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30

Deep Metazoan Phylogeny 2011
New data, new challenges

11.–14. October 2011

Programme and Abstracts

Munich 2011

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Zitteliana	B 30	78 Seiten	München, 1.10.2011	ISSN 1612-4138

Preface

The international conference "Deep Metazoan Phylogeny 2011 – new data, new challenges", held from 11-14 October 2011 at the Ludwig-Maximilians-Universität München in the Palaeontological Museum Munich, brings together mathematicians, theoreticians, molecular systematists, and morphologists who aim at resolving deep branches in the animal tree of life for a better understanding of the evolution and diversification of multicellular life on Earth. During the conference, new data, new analytical tools and new results will be discussed. Challenges and pitfalls in phylogeny reconstruction based on molecular and/or morphological data will be identified, aiming for a critical and constructive view of the state of the art of the metazoan tree of life.
The meeting will consist of sessions with several invited leaders in the field and open sessions with shorter presentations. In addition, there will be ample space and time to present posters as well as a distinguished public evening lecture.
The conference is the second of its kind (the first one was held at the Humboldt Universität Berlin in March 2009) and is organised in cooperation with the Priority Programme "Deep Metazoan Phylogeny" (SPP 1174) of the German Research Foundation (DFG). The priority programme, which ran for six years from 2005 until 2011, is a joint effort of more than 20 participating workgroups that has brought together molecular, morphological and bioinformatic expertise with the goal to establish a robust backbone metazoan phylogeny. Details on the priority programme can be found at http://www.deep-phylogeny.org.
We wish all participants a fruitful and lively conference and many stimulating discussions.

for the organising committee

Gert Wörheide
(Chair of local organising committee)

Wolfgang Wägele
(Coordinator of the Priority Programme)

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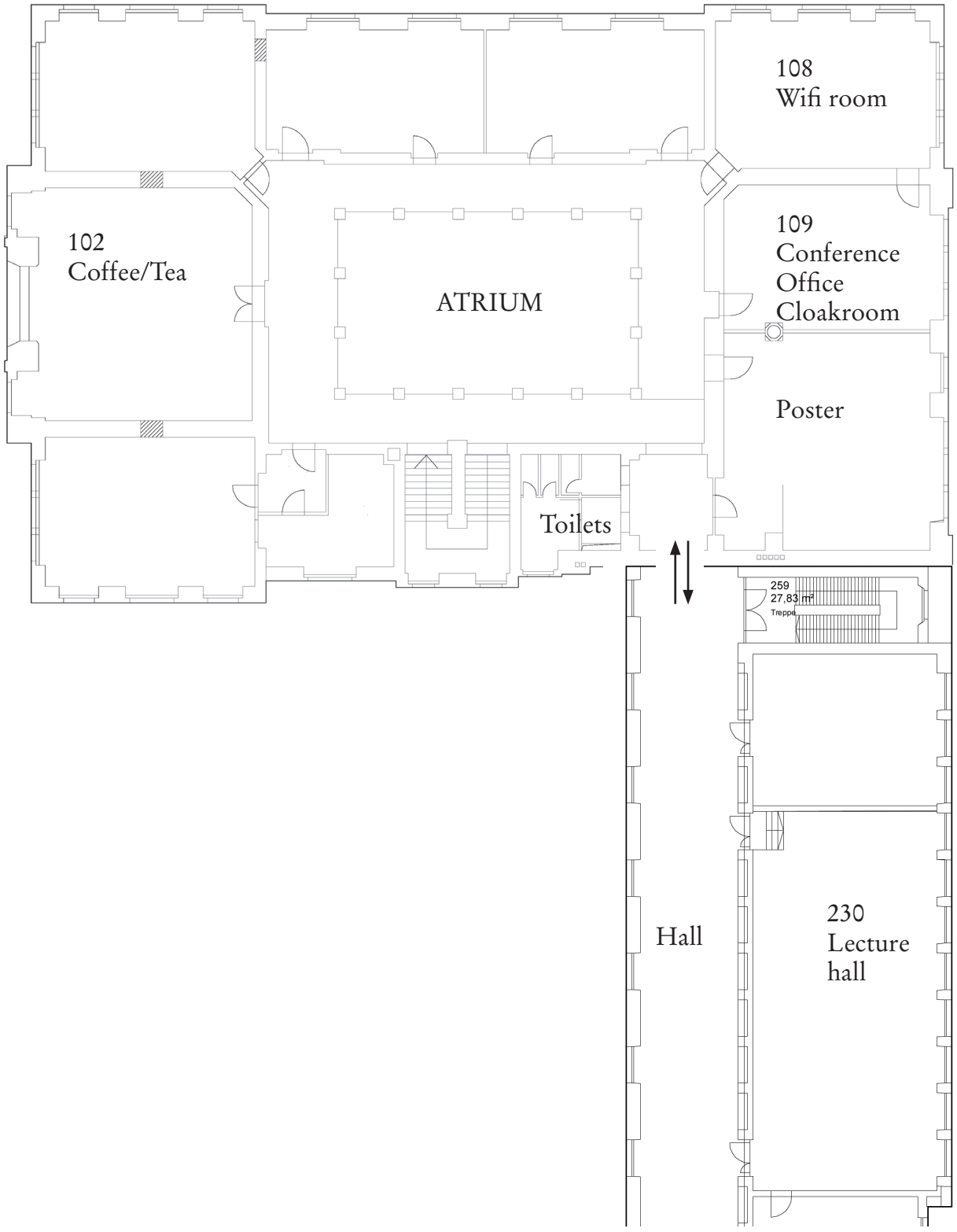

Programme

Symposium 1: Innovations in analyses of molecular and morphological data Wednesday, October 12, 2011		
Time	**Speaker**	**Titel**
8.30-9.00		Opening Ceremony Welcome addresses
9.00-9.30	Misof, B.	Introduction
9.30-10.00	Anisimova, M.	Fast and accurate evaluation of phylogenetic clade support
10.00-10.30	Stamatakis, A.	Fishing in the dark: Trying to identify rogue taxa
10.30-11.00		*Coffee break*
11.00-11.15	de Oliveira Martins, L. & Posada, D.	Inference of species tree distribution using a probabilistic reconciliation cost
11.15-11.30	Nguyen, M. A. T. et al., von Haeseler, A.	MISFITS: Evaluating the goodness of fit between a phylogenetic model and an alignment
11.30-11.45	Rota Stabelli, O. et al.	Parallel codon usage and compositional bias in deep phylogenomic
11.45-12.00	Conrad et al., Poustka, A. J.	Runtime optimation of complex mixture models of phylobayes for large scale phylogenetic tree reconstruction using GPU`s.
12.00-13.30		*Lunch*
13.30-14.00	Boussau, B. et al.	Integrative models of genome evolution
14.00-14.30	Kück, P. et al.	Detection of bias in simulated and real data
14.30-14.45	Wilkinson, M. & Day, J.	Testing hard polytomies with partial splits
14.45-15.00	Groussin, M. et al.	The COaLA Model: a Time Non-Homogeneous Model of Evolution Based on a Correspondance Analysis
15.00-15:15	Klopfstein, S. et al.	How deep is the hymenopteran tree? A total-evidence approach to dating with fossils
15.15-15.30	Bernt, M. & Middendorf, M.	Rearrangement Analysis for Large Sets of Gene Orders: Towards Reconstructing the Evolution of Metazoan Gene Orders
15.30-16.00		*Coffee break*
16.00-16.30	Stadler, P.	Molecular morphology: higher order characters derived from sequence data
16.30-16.45	Vogt, L. & Grobe, P.	Using the matrix module of Morph•D•Base for collaboratively editing character matrices live and online
16.45-17.00	Böhmer, C. et al.	Hox code and vertebral morphology in archosaurs
17.00-17.15	Greenwood, J. et al.	Mapping metazoan morphospace
17.30-20.00		**Poster session with bavarian beer**

Symposium 2: Molecular phylogeny: new markers and phylogenomic analyses Thursday, October 13, 2011		
Time	**Speaker**	**Titel**
9.00-9.30	Wörheide, G.	Introduction: the status quo of higher-level metazoan phylogeny based on phylogenomic analyses
9.30-10.00	Philippe H.	Resolving difficult phylogenetic questions: why adding more sequences is not enough
10.00-10.30	Lavrov, D. V.	Mitochondrial genomic diversity in non-bilaterian animals: implications for phylogeny and evolution
10.30-11.00		*Coffee break*
11.00-11.15	Schierwater, B. et al.	Can we resolve the base of the Metazoa: If yes, why not?
11.15-11.30	Ryan, J. et al.	The genome of the ctenophore Mnemiopsis leidyi and its impact on our understanding of animal history
11.30-11.45	Nosenko, T. et al.	Early metazoan phylogeny: identifying obstacles and solutions
11.45-12.00	Huchon, D. et al.	Illuminating the phylogenetic position of Myxozoa using next-generation sequencing
12.00-13.30		*Lunch*
13.30-14.00	Peterson, K. J.	MicroRNAs and the Evolution of Metazoan Complexity
14.00-14.30	Hausdorf, B.	Phylogenomic relationships between lophotrochozoan phyla – phylogenetic signal versus systematic errors.
14.30-14.45	Merkel, J. et al.	A morpho-molecular approach to assess phylogeny – first developmental data of Entoprocta
14.45-15.00	Wey, A. R. et al.	About wheels, thorns and trees – The phylogeny of Syndermata in the light of EST data
15.00-15:15	Lieb, B.	What do DNA, RNA and proteins tell us about molluscan phylogeny?
15.15-15.30	Helm, C. et al.	On the phylogenetic position of Myzostomida – integrating molecules and morphology
15.30-16.00		*Coffee break*
16.00-16.30	von Reumont, B.	Discovering the evolution of arthropods: prospects and pitfalls of molecular methods including phylogenomic data
16.30-16.45	Burmester, T. et al.	A phylogenomic approach to arthropod relationships and divergence times
16.45-17.00	Simon, S. & Hadrys, H.	Pterygote phylogenomics: The evolutionary history of genes and their impact on the topology
17.00-17.15	Meusemann, K. et al.	Phylogeny of primary wingless hexapods: chances, challenges and pitfalls of "phylogenomic" approaches
17.15-17.30	Pisani, D. et al.	MicroRNA and phylogenomics congruently resolve the phylogenetic relationships of the Tardigrada within Ecdysozoa
17.30-19.00		**Poster session with bavarian beer**
19.00-19.45	Donoghue, P.	**Evening lecture:** Reconciliation of fossils, molecules and morphology.

Symposium 3: The evidence found in morphology Friday, October 14, 2011		
Time	**Speaker**	**Titel**
9.00-9.30	Richter, S.	The role of morphology in evolutionary research
9.30-9.45	Nickel, M. et al.	Evolution of body contractility in early branching Metazoa – what morphology of Porifera and Placozoa tells us
9.45-10.00	Gruhl, A. et al.	Minicollagen expression supports homology of myxozoan and cnidarian organelles
10.00-10.30	Loesel, R.	Reviewing neurophylogeny – advances since the turn of the millennium
10.30-11.00		*Coffee break*
11.00-11.15	Hejnol, A.	Reconstructing the ground pattern of the Acoelomorpha – molecular patterning of the blind gut, nervous system and other features
11.15-11.30	Rieger, V. et al.	Development of the nervous system in hatchlings of Spadella cephaloptera (Chatognatha)
11.30-11.45	Purschke, G.	Unpigmented ciliary photoreceptor cells and organs in Annelida – diversity and importance for in-group phylogenetic relationships
11.45-12.00	Ullrich-Lüter, E. M. et al.	Function and evolution of echinoid photoreceptors
12.00-13.30		*Lunch*
13.30-14.00	Lowe, C.	Uncoupling morphological and molecular evolution: deep deuterostome origins of the vertebrate head developmental program
14.00-14.30	Stach, T.	Phylogenetic patterns from morphogenetic processes
14.30-14.45	Fritsch, M. & Richter S.	From a clam shrimp to a water flea: evolutionary insights from developmental sequences in the nervous system of branchiopod larvae (Crustacea)
14.45-15.00	Maas, A. et al.	Deep crustacean phylogeny
15.00-15:15	Pennerstorfer, M. & Scholtz, G.	Early cleavage in Phoronida shows spiral features
15.15-15.30	Ruthensteiner, B. et al.	Highly variable patterns in development of metanephridial and coelomic system in molluscs
15.30-16.00		*Coffee break*
16.00-16.30	Laubichler, M. D.	Reconstructing ancestors: the lessons from developmental evolution
16.30-16.45	Koch, M. et al.	Morphogenesis and homology of coeloms and nephridia in annelids and arthropods
16.45-17.00	Kaller, T. et al., Hausen, H.	The “division of labour model” for cell type specialization of annelid cerebral eyes
17.00-17.15	Schmidt-Rhaesa, A. & Rothe, B. H.	The nervous system of Nemathelminthes – is the taxon Nemathelminthes valid?
17.15-17.45	Jenner, R. A.	Please mind the gaps: exploring the limits of our understanding of animal body plan evolution
17.45-18.15	DMP Organizers	Concluding Remarks: Deep Metazoan Phylogeny – where to now?; Poster award
19.00-23.00		**Conference Dinner**

Molecular phylogeny: new markers and phylogenomic analyses - Poster B1

Do developmental toolkits of the basal metazoans carry phylogenetic signal?

Marcin Adamski[1], Sofia Fortunato[1], Brith Bergum[1], Sven Dirk Leininger[1], Hans Tore Rapp[2], Maja Adamska[1]
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Branching order of the basal metazoans (sponges, ctenophores, cnidarians and placozoans) remains a contentious issue, and is additionally complicated by the possible paraphyly of sponges. To resolve the deep branches of the animal tree of life, it is thus necessary to include genomes representing all three sponge lineages: demosponges, homoscleromorphs and the calcarea. Until recently, the genome of demosponge *Amphimedon queenslandica* served as the only representative of sponges.

Here we report on progress of sequencing, assembly and analysis of the genome of a calcareous sponge, *Sycon ciliatum* . The genome and transcriptome have been sequenced using combination of the "next generation" Illumina and 454 sequencing technologies, as well as Sanger sequencing. Assembled genome covering approx. 220 megabases is now being annotated using staged transcriptome sequences from reproductive and non-reproductive adults, larvae, juveniles and regenerating fragments.

We have focused our initial analysis on selected components of the developmental toolkit: signaling pathways (wnt, tgf-beta, hedgehog and notch) and developmental transcription factors (t-box, sox, fox, homeobox and bhlh families). Many of these gene families are significantly larger in *Sycon* than in *Amphimedon* . At the same time, within given gene family the two sponges often contain different complements of paralogs shared with the eumetazoans. This suggests that genomes of extant sponges were shaped by significant gene loss and lineage-specific expansion of gene families. We conclude that care should be taken when attempting to use gene content as one of ways to unravel phylogenetic relationships.

Innovations in the analyses of molecular and morphological data - Invited

Fast and accurate evaluation of phylogenetic clade support

Maria Anisimova
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I will discuss fast approximate likelihood-based methods for evaluating branch supports of inferred phylogenies (aBayes, aLRT and SH-aLRT), and how these compare to more traditional Bayesian and maximum likelihood bootstrap supports. Model violations make it almost impossible for any support measures to be interpreted as probabilities of inferred clades to be true. An interpretation of branch support based on frequentist-like error rates is more informative. The concepts are illustrated in simulations and with examples from real data.

Overlap in appearance of the protonephridia and the metanephridial system in a mollusc

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As typical for many spiralian taxa, in the polyplacophoran mollusc *Lepidochitona corrugata* two types of excretory systems are formed during development: The anteriorly located, larval-juvenile, paired protonephridia (head kidneys) and the posterior juvenile-adult metanephridial system. The protonephridia exhibit two remarkable features: (1) They achieve their peak level of development (size, structural differentiation) after metamorphosis, thus in the juvenile life phase. (2) The organs form voluminous pouch-like differentiations in the duct, the protonephridial kidneys, previously unknown from molluscan protonephridia. The metanephridial system, consisting of pericardium plus heart and the kidney, is formed during early juvenile development from an anlage giving rise to all components of the organ system. Both organ complexes, the protonephridia and the metanephridial system, overlap in presence for a substantial period during juvenile development and they also show striking resemblances. These include the ultrafiltration sites with slits between regularly arranged pedicles and the reabsorptive differentiations of the ducts (kidneys), which show identical histology and cytology.

The close similarities in organisation indicate that there is a serial (iterative) homology of protonephridia and the metanephridial system at the level of organs within the Mollusca. Furthermore, the elaborate protonephridial kidney of juvenile polyplacophorans might shed light on the homology relations of anterior located kidneys of adult monoplacophorans, which might represent homologues of head kidney protonephridia.

Nemertean nervous system: A comparative analysis

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During the last decade immunochemical methods were used for analyzing spiralian nervous system. While there are many studies available for, e.g., platyhelminthes, annelids or molluscs, only a single nemertean species, the heteronemertean *Lineus viridis* , has been studied. Since heteronemerteans represent a derived clade within Nemertea, primary conditions in the nervous system of nemerteans can hardly be inferred from this study. In order to provide a sound picture of the primary design of nemertean nervous system, specimens particularly belonging to basally branching groups were examined using 3D-reconstruction techniques based on histological slices. Immunochemistry was applied to reveal the anatomy of the peripheral nervous system. The different nerve plexus turned out to be promising characters for unraveling the internal relationship of nemerteans, since their neurites are differently arranged in various body parts. Another promising set of characters are the neuronal somata revealed by classical Azan staining. According to the data achieved, the central nervous system (CNS) of nemerteans consists of a brain which surrounds the rynchocoel and two lateral medullary cords which run to the posterior of the animal where they unite. The brain and lateral medullary cords of nemerteans is composed of a central neuropil which is surrounded by a layer of cell somata. The nemertean nervous system displays an unexpected anatomical diversity which includes positional variation with respect to the body wall muscles as well as differences in the arrangement of the neurites in the neuropil of the brain, the cell somata and the possession of a cerebral organ.

Innovations in the analyses of molecular and morphological data - Oral Presentation

Rearrangement analysis for large sets of gene orders: Towards reconstructing the evolution of metazoan gene orders

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Mitochondrial gene orders are supposed to be a good source of information for phylogenetic investigations, particularly for the analysis of deep metazoan phylogenetic relationships. One possibility to access this information is to reconstruct parsimonious rearrangement scenarios, e.g., for pairs of species or along the edges of a given phylogenetic tree starting from the leaves that correspond to the gene orders of contemporary species.

CREx is a heuristic method for computing short pairwise rearrangement scenarios. Compared to other methods CREx has the advantage that it considers four different types of gene order rearrangement operations: inversions, transpositions, inverse transpositions, and tandem duplication random loss operations. This makes CREx suitable for studying genome rearrangements in metazoan mitochondrial genomes.

Here we present a method for selecting a reliable set of pairwise rearrangement scenarios for a large set of gene orders. The method is based on the set of all pairwise rearrangement scenarios that are reconstructed with CREx and from which a subset is selected. The reconstructed rearrangements are organised in a graph that is called rearrangement inventory graph (RI-graph). The new method has been applied to the gene orders of all known complete mitochondrial genomes. The resulting RI-Graph gives an unprecedented comprehensive overview of likely rearrangements that occurred within the different phyla. Many of the automatically computed rearrangement scenarios within the RI-Graph were in agreement with published results. Additionally, several interesting previously unknown scenarios which are potential alternatives to published rearrangement scenarios have been identified.

The evidence found in morphology - Poster C3

Neuroanatomy in apterygote insects: the brain of Diplura

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The brain of representatives of both suborders of Diplura was investigated using 3D-reconstruction of semithin section series and antibody staining. Diplura possess elaborate mushroom bodies, a complex deutocerebrum with spheroidal glomeruli (which differ significantly in size and number between Dicellurata and Rhabdura), and a central body that is divided into discrete columns which are organized in three layers. In *Catajapyx* one of the mushroom bodies is interconnected across the midline, a condition unique among hexapods. The brain organization of Diplura is compared to other apterygotes. While Protura and Archaeognatha lack mushroom bodies, they are present in Zygentoma and possibly in Collembola. The evolutionary origin and transformations of the various brain structures in early hexapods are discussed.

Innovations in the analyses of molecular and morphological data - Oral Presentation

Hox code and vertebral morphology in archosaurs

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A characteristic feature of sauropodomorph dinosaurs is not only highly complex vertebral morphology, but also highly variable vertebral count. The exact mode and pattern of variation is largely unknown. In the absence of other criteria, such as specific soft tissue associations, or genetic information, axial morphology is the only clue to resolve this issue.

Hox genes are of considerable importance in anteroposterior patterning of the metazoan body plan. In vertebrates, the functions of this special group of homeotic genes include the specification of the vertebral shape. It has been proposed that a unique or highly distinctive axial *Hox* code (a combination of *Hox* genes) expressed in each somite specifies each of the different vertebral morphologies. This link between gene expression and morphology suggests that *Hox* genes may have played an important role in the evolution of specific axial variation.

The study of morphological variation as a proxy for *Hox* gene expression provides an opportunity to re-examine aspects of morphology in extinct taxa and address questions that have long been problematic for evolutionary biologists.

First, we will establish the *Hox* code for the formation of the presacral vertebral column in recent archosaurs and reconstruct the ancestral *Hox* code for archosaurs on this basis. Second, we will test whether there is a direct linkeage between change in *Hox* gene expression and quantifiable morphology of presacral vertebrae in recent archosaurs. Third, we will try to establish *Hox* gene expression in fossil archosaurs, including sauropodomorphs, on the basis of quantifiable changes in morphology.

Innovations in the analyses of molecular and morphological data - Invited

Integrative models of genome evolution

Bastien Boussau[1,2], Gergely Szollosi[1], Laurent Duret[1], Manolo Gouy[1], Eric Tannier[1], Vincent Daubin[1]
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Species trees are usually built as an average of the phylogenetic signal of at most a few dozens of gene families. These gene families are selected because of their simple history, apparently devoid of duplications and losses. However, these gene families may have undergone hidden duplication and loss events, in which case their phylogeny may differ from the species phylogeny: in such circumstances, the reconstructed species tree may differ from the true species tree. Contrary to such common approaches, we propose to model gene family evolution in the presence of gene duplication and loss, and consequently separately infer gene family trees and species tree. Importantly, this enables inferring species trees based on all gene families in genomes, and based on the phylogenetic information contained in events of gene duplication and loss. In this model, each branch of the species tree is associated to particular duplication and loss parameters to accommodate heterogeneity in the processes of genomic evolution. We explain how one can efficiently compute the likelihood of a species tree and gene family trees with such a model, and present its parallel implementation in PHYLDOG, a program able to analyze simultaneously dozens of species and thousands of gene families in a statistical framework. We show that PHYLDOG performs very well on simulated data, and we reveal general trends of genomic evolution by applying it to more than 7000 gene families in 37 whole genome sequences from mammalian species.

Molecular phylogeny: new markers and phylogenomic analyses - Poster B2

A one-two punch: Anthozoans are characterized by extremely low rates of mitochondrial DNA sequence evolution and variable nuclear markers remain elusive

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Reconstructing relationships among cnidarians is complicated by extremely low rates of mitochondrial (mt) DNA sequence evolution within anthozoans. With the exception of some stony corals, anthozoans examined to date are characterized by synonymous substitution rates 50-100 times slower than most metazoans and variation is almost nonexistent at the intraspecific level. Currently applied nuclear markers (i.e. , nuclear ribosomal cistron 18S-ITS1-5.8S-ITS2-28S) are not sufficiently variable to differentiate some putative species.

To further explore the rate of mtDNA sequence evolution within anthozoans, we sequenced complete mitochondrial genomes for six putative species of black corals (Hexacorallia: Antipatharia: Leiopathidae) from the Gulf of Mexico, Western N. Atlantic, N. Pacific, and Mediterranean Sea. Among the six genomes (length: 21,669 bp each), we observed only 70 variable sites, 32 of which were autapomorphies within a single individual.

Anthozoan systematists and taxonomists face a daunting challenge: in addition to slow mt sequence evolution and a lack of variable nuclear markers, simple body plans reduce the number of morphological characters available to define a species. Mosaics of characters currently distinguish actiniarians (sea anemones) and evolutionary relationships are largely based on an absence of features. We are currently searching for variable nuclear markers both for species-level identification and phylogenetic reconstruction of the order (1,200 species in 46 families). Variable markers will ultimately help determine which external / internal morphological characters are species-specific. Our initial screening of novel nuclear markers across a broad sampling of the genus *Aiptasia* will be presented.

Molecular phylogeny: new markers and phylogenomic analyses - Oral Presentation

A phylogenomic approach to arthropod relationships and divergence times

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Arthropods represent the most diverse and specious animal phylum. Although there is conclusive evidence that arthropods are member of the superphylum Ecdysozoa, its actual sister taxon has still to be determined. Likewise, the relationships among the arthropods are matter of intense debate. We employed a phylogenomic approach to resolve the arthropod tree of life. Expressed sequence tags (ESTs) were obtained from the priapulid Halicryptus spinulosus, the scorpion Pandiunus imperator, the harvestman Phalangium opilio, the sunspider Gluvia dorsalis, the pseudoscorpion Chelifer cancroides, the whip scorpion Mastigoproctus giganteus, the whip spider Euphrynichus bacillifer, the centipede Scolopendra subspinipes and the diplopod Polyxenus lagus by next generation pyrosequencing. Phylogenetic analyses employed >100 selected orthologous genes and included more than 100 arthropod species. First results show that Tardigrades are not closely related to the arthropods, but form a common clade with the Nematoda. Arachnids were found paraphyletic because the Acari (tick and mites) occupy a basal position within the Euchelicerates. The position of the Myriapoda still remains unresolved. A molecular clock approach suggest that arthropods emerged ~600 million years ago (MYA). Onychophorans and euarthropods split ~574 MYA, Pancrustacea and Myriochelata ~562 MYA, Myriapoda and Chelicerata ~555 MYA, and paraphyletic Crustacea and Hexapoda ~510 MYA. Endopterygote insects appeared ~390 MYA.

Runtime optimation of complex mixture models of phylobayes for large scale phylogenetic tree reconstruction using GPU`s.

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The complete genome sequences and hence the availability of all genes of thousands of organisms are upcoming. Phylogenetic reconstructions using extremely computing expensive algorithms such as CATGTR of the phylobayes package, which may be ideal to reconstruct deep phylogenies and correct for long branch attraction errors (LBA) are becoming impossible tasks for very large datasets. For this reason we have begun to explore the possibilities to develop parallelised versions of the CATGTR module of phylobayes to improve its propagate function. It is hoped to reduce runtime by replacing and improving the used matrices by functions of the JCuda package. The porting of data necessary for runtime is being tested and realised in two different approaches. With the first possibility the porting is achieved by using the ICE package. Here, a server is started on the graphics processing unit (GPU), which then receives the necessary data from a client started by phylobayes, processes them and sends them back.

The second possibility for the porting can be completely processed on the GPU itself. Here, the aim is to start the Java Native Interface by phylobayes itself, to enable the direct access to the needed Java(JCuda)-functions out of the C++ function.

Preliminary benchmarks will be presented.

Innovations in the analyses of molecular and morphological data - Oral Presentation

Inference of species tree distribution using a probabilistic reconciliation cost

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The species tree can differ from estimated gene trees not only by stochastic factors but also by biological phenomena like horizontal gene transfer, incomplete lineage sorting or duplications and losses. As we accumulate more data from gene families, we expect that the signal from the species tree can be reconstructed despite these confounding factors. In the present work we develop a hierarchical Bayesian model that estimates the posterior distribution of species trees by importance sampling of the phylogenies for a group of gene families over these given species.

Our model is based on the distance between each gene family tree and the species tree, where the distance is calculated as the most parsimonious scenario of duplications, losses, and root location - that is, the reconciliation cost. This model can be interpreted as an extension of the gene tree parsimony, where instead of searching for the species tree that minimizes the total reconciliation cost we try to infer the distribution of species trees, with frequencies proportional to this reconciliation cost. Uncertainty in the gene phylogenies is taken naturally into account, and for unrooted gene trees the reconciliation cost will be the minimum over all possible rootings. The importance sampling depends on a previous Bayesian phylogenetic analysis of each gene family, and will re-weight each individual gene tree based on its agreement with the other gene families.

Molecular phylogeny: new markers and phylogenomic analyses - Poster B3

Molecular paleobiology of early-branching animals: integrating DNA and fossils elucidates the evolutionary history of hexactinellid sponges

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Reconciliation of paleontological and molecular phylogenetic evidence holds great promise for a better understanding of the temporal succession of cladogenesis and character evolution, especially for taxa with a fragmentary fossil record and uncertain classification. In zoology, studies of this kind have largely been restricted to Bilateria. Hexactinellida (glass sponges) readily lend themselves to test such an approach for early-branching (non-bilaterian) animals: they have a long and rich fossil record, but for certain taxa paleontological evidence is still scarce or ambiguous, which is further exacerbated by a lack of consensus for taxonomic interpretations, and discrepancies between neontological and paleontological classification systems. Using conservative fossil calibration constraints and the largest molecular phylogenetic dataset assembled to date for this group, we infer divergence times of crown-group Hexactinellida in a Bayesian relaxed molecular clock framework. With some notable exceptions, our results are largely congruent with interpretations of the hexactinellid fossil record, but also indicate long periods of undocumented evolution for many groups. This study highlights the potential of an integrated molecular/paleobiological approach to reconstruct the evolution of challenging groups of organisms such as sponges.

Molecular phylogeny: new markers and phylogenomic analyses - Evening Lecture

Reconciling fossils, molecules and morphology in deep metazoan phylogeny

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In these more enlightened times it just seems ironic that there was once a heated controversy over the competing roles of morphology and molecules in elucidating evolutionary history. To be sure, it will never be possible to recover sequence data from the fossil organisms that populate the deep branches in metazoan phylogeny. But if our ultimate aim is to uncover organismal evolution – even through comparative genomics or comparative development – the fossil record remains integrally germane. Palaeontological data inform on the extent of evolutionary history, on the sequence and tempo of phenotypic character evolution and their geologic context also informs on the extrinsic environment and its evolution. However, there is nothing particularly unique about palaeontological data – it is much like any other kind of morphological data. Nevertheless, fossil data have been singularly influential in testing hypotheses – e.g. of development evolution, or the nature of ancestral organisms - because fossils have been all too frequently overlooked. Thankfully, there is a growing appreciation of the value of palaeontological data. At the same time, palaeontologists are increasingly recognizing that evolutionary history has not been written solely in stone, that it is possible to address core palaeontological problems using comparative developmental genetics to test hypotheses of homology, and using molecular phylogenetics to resolve phylogenetic problems. The development of mixed model phylogenetic methods are particularly promising in facilitating the comparative analysis of fossil and living taxa, drawing upon the power of both comparative morphological and molecular data, to better constrain understanding, even of Deep Metazoan Phylogeny.

The evidence found in morphology - Poster C4

Molecular characterization of photoreceptor cells in *Macrostomum lignano* (Macrostomida, Plathelminthes)

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In order to decipher evolutionary changes at the phylum level the understanding of the evolution of the "fundamental unit of multicelluar organisms" – the cell types – is gaining importance as a basic principle. This cell type approach, also known as "molecular fingerprinting", requires the collection of comparable data sets across different phyla. Recent work established a molecular fingerprint for various sets of photoreceptor cells in the marine annelid *Platynereis dumerilii* . The aim of my project is to complement and complete profiling data on the photoreceptor cells of the meiobenthic flatworm *Macrostomum lignano* , an emerging reference animal. Combined analysis of the molecular data with morphological information obtained by electron microscopy in *M. lignano* will be compared with similar data obtained for other lophotrochozoan groups. Our study is expected to shed new light on the evolution of photoreceptor cells within Lophotrochozoa.

Molecular phylogeny: new markers and phylogenomic analyses - Poster B4

A consistency-based reconstruction of the fungal tree of life

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The kingdom of fungi provides model organisms for biotechnology, cell biology, genetics, and life sciences in general. Only when their phylogenetic relationships are stably resolved, individual results from fungal research can be integrated into a holistic picture of biology. However, and despite recent progress many deep level relationships within the fungi remain unclear. Here we present the first phylogenomic study of an entire eukaryotic kingdom that uses a consistency criterion to strengthen phylogenetic conclusions. We reason that splits recovered with independent data and different tree reconstruction methods are likely to reflect true evolutionary relationships. Two complementary data sets based on 99 fungal genomes and 109 fungal EST sets analyzed with four different tree reconstruction methods shed light from different angles on the fungal tree of life. Three further data sets address specifically the phylogenetic position of Blastocladiomycota, Ustilaginomycotina and Dothideomycetes, respectively. The combined evidences from the resulting trees support the deep-level stability of the fungal groups towards a comprehensive natural system of the fungi. Our analysis revealed a methodologically interesting side aspect. Enrichment for EST encoded data –a common practice in phylogenomic analyses– introduces a strong bias toward slowly evolving and functionally correlated genes. Consequently, the generalization of phylogenomic data sets as collections of randomly selected genes cannot be taken as granted. A thorough characterization of the data to assess possible influences on the tree reconstruction should be therefore become a standard in phylogenomic analyses.

The evidence found in morphology - Poster C5

Morphogenesis in sponges and their phylogenetic significance

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In Metazoa, there are two types of morphogenetic processes: mesenchymal and epithelial ones. To understand the evolution of morphogenesis during animal diversification, it is necessary to compare these processes between sponges and eumetazoans. Sponges branch basally in the metazoan phylogenetic tree and are composed of four distinct lineages. Recent molecular studies propose that Homoscleromorpha are distinct from Demospongiae in which they were traditionally classified. To this purpose, the Homoscleromorpha lineage is really worth studying since it is notably the only sponge group to possess a basement membrane with collagen IV and specialized cell-junctions. The consequence of this organization is the predominance of epithelial morphogenesis during their embryonic development, metamorphosis, growth, asexual reproduction and regeneration. In contrast, the other three sponges clades (Hexactinellida, Demospongiae and Calcarea) are characterized by mesenchymal morphogenesis.

Presently, there are two hypotheses concerning sponges phylogenetic status. The first one proposes the sponge monophyly. In this case, the epithelium appears either in the common ancestor of Metazoa, (and have probably been lost in Hexactinellida, Demospongiae and Calcarea branches), or this character has been acquired independently in the branches leading to Homoscleromorpha and Eumetazoa. In the sponge paraphyly hypothesis, the epithelium has been acquired only once in the branch leading to Homoscleromorpha and Eumetazoa clades. In both cases, Homoscleromorpha appears to be the most relevant sponge group to study for comparison with eumetazoan taxa.

Molecular phylogeny: new markers and phylogenomic analyses - Poster B5

Horny sponges and their affairs: On the phylogenetic relationships of keratose sponges

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The demosponge orders Dictyoceratida and Dendroceratida comprise the keratose (or "horny") sponges, which are (mostly) devoid of own mineral skeletal elements, but possess an elaborate skeleton of organic fibres instead. This paucity of complex mineral skeletal elements makes their unambiguous classification and phylogenetic reconstruction based on morphological features difficult. Here we present the most comprehensive molecular phylogeny to date for the Dendroceratida, Dictyoceratida, and also the Verongida, based on independent mitochondrial and nuclear markers. We validate the coherence of all classically (morphologically) recognized orders, families and subfamilies, discuss the significance of keratose morphological and chemotaxonomic characters and suggest adapted definitions for the classification of dendroceratid, dictyoceratid, and verongid higher taxa. We find chondrosid sponges nonmonophyletic with respect to Halisarcida. Verongida and Dendroceratida are monophyletic but most of their classically recognized families cannot be recovered, which indicates that the distinction between dendritic and anastomose skeletal features is not significant at this level of classification. Dysideidae are the sister-group to the remaining Dictyoceratida, Irciniidae are a distinct clade, but Thorectidae and Spongiidae cannot be separated with the molecular markers used. We also suggest the name Verongimorpha for the clade combining verongid, chondrosid and halisarcid taxa.

The evidence found in morphology - Poster C6

Neurophylogeny of molluscs

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The nervous system of invertebrates is considered to be a very conservative organ system and thus can be helpful to elucidate questions of phylogenetic relationships. Up to now neurophylogenetic studies have been mainly focussed on arthropods, where in-depth studies on major brain structures are abundant. In contrast the nervous system of the second largest phylum of invertebrates, the molluscs, is as yet hardly investigated in detail. We therefore initiated an immunohistochemical survey to contribute new neuroanatomical data for several molluscan taxa, especially the lesser known Caudofoveata, Solenogastres and Scaphopoda, focusing on the cellular architecture and distribution of neurotransmitters in the brain. Here we present an overview of central nervous system architectures across molluscs in an attempt to reconstruct the neurophylogeny of this phylum.

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Molecular phylogeny: new markers and phylogenomic analyses - Poster B6

Distinguishing signal, noise and bias in early animal evolution: The difficult problem of the sponge phylogeny

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Early animal relationships are still hotly debated, and three main hypotheses have been proposed in the last few years. The first suggests that the sponges represent the monophyletic sister group of all the other Metazoa. The second suggests that sponges plus the Coelenterata and perhaps the Placozoa represent the sister group of all the other Metazoa (an hypothesis named Diploblastica), and the third suggests that sponges are paraphyletic, with the Demospongiae representing the sister group of all the other Metazoa, and a Homoscleromorpha representing the sister group of the Eumetazoa.

Recently evidence was provided suggesting that Diploblastica could be dismissed as the result of paralogy, alignment errors and tree reconstruction artifacts. However, it is still unclear whether sponges represent the monophyletic or the paraphyletic sister group of Eumetazoa. Here, we shall show results of reanalyses of two recently published data sets (Pick et al. 2010 and Philippe et al. 2009) and illustrate how the support for alternative sponge phylogeny changes when potential sources of phylogenetic bias are taken into consideration.

Our results confirm that Diploblastica is a phylogenetic artifact. In addition to that they also show that whether sponges are monophyletic (Pick et al. 2010 and Philippe et al. 2009) or paraphyletic as previously postulated by Sperling et al. (2009) is still unclear. Current evidence to resolve the phylogeny of the sponges is scant and more data and even better analyses might be necessary before a solution to this evolutionary problem will be found.

The evidence found in morphology - Oral Presentation

From a clam shrimp to a water flea: Evolutionary insights from developmental sequences in the nervous system of branchiopod larvae (Crustacea)

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Development is a continuous progress and involves a series of discrete developmental stages. Each developmental stage is separated from the subsequent by transformation of morphology. This progress in which discrete developmental forms follow a particular chronology is known as a developmental sequence. Within these sequences, distinct changes in chronology may appear and are considered as evolutionary transformations (heterochronic events).

In recent years developmental investigations of arthropods have seen a great revival. This has also brought about a renewed interest in the studies of evolutionary transformations. We are interested in the nervous system development and the evolutionary novelties within the Branchiopoda (Crustacea). One of the most interesting riddles in crustacean evolution is the origin of the Cladocera derived from a "conchostracan"-like ancestor. The current hypothesis is that the water-fleas evolved from a "sexually mature larvae" of a conchostracan-like ancestor. Herein, we present and compare the larval development of a representative of Spinicaudata, *Leptestheria dahalacensis* with that of Cyclestherida, *Cyclestheria hislopi*, the cladoceran sister group with conchostracan-like habitus but also cladoceran-like development. The nervous system ontogeny was investigated by alpha-tubulin markers and the expression pattern of a neurotransmitter, serotonin. To compare on the one hand the free swimming larvae in *L. dahalacensis* and on the other hand the "embryonized" larvae in *C. hislopi* we documented their developmental sequences and applied the event pairing method to show that the evolutionary transformations from a conchostracan-like ancestor to a water-flea appeared as a two-step-process.

Molecular phylogeny: new markers and phylogenomic analyses - Poster B7

The miRNA complement of *Gyrodactylus salaris* (Platyhelminthes, Monogenea)

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MiRNAs are single-stranded, 22 nucleotide long, non-coding transcripts derived from different genome encoded hairpin precursors that regulate gene expression negatively. They represent the most recently discovered gene regulators and are involved in a broad variety of biological processes. Gyrodactylus is an extremely diverse and widely distributed and species-rich genus of small ectoparasitic monogenean flatworms (500µm size in average). Gyrodactylus salaris has recently been introduced to Norway and caused severe damage to infected Atlantic salmon (Salmo salar) stocks since.

We extracted microRNA from 100 pooled Gyrodactylus salaris individuals, and subjected it to 2nd generation sequencing (Illumina GA2). We obtained 18 million smallRNA reads in total. We compared the high quality reads to the mirBASE database and checked them also against the available parts of the genomes of the closely related Schmidtea mediterranea and Schistosoma japonicum. This delivered a comprehensive first-glance set of candidate Gsa-miRNAs.

A main focus of the Evolutionary Parsitology Group at the NHM in Oslo is the genome sequencing project of Gyrodactylus salaris, which so far delivered data from a 454 run assembled in contigs, and 3 Illumina GA2 lanes.We checked each of our Gyrodactylus salaris miRNA reads against this preliminary Gyrodactylus salaris genome data, which identified and confirmed several of the candidate miRNA.

Molecular phylogeny: new markers and phylogenomic analyses - Poster B8

Phylogenetic position of the interstitial annelid taxa *Apharyngtus punicus* and Dinophilidae of supposedly paedomorphic origin

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Several annelid taxa are prominent members of marine interstitial habitats. Because of their small body size of a less than a few milimeters and apparently simple organisation (e.g. a few, vaguely differentiated segments, simple or lacking parapodia and chaetae, ventral ciliary gliding bands, etc.), some of them, such as *Apharyngtus punicus* and Dinophilidae, had been considered as primitive annelids. Conversely, these interstitial taxa were regarded as secondarily simplified annelids evolved by paedomorphosis, which is the retention of larval or juvenile characters in the adult stages of their descendants. Moreover, paedomorphosis has been regarded as the major evolutionary process responsible for the permanent colonization of interstitial habitats by meiofauna organisms in general. For example, besides a close relationship of *Apharyngtus punicus* and Dinophilidae, morphological data indicated a paedomorphic origin within Eunicida, or more precisely within "Dorvilleidae". However, first molecular phylogenetic analyses raised doubts on these hypotheses. Herein, using mitogenomic data, we show that a sistergroup relationship between *A. punicus* and Dinophilidae is strongly supported. The unpaired posterior copulatory organ in both taxa is eventually an autapomorphy for this clade. On the other hand, a closer relationship to Eunicida could not be retrieved. Hence, their origin by paedomorphosis is not as certain as proposed based on morphological data.

Innovations in the analyses of molecularand morphological data - Poster A1

An accurate algorithm of cubic complexity to build supertrees

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The problem statement. Important desired properties of an algorithm to construct a species tree (supertree) by reconciling input trees are its low complexity and applicability to large biological data. During "reconciliation" the algorithm minimizes the total cost of mappings of individual trees into the desired supertree over all input trees and inferred evolutionary events. Even if only duplication and loss events are allowed, this problem is proved to be NP-hard. In practice, supertree building algorithms, including various heuristic solutions, suffer from exponential complexity.

The solution. We propose a reformulation of the supertree building problem: the supertree is sought for such that it does not contain clades incompatible with those existing in the input trees. This requirement is biologically natural and allows a solving algorithm of cubic complexity. Our model incorporates duplications, losses, gains and horizontal transfers. It was extensively tested with simulated and biological trees and was shown to possess a square complexity in average even under the assumption of HGTs. Under no HGTs, the algorithm is mathematically correct and possesses the longest running time of n^3 x m^3, where n is a the number of input trees, and m is the total number of species. The corresponding program super3GL and its testing are freely available at http://lab6.iitp.ru/en/super3gl. The program is capable of processing large data (hundreds of species and thousands of trees simultaneously), including polytomic and unrooted trees. It is effectively implemented for both multiprocessor platforms with MPI-1.2, and single-CPU machines.

Mapping metazoan morphospace

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The evo-devo revolution was stimulated in part by Gould´s Wonderful Life thesis, that the Cambrian was an interval of biological innovation in which most animal bodyplans were established. While biologists have sought to explain this phenomenon of organismal disparity, it has only been codified at the level of local clades. We sought to characterise disparity at Class level for all animal phyla using the cladistic matrix implicit in Peter Ax's Phylogenetic system and performing Non-metric Multidimensional Scaling to summarise the variation within the bodyplans of living clades. We also sought to test the hypothesis that enigmatic Cambrian problematica represent fundamentally distinct bodyplans, by resolving these fossils to their agreed phylogenetic position and then optimizing their unknown character states. Fossil taxa do not contribute materially to the occupation of morphospace, perhaps because so much of their biology must be inferred based on their phylogenetic position. Thus, fossils either do not or cannot contribute to our understanding of the evolutionary exploration of morphospace except in terms of their inherent temporal constraints. Most phyla achieve maximal disparity early in their evolutionary history – with the exception of Arthropoda and Chordata, which underwent progressive expansion through the Phanerozoic. We tested hypotheses of causality by assessing the degree of correlation between our cladistic dataset and comparable matrices representing protein, cell type, and microRNA diversity. Disparity exhibits a strong correlation with expansions in cell type and microRNA diversity, but not proteomic complexity, suggesting that it evolved in hand with developmental regulation but not protein repertoire expansion.

The COaLA Model: a time non-homogeneous model of evolution based on a correspondance analysis

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In this work, we focused on the development of a new time non-homogeneous evolutionary model for protein sequences in the Maximum Likelihood (ML) framework. In classic approaches, the Markovian substitution process is supposed to be constant over time (homogeneous and stationary model). Ergo, all species share the same equilibrium frequencies in terms of amino-acid whereas in reality, variations of compositions are frequently observed between species. Heterogeneous amino acid compositions were proved to bias phylogenetic reconstructions of various groups of organisms, including within Metazoa, at both the nuclear and mitochondrial levels. Moreover, it has been shown as well that homogeneous models may also be poor to estimate ancestral compositions and sequences along a phylogenetic tree. To relax the homogeneity hypothesis, the usual approach is to allow the different branches of a phylogenetic tree to have their own free equilibrium frequencies. The major drawback of such a modeling is the unrealistic number of parameters involved in the model. We propose here a way to model the non-homogeneity of the evolutionary process by considerably reducing the number of parameters, thanks to the use of a Correspondance Analysis that allows to explore a sub-space of the total variance originally present in the data. It then becomes feasible to use such models in the ML framework, in a reasonable time.

Simulation experiments showed that the COaLA model (COrrespondance and Likelihood Analysis) performs really well in estimating the ancestral amino-acid frequencies. The model was also used on different biological data sets and interesting results will be presented.

The evidence found in morphology - Oral Presentation

Minicollagen expression supports homology of myxozoan and cnidarian organelles

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Recent phylogenomic analyses suggest a cnidarian affinity for the parasitic Myxozoa, but phylogenetic analyses based on 18S rDNA are not always consistent with this interpretation. The most convincing synapomorphy of myxozoans and cnidarians is the possession of cell organelles with extrusible filaments: nematocysts in the free-living cnidarians and polar capsules in myxozoans. However, homology of these organelles has not been tested in detail. Cnidarian nematocyst walls are reinforced by minicollagens - proteins unique to Cnidaria and therefore regarded as phylum-specific markers (Milde et al. 2009 Genome Biol. 10:1). A putatively homologous minicollagen gene, Tb-Ncol-1, has now been found in a survey of ESTs in the myxozoan *Tetracapsuloides bryosalmonae* (Holland et al. 2011 Proc. R. Soc. B 278:546-553). To test whether Tb-Ncol-1 gene products are utilised in a similar way to minicollagens in cnidarian nematocysts we use an antibody to localise the Tb-Ncol-1 protein in *T. bryosalmonae* during polar capsule morphogenesis . Tb-Ncol-1 immunoreactivity firstly appears in small vesicles in the cytoplasm of the capsulogenic cells. As these vesicles enlarge Tb-Ncol-1 is distinctly localised in the vesicle walls except for the site where the polar filament is presumably forming. Following further maturation of the polar capsules, Tb-Ncol-1 immunoreactivity fades, consistent with hydrozoan nematogenesis where masking of antigenic sites occurs during minicollagen cross-linkage. The overall pattern revealed is highly similar to morphogenesis in cnidarian nematocysts, thus supporting homology between polar capsules and nematocysts and a common ancestry of Myxozoa and Cnidaria.

The evidence found in morphology – Poster C7

The first sequenced genome of a twisted-wing parasite (Insecta: Strepsiptera) and its phylogenetic implications

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Twisted-wing parasites are endopterygote insects with a highly derived morphology and life history, whose phylogenetic relationship has proven notoriously difficult to resolve ("The Strepsiptera problem"). We sequenced the genome of a twisted-wing parasite with the aim to utilize information of whole genomes to clarify the phylogenetic affinities of this intriguing and enigmatic group of insects. The genome was sequenced to an estimated >14x coverage with 454-pyrosequencing. Using a combination of ab initio and evidence-based gene prediction, we annotated ~13,000 genes with high confidence. Roughly 4,500 of these proved to be orthologous among endopterygote and paraneopteran insects. After removing ambiguously aligned sites, the dataset of orthologous genes consisted of 1.8 million codon sites. To minimize a confounding impact of inhomogeneous nucleotide or amino acid frequencies among sequences in the phylogenetic analysis, we analyzed RY-recoded second codon positions only. Maximum likelihood estimates overwhelmingly suggest a close phylogenetic relationship of twisted-wing parasites and beetles. Hadamard conjugation indicates no plausible conflict in the phylogenetic signal. An independent phylogenetic estimate derived from corrected rearrangement distances of chromosomal gene order gives congruent results.

We are currently analysing other genomic meta characters like protein domain content, presence/absence of miRNAs and snoRNAs, and the position of introns within genes.

Molecular phylogeny: new markers and phylogenomic analyses - Invited

Phylogenomic relationships between lophotrochozoan phyla – phylogenetic signal versus systematic errors

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One of the major rearrangements of the animal phylogeny based on molecular data was the shift of the lophophorate lineages from the base of Deuterostomia into Protostomia, where they were amalgamated with phyla characterized by trochophora larvae and/or spiralian cleavage to form Lophotrochozoa. Although the existence of this assemblage of phyla has been affirmed by various molecular data, their interrelationships remained puzzling. In the past years, especially phylogenomic analyses suggested new hypotheses about the relationships between lophotrochozoan phyla like Kryptozoa uniting Nemertea, Brachiopoda and Phoronida and resurrected old ones like the classical Bryozoa including Ectoprocta, Entoprocta and Cycliophora. The reliability of such hypotheses is discussed in consideration of bias in compositional heterogeneity of sequences and in substitution rates between taxa that may cause systematic errors in phylogenetic inference.

The evidence found in morphology - Oral Presentation

Reconstructing the ground pattern of the Acoelomorpha - molecular patterning of the blind gut, nervous system and other features

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Molecular and morphological data place the Acoelomorpha, a taxon that comprises the taxa, Acoela, Nemertotodermatida and Xenoturbellida, as the sister group to all the remaining bilatarian animals. Although this view has been recently challenged, these animals show a number of features that are thought to be ancestral for the Bilateria and thus bridge the transition of a Cnidarian-Bilaterian ancestor into the more complex Protostome-Deuterostome stem species. However, the Acoelomorpha are not uniform and some characters, such as the organization of the nervous system and the position of the mouth differ between the taxa. To reconstruct the ancestral characters of the acoelomorph stem species, we expanded recent studies on acoels to the sister group Nemertodermatida. Here we present new data on the molecular and morphological patterning of the digestive and nervous system of the nemertodermatid *Meara stichopi* . The molecular architecture of the digestive system seems to be highly conserved between acoels and nemertodermatids - especially the fact that several bilaterian hindgut markers are expressed in specific regions of the male gonoduct. The nervous system in contrast, differs between acoels and nemertodermatids, in that the nemertodermatids show more similarities to that of *Xenoturbella* than that of acoels. This suggests that the condensation of the acoel nervous system into the brain and multiple nerve cords has evolved independently.

Molecular phylogeny: new markers and phylogenomic analyses - Oral Presentation

On the phylogenetic position of Myzostomida – integrating molecules and morphology

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Myzostomids are minute, soft-bodied marine worms, associated with echinoderms since the Carboniferous. Due to this long history of their host-specific adaptation they have developed a highly derived body plan. While some of their morphological characters show similarities to annelids (e.g., trochophore-like larvae and parapodia-like structures), previous molecular analyses related myzostomids to either Annelida or Platyzoa and have therefore not been able to resolve the phylogenetic position of myzostomids. To investigate the phylogenetic position of these enigmatic worms we sequenced the transcriptome (mRNA-seq and small RNAs) of pooled adult individuals of the protandric *Myzostoma cirriferum* with Solexa Sequencing Technology. Moreover, we used immunocytochemical methods and confocal laser scanning microscopy to map the distribution of several neuronal markers, including serotonin and synapsin, in juvenile and adult specimens of *Myzostoma cirriferum*. Furthermore, we conducted an in-situ hybridization study of the PIWI-gene, a stem cell marker with putative phylogenetic informative gene expression. Summarizing all data generated, we found conclusive support that myzostomids are part of the annelid radiation, with which they share a unique gene order of mitochondrial proteins, several specific microRNA families, a segmented nervous system, and a trochophora-like larval stage. Gene tree parsimony analysis of 1878 genes recovers myzostomids as the annelid sister taxon. Gene expression studies gave no evidence for the presence of the unique replacement system for epidermal cells typical for flatworms.

The evidence found in morphology - Poster C8

Immunocytochemical analysis of neuronal patterns in Acoelomorpha

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Since their first description, the phylogenetic position of the enigmatic Acoelomorpha is discussed controversially. Originally, the acoels were associated with flatworms, but molecular systematic analyses suggest they are a sister group to all other bilaterians. However, a recent molecular investigation based on microRNAs, mitochondrial genome sequences and EST-data has placed acoelomorphs as an ingroup of deuterostomes closely related to Ambulacraria (echinoderms and hemichordates). The clarification of the exact phylogenetic position of acoels has fundamental implications for our understanding of the evolution of bilaterian organ systems, in particular the nervous system. In order to clarify the presence of brain-like structures in acoels, which is neglected by some authors, and to describe the organization of the nervous system, we investigated neuronal patterns in adult acoels. We used immunocytochemical methods and confocal laser scanning microscopy and analysed the distribution of neuronal markers in the nervous system of *Convolutriloba* sp.. In particular the neuronal distribution of tyrosinated αtubulin indicates the existence of orthogonal nerve fibres and the presence of a brain-like structure in Acoelomorpha, thus contradicting the assumption that these animals bear a diffuse nerve net. We discuss out findings in the light of the current discussion regarding the phylogenetic position of acoels.

The evidence found in morphology - Poster C9

A WNT/SFRP signalling system acts in specification of the ancestral eumetazoan body axis

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SFRPs are secreted proteins shown to act as modulators of Wnt signalling by direct binding to Wnt ligands in the extracellular space. Previously, it has been shown that Wnt signalling is one of the key factors in axis formation in metazoan embryos. In cnidarians, wnt signalling genes are activated at the blastoporal organizer and confer positional values along the major oral-aboral body axis. Now, we have characterized the cnidarian sFRP1/2/5 genes and have studied their involvement in axial patterning during development. In both Nematostella and Hydra, an sFRP1/2/5 ortholog is active at the aboral pole of the polyp. During early Nematostella embryogenesis, expression is restricted to the aboral pole, where no wnt genes are activated. This complementary expression pattern was also observed during asexual bud formation in Hydra. Oralization of the main cnidarian body axis by ectopic activation of Wnt/beta-Catenin signalling results in a down-regulation of aboral sFRP activity. Morpholino-mediated knock-out of sFRP1/2/5 in early Nematostella embryos, in contrast, results in a termination of aboral development roughly at the gastrula stage, but it also affects positional values along the entire oral-aboral body axis. In summary, our data suggest that an antagonistic Wnt-sFRP system is a central player in setting up positional values along the cnidarian major oral-aboral body axis. Since preliminary results in all bilaterian groups studied by now show anterior activity of sFRPs and posterior activity of Wnts, bilaterians seem to have inherited an ancestral mechanism to pattern their primary body axis.

Molecular phylogeny: new markers and phylogenomic analyses - Oral Presentation

Illuminating the phylogenetic position of Myxozoa using next-generation sequencing

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Myxozoa are parasites with a very simple body organization but a complex life cycle that typically alternates between an annelid host and a fish host. Until recently these organisms were placed in their own phylum. However, sequence-based molecular phylogeny and the presence of polar capsules resembling cnidocyst support the idea that they are members of the phylum Cnidaria. Evolutionary analyses of this group are limited by lack of genomic data: except for 18S rRNA sequences, very few genes have been sequenced for these species. In order to improve our understanding of myxozoan genome evolution, and to clarify their phylogenetic relationships, we conducted de novo genomic sequencing of Kudoa iwatai (Myxosporea: Multivalvulida). We here present preliminary sequencing results based on Illumina technology. The analysis of the obtained reads is a challenging task since no reference myxozoan genome is available. Furthermore, the DNA sample sequenced contains both fish and myxozoan reads. Separating the two is a demanding task, because the genome of the host fish is also unknown. To this end, putative fish reads were identified by blasting each read to other fish genomes and ESTs. The remaining myxozoan reads were then assembled. Our obtained genomic data provide the first insight into the myxozoan nuclear genome. One surprising result is that we could not identify mitochondrial sequences in the assembly. This can either indicate the lost of mitochondria, or a bias of the next generation sequencing technology. We further present preliminary phylogenetic analysis based on the obtained myxozoan protein sequences.

The evidence found in morphology - Poster C10

Phylogeny and geographic distribution of deep-sea hydrothermal vent crustacean copepods of Dirivultidae (Siphonostomatoida)

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Dirivultidae Humes & Dojiri, 1980 is a diverse group of siphonostomatoid copepods endemic (=obligate) for deep-sea hydrothermal vents and recorded from many sites of the Atlantic and Pacific Oceans. Both morphological and phylogenetic analyses suggest that most of dirivultids are characterizing by free-living mode of life and presumably feed on bacteria; only one derived group of dirivultids' genera can be considered as obligate symbionts of siboglinid worms and bivalves. The phylogenetic analysis clearly shows that mentioned group of symbiotic dirivultids evolved independently from other diverse taxa of siphonostomatoids associated with invertebrates and fishes. East Pacific, West Pacific and Mid-Atlantic Ridge are the only geographic regions characterizing by endemic genera. General pattern of dirivultid distribution revealing from phylogenetic tree suggests that Mild-Atlantic Ridge is the region inhabited by representatives of the most derived and presumably youngest taxa of dirivultids. Direction of transition of dirivultids to the Atlantic Ocean from the Pacific Ocean is discussed.

The evidence found in morphology - Poster C11

Evolutionary ecology of basic metazoans from a historical viewpoint: Palaeontological evidence of sponges

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In the fossil record, and according to most phylogenetic threes, Porifera is the oldest Metazoa taxon. Although great progress has been achieved, phylogeny and systematics of the recent and fossil Porifera are still ambiguous and largely unresolved. Sponge taxonomy is traditionally based on skeletal characters. Molecular investigations help testing morphologically based taxonomic classification shemes, but results are sometimes ambigous. Study of fossil material is an alternative method for providing independent evolutionary-ecological modela of recent taxonomic distribution. Where molecular data are scarce or inconsistent, sometimes palaeontological data are available and suitable for providing, or testing, phylogenetic hypothesis. Hexactinellida is a poriferan taxon, for which only fragmental molecular data so far exist, but with a comparably good fossil record. According to morphology, Hexactinellida is a conservative group, whose Mesozoic fossils are commonly identified to a genus level. By comparison with recent taxa Most extant hexactinellid genera can be traced back to the Late Cretaceous, and its Palaeozoic fossils may be identified to a family level. As we look back into the Early Palaeozoic, the taxonomic resolution successively decreases. Nevertheless, fossils of siliceous sponges can be found even in Late Proterozoic sediments of Ediacaran age (about 543 MY old). From Early/Middle Cambrian, all three Poriferan classes are well documented. As one of the latest of the groups, Carboniferous stem linneage representatives of Homosclerophorida are documented by isolated spicules, probably derived from or a tetractine-bearing demospongiaen group. Fossils can be used in systematics to help reconstructing the underlying evolutionary processes.

Please mind the gaps: exploring the limits of our understanding of body plan evolution

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As we draw nearer to a consensus on the phylogeny of Metazoa, we must confront the challenge of clarifying the diverse traits that typify body plans, including behavioral, morphological, embryological, genomic, and ecological traits, and integrate these into a coherent evolutionary narrative in the context of the established phylogeny. A significant hurdle to this goal is the existence of knowledge gaps. One type of gap can be bridged relatively easily, at least in principle, by generating new data on poorly studied taxa. Another type of gap reflects our limited understanding of the ground patterns of some higher-level taxa, which can be remedied by further research on their internal phylogenetic relationships. A third type of knowledge gap cannot so easily be overcome. The crown body plans of higher-level taxa are generally phenotypically very distinct, and we may have little more than our imagination to bridge them. Notably, some recent phylogenomic analyses have united such phenotypically dissimilar taxa that these sister group hypotheses have been given names expressing great surprise (e.g. Kryptrochozoa and Miracrustacea). Understanding the divergence of such disparate body plans is very difficult, unless facilitated by fortuitous discoveries of fossil or living taxa with intermediate body plans. Unless our luck is significantly up in the near future, I expect that most higher-level animal taxa will remain separated by wide gaps in body plan organization. It will therefore remain a great challenge to formulate testable scenarios for animal body plan evolution, and to choose among competing hypotheses.

The "division of labour model" for cell type specialization in the evolution of annelid cerebral eyes

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Many annelids have two different sets of pigmented rhabdomeric eyes, dedicated larval and adult eyes. According to our molecular and structural data on the development and functional aspects of the individual eye cell types from three species, the errant polychaete *Platynereis dumerilii*, and the sedentary polychaetes *Capitella teleta* and *Helobdella robusta*, this duality arose in the annelid stem lineage by duplication from a single pair of precursor eyes. The evolutionary history of the annelid eyes, however, obviously is complex and is best explained by functional segregation of rather multifunctional cell types pinpointing pitfalls for homology assessments. The data suggest that the precursor eye was composed of cells which had both shielding and visual pigments and were expressing a large set of well known eye developmental genes like pax6, dac, eya, six1/2 and others. Cellular duplication and specialization events gave rise to the functionally divergent annelid larval and adult eyes, which is corroborated by our ultrastructural data on various species in the major annelid lineages. Along with the functional divergence, the expression of selector genes and their downstream differentiation batteries was lost from sister cell types. Our gene expression and structural data are congruent with recent phylogenomic analyses on annelid evolution, in that the complex architecture of errant polychaete adult eyes corroborates the re-erection of the clade Errantia. A common origin of leech phaosomal and capitellid adult eye photoreceptor cells is likely and in line with the inclusion of clitellates into sedentary polychaetes.

The evidence found in morphology - Poster C12

The development of the mesoderm and associate structures in the hemichordate *Saccoglossus kowalevskii*: Left-right asymmetries in a non-chordate deuterostome

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Morphological left-right asymmetries can be found in different animal phyla along the protostomes and deuterostomes. In chordates, a part-group of deuterostomes, asymmetries are well documented in numerous studies. These are e.g. the heart and visceral organs in vertebrates, the asymmetric folded gut in urochordates or the radically asymmetric larval head and development of gill slits in cephalochordates, to name but a few. In order to find out if these morphological asymmetries are novelties of the chordates or could already have been present in a deuterostome ancestor, we studied developing morphological structures of a stem-deuterostome. In order to trace the developmental fate of the endodermal and mesodermal structures, we use modern semithin and ultrathin serial sectioning of whole developmental stages of the direct developer *Saccoglossus kowalevskii* , and constructed complete 3D models of each stage. Our data show that the five main mesodermal coelomic cavities derive from the archenteron by the way of enterocoely. In contrast, the pericardial coelom is ontogenetically derived from the ectoderm and develops by schizocoely. The unpaired protocoel opens to the exterior through a single proboscis pore that develops at the left side. Furthermore, we detected an asymmetrical Anlage of the paired gill pores. Moreover, we found that the connection between pharynx and intestine, namely the oesophagus, breaks symmetry to form a right-coiled tube later during development. These findings will be discussed phylogenetically and their implications will be interpreted.

Innovations in the analyses of molecular and morphological data - Oral Presentation

How deep is the hymenopteran tree? A total-evidence approach to dating with fossils

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Phylogenies are usually dated by calibrating interior nodes against the fossil record. This relies on indirect *ad hoc* methods that, in the worst case, misrepresent the fossil information. Here, we compare standard node dating to an approach based on a total evidence analysis of fossil and extant taxa within a Bayesian context. As a test case, we focus on the early evolution of the insect order Hymenoptera. For node dating, we use nine calibration points derived from the fossil record, while total-evidence dating is based on 343 morphological characters scored for 45 fossil (4-20% complete) and 68 extant taxa. In both cases we used molecular data from five markers (about 5 kb) for the extant taxa. We employ relaxed-clock models to accommodate rate variation across the tree but find it necessary to introduce a rooting constraint to avoid errors in tree topology. The order Hymenoptera is estimated by our approach to date back to the Carboniferous with an approximate age of 309 My (291-347 My). Despite considerable uncertainty in the placement of most fossils, we find that they contribute significantly to the estimation of divergence times, as indicated by usually narrower posterior distributions that are less sensitive to prior assumptions when fossils are included as terminals. From a theoretical standpoint, total-evidence dating is preferable simply because it explicitly incorporates the fossil data instead of relying on secondary interpretation. Our results suggest that it can also improve the precision and accuracy of divergence time estimates.

Morphogenesis and homology of coeloms and nephridia in annelids and arthropods

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The musculature and circulatory system of arthropods are traditionally considered to develop out of transitory, serially arranged coelomic body cavities by disintegration and transformation of their epithelial lining. Remnants of the embryonic coeloms are believed to persist in postembryonic stages as the sacculi of the nephridia. Support for this view was mostly inferred from light microscopical studies of organogenesis and until recently remained biased upon the former assumption that the panarthropods are most closely related to annelids. The Ecdysozoa-hypothesis on the origin of panarthropods from nemathelminth-like worms caused us to re-investigate coelomogenesis by transmission electron microscopy. Our studies reveal that particularly in yolk-rich areas of arthropod embryos it is impossible to reliably distinguish primary and secondary body cavities by light microscopy. The occurrence of coelomic cavities proved to be highly variable, ranging from segmental arrangements (Pterygota) to spatial and temporal restriction to some segments (e.g. Xiphosura, Araneae) to entire absence (e.g., Pycnogonida, Branchiopoda, Collembola). When present, the cellular lining of the coeloms never contributes to the formation of muscles, including the heart. The nephridia and their sacculi consistently develop within massive mesodermal cell clusters independent of any transitory coelom; the nephridiogenesis shows more resemblance to protonephridia than to metanephridial systems. Functionally the transitory coeloms seem to be largely dispensable, which might explain their strikingly variable occurrence in arthropods. Although a historic constraint (i.e., inherited information) for their occurrence cannot be excluded, our insights substantially reduce the body of evidence for the homology of coeloms and nephridia in arthropods and annelids.

Scyphozoan larva metamorphosis – phylogenetic consequences

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Today we understand that molecular data or morphology description at certain stages ontogeny considered independently and out of context of organism development do not help greatly in understanding of phylogeny of certain taxa. Detailed investigations of the organism development and its morphological alterations during entire ontogeny are required for interpreting both the peculiarities of organism structure and the origin of such peculiarities in the phylogenetic context. As an example we present the data on metamorphosis of scyphozoan larva *Aurelia aurita*. In spite of being a textbook "organism" the details of scyphozoan larva development and metamorphosis remained till now obscure. The larva competent for metamorphosis is composed of two distinct tissue layers. Our investigations reveal that during settlement and metamorphosis into primary polyp such larval organisation undergoes certain alteration. As a result the lining of the gastric cavity of the primary polyp has double origin: the inner surface of manubrium originates from ectoderm of the larva posterior pole. These finding are in contradiction with previous data (Yuan et al., 2008). We argue that revealed mode of scyphozoan larva metamorphosis is the modified and simplified variant of anthozoan primary polyp with ectoderm pharynx development.

The evidence found in morphology - Poster C14

Morphogenetic approach for the analysis of form diversity

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Traditional classification of multicellular organisms rests on the analysis of whole amount of morphological, anatomical, cytological, biochemical, molecular, etc. characters mostly of modern organisms. That allows to classify suitably the known objects and in some cases to formulate certain conclusions on the phylogenetic relationship and evolution of groups within particular taxon. However, the conditions of historical similarities and differences between organisms can be diverse. The nowadays data support the great role the convergences and parallelisms play, in spite of ancestor inheritances, in the process of organism evolution. It is evident that the interaction between the genotype and phenotype is the complex multidimensional (non-linear) web of processes including pleiotropy, self-organisation, mechanical interactions and environmental regulative signals contributing to the final organism morphology. At that, the spectrum of real forms has its limitations based not exceptionally upon the presence of exact genes and proteins but is the result of all epigenetic interactions between molecules, cells, tissues and environment realised in the organism development.

In such a case, the morphogenetic approach looks promising for solving the systematic and phylogenetic problems. This approach rests on unrevaling the mystery of form transformation based on the knowledge of possible (allowable) for this group morphogenetic processes, not on discovering of the genetic relations or classification of great number of forms. As an example we analysed the diversity of spatial organisation of shoots in thecate hydroids (Cnidaria, Hydroidomedusa, Leptomedusae). The main tendencies and constraints of evolutionary complexity increase in thecate hydroids colonies are uncovered.

Innovations in the analyses of molecular and morphological data - Invited

Detection of bias in simulated and real data

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We analysed the robustness and efficiency of Maximum Likelihood in respect to different subclasses of the typical 4-taxon long branch case in multiple taxon topologies. The analyses were performed over a broad range of different branch length conditions and model parameters. Although the inclusion of a mixed-distribution model (Gamma+I) fits our data much better than a Gamma distribution or invariant sites proportion model alone, our results show that for some topologies and branch lengths the reconstruction success of maximum likelihood is still low for alignments with a length of 100,000 base positions even if the model assumptions are correct. Thus the risk of obtaining a wrong topology increases even if ML is used in the reconstruction process and highly depends on given model parameters and branch length relations in the true topology that shall be reconstructed.

To identify taxa which will most likely be misplaced in trees and which negatively influence the tree-likeness of the data we developed AliGROOVE, a new tool to visualize the quality of sequence similarity in multiple alignments. AliGROOVE summarises site scores of profiles of sequence similarity over the whole alignment length from each pairwise comparison and translates the obtained scoring distances into a similarity matrix. We used simulated data to see whether this approach is sensitive enough to pick up ambiguously aligned single taxa or groups of taxa. Additionally, we applied AliGROOVE on empirical data. Results of tests are subsequently put into relation to observations of our simulated data analyses.

The evidence found in morphology - Invited

Reconstructing ancestors: The lessons from developmental evolution

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Reconstructing ancestral forms has been a major part of analyzing the history of life on earth. For a long time this has been the purview of comparative anatomy, morphology and paleontology. However, for those deep ancestral forms that did not leave any fossil traces embryological data were used as evidence, most prominently by Ernst Haeckel in his *Gastraea Theory*. In the second half of the 20th century reconstructing concrete ancestral forms has been overshadowed by an operational approach to reconstructing phylogenetic relationships based on molecular and morphological data. More recently, in the context of *developmental evolution*, the reconstruction of ancestral forms has been revived and developmental data play again a major role. These reconstructed forms, such as *Urbilateria* represent concrete hypotheses based on a functional understanding of shared elements of the genetic toolkit and of deeply conserved elements of gene regulatory networks. They are also the basis for formulating scenarios of how evolutionary changes in underlying developmental systems can explain major transformations in phenotypic evolution. This talk will sketch the history of attempts to reconstruct deep ancestral forms and explore the role of such reconstructions in transforming evolutionary biology into a causal-mechanistic science.

Molecular phylogeny: new markers and phylogenomic analyses - Invited

Mitochondrial genomic diversity in non-bilaterian animals: implications for phylogeny and evolution

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Mitochondria – the energy producing organelles present in most eukaryotic cells – contain their own genome (mt-genome or mtDNA), separate from that of the nucleus. While mt-genomes of bilaterian animals are relatively uniform, those of non-bilaterian animals (phyla Cnidaria, Ctenophora, Placozoa, and Porifera) display remarkably different modes and tempos of evolution. Furthermore, large differences in mtDNA organization are found within Porifera and Cnidaria. Here I review our current understanding of mtDNA evolution in non-bilaterian animals and its implication for phylogenetic inference based on mitochondrial data.

The evidence found in morphology - Poster C15

Retinula axons of Pycnogonida and their terminals in the visual neuropils: Ancestral chelicerate features?

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The phylogenetic relationships of Pycnogonida – or sea spiders – within the Arthropoda have been controversial in the last century. Neuroanatomical features – especially the innervation of the protocerebrum – have contributed important arguments in this discussion. In arthropods the protocerebrum is primarily responsible for the visual system. Due to its phylogenetic relevance the visual system of arthropods is well studied, which is underlined by the Tetraconata concept (Crustacea + Insecta), where the structure of the eyes is eponymous. Pycnogonids possess an ocular tubercle with four ocelli generally interpreted as median eyes, while classical lateral eyes are absent. Our knowledge on the visual neuropils connected to the eyes is cursory at the moment.

In this study we analyse the visual system of three pycnogonid species of two families with several neuroanatomical methods: Cobalt backfills, Golgi technique, osmium-ethyl gallate procedure, 3D-reconstruction and transmission EM. It is revealed, that a paired nerve connects the median eyes with the brain. In the protocerebrum two optic neuropils are found. The classical optic neuropil, described by Hanström and Winter, can be approved. But surprisingly and in contrast to Hanström and Winter terminals of retinula cells are found in a second optic neuropil considerably deeper in the protocerebrum – close to where the arcuate body is assumed. These features – two target regions of the median eye nerv and their position in the protocerebrum – are very similar to the situation of the median eyes of Limulus polyphemus (Linnaeus, 1758) and thus supports the close relationship of Xiphosura and Pycnogonida.

Molecular phylogeny: new markers and phylogenomic analyses - Oral Presentation

What do DNA, RNA and proteins tell us about molluscan phylogeny?

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Despite the economical, ecological and scientific importance of the Mollusca, the phylogenetic relationships among the major lineages of this Phylum are still largely unresolved. The great disparity in morphology among the major lineages of Mollusca has prompted several competing phylogenetic hypotheses, and molecular studies widely have failed to robustly resolve mollusc class-level relationships. We have initiated several new approaches to resolve the evolutionary relationships among the major lineages of Mollusca: (i) we generated EST data to reconstruct a phylogenetic tree of the Mollusca and also their potential relatives, (ii) we evaluated a reduced data matrix to make such an approach more practical, (iii) we re-evaluated the 18S data of 400 mollusks, and (iv) we analyzed the genes and the primary structures of hemocyanins to unravel the phylogenetic relationship within Mollusca. The results, and the advantages and limitations of the different approaches will be presented and discussed.

Reviewing neurophylogeny: advances since the turn of the millenium

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Neuroanatomical studies have demonstrated that the architecture and organization of the central nervous system and the brain is highly conserved within the major animal clades. The morphology of nerve cells and their neuropilar arrangement provide robust characters for phylogenetic analyses. Characters that have been used for evolutionary considerations in e. g. arthropods are architectural features of major brain centers such as the optic lobe neuropils, the mushroom bodies, and the central complex. These studies agree with molecular phylogenies in demonstrating that crustaceans and hexapods together comprise the taxon Tetraconata. Another interesting finding is that the onychophoran brain shares striking similarities with the brain of chelicerates suggesting an archaic relationship of the onychophora with a chelicerate stem lineage. This talk will provide a brief summary on the history and concepts of a field that is now termed "neurophylogeny". Recent advances in using neuroanatomical characters for resolving the animal tree of life will be highlighted.

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Uncoupling morphological and molecular evolution: deep deuterostome origins of the vertebrate head developmental program

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Much of what we understand about the evolution of the vertebrate head has been derived from classical morphological studies on the diversity of living chordates, both complex and simple, and their early fossil record. The closest phyla to chordates have generally thought to have morphological structures that are too divergent to be informative as a comparative out group to reconstruct the early evolution of chordates, and the innovations that lead to the emergence of the vertebrate head. Recent research in vertebrate molecular genetics has identified much of the developmental program responsible for setting up the vertebrate head. Our work suggests that hemichordates, which are closely related to chordates, but with their own unique morphologies, possess much of the early genetic program that was thought to have evolved in association with the complex structural innovations of the vertebrate head. We explore the implications of this work for our understanding of morphological evolution and why sampling animal diversity is key to understanding the early evolutionary origins of animal form and function.

The evidence found in morphology - Poster C16

Morphological phylogenetic analysis of vent shrimps: probable impact of geomorphology to speciation of hydrothermal fauna

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Alvinocaridid shrimps are the dominant group in the hydrothermal communities of the Mid-Atlantic Ridge (MAR) and make significant contribution to vent communities of other oceans. The present COI nucleotide divergence estimates reveal that recent species of vent- and seep-obligate shrimp constitute a monophyletic group (Shank et al., 1999). We performed morphologically-based phylogenetic analyses based on numerous characters and revealed two main clades and 26 species of vent shrimps distributed through Atlantic, Indian, and Pacific Oceans. Results of the phylogenetic analyses were put on geographic map and patterns of the species distribution were discussed.

Most vent shrimp species in the Indo-Pacific area are characterized by local species ranges, each species occupying a single hydrothermal/seep field. Conversely, in the Atlantic Ocean species ranges are stretched along MAR, each species usually occupying several hydrothermal/seep fields. Many variable populations of the genus *Alvinocaris* , dispersed along the ridge, were found to belong to the same species, *Alvinocaris markensis* .

Results give an evidence for a much faster speciation in the Indo-Pacific area, probably associated with effective isolation between the populations inhabiting neighboring vent fields. Isolation fails to be effective in the Atlantic Ocean, probably due to the geomorphology: well-defined rift valley may serve as a corridor for dispersal of shrimp larvae, thus providing significant gene exchange and preventing isolation.

The evidence found in morphology - Oral Presentation

Deep crustacean phylogeny

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Illuminating the deep phylogeny on any taxon is most reliable if ancient witnesses of deep time are known, i.e. as fossil species being as old as possible. Crustacea is an arthropod taxon with a long fossil record dating back to the Cambrian, i.e. they are at least 520 Ma old. Such early fossils are exclusively from the "Orsten" lagerstätten occuring world-wide. Characteristic of this type of preservation, these fossils are three-dimensionally preserved and display externally as many details as their extant counterparts. Several of the fossil species could be assigned to specific in-group Crustacea, but the majority is not part of the crustacean crown group, the Eucrustacea. Particularly these "Orsten" crustaceans tell us much about early crustacean evolution. Details of their morphologies and, even, ontogenetic patterns have been accumulated through the last six years, which led to very detailed information about the ground pattern of the Crustacea s.l. and Eucrustacea, and evolutionary steps in-between. Crustacea s.l. are characterized by three anterior appendages specialized for locomotion and food intake. Further evolution within Crustacea was affected by heterochronic events that are mainly evident in the morphology of the postantennular cephalic appendages. For example, a special setiferous outgrowth, originally appearing late in development on two postantennular limbs, becomes pre-displaced into earlier ontogenetic stages subsequently. This and the transformation of this so-called "proximal endite" on the anterior two postantennular limbs ("antenna", "mandible") into a large basal limb portion, the coxa, emphasise the strong connection of locomotion and nutrition during crustacean evolution.

A morpho-molecular approach to assess phylogeny – first developmental data of Entoprocta

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Among the four major bilaterian superclades – Acoelomorpha, Deuterostomia, Ecdysozoa and Lophotrochozoa – the latter expresses the largest diversity of bodyplans. It ranges from worm-shaped groups such as annelids, flatworms and nemertines to creeping taxa such as gastropods and the highly motile free-swimming cephalopods. Entoprocta is a group of sessile, solitary or colonial living marine invertebrates with a typical tentacle crown. Although their inclusion within Lophotrochozoa is widely accepted, their phylogenetic position within this superclade remains unresolved. While some traditional morphological and some recent molecular studies propose a close relationship to Ectoprocta, others suggest affinities to Mollusca and/or Cycliophora. *Hox* genes are known to have significant functions in animal bodyplan formation. By the use of in situ hybridization techniques, we will investigate the expression pattern of different *Hox* genes in order to identify their role in entoproct development. So far, we were able to identify the homeobox sequence of three different *Hox* genes of the entoproct *Pedicellina cernua* : the anterior *Lab*, the central *Lox5* and the posterior Post2 . The homeodomain of the *ftz* -like gene *Lox5* shows striking similarities to other Lophotrochozoans. By comparative analyses of the developmental data and the obtained gene sequences with other lophotrochozoan phyla we hope to elucidate the role of the target genes in entoproct development and to obtain insights into the evolution of this yet cryptic lophotrochozoan phylum.

Phylogeny of primary wingless hexapods: chances, challenges and pitfalls of "phylogenomic" approaches

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Phylogenetic relationships among apterygote hexapod lineages (Protura, Diplura, Collembola,

Archaeognatha and Zygentoma) are still a matter of debate. In the last decade, several contradicting hypotheses, e.g. "Ellipura" (Protura + Collembola) vs. "Nonoculata" (Protura + Diplura) or the monophyly vs. a para- or polyphyly of hexapods gained partly equivocal support from morphological, developmental and molecular studies. The inclusion of all primary wingless orders is crucial to reliably resolve deep hexapod and euarthropod relationships, but the molecular data has been very sparse for these taxa. We provide new EST data covering all primary wingless hexapod orders. Within this phylogenomic approach, we carefully assessed data quality (e.g. orthology prediction, alignment masking, selection of genes with advanced reduction heuristics). Our results corroborate the monophyly of Hexapoda, Nonoculata and Ectognatha, but show the need for research on the fate of non-random signal in phylogenomic datasets.

Molecular phylogeny: new markers and phylogenomic analyses - Poster B9

Twenty ribosomal genes provide high resolution on deep molluscan phylogeny and the comparison of three laboratory sampling strategies

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Phylogenomic datasets are the molecular method of choice to infer basal splits of the molluscan phylogeny. Though, the Mollusca are highly divers and comprise approximately 200,000 species. Due to this species richness combined with their great morphological and molecular variability, alternative and taxon rich datasets are worth to be collected and explored. We compare a tree inferred using phylogenomic data with a tree inferred using a subset of only twenty ribosomal protein genes. Both alignments led to a ML-tree sharing the same nodes of class level branching pattern in molluscs. Hence, the position of cephalopods is statistically not supported using our small dataset. Three different methods to sample ribosomal protein genes for additional taxa are presented: a) RT-PCR based amplification using gene specific forward primers, b) DIG labeling of target clones in cDNA libraries and c) separation of target mRNA directly from total RNA extractions via biotinylated DNA probes. Target-oriented sequence sampling of selected ribosomal protein genes is practical, has the potential to reduce the financial burden of sequencing, and will allow the broader insight into the phylogeny of molluscs.

Molecular phylogeny: new markers and phylogenomic analyses - Poster B10

Variations on a theme - mitochondrial gene order and the phylogeny of Bilateria

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Compared to other Eukaryota and even to Choanozoa, Porifera and Placozoa, mitochondrial genomes of Bilateria show a very condensed organization with only 37 genes and little or no non-coding sequences separating the genes. Although mitochondrial gene order is often conserved in animal phyla there is much variation between and within phyla. The small transfer RNA genes are much more often subject to translocations than larger genes. Looking only at protein-coding and ribosomal RNA genes it is possible to hypothesize ancestral gene orders for Deuterostomia, Lophotrochozoa and Ecdysozoa. In contrast there are several equally parsimonious alternatives for the ground pattern of Bilateria. The highest degree of variation is found in Mollusca, Brachiopoda and Ectoprocta. In principle, shared derived gene orders can be useful as apomorphic characters in a phylogenetic analysis. For a comprehensive analysis of the interrelationship of the metazoan phyla mitochondrial gene order is of limited value. Even homoplasious events are possible – among Lophotrochozoa independent similar inversions can be seen in molluscs and phoronids. But at least some questions may be solved with support from this dataset, e.g. concerning the phylogenetic positions of Xenoturbellida (with deuterostomes) and Myzostomida (with annelids).

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Innovations in the analyses of molecular and morphological data - Oral Presentation

MISFITS: Evaluating the goodness of fit between a phylogenetic model and an alignment

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As models of sequence evolution become more and more complicated, many criteria for model selection have been proposed, and tools are available to select the best model for an alignment under a particular criterion. However, in many instances the selected model fails to explain the data adequately as reflected by large deviations between observed pattern frequencies and the corresponding expectation. We present MISFITS, an approach to evaluate the goodness of fit (http://www.cibiv.at/software/misfits). MISFITS introduces a minimum number of "extra substitutions" on the inferred tree to provide a biologically motivated explanation why the alignment may deviate from expectation. These extra substitutions plus the evolutionary model then fully explain the alignment. We illustrate the method on several examples.

The evidence found in morphology - Oral Presentation

Evolution of body contractility in early branching Metazoa – what morphology of Porifera and Placozoa tells us

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Early muscle cell evolution has been discussed for over a century. However, the emergence of contractile muscle filaments is still an unresolved mystery. The Cnidaria posses the first muscle cells among the Metazoa, while the Porifera and Placozoa are muscleless. Nevertheless, both display a remarkable range of body contractility, but the effector cells are still debated. Two competing hypotheses on sponge contractile cells were postulated: (1) mesohyl contraction actinocytes ("myocytes"). (2) epidermal contraction by pinacocytes. In the Placozoa, the mesenchymal fibre cells are regarded contractile. Only indirect evidence, like cell shape or the presence of cytoplasmic filaments supports contractility of those cells. We present comprehensive data on sponge contractility including all four major sponge taxa, Demospongiae, Hexactinellida, Calcarea and Homoscleromorpha. In addition, the contractile behavior of *Trichoplax adhaerens* is addressed. A modern functional morphology approach based on in vivo and 3D imaging techniques (i.e. SRμCT), provides evidence for epithelial contractility. In conclusion, epithelial contractility might be a character of the metazoan ground pattern. Most likely such early contractile epithelia lacked functional compartmentalization like in cnidarian epithelio-muscle cells. The resulting evolutionary scenario suggests that the transition from a general cytoskeleton contractility (also found in unicellular members of the Opistokonta) to the muscle specific, specialized filament contractility, occurred early within the metazoan stem group. The contractile epithelia in Porifera and Placozoa might both be derived, but nevertheless share a functional root on the gene and protein level. This hypothesis will have to be tested using genomic data and gene expression analysis.

Molecular phylogeny: new markers and phylogenomic analyses - Oral Presentation

Early metazoan phylogeny: identifying obstacles and solutions

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Recent advances in DNA-sequencing technologies have overcome the problem of limited gene sampling for inferring phylogenetic relationships between major animal lineages. Within the last decade, animal phylogenetics has progressed from single-gene trees to phylogenies constructed based on concatenated alignments of hundreds of genes. Nevertheless, the relationships between the five major metazoan lineages – Porifera, Ctenophora, Cnidaria, Placozoa and Bilateria, still remain subject of controversy. Recent studies addressing deep-level metazoan relationships resulted in a collection of conflicting topologies, which are not easy to compare since they have been generated using different tree-building algorithms and different taxon and gene sampling strategies.

To gain a better understanding of the underlying causes of the observed incongruence among recently published metazoan phylogenies, we constructed and analyzed two non-overlapping multigene matrices that have comparable lengths, similar number of variable sites and identical taxon sampling. We followed a fixed computational procedure for gene selection, orthology assignment, and building of sequence alignments. The concatenated gene sets were subjected to phylogenetic analysis using several amino acid substitution models available under the maximum likelihood and Bayesian framework. The result of these analyses showed a crucial effect of the choice of substitution model on the animal tree topology. To reveal the factors that affect support on the basal nodes of metazoan trees and cause incongruence between two topologies obtained using one tree-reconstruction method, we performed a leaf stability assessment, taxon-specific amino acid composition bias analyses and estimated saturation level in the two multigene matrices. Results of these analyses will be discussed.

The evidence found in morphology - Poster C17

Early cleavage in Phoronida shows spiral features

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The view that early cleavage in Phoronida follows a radial pattern is widely accepted. Nonetheless, existing studies are not all consistent in this point. Several authors report occasional observations of embryos displaying "spiral" cleavage features, and for one species (Phoronopsis viridis) cleavage is described as entirely spiral. These observations, however, are often considered as being the result of artifacts and misinterpretations. Molecular phylogenies put Phoronida with protostome taxa characterized by spiral development into the Lophotrochozoa. We investigated two species, Phoronis muelleri and Phoronis pallida, applying for the first time morphological methods of 4D microscopy, fluorescent staining, and CLSM on phoronid cleavage. Early cleavage pattern is largely similar between these species and can be characterized as holoblastic, adequal, and more or less synchronous. From third cleavage onwards, we found a pattern of oblique spindle orientations and divisions of blastomeres in alternating dextral and sinistral direction. This pattern, which is more consistent in the animal and vegetal most tiers of cells, mostly results in four blastomeres encircling the poles of the embryo. We found no indications for a classical radial cleavage. In contrast, our study shows that cleavage in both investigated species is highly corresponding to that described as spiral in Ph. viridis. All three species display characters consistent to the pattern of spiral cleavage, especially if compared to taxa such as Nemertea or some Annelida. Hence, we suggest that our findings present morphological support for a lophotrochozoan / spiralian affinity of Phoronida.

Innovations in the analyses of molecular and morphological data - Poster A2

A new approach to process and phylogenetically analyze sequences from public databases, applied to infer the phylogeny of Hymenoptera

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Massive amounts of molecular sequence data have been accumulated over the last years by the scientific community, and there is high and widespread interest in using these data for comprehensive phylogenetic analyses. To this end, we developed a novel bioinformatic pipeline for downloading, formatting, filtering and analyzing public sequence data deposited in GenBank. With this pipeline, it is possible to produce phylogenetic trees for any taxonomic group and to monitor new data and tree robustness in a taxon of interest.

We exemplarily used the pipeline to investigate the phylogeny of Hymenoptera (sawflies, bees, wasps, and ants). After downloading and processing more than 120,000 sequences, our pipeline produced a supermatrix with more than 80,000 sites and 1,146 species. The dataset was phylogenetically analyzed with a maximum likelihood approach. In the inferred tree 'Symphyta' (sawflies) was paraphyletic, consistent with previous studies,. Within Apocrita (wasp-waisted wasps), we found the following phylogenetic relationships: Stephanoidea + (Ichneumonoidea + (Proctotrupomorpha + (Evanioidea + Aculeata))). Despite the huge amount of data, data coverage is still low and unbalanced. Therefore, additional sequence data have to be generated to reliably infer the phylogeny of Hymenoptera.

Molecular phylogeny: new markers and phylogenomic analyses - Invited

microRNAs and the evolution of metazoan complexity

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As a historical science Evolutionary Biology is broadly studied by workers who usually focus on either evolutionary pattern or evolutionary process. This is because the types of data used to elucidate the patterns of life are largely divorced from the processes that evolve life. For example, the sorts of data now being used to build the metazoan phylogenetic tree, whether it be ESTs or mitochondrial genomes, are mute about how animals initially evolved, diversified, complexified and simplified over their near 800 million year evolutionary history. One new source of phylogenetic information though, microRNAs (miRNAs), may also shed insight into key questions surrounding the evolution of animals, and in particular animal complexity. Unlike the transcription factors and other components of the developmental tool kit that miRNAs regulate, new clade-specific miRNAs are continuously being acquired through time in all animal lineages studied to date, and thus miRNAs can be used as a source of phylogenetic information. In addition though, large increases to the miRNA repertoire are associated with increases to animal complexity, including at the base of the bilaterians and at the base of the vertebrates, and where studied, the most copiously expressed miRNAs in clade-specific tissues are clade-specific miRNAs. On the other hand, simple animals (e.g., sponges) have few miRNAs, and losses of miRNAs within the bilaterians are associated with instances of secondary morphological simplification, as seen in, for example, rotifers and acoel flatworms. Therefore, miRNAs simultaneously shed insight into both the evolutionary pattern and at least some of the processes underlying animal evolutionary history.

Molecular phylogeny: new markers and phylogenomic analyses - Oral Presentation

MicroRNA and phylogenomics congruently resolve the phylogenetic relationships of the Tardigrada within Ecdysozoa

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Morphological data traditionally recovers Onychophora (Velvet worms), Tardigrada (Water bears) and Arthropoda (e.g. crabs, wasps, centipedes) within the monophyletic group Panarthropoda. However, studies of molecular sequence data provide support for alternative placements of Tardigrada within the Ecdysozoa; most often grouping tardigrades closer to the cycloneuralian clade Nematoda (round worms). This result is suspicious however, as the branches associated with both the Tardigrades and the Nematoda are very long, suggesting the nematode-tardigrade grouping might represent a long-branch attraction (LBA) artefact. In order to test the hypotheses of tardigrades relationships, we have analysed two independent genomic data sets: (1) a large EST data set and, (2) microRNAs for all relevant taxa, including newly sequenced microRNAs for Tardigrada and Onychophora. Using careful experimental manipulations – such as: comparisons of model fit, signal dissection, and taxonomic sampling – we were able to show that support for a Nematoda plus Tardigrada group derives from the phylogenetic artefact of long branch attraction (LBA). Our small RNA libraries fully support our EST analysis, as no microRNAs were found to link Tardigrada with Nematoda, while a microRNA (miR-276) was found to be shared by all panarthropod groups. Our data sets yielded congruent results, provide compelling evidence in favor of monophyletic Panarthropoda, and suggest that Onychophora is most likely the sister group to Arthropoda. Overall, our findings provide a solid foundation to better understand the origin of the arthropods body plan.

The evidence found in morphology - Oral Presentation

Unpigmented ciliary photoreceptor cells and organs in Annelida - diversity and importance for in-group phylogenetic relationships

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There are two distinct types of photoreceptor cells (PRCs) in Annelida: rhabdomeric and ciliary PRCs. The cerebral pigmented eyes exclusively employ rhabdomeric PRCs and recently a hypothesis explaining the evolution of these eyes has been put forward. By contrast, ciliary PRCs generally occur without shading pigment with inconspicuous supportive cells in so called unpigmented ocelli or as isolated cells in the form of phaosomes. Within Annelida these presumed ciliary PRCs are structurally different and obviously a confusing diversity exists. Therefore, until now it is unclear how their evolutionary history in this taxon is. On the other hand this diversity indicates their possible importance as morphological characters for phylogenetic analyses. Although apparently widely distributed among the annelid subgroups, ciliary PRCs are generally present in representatives of the more basal branches and in Errantia, whereas in many subgroups of Sedentaria no records exist to date probably indicative for their absence in these groups. The more basal annelid subtaxa show the greatest diversity, whereas within Errantia each of the major subgroups Phyllodocida, Eunicida, Amphinomida and Orbiniidae possesses a specific type of ciliary photoreceptive organ. Within Sedentaria ciliary PRCs either have been lost several times independently or only once subsequently followed by secondary accession in certain lineages.

Molecular phylogeny: new markers and phylogenomic analyses - Poster B11

Dating the arthropod tree of life employing expressed sequence tags (ESTs)

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Dating divergence times of animal taxa have always been of major interest to biology. Molecular sequences do not only allow the reconstruction of phylogenetic relationships among taxa, but also provide information on the approximate divergence times. DNA and protein sequences provide a rich source of information to infer life history by molecular clock approaches. Still, there is little agreement between fossils and molecular clock studies when inferring deep nodes. The fossil record dates the origin of most multicellular animal phyla during the Cambrian explosion less than 540 million years ago (mya), whereas molecular clock calculations usually suggest much older dates. In our approach we analyzed a large multiple sequence alignment derived from Expressed Sequence Tags and genomes comprising 129 genes (37,476 amino acid positions) and 117 taxa, including 101 arthropods. By applying a Bayesian relaxed clock framework and multiple, carefully selected calibration points, we obtained divergence time estimates that were robust to different priors, substitution rates and missing data. We calculated that the arthropods emerged ~620 mya. Onychophorans and euarthropods split ~600 mya, Pancrustacea and Myriochelata ~570 mya, Myriapoda and Chelicerata ~560 mya, and "Crustacea" and Hexapoda ~515 mya. Endopterygote insects appeared ~390 mya. These dates are considerably younger than most previous molecular clock estimates and in better agreement with the fossil record. However, a Precambrian origin of arthropods and other metazoan phyla is still supported. Our results demonstrate the applicability of large datasets of random nuclear sequences for the timing of multicellular animal evolution.

Innovations in the analyses of molecular and morphological data - Poster A3

Estimating the processes of evolutionary change of single characters by replacing character states with arrays of alternative characters

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We discuss a procedure of estimating the processes of evolutionary change by means of using alternative characters. For instance in DNA sequences there are four character states A,G, c, t. These character states can be substituted by six alternative characters. For each of these alternative characters the change during evolution can be explained by a shot-hit-repair model. This model assumes that there is steadily some shooting resulting in the destruction of the DNA at different positions (=characters). The probability per shot that a position is hit (hit probability) and destroyed differs at different positions. If a position is hit it has to be repaired. But in different alternative characters the probability that one of the two states is used for the repair differs; there are different preferences. The hit probability and the preference define the stochastic matrix of an alternative character. They define too a function similar to that of radioactive decay which describes how the probability of no difference between two species decreases with the number of shots. If we use estimates of evolutionary distances as approximations of the number of shots, we can fit the curves determined by two unknown parameters. If we have fit such curves for all six alternative characters of one position we can combine the results and return to the original states A, G, c, t. If the stochastic matrices of single characters are kown a lot is gained. But it should be realized that stochastic matrices are too changed by evolution.

The evidence found in morphology - Invited

The role of morphology in evolutionary research

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Morphology is generally understood as the structure, form and pattern of organisms, something organisms are characterized by, and is often used in the alternatives morphological versus molecular data. Primarily, however, morphology is a discipline in biology. Although morphology is often believed to be restricted to the description of structures, or described as a "purely formal" discipline, morphology is in fact the science of form and structure and includes analytical and synthetic processes for explaining them (sensu Riedl). (Evolutionary) Morphology comprises: descriptive morphology, comparative morphology – which in the framework of evolutionary morphology is essentially homology research - and finally causal morphology, which seeks to provide evidence for the direction and mechanisms of evolutionary transformations. Morphology as a discipline is closely related to other disciplines, in particular physiology, developmental biology and evolutionary biology for all three of which it lays the foundation. Herein we elaborate the various aspects of morphology as a discipline, showing that it is indeed a biological discipline in its own right.

The evidence found in morphology - Oral Presentation

Development of the nervous system in hatchlings of *Spadella cephaloptera* (Chaetognatha)

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Chaetognaths are small, marine predators which are present in abundance in plankton communities. Chaetognath development is not yet well understood and our present study sets out to further the knowledge in this area. We examined the epibenthic Spadella cephaloptera because we could obtain developmental stages of a determined age under controlled conditions. The present study combines several techniques to analyze the formation of the nervous system in newly hatched animals. Sections through the trunk region reveal the dimension of the developing ventral nerve center (VNC) and the cells it contains. We relate this to data we obtained by immunhistochemical detection of BrdU, RFamides and synapsin. *In vivo* labeling with the proliferation marker BrdU revealed the mitotic activity in the VNC and the fate of the proliferating cells during the first week after hatching. The detection of synapsin and RFamides was used as an indicator of the differentiation of neuronal structures. We found that the developing VNC is the most dominant structure in the hatchling trunk and neurons, putative glia cells and neuronal precursors are present. Utilizing BrdU demonstrates that the large precursor cells divide several times, producing smaller, non-mitotic cells with each division. At hatching RFamides and synapsin are present in the VNC and to a lesser extend also in the brain. We mapped the development of these systems for several days after hatching until the anatomy of the nervous system resembled that in adults. This study is part of the DFG-Program Deep Metazoan Phylogeny (grant HA2540/7-1/2/3).

Molecular phylogeny: new markers and phylogenomic analyses - Poster B12

Are sea anemones (Cnidaria, Actiniaria) monophyletic? First phylogenetic higher-level classification for the order

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Sea anemones (order Actiniaria) are among the most diverse and successful members of the anthozoan subclass Hexacorallia, being found in all benthic marine habitats at all depths and latitudes. Actiniaria comprises approximately 1200 species of solitary and skeleton-less polyps lacking any morphological synapomorphy. Despite their morphological simplicity as tissue-grade organisms, sea anemones are an ancient lineage whose members display remarkably diverse life history strategies.

Because anemones are characterized by an absence of attributes that define other hexacorallian orders and are so diverse anatomically, it has been hypothesized that the order is paraphyletic. Although monophyly is anticipated based on cnidarian higher-level molecular phylogenetic studies (typically as the sister group to hexacorallian orders Antipatharia, Corallimorpharia, Scleractinia and Zoanthidea), to date, monophyly has not been explicitly addressed. Previous studies emphasized relationships among anthozoans, and therefore did not sample sea anemones well enough to provide a comprehensive picture of their evolutionary history.

Current phylogenetic analyses demonstrate the inadequacy of existing morphological-based classifications within Actiniaria; none of the superfamilial groupings, and most families and genera that have been rigorously studied are monophyletic, indicating conflict with the current hierarchical classification scheme. Additionally, studies have been focused only on the suborder Nynantheae, main suborder of the three currently recognized within Actiniaria.

We test the monophyly of Actiniaria using 2 nuclear and 3 mitochondrial genes as well as multiple analytical methods. In addition, our analyses are the first including representatives of all three suborders within Actiniaria. Based on well-supported clades, we propose a new higher-level classification for Actiniaria.

Innovations in the analyses of molecular and morphological data - Oral Presentation

Parallel codon usage and compositional bias in deep phylogenomic

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Deep phylogenomic analyses are usually performed using amino acids, but it is unclear whether they should be preferred to nucleotides. We address this problem by exploring a phylogenomic dataset of arthropods whose highly supported nucleotide topology is incongruent with a weaker supported amino acid one.

This incongruence has been suggested to be due to signal concentrated in synonymous serine codon families that cannot be traced using amino acids. Indeed, we show that when serine codons are recoded as gaps, the nucleotide phylogeny converge on the amino acid one. As a counterproof, a new amino acid character recoding using 21 or 23 states, designed to account for synonymous codons, recovers the nucleotide topology.

We show, however, that different lineages are differently biased in their usage of synonymous codons, and that these biases are correlated with the nucleotide composition biases, a notorious source of not-phylogenetic signal. Serine codon usage bias is also correlated with the topology derived from the nucleotides (but not the amino acids) sequences. These results suggest that nucleotide topology is influenced by a compositionally driven, parallel synonymous codon usage bias, to which amino acids data should be invariant.

In conclusion, high supports for certain nodes in the nucleotides topology are likely the result of a not-phylogenetic signal. On the other hand, corresponding amino acids do not bring enough information to resolve unambiguously the phylogeny. From a methodological point of view, amino acids are potentially less prone to artifacts than nucleotides and likely more suited for deep-time phylogenomic studies.

The evidence found in morphology - Oral Presentation

Highly variable patterns in development of the metanephridial and coelomic system in molluscs

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We investigated the development of the metanephridial system of the polyplacophoran *Lepidochitona corrugata* and the bivalve *Mytilus galloprovincialis* in detail with a strict 4-dimensional approach. In *L. corrugata* there is a common, terminally located, unpaired anlage that hollows and widens. The metanephridial components differentiate from the ventro-lateral wall of this anlage; the remaining portions give rise to pericardium and heart. In *M. galloprovincialis* the metanephridial organs undergo a functional protonephridial stage. The paired organs appear during the larval phase and become connected to the anlage of the pericardium that later develops from an unpaired anlage. This variable pattern in nephrogenesis is supported by previous literature and our preliminary data of other molluscs: In the scaphopod *Antalis entalis* and the solenogaster *Wirenia argentea* we found a transitory protonephridial stage. In contrast, in the gastropod *Ovatella myosotis* we found a common origin of the metanephridial and circulatory system.

The varying development mode may be due to different functional constraints (e.g. larval or developmental type) or even the result of modifications in the early cleavage patterns. In any case, some conventional ideas on the ontogenetic origin of this organ system should be dropped. We could not track down anything resembling a "mesodermal band" in the two species that were closely examined (*L. corrugata* , *M. galloprovincialis*). Since there is no general program for nephrogenesis in molluscs, distinct differences of nephrogenesis in annelids are vanishing. Accordingly, ontogenesis provides no evidence for rejecting the homology of the metanephridial system of the two phyla.

Molecular phylogeny: new markers and phylogenomic analyses - Oral Presentation

The genome of the ctenophore *Mnemiopsis leidyi* and its impact on our understanding of animal history

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Despite great strides in the areas of phylogenomics, and phylogenetics, the early history of animals -- and especially the relationships between the earliest branching lineages (i.e., Porifera, Placozoa, Ctenophora, Cnidaria, and Bilateria) -- remains ambiguous. Functional data from non-bilaterian species holds the promise of shedding light on the origin of metazoan multicellularity and the molecular basis of morphological complexity. However, the ambiguity surrounding the relationships at the base of the animal tree has made it difficult to confidently interpret this functional data. One of the most significant hurdles has been the absence of whole-genome data from a ctenophore species. Here, we report the results of the sequencing, annotation, and initial analysis of the ~150-megabase genome of the ctenophore, *Mnemiopsis leidyi* . Many of the crucial elements of the animal genetic toolkit are present in the *Mnemiopsis* genome, including most homeobox classes and many Wnt and TGF-beta signaling pathway components. However, *Mnemiopsis* and the poriferan *Amphimedon queenslandica* are missing similar sets of genes that are often present in placozoan, cnidarian, and bilaterian genomes. We hypothesize that the majority of these shared absences represent a plesiomorphic distribution pattern, and that therefore placozoans, cnidarians, and bilaterians form a clade exclusive of the Porifera and Ctenophora. We have named this clade the ParaHoxozoa. Our results, provide a starting point from which functional data within these lineages can be interpreted and suggest that many important developmental "toolkit" components arose after a number of complex morphological features, for example, the nervous and musculature systems.

Molecular phylogeny: new markers and phylogenomic analyses - Oral Presentation

Can we resolve the base of the Metazoa: If yes, why not?

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A hot ongoing debate concerns the recent animal phylum closest to the hypothesized Urmetazoon, the very first metazoan animal. Different animal groups have been postulated to branch of first after the metazoan animals' ancestor. Most often sponges (phylum Porifera) have been seen in a basal position but recent data also support scenarios, where placozoans, the morphologically simplest organized animals, are placed at the very base of the Metazoa. Modern molecular phylogenetic analyses undertaken to infer basal metazoan relationships have failed to provide a clear answer even when hundreds of genes were included in the analysis. The largest data sets lead to different and partially highly contradictive evolutionary scenarios. The observation that even the highly derived ctenophores were found basal in some analyses reflects how ill-suited huge but holey data matrices can be. We present results on basal metazoan relationships using highly saturated gene matrices based on new transcriptome and genome data from different basal metazoans.

The evidence found in morphology - Oral Presentation

The nervous system of Nemathelminthes - is the taxon Nemathelminthes valid?

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The taxon Nemathelminthes expresses the sister-group relationship between the taxa Gastrotricha and Cycloneuralia (composed of Nematoda, Nematomorpha, Priapulida, Kinorhyncha and Locicifera). The talk summarizes the structure of the nervous system in these taxa, including evolutionary patterns and open questions. One result is that gastrotrichs possess a type of brain which is different from that in Cycloneuralia. Considering that molecular data do not reveal a close relationship between gastrotrichs and cycloneuralians, the validity of the sister-group relationship between these two taxa becomes questionable and Nemathelminthes might not be a monophyletic taxon.

Molecular phylogeny: new markers and phylogenomic analyses - Poster B13

Molecular phylogeny of lithistid sponges (Porifera: Demospongiae) supports resolution of pattern and timing of demosponge evolution

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Demospongiae is the largest and most successful group of Phylum Porifera (~ 90 % of all extant species). Unfortunately, the fossil record of most taxa is scarce and the phylogenetic relationships cannot be assessed unambiguously with morphology alone, due to the lack of informative characters. The polyphyletic group of lithistid sponges, with yet uncertain relationships to other demosponge lineages, provides the richest fossil record for sponges due to their rigid skeleton of articulated silica spicules (desmas). Molecular palaeobiological analyses of extant taxa of this important group can be used to understand their evolution and phylogenetic position within demosponges, and provide robust calibration points for molecular clock analyses.

With a sampling of more than 240 specimens, covering 14 families and 25 genera, this work presents the to date broadest molecular systematic study of lithistid sponges, using independent mitochondrial protein coding and nuclear ribosomal markers.

Our first results indicate a sister-group relationship of the lithistid families Theonellidae, Corallistidae, Phymatellidae, Pleromidae and Macandrewiidae to the non-lithistid Order Astrophorida. They all possess triaene ectosomal spicules, a distinguishing character for astrophorid sponges. However, Family Desmanthidae lacks triaenes and reveals a close relationship to halichondrid sponges. The family Vetulinidae indicates affinities to freshwater sponges and is clearly distant to the other lithistid taxa.

Our results are compared with previous phylogenies of lithistid sponges and in addition their rich fossil record is used to reconstruct timing and radiation patterns of demosponge lineages with a molecular clock approach.

Molecular phylogeny: new markers and phylogenomic analyses - Poster B14

Mitogenomic analysis of decapod phylogeny

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For comprehensive study of decapod phylogeny on mitochondrial genome level, we completely sequenced 13 decapods. Together with available 32 decapods from GenBank, the datasets now covered all major decapod taxa. From the sequence aspect, Maximum likelihood (ML) and Bayesian inference (BI) of nucleotide, genome and amino acid datasets revealed similar topologies at the higher level relationships: Brachyura, Anomala), Thalassinida), Astacidea), Achelata), Stenopodidea), Caridea), Dendrobranchiata). Only Polychelida received two different positions: the basal branch of Reptantia in ML analysis of amino acid data and the sister group of Astacidea in the resting analyses. On the family level, Thalassinida is paraphyletic, which is consistent with some morphological and some recent molecular results (e.g. de Saint Laurent 1973, Tsang et al. 2008), other taxa are monophyletic. These major results confirm some of the traditional morphological views. In the gene arrangements aspect, two notable features in astacid mitogenomes evolution have been observed: a huge inversion happened in Procambarus fallax f. virginalis, Homarus gammarus and one priapulid Priapulus caudatus is supposed to be of convergent nature within the Ecdysozoa; complete loss of protein coding gene nad2 in H. gammarus and partial loss in Enoplometopus occidentalis are supposed to be synapomorphic character for Nephropidae. Additionally, a new gene rearrangement model – "invertion triggered duplication" model is also proposed accooding to decapod gene rearrangements. Anyhow, the mitogenomes show a good potential to resolve the relationship within Decapoda.

Molecular phylogeny: new markers and phylogenomic analyses - Oral Presentation

Pterygote phylogenomics: The evolutionary history of genes and their impact on the topology

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The introduction of the next-generation sequencing technologies led to a revolution in molecular systematics. Instead of using only one gene to infer a species tree molecular systematic studies are using today even more than 1,000 genes to resolve a phylogenetic question. This change in the phylogenetic studies has changed the issues that have to be handled. The so-called phylogenomic era have brought up a major new challenge – the gene selection. Recent discussion in phylogenomic studies centers also on the data quality and inference methods, both known to reinforce systematic bias. Here, one important factor contributing also to the data quality is the evolutionary history of the genes which compose the data sets as they are also of relevance for the resulting topology.

In our new approach we have started to analyze the impact of the selected genes on the resulting topology using the wealth of published sequence information (EST- and genome-projects) for pterygote species (winged insects) in addition to newly generated EST data (funded by the DFG special priority program "Deep Metazoan Phylogeny"). We selected individual proteins according to their biological function with the assumption that they harbour the same evolutionary history along the branches of the organismal phylogeny and that different evolutionary signals are a result of the different evolutionary processes that act upon the genes. The data matrices will further serve to gain a better knowledge of the major macro-evolutionary key innovations which occurred in insect evolution (origin of insect wings, wing folding and complete metamorphosis).

Molecular phylogeny: new markers and phylogenomic analyses - Poster B15

Phylogeny of coral-inhabiting barnacles (Cirripedia; Thoracica; Pyrgomatidae) with a closer look at the *Savignium* group

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The traditional phylogeny of the coral-inhabiting barnacles, the Pyrgomatidae, is based on morphological characteristics, mainly of the hard parts. It has been difficult to establish the phylogenetic relationships among Pyrgomatidae because of the apparent convergence of morphological characteristics, and due to the use of non-cladistic systematic, which emphasize ancestor-descendant relationships rather than sister-clade relationships. Our phylogenetic results allowed us to reject previous classifications of Pyrgomatidae based on morphological characteristics. The hydrocoral barnacle *Wanella* is not found on the same clade as the other pyrgomatids, but rather, with the free living balanids. Our results also suggested the possibility of paraphyly of the Pyrgomatidae. Fusion of shell plate and modification of the opercular valves is a homoplasious feature that occurred more than three times on different clades. Even the monophyletic position of the "*Savignium*" group, barnacles with fused shell and elongated scuta, comprising four nominal genera, is not supported. The different taxa of the genus *Savignium* are placed on different clades. Moreover the traditional systematic does not reflect the existence of distinct ESUs within a nominal species. Populations of the nominal species *Trevathana dentate* occupying different host corals display clear genetic differences, suggesting that the barnacles from these five different coral genera represent five distinct ESUs. These species display host specificity at least at the generic level.

Phylogenetic patterns from morphogenetic processes

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The so-called biogenetic law "ontogeny recapitulates phylogeny" is currently reanimated in form of the "molecular phylotypic stage." I argue that both concepts are empirically questionable and logically untenable. Instead, I propose to include ontogenetic characters from all available organismic levels in formal cladistic analyses in order to properly evaluate potential evolutionary information and to infer phylogenetic hypotheses. Using examples from comparative developmental morphology of deuterostomes, I suggest how embryological data could be profitably utilized in a phylogenetic context. Simultaneously, I demonstrate the recent progress in microscopical techniques and its effect on embryological research. Computer assisted three-dimensional reconstructions allow detailed comparisons that can be used to propose hypotheses of primary homology. Adding the fourth ontogenetic dimension, time, considerably increases the number of characters that can be investigated and reveals similarities in embryological processes, such as between neurulation in chordates and neurulation of the collar cord in enteropneusts. Similarly, 4D-microscopy can reveal correspondences between morphogenetic events on a cellular level. Moreover, this latter technique elegantly reveals precise cell-lineages at a level unattainable for traditional methods. These advances together with the current explosion of molecular data and in combination with internet-based research tools such as databases and interactive collaborative phylogenetic matrices hold great potential for comparative morphology.

Hair cells in Tunicata: when did the lateral line evolve?

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Hair cells are secondary sensory cells present in the lateral line and inner ear of vertebrates, where they function as mechanoreceptors. We characterize secondary sensory cells in the vicinity of the mouth openings in ascidians, salps, pyrosomes, doliolids, and appendicularians. The sensory cells of ascidians vary in morphology, and in some species strongly resemble vertebrate hair cells, bearing cilia situated to one side of a crescent-shaped bundle of stereovilli that are graded in length. Sensory cells together with supporting cells form the so-called coronal organ. Secondary sensory cells are also present in the pelagic tunicate species investigated with the exception of the salp *Thalia democratica* . Therefore, we conclude that secondary sensory cells in the coronal organ situated at the mouth opening represent a plesiomorphic feature of tunicates. In addition, we compare tunicate secondary sensory cells with those present in Cephalochordata and Craniata, and discuss the possibility that they are homologous across all chordates.

Molecular morphology: higher order characters derived from sequence data

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The availability of complete genome-wide sequence information for large numbers of taxa provides new opportunities and poses new challenges for phylogenetic analysis. Implicitly, the genome sequence encode higher level features that in themselves contain phylogenetic information that can be analyzed independent of models of sequence information. Examples are repetitive elements, gene content and gene order, locations of introns, microRNA content, and RNA structures. Such features can serve as highly informative and relatively homoplasy-free characters, akin to morphological approaches. In order to make these features usable for large scale phylogenetic studies, however, one first has to extract them from the genomic sequence data. In my presentation I will review recent progress in this area, with an emphasis of deep metazoan phylogeny.

Fishing in the dark: Trying to identify rogue taxa

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The identification of rogue taxa, that is, taxa that randomly scatter across a phylogenetic tree, for instance, because of lack of signal, ambiguous signal, or chimeric sequence data is a current challenge in phylogenetics. I will outline some recent algorithmic approaches and experimental results to identify rogue taxa for two distinct classes of rogue identification:
1. A posteriori rogue identification, that is, identification of rogues by means of a set of bootstrap replicate trees.
2. A priori rogue identification, that is, identification (and removal) of rogues prior to conducting a resource-intensive bootstrap analysis.www: www.exelixis-lab.org

The evidence found in morphology - Poster C19

Morphology of the ventral nerve cord in Cephalocarida and Remipedia (Crustacea) and phylogenetic implications

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Since most external morphological features of Cephalocarida have been interpreted as plesiomorphic, early morphologists have placed the taxon as "most basal" within Crustacea. Moreover, a number of features in the cephalocarid brain have recently been suggested to closely represent the mandibulate ground pattern. Recent molecular studies, however, rather support a sister-group relationship between Cephalocarida and Remipedia. It was shown that the ventral nerve cord of all arthropods contains an evolutionarily conservative pattern of serotonin-like immunoreactive neurons. The latter can be specified in detail by the number and course of their neurites and by the segmental commissures to which they contribute. To investigate this phylogeneticly interesting pattern in Cephalocarida and Remipedia, we applied immunohistochemical stains and nuclear counter stains to whole mounts and vibratome sections, analyzing stained specimens with confocal laser scanning microscopy and computer-aided 3D-reconstruction. Our study revealed a number of correspondences between Cephalocarida and Remipedia that strongly suggest homology. In certain trunk segments, both taxa feature six pairs of serotonin-like immunoreactive somata, with one anterior pair contributing neurites to an anterior commissure, three central pairs whose neurites take diverse courses, and two posterior pairs contributing neurites to a posterior commissure. This immunoreactive pattern differs from all other studied tetraconates, which show at most four pairs of serotonin-like immunoreactive somata per segment, a number that has been suggested to be representative for the ground pattern of Tetraconata.

Molecular phylogeny: new markers and phylogenomic analyses- Poster B16

Alternative view on deep molluscan evolution

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Mollusca are old, diverse, ubiquitous, relevant to many disciplines, and have a formidable fossil record. Though, interrelationships of the eight extant classes, the identity of numerous aberrant fossils, and the early molluscan evolution are basically unresolved. Innumerable palaeontological and anatomical approaches added important information, but hypotheses proposed on early molluscan phylogeny remain contradictory. Most researchers and textbooks trust the Conchifera concept, comprising all shell bearing molluscs except for Polyplacophora. Usually, polyplacophorans are thought either to form a clade called Testaria with Conchifera, or a clade Aculifera with also spicule-bearing aplacophoran "worm-molluscs". Rather than supporting any of these conventional hypotheses, molecular systematic studies recovered a well-supported clade Serialia, composed of the single-shelled Monoplacophora and Polyplacophora. However, all previous multi-locus studies suffered from contamination and limited taxon sampling; in particular, just single monoplacophoran species were available. Here we present results from comprehensive, exhaustively quality checked data sets of five mitochondrial and nuclear loci. All eight molluscan classes are covered by multiple representatives, including five monoplacophoran species; we are the first to include both currently recognized families. The topology recovered supports the Serialia idea, and rejects major traditional concepts of molluscan class interrelationships. We also are the first to estimate divergence times of major molluscan lineages by relaxed molecular clock analyses on base of several sets of fossil calibration points. An alternative scenario on early molluscan evolution emerges.

Molecular phylogeny: new markers and phylogenomic analyses - Poster B17

Evolution of the epithelial sodium channel and the sodium pump are linked to the development of multicellularity in the Metazoan kingdom.

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Despite large changes in salt intake, the mammalian kidney is able to maintain the extracellular sodium concentration and osmolarity within very narrow margins, thereby controlling blood volume and blood pressure. In the Aldosterone Sensitive Distal Nephron (ASDN), aldosterone tightly controls the activities of ENaC and Na,K-ATPase, the two limiting factors in establishing transepithelial sodium transport. It has been proposed that the ENaC/degenerin gene family is restricted to Metazoans whereas the alpha and beta-subunits of Na,K-ATPase have homologous genes in prokaryotes. This raises the question of the emergence of osmolarity control. By exploring recent genomic data of diverse organisms, we found that: i) ENaC/Degenerin exists in all of the Metazoans screened, including non bilaterians, and by extension was already present in ancestors of Metazoa. ii) ENaC/Degenerin is also present in Naegleria gruberi, an eukaryotic microbe, consistent with either a vertical inheritance from the Last Common Ancestor of Eukaryotes or a lateral transfer between Naegleria and Metazoan ancestors. iii) The Na,K-ATPase beta-subunit is restricted to Holozoa, the taxon that includes animals and their closest single-cell relatives. Since the beta-subunit of Na,K-ATPase plays a key role in targeting the alpha subunit to the plasma membrane and has an additional function in the formation of cell junctions, we propose that the emergence of Na,K-ATPase, together with ENaC/Degenerin, is linked to the development of multicellularity in the Metazoan kingdom. The establishment of multicellularity and the associated extracellular compartment ("internal-milieu") precedes the emergence of other key elements of the aldosterone signaling pathway.

The evidence found in morphology - Oral Presentation

Function and evolution of echinoid photoreceptors

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Light triggered behaviors in echinoids have been reported since the late 19th century but the corresponding receptor structures have remained enigmatic until genomic data of the purple sea urchin (*Strongylocentrotus purpuratus*) became available. Combined with results of morphological studies, these data enabled us to identify and characterize photoreceptors in echinoid podia and allows to draw conclusions regarding their function and evolution. *Pax6*, an essential transcription factor for eye development in many metazoan animals, is present at the site of the developing echinoid photoreceptors and they express an opsin ortholog of photopigments found in visual photoreceptors of protostomes as well as in *Branchiostoma* Hesse and Joseph cells and vertebrate photoreceptors for circadian rhythm. Echinoid photoreceptors, like protostome ones, display a microvillar morphology. We thus propose common origin of all these photoreceptors with the echinoid ones displaying a unique functional arrangement within the animal kingdom. Despite the lack of light shielding pigment granulae the receptors at the podial bases are effectively shaded by the roundish echinoid skeleton allowing the animal to detect the direction of a light source and to function as one huge "compound eye". Asteroid photoreceptors known to have a role in phototaxis also react with a highly specific antibody produced against the echinoid rhabdomeric opsin and we thus propose a visual function for this receptor type at the base of deuterostomes. Deployment of this photorector cell type in circadian rhythm might thus have evolved as late as in the chordate stemline.

Molecular phylogeny: new markers and phylogenomic analyses - Poster B18

Molecular phylogeny of the carnivorous sponge family Cladorhizidae: implications for the systematics of Poecilosclerida

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Among the species-rich demosponge order Poecilosclerida, members of the family Cladorhizidae are well-known for their carnivorous habit. From a systematic point-of-view, Cladorhizidae represents a problematic taxon for the accepted classification of Poecilosclerida. In this respect, the family lacks a "strong synapomorphy", and its high diversity of chelae is at odds with the sub-ordinal classification of poecilosclerid sponges. The pivotal role of cladorhizid sponges in the systematics of the order Poecilosclerida has been repeatedly recognized: the diversity of micro-spicules observed in carnivorous sponges —even restricting the analysis to Cladorhizidae— could fit the definition of several poecilosclerid families in the sub-orders Mycalina and Myxillina, and could mean that the classification of the order Poecilosclerida deserves to be revised. Here, we present a molecular phylogenetic analysis of the family Cladorhizidae and clarify their relative systematic position within the order Poecilosclerida.

The evidence found in morphology - Poster C20

Report on the activities of the International Zoomorphological Standards Consortium

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In the age of the semantic web and the use of databases in everyday biological research practice, standardization of data and metadata become increasingly important and respective initiatives started in various academic communities. Based on an initiative from last year, an international consortium for developing data and metadata standards for zoomorphology formed during the *2nd International Congress of Invertebrate Morphology* this year. I will report on the progress and activities of the initiative and the resulting International Zoomorphological Standards Consortium.

Innovations in the analyses of molecular and morphological data - Oral Presentation

Using the matrix module of Morph•D•Base for collaboratively editing character matrices live and online

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Morph•D•Base (www.morphdbase.de) is an online database for storing morphological metadata and graphical material according to modern standards using controlled vocabularies like DarwinCore. The matrix module allows generating phylogenetic character matrices, in which each cell can be linked to relevant specimen, taxa, media, and literature entries within *Morph•D•Base* as well as to external web resources. This allows detailed documentation of all relevant information, satisfying the requirement for reproducibility and transparency. Character and character state definitions in *Morph•D•Base* are given in "free text" and in future also as schematized codings (adapted from Sereno's *neomorphic* and *transformational* coding schemes). User will also be able to use terms and concepts from anatomy ontologies (e.g. OBO, www.obofoundry.org), resulting in marked-up character and state definitions/codes, which significantly increases overall semantic transparency of matrices as well as comparability between them. The matrix editor possesses many additional features for managing and collaboratively editing matrices, including live editing with dynamic update of the web interface, color labeling of cells/rows/columns, scheduled-notifications, change tracking, and progress markers. Further in development are a chat-functionality, commenting on various input fields, and import/export of NEXUS and NeXML files. It will also offer two innovative features not found in any other matrix editor: (i) coding of alternative characters for competing homology hypotheses; (ii) specification of class-subclass and part-whole relationships between characters, which can be used to automatically preclude inconsistent combinations of certain character state combinations in absent/present codings. *This study was supported by the Deutsche Forschungsgemeinschaft DFG (VO 1244/3).*

Molecular phylogeny: new markers and phylogenomic analyses - Poster B19

Molecular phylogenies are in strong conflict with the current classification of calcareous sponges

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For certain metazoan taxa, establishing a robust phylogenetic classification can be a challenging task. Especially non-bilaterian metazoans such as sponges often lack informative morphological characters due to their simple organization. Calcareous sponges (Phylum Porifera, Class Calcarea) are an extreme example of this challenge. Despite numerous efforts to establish a well-supported phylogenetic system, the currently accepted classification is based on debatable hypotheses regarding the evolution of certain morphological characters. Several of these hypotheses were questioned by results of previous analyses of ribosomal RNA gene data. By extending the currently available data, we provide new and previously unconsidered hypotheses about the evolution of Calcarea. With the data we can reject several phylogenetic hypotheses about morphological evolution, which underlie the current classification of this class. According to our results, the taxonomy of Calcarea is in desperate need of a thorough revision that cannot be achieved by considering morphology alone. Our hypotheses require further testing with independent molecular markers. We discuss the potential use of mitochondrial genes for this purpose.

The evidence found in morphology - Poster C21

Phylogenetic implications from photoreceptors in Nemertea

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Ciliary pigmented cerebral photoreceptors have been reported to occur exclusively in vertebrates. In other invertebrate taxa the pigmented cerebral photoreceptors comprise rhabdomeric receptor cells. This goes along with a stereotypical expression of ciliary and rhabdomeric opsins, respectively. However, pigmented cerebral photoreceptors with ciliary receptor cells have been observed in larvae of numerous invertebrate taxa (e.g. in representatives of nearly all spiralians). In nemerteans only the cerebral photoreceptors in juveniles and adults of the derived Neonemertea have been studied. In Lineus viridis , the eye develops from an anlage consisting of only a few cells to a rhabdomeric photoreceptor comprising numerous pigmented, corneal, and receptor cells. In order to get data on the larval cerebral photoreceptors the eyes of larvae of palaeo- and hoplonemerteans were examined using transmission electron microscopy. In the basally branching palaeonemertean species studied the larval photoreceptor consists of few cells of two types: pigmented and ciliated receptor cells, whereas in hoplonemertean larvae the photoreceptor is rhabdomeric. Moreover, the photoreceptors in hoplonemerteans show a remarkable similarity to the organization of the adult photoreceptor suggesting that they are identical. It is assumed that the ciliary photoreceptors of palaeonemerteans represent the ancestral type of eyes in Nemertea, thus providing another case of pigmented cerebral photoreceptors in spiralian larvae. Studies to elucidate the type of opsins expressed in both the rhabdomeric and the ciliary eyes of Nemertea are in progress.

Molecular phylogeny: new markers and phylogenomic analyses - Invited

Discovering the evolution of pancrustaceans within arthropods: prospects and pitfalls of molecular methods including phylogenomic data

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The reconstruction of the evolutionary history of crustaceans and arthropods is still difficult addressing internal relationships, but also revealing the likely crustacean sistergroup to Hexapoda. Recent molecular studies corroborate Myriapoda as sistergroup to Pancrustacea with paraphyletic crustaceans supporting Remipedia or Remipedia + Cephalocarida as sistergroup to Hexapoda. However, the position of Remipedia and several other groups like Malacostraca within crustaceans still remains ambiguous based on different data sources. A likely scenario of euarthropod evolution based on EST data is, that Remipedia represent the possible link to Hexapoda conquering land habitats.

In the presented phylogenomic approach first 454 EST data of Remipedia were included. Genes were selected from the unreduced dataset applying the matrix reduction software MARE. All reconstructed topologies highly support Remipedia as sistergroup to Hexapoda. The results further support recent studies concluding that critical data evaluation is crucial and new methods are essential for prospective phylogenetic analyses.

To estimate the reliability of the tree reconstructions from phylogenomic data is a major challenge and the handling of long branch taxa is still problematic. This and further issues, e.g. the gene selection and the identification of informative genes are essential to improve our understanding of molecular evolution and phylogenomic data. However, to enlight pancrustacean evolution, it is still crucial to collect more crustacean key taxa (e.g. Cephalocarida). The presented analysis includes first 454 data of Remipedia, Ostracoda, Mystacocarida and Leptostraca. Until now, an overhead of decapod EST sequences is published, while data for non-decapods are very sparse.

Molecular phylogeny: new markers and phylogenomic analyses - Poster B20

Phylogenomic analyses of annelid phylogeny - the influence of adding new taxa

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Annelida is a highly diverse animal phylum with over 15,000 described species. Whereas the monophyly of the approximately 80 higher ranked taxa usually classified as families was well established, relationships between those taxa remained controversial. In a phylogenomic analyses mainly based on traditional Sanger EST-sequencing we recovered a well-supported phylogeny with strong support for two major splits (Errantia and Sedentaria) including the biggest fraction of annelid diversity, indicating that life-history characters are phylogenetically informative. Moreover, Clitellata form a subgroup of the latter and are nested within a part of the former Scolecida. A sister group relationship to all other annelids can be rejected without doubt. Chaetopterids, myzostomids, and sipunculids grouped outside this core Annelida, now named Pleistoannelida, in the basal part of the tree. The position of Echiura and Siboglinidae within Sedentaria can be confirmed and is strongly supported. Using Solexa-based mRNA sequencing, we added eight more taxa, partly of hitherto unrepresented annelid families, to our dataset. Using ML-based analyses, we found additional support for the backbone of the annelid tree as described above. Additionally, we performed sensitivity analyses to estimate the influence of outgroup choice and ingroup taxon sampling. Ancestral character state reconstructions of last common ancestors of major annelid clades are discussed in the light of the fossil record.

Molecular phylogeny: new markers and phylogenomic analyses - Oral Presentation

About wheels, thorns and trees – The phylogeny of Syndermata in the light of EST data

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Syndermatans are part of the lophotrochozoan clade in the metazoan tree of life. They comprise minute (<1mm) and mostly free-living "wheel animals" (Rotifera) on the one hand and obligate endoparasitic "thorny-headed worms" (Acanthocephala) of up to 70 cm length on the other hand. Despite vast differences in morphology, the monophyly of Syndermata is rather undisputed. Their internal phylogeny, however, has been debated for more than twenty years.

Within the DMP framework, we have produced plenty of EST data of syndermatans, including Seisonidea, a special epizoic taxon of rotifers that was formerly only scarcely covered by molecular data. We extracted sequences of ribosomal proteins or applied a broader search for gene orthologues and reconstructed molecular phylogenies based on the largest sequence datasets available for these taxa. The results consistently show a closer relationship of bdelloid rotifers to the morphologically distinct Acanthocephala than to monogonont rotifers, revealing the taxon "Eurotatoria" as paraphyletic. Recently, we were able to confidently resolve the position of the epizoic Seisonidea inside the syndermatan clade as sister group to the endoparasitic acanthocephalans, providing interesting implications for the evolution of parasitism. Additionally, the topology indicates loss events of complex morphological traits in the syndermatan lineages.

Furthermore we evaluated the suitability of ribosomal protein (RP) sequences for phylogenetic reconstructions in syndermatans. Our findings clearly indicate that some RP sequences can bias the analysis, especially when long branches are present, and that a suitable subset of RP data should be selected for phylogenetic reconstructions.

Molecular phylogeny: new markers and phylogenomic analyses - Poster B21

The phylogeny of Acanthocephala in the light of complete mitochondrial genome data

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Acanthocephalans ("thorny headed worms") are endoparasites of up to 70cm length that use vertebrates as their definite hosts. They are widely accepted as a subtaxon of the Syndermata and therefore as close relatives of the minute (<1mm) and mostly free-living "wheel animals" (Rotifera). The monophyly of Rotifera (classes Monogononta, Bdelloidea and Seisonidea), however, is questionable with respect to acanthocephalans, as has been shown in several recent studies. Furthermore, the relationships between the three acanthocephalan groups are controversially discussed.

Until 2011, only three syndermatan mt genomes were available, covering only half of the existing taxon classes. Within the DMP framework, we have amplied and sequenced four syndermatan mitochondrial genomes, including one bdelloid rotifer, one Palaeacanthocephala and two acanthocephalans from taxa that were formerly not covered by broad molecular data (Eo- and Archiacanthocephala). We investigated mt gene repertoire, gene order and tRNA structures and used the derived amino acid sequences of the encoded proteins to reconstruct phylogenies.

Our results reveal interesting features of syndermatan mt genomes in terms of e.g. rRNA size variation and structural modifications of tRNAs. The phylogenetic reconstructions support recent indications for paraphyletic Eurotatoria. Confirming our EST-based work, we can conclusively sort out three of five postulated hypothesis of the internal syndermatan phylogeny. We also answer several questions regarding the internal phylogeny of acanthocephalans. The obtained topology implies massive gain and loss events of complex morphological traits during the evolution of the acanthocephalan lineages.

Innovations in the analyses of molecular and morphological data - Oral Presentation

Testing hard polytomies with partial splits

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It has been suggested that some parts of the Metazoan tree are hard to infer because divergences occurred quickly producing short internal branches with too few changes (morphological and molecular) on these branches to provide good evidence for the reality of the branch. This line of reasoning is common in phylogenetics when analyses fail to resolve relationships and it is claimed that polytomies in inferred trees are hard (real). Hard polytomy hypotheses are most obviously tested through the generation of additional data that may or may not allow resolution of the polytomy. In the absence of additional data, limited testing of hard polytomy hypotheses may be achieved using partial splits. Well supported partial splits can be incompatible with hard polytomy hypotheses and thus can lead to their rejection or refinement. I will illustrate several approaches that can be used to discover well-supported partial splits using Metazoa as an example. The methods are relevant to the discovery of relatively unstable taxa, whether those taxa comprise single leaves or entire clades.

Molecular phylogeny: new markers and phylogenomic analyses - Invited

The status quo of higher-level metazoan phylogey based on phylogenomic analyses

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Higher-level metazoan relationships have been controversial since the early single-ribosomal gene phylogenies have proposed the „new animal phylogeny". Nowadays, expanding molecular datasets and continuing advances in phylogenomic methods are increasingly used, aiming for a robust animal backbone phylogeny. However, while many deep intra-bilaterian relationships are largely uncontentious, several important nodes remain difficult to resolve even with large amounts of sequence data. For example, some recent large-scale metazoan phylogenomic analyses found no unequivocal support for the relationships among non-bilaterian animals, the position of acoelomorph flatworms and *Xenoturbella* as the sister-group to the remaining Bilateria remains debated, similar to the still unresolved position of the Chaetognatha. However, a well solved and supported backbone phylogeny of animals is needed to correctly reconstruct the evolution of the Metazoa in deep time. Some of the still open questions and remaining issues will be highlighted to open the symposium on „Molecular phylogeny: new markers and phylogenomic analyses".

Molecular phylogeny: new markers and phylogenomic analyses - Poster B22

DNA palindromes as a new and effective phylogenetic marker

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Phylogenetic markers span to extremes. At one extreme are neutrally evolving characters that are ideal for both phylogenetic reconstruction and dating speciation and gene duplication events, but suffer from two disadvantages: 1) they are not suitable for deep phylogenies because of rapid substitution saturation, and 2) they do not give us clues as to the evolutionary interaction between DNA and environment. The other extreme are represented by phenotypic characters such as morphological traits whose phylogenetic signals are typically maintained by strong purifying selection. DNA palindromes and RNA stem-loop structures are typically the recognition sites for a variety of molecular machinery operating in the transcription, translation and genome duplication processes. A nucleotide sequence has its unique palindromic landscape associated with its molecular function. These palindromic landscapes constitutes a class of molecular phenotypes whose phylogenetic potential has not been explored.

Here I present a preliminary analysis of palindromic data to show that palindromes can be used to recover both shallow and deep phylogenies. The analysis does not require sequence alignment and therefore circumvent the chick-and-egg problem in multiple alignment (i.e., a good guide tree is needed for a good alignment which is in turn needed to produce a good guide tree). In particular, the dynamic change of palindromes along different evolutionary lineages is expected to tell us evolutionary interactions between DNA and the cellular machinery it encodes.

Molecular phylogeny: new markers and phylogenomic analyses - Poster B23

Hidden parapatric speciation in the reef-building coral *Heliopora coerulea*

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The blue coral Heliopora coerulea is the sole extant member of the alcyonarian order Helioporacea. Although this species is once widely distributed in tropical and subtropical regions, its current distribution is limited due to its preference of specific environment and also human disturbances. It is at present regarded as Vulnerable under Criterion A4cde of the IUCN Red List Category. Because this species has wide range of planktonic larval duration (a few hours to up to 30 days), reef-connectivity studies are essential for its conservation. Hence, we examined the population genetic structure of H. coerulea collected from Southeast Asia (Thailand, Philippines) and West Pacific (Palau, Taiwan and Japan) region, using microsatellite makers. Two major genetic clades were found irrespective of geographic distances indicating that continuous (or neighboring) populations do not mate and exchange larvae randomly. The two clades are incongruent with different skeletal morphologies but some trends are found: clade A often appears in small branch shape and favors reef-slopes rather than inside fringing reef and cladeB often appears in leaf-shape and favors rather calm situation inside fringing reefs. Further genetic analysis revealed CladeA had stronger gene flow than Clade B, implying possible difference in larval ecology and/or ecological post-settlement selection between the two hidden species.

Molecular phylogeny: new markers and phylogenomic analyses - Poster B24

Tracing of Malaysian indigenous mahseers (cyprinids) phylogeny through partial sequences of cytochrome oxidase II gene

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Mahseer are endemic to Asia and there are comprises of three genera. *Tor*, *Neolissochillus* and *Naziritor* . There are 17 species under the genus *Tor* from all across Asia but only 3 species reported in Malaysia namely *Tor tambroides* , *Tor douronensis* and *Tor tambra* . Among the Malaysian mahseers, the taxonomic differentiation of *T. douronensis* and its related species, *T. tambroides* and *Neolissochilus stracheyi* are highly controversial with many conflicting descriptions among different authors. The present study aimed to clarify the phylogenetic relationship of the three Malaysian indigenous mahseers by utilizing direct sequencing of the mitochondrial (mtDNA) cytochrome oxidase II (COII). A total of 595bp of the mtDNA COII gene was successfully sequenced for 15 individuals of 3 species of Mahseer comprising of genera *Tor* and *Neolissochilus*. The maximum parsimony tree showed 2 major clades generated from sequences of Malaysian Mahseer. The first clade is belonging to Tor congeners while the second clade comprised all samples of *N. stracheyi*. This method of analysis, was positioned *N. stracheyi* as sister taxa to *Tor* congeners with high bootstrap support (93%). The findings from this present study are generally concordance with the current taxonomic classifications of mahseer based on morphology.The generated phylogenetic tree also supported the monophyletic status between the two malaysian mahseers of the genus *Tor* (*T. douronensis* and *T. tambroides*). The current findings validate the current reclassication of *N. stracheyi* (previously classified as *Tor soro*) from the genus Tor into the genus *Neolissochilus* based on the absence of median lobe.

Estimating the phylogeny and divergence times of Malaysian *Puntius* using mitochondrial and nuclear genes

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Puntius spp has the largest number of species in the Asian tropics with some unsolved taxonomic problems at the species level. The phylogenetic relationships are inferred from DNA sequences of the three mitochondrial genes (Cytochrome oxidase b (875 bp), Cytochrome oxidase c (498 bp), 16s ribosomal RNA (574) and two nuclear genes, Recombination activating gene 2 (863 bp) and Beta actin (913 bp). A multi-locus molecular phylogeny was constructed and calibrated using two fossil dates to estimate divergence times within the Cyprinid family. The topologies resulting from maximum parsimony, maximum likelihood and Bayesian analyses of combined genes are broadly congruent with each other. Two distinct clades within the genus were obtained with high bootstrap values, namely Clade I (*P. schwanenfeldii* , *P. bulu* , *P. gonionotus* , and *P. daruphani*) and Clade II (*P. fasciatus* , *P. tetrazona hexazona* , *P. tetrazona partipentazona* , *P. lateristriga* , *P. binotatus* and *P. everetti*). Divergence times estimated from nuclear and mitochondrial DNA data calibrated in the data set showed a clear history of diversification over the last 47.87 million years ago (MYA) for cyprinid, and 26.85 (MYA) for *Puntius* and supported early Oligocene origins for this genus.

Atrium of the palaeontological museum Munich with *Gomphotherium* aff. *steinheimense* (KLÄHN) in the foreground

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