. The field of vascular biology is focused primarily on proximate mechanisms in health and disease. Comparatively little attention has been given to the evolutionary basis of the cardiovascular system. Here, we employ a comparative approach to review the phylogenetic history of the blood vascular system and endothelium. In addition to drawing on the published literature, we provide primary ultrastructural data related to the lobster, earthworm, amphioxus, and hagfish. Existing evidence suggests that the blood vascular system first appeared in an ancestor of the triploblasts over 600 million years ago, as a means to overcome the time-distance constraints of diffusion. The endothelium evolved in an ancestral vertebrate some 540-510 million years ago to optimize flow dynamics and barrier function, and/or to localize immune and coagulation functions. Finally, we emphasize that endothelial heterogeneity evolved as a core feature of the endothelium from the outset, reflecting its role in meeting the diverse needs of body tissues.

(45)

Rodriguez ZB, Perkins SL, Austin CC (2018)

Multiple origins of green blood in New Guinea lizards

Science Advances 4: eaao5017

Abstract

Several species of lizards from the megadiverse island of New Guinea have evolved green blood. An unusually high concentration of the green bile pigment biliverdin in the circulatory system of these lizards makes the blood, muscles, bones, tongue, and mucosal tissues bright green in color, eclipsing the crimson color from their red blood cells. This is a remarkable physiological feature because bile pigments are toxic physiological waste products of red blood cell catabolism and, when chronically elevated, cause jaundice in humans and all other vertebrates. Although these lizards offer a promising system to examine the evolution of extraordinary physiological characteristics, little is known about the phylogenetic relationships of green-blooded lizards or the evolutionary origins of green blood. We present the first extensive phylogeny for green-blooded lizards and closely related Australasian lizards using thousands of genomic regions to examine the evolutionary history of this unusual trait. Maximum likelihood ancestral character state reconstruction supports four independent origins of green blood. Our results lay the phylogenetic foundation necessary to determine the role, if any, of natural selection in shaping this enigmatic physiological trait as well as understanding the genetic, proteomic, and biochemical basis for the lack of jaundice in those species that have independently evolved green blood.

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(46)

Kieneke AI, Arbizu PM, Ahlrichs WH (2008)

Anatomy and ultrastructure of the reproductive organs in Dactylopodola typhle (Gastrotricha: Macrodasyida) and their possible functions in sperm transfer

Invertebrate Biology 127: 12-32

Abstract

The reproductive anatomy of gastrotrichs is well known for several species, especially for the marine taxon Macrodasyida. However, there is little information on the reproductive organs and the modes of mating and sperm transfer in putative basal taxa, which is necessary for accurate reconstruction of the ground pattern of the Gastrotricha. We present the first detailed morphological investigation of the reproductive system of a putative basal gastrotrich, Dactylopodola typhle, using transmission and scanning electron microscopy, histology, and microscopic observations of living specimens. Dactylopodola typhle is a hermaphrodite that possesses paired female and male gonads, an unpaired uterus with an outlet channel that we call the cervix, and an additional accessory reproductive organ, the so-called caudal organ. We hypothesize that the hollow, secretory caudal organ serves for picking up autospermatozoa (self-sperm), for spermatophore formation, and finally for transferring the autospermatophore to a mating partner. The allospermatophore (foreign spermatophore) is stored within the uterus where fertilization occurs. We think that the mature and fertilized egg is released through the cervix and the dorsolateral female gonopore, and not by rupture of the body wall. Based on the morphology, we provide a plausible hypothesis for spermatophore formation and transfer in D. typhle. Preliminary phylogenetic considerations indicate that the stem species of Macrodasyida, perhaps that of all Gastrotricha, had paired ovaries and paired testes, an unpaired uterus, and only one accessory reproductive organ.

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Prud'homme B, De osa, R, Arendt D, Julien JF, Pajaziti R, Dorresteijn AWC, Adoutte A, Wittbrodt J, Balavoine G (2003)

Arthropod-like expression patterns of engrailed and wingless in the annelid Platynereis dumerilii suggest a role in segment formation

Current Biology 13: 1876-1881

Abstract

The origin of animal segmentation, the periodic repetition of anatomical structures along the anteroposterior axis, is a long-standing issue [1] that has been recently revived by comparative developmental genetics [2-6]. In particular, a similar extensive morphological segmentation (or metamerism) is commonly recognized in annelids and arthropods. Mostly based on this supposedly homologous segmentation, these phyla have been united for a long time into the clade Articulata [7, 8]. However, recent phylogenetic analysis [9-10] dismissed the Articulata and thus challenged the segmentation homology hypothesis [11]. Here, we report the expression patterns of genes orthologous to the arthropod segmentation genes engrailed and wingless in the annelid Platynereis dumerilii. In Platynereis, engrailed and wingless are expressed in continuous ectodermal stripes on either side of the segmental boundary before, during, and after its formation; this expression pattern suggests that these genes are involved in segment formation. The striking similarities of engrailed and wingless expressions in Platynereis and arthropods may be due to evolutionary convergence or common heritage. In agreement with similarities in segment ontogeny and morphological organization in arthropods and annelids, we interpret our results as molecular evidence of a segmented ancestor of protostomes.

48

Moller PC, Ellis RA (1974)

Fine structure of the excretory system of Amphioxus (Branchiostoma floridae) and its response to osmotic stress

Cell and Tissue Research 148: 1-9

Abstract

The excretory organs of Amphioxus occur as segmentally arranged structures throughout the pharyngeal region and may be divided into three components: the solenocytes, the renal tubule, and the renal glomerulus.

The solenocytes possess foot processes that rest upon the coelomic surface of the ligamentum denticulatum. The tubular apparatus of the solenocytes consists of ten triangular rods surrounding a central flagellum. The distal end of the tubular apparatus enters branches of the renal tubule. The renal tubule eventually opens into the atrial cavity of Amphioxus.

The renal glomerulus is a sinus within the connective tissue of the ligamentum denticulatum where it connects elements of the branchial circulation with the dorsal aorta. The renal glomerulus, like other blood vessels of Amphioxus, lacks an endothelial lining.

If Amphioxus is adapted to artificial sea water at different concentrations there is no change in kidney morphology suggesting that Amphioxus is either is osmotic with its environment or is osmoregulating with other organs.

(49)

Hosken DJ, Stockley P (2004)
Sexual selection and genital evolution
Trends in Ecology and Evolution 19: 87-93

Abstract

Genitalia are conspicuously variable, even in closely related taxa that are otherwise morphologically very similar. Explaining genital diversity is a longstanding problem that is attracting renewed interest from evolutionary biologists. New studies provide ever more compelling evidence that sexual selection is important in driving genital divergence. Importantly, several studies now link variation in genital morphology directly to male fertilization success, and modern comparative techniques have confirmed predicted associations between genital complexity and mating patterns across species. There is also evidence that male and female genitalia can coevolve antagonistically. Determining mechanisms of genital evolution is an important challenge if we are to resolve current debate concerning the relative significance of mate choice benefits and sexual conflict in sexual selection.

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(50)

Annona G, Holland ND, D'Aniello S (2015)
Evolution of the notochord
EvoDevo 6: 30

Abstract

A notochord is characteristic of developing chordates (which comprise amphioxus, tunicates and vertebrates), and, more arguably, is also found in some other animals. Although notochords have been well reviewed from a develop-mental genetic point of view, there has heretofore been no adequate survey of the dozen or so scenarios accounting for their evolutionary origin. Advances in molecular phylogenetics and developmental genetics have, on the one hand, failed to support many of these ideas (although, it is not impossible that some of these rejects may yet, at least in part, return to favor). On the other hand, current molecular approaches have actually stimulated the revival of two of the old proposals: first that the notochord is a novelty that arose in the chordates, and second that it is derived from a homologous structure, the axochord, that was present in annelid-like ancestors. In the long term, choosing whether the notochord is a chordate novelty or a legacy from an ancient annelid (or perhaps an evolutionary derivative from precursors yet to be proposed) will probably require descriptions of gene regulatory networks involved in the devel-opment of notochords and notochord-like structures in a wide spectrum of animals. For now, one-way forward will be studies of all aspects of the biology of enteropneust hemichordates, a group widely thought to be the key to under-standing the evolutionary origin of the chordates.

(51)

Nilsson DE (2009)
The evolution of eyes and visually guided behavior
Philosophical Transactions of the Royal Society B: Biological Sciences 364: 2833-2847

Abstract

The morphology and molecular mechanisms of animal photoreceptor cells and eyes reveal a complex pattern of duplications and co-option of genetic modules, leading to a number of different light-sensitive systems that share many components, in which clear-cut homologies are rare. On the basis of molecular and morphological findings, I discuss the functional requirements for vision and how these have constrained the evolution of eyes. The fact that natural selection on eyes acts through the consequences of visually guided behaviour leads to a concept of task-punctuated evolution, where sensory systems evolve by a sequential acquisition of sensory tasks. I identify four key innovations that, one after the other, paved the way for the evolution of efficient eyes. These innovations are (i) efficient photopigments, (ii) directionality through screening pigment, (iii) photoreceptor membrane folding, and (iv) focusing optics. A corresponding evolutionary sequence is suggested, starting at non-directional monitoring of ambient luminance and leading to comparisons of luminances within a scene, first by a scanning mode and later by parallel spatial channels in imaging eyes.