Meeting report

150 years beyond Darwin's *Origin of species*: finding new approaches to reconstruct early animal phylogeny

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The conference 'Celebrating Darwin: From the Origin of Species to Deep Metazoan Phylogeny' was held at the Humboldt University in Berlin, from 3 to 6 March 2009. Specialists from the fields of bioinformatics, molecular biology, developmental biology, comparative morphology and paleontology joined forces to present and discuss novel approaches in reconstructing the still unresolved early branching patterns of the metazoan tree of life.

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1. INTRODUCTION

The field of phylogenetics, i.e. the study of evolutionary relationships between groups of organisms, has undergone dramatic changes during the last two decades. While most phylogenetic trees and classifications found in textbooks have been constructed the 'traditional way' by morphologists using anatomical characters, the advance of nucleotide and protein sequencing techniques has shifted the focus of phylogeneticists towards molecular data. The analysis of sequence data depends upon sophisticated mathematical algorithms to handle the sheer amount of information. Therefore, modern evolutionary research depends on tools that are generated by bioinformatic experts. Whereas phylogenetic studies are usually carried out on extant organisms, the aim is nevertheless to reconstruct a process that has occurred in the past. Thus, the resulting trees must be in accordance with the fossil record. Consequently, the field of paleontology plays a major role in phylogenetics, as well. A constant exchange of information and ideas between morphologists, geneticists, mathematicians and paleontologists is essential to advance our knowledge of the evolutionary past. And advance is truly needed because even 150 years after Darwin's *On the origin of species* (Darwin 1859), the origin of most major animal groups is still a matter of debate. With

an average of 15 phylogenetic trees published per day (Rokas 2006) the picture is not necessarily getting clearer. Many trees contradict each other. This is in part due to the different types of information that are used to infer phylogenetic relationships and is also owing to different mathematical models underlying the construction of evolutionary trees. The disagreements also reflect the fact that the construction of a phylogenetic tree is an inherently uncertain process of statistical inference.

What is needed are new approaches to combine the available information, assess the quality of the data used and search for novel characters that might aid in reconstructing the early branching points of the tree of life. To get a start on achieving this goal, specialists from various fields of biology gathered at a conference in Berlin in March to exchange ideas and develop new concepts for retracing evolutionary events that occurred half a billion years ago.

2. THE DEEP METAZOAN PHYLOGENY PROGRAMME

The conference (local coordinator: Gerhard Scholtz, Humboldt-University) was organized by members of the German Research Foundation's priority programme Deep Metazoan Phylogeny (DMP). This programme currently comprises 24 research groups from 15 universities. Specialists from the areas of bioinformatics, molecular biology and morphology work together in a synergistic approach to reconstruct the still unresolved early branching patterns of the metazoan tree of life.

The DMP project is now in its fourth year. With the intention of presenting what has been achieved so far to a wide audience and to join forces with international colleagues, DMP organized the conference 'Celebrating Darwin: From the Origin of Species to Deep Metazoan Phylogeny' at the Humboldt University in Berlin from March 3 to 6 2009. In all, 180 scientists from 17 nations attended the meeting, whose scientific part comprised 50 talks, 51 posters and a panel discussion.

3. EARLY ANIMAL RADIATION: STILL A PUZZLE

The conference focused on unraveling the basal branching pattern of the metazoan (multicellular animals) tree of life, i.e. on evolutionary events that occurred before and throughout the so-called Cambrian radiation. During this period that lasted from approximately 540–500 Myr ago, most major groups of complex animals that still exist today appeared in the fossil record. Some taxa like sponges or cnidarians are most likely older, dating back to the Pre-Cambrian Ediacara era. Consequently, the separation of major bilaterian phyla most likely took place between the Ediacaran period and the Middle Cambrian. If we want to understand what happened during this era, we are faced with the challenge of reconstructing events that happened within a relatively short geological time frame. Since then, evolution has altered the organismic world for more than half a billion years, thereby blurring cues on the early branching patterns of the animal tree of life. Until now, there has been no consensus of what the basic nodes of the tree looked like. Are sponges the sister group to the

remaining multicellular animals or are the metazoans a group within the sponges? Other investigations suggest that not the sponges but the placozoans, feature-poor flat creatures, are the most basal animals. These are just a few examples of alternative evolutionary scenarios that are under debate and were discussed at the Berlin conference.

4. FINDING WAYS TO RECONSTRUCT EVOLUTIONARY EVENTS THAT OCCURRED HALF A BILLION YEARS AGO

In his welcome address, Wolfgang Wägele (Museum Koenig, Bonn), the coordinator of the DMP programme, stressed that it was not the goal of the conference to present even more trees but to discuss new concepts, find novel characters from which to derive phylogenetic relationships and exchange ideas for developing advanced tools in data analysis and data quality assessment. Different approaches have frequently resulted in conflicting trees. However, seemingly contradictory findings have to be reconciled and interpretations have to be found for why, for instance, morphological results are often not congruent with molecular data. One example of this problem that has led to lively discussions for many years is the relative position of annelids and arthropods within the animal tree of life. While traditionally, based on similarities of the body plan, these two groups were united as the Articulata, molecular studies place annelids and arthropods in two different superphyla, the Ecdysozoa and Lophotrochozoa. Assuming that the latter is true, this hypothesis implicates repeated and independent evolution or, alternatively, multiple loss of highly complicated structures. As yet there are no ideas of how to explain such evolutionary scenarios in a plausible way. These problems not only arise when comparing molecular with anatomical findings but conflicting trees also arise when phylogenies are built upon different sets of genes or identical data are analysed with different mathematical models.

The following presentations were assigned to three symposia. The first one, titled 'Innovations in analyses of molecular data' contained talks that proposed advanced algorithms and novel methods to compute molecular information. An introduction to the symposium was given by Bernhard Misof (University of Hamburg), who summarized problems and possible solutions of sequence data analysis. Misof outlined that with increasing amounts of sequence data, stochastic errors may vanish but systematic biases will remain a problematic issue. Erroneous branching points that are built upon biased data are likely to go undetected because classical measures of robustness (e.g. bootstrapping) cannot assess the amount of bias in the analysis, concluding that data quality counts more than ever. The subsequent talks dealt with different theoretical aspects of tree-building algorithms, data quality evaluations and new ideas on nucleotide sequence evolution.

Presentations in the second symposium 'Molecular phylogeny: new markers and phylogenomic analyses' gave an overview of the current state of molecular analyses concerning specific questions in animal

phylogeny. Topics that were covered included the search for the root of the metazoan tree, an estimate of the genetic complexity of the last universal ancestor of the Metazoa and molecular aspects of the evolution of segmentation, to name just a few. Several talks discussed the usefulness of different types of molecular data such as selected single genes, whole-genome approaches, expressed sequence tags or rare genomic events for the reconstruction of animal relationships. In his talk, Casey Dunn (Brown University, Providence) took a glimpse into the near future, suggesting that owing to constantly falling prizes for gene sequencing, the amount of molecular data available will no longer pose a problem. Rather, cut-backs in the support for classical zoology cause a lack of trained taxonomists, which in turn might lead to poor or incorrect species sampling. Another limiting factor will be the enormous computational power that is needed to analyse large molecular datasets. Dunn named an overwhelming number of more than 6000 CPUs that worked in parallel for a total time of more than 2 million hours at the IBM BlueGene/L supercomputer in San Diego, which his group needed to calculate their latest tree.

The final symposium 'The indispensability of morphology' focused on the relevance of morphological findings in modern phylogenetics. Several talks covering the disciplines of comparative anatomy, developmental biology and paleontology demonstrated the importance of morphological findings in testing evolutionary hypothesis that are proposed based on molecular data. Claus Nielsen (University of Copenhagen) laid out that, while nowadays anatomical findings play only a minor role in erecting new trees, the field of morphology is, nevertheless, indispensable for envisioning phylogenetic pathways, reconstructing ancestral bodyplans and describing adaptive values of evolutionary changes. All this is necessary for assessing the plausibility of a proposed tree. Other presenters focused on selected organs such as the central nervous system, the eyes and on embryology and discussed the findings in the light of novel phylogenetic hypothesis. Two talks on paleontology demonstrated the informative value of fossils in evolutionary research. Stefan Bengtson (Swedish Museum of Natural History) showed how modern synchrotron-based X-ray microtomography enables investigators to study the internal structure of animal tissue that is more than half a billion years old. Using state-of-the-art techniques, it was, for example, possible to demonstrate the presence of cnidocytes in the oldest cnidarian-like animals. Jes Rust (University of Bonn) made the point that fossils still represent the most important documents of the historical aspects of phylogenesis. Using the example of whales, Rust outlined that for this group not only is a relatively complete fossil record to retrace evolutionary events available, but that well-preserved foetal skeletons that are positioned for head-first delivery in the female body also indicate that early whales that were already adapted to life in water still gave land-based birth, which is an example of how paleontology can sometimes even reconstruct the behaviour of extinct species. (For a complete list of speakers and topics please visit www.dmp2009.org.)

5. MODERN PHYLOGENETIC RESEARCH: WHAT LIES AHEAD

The basal nodes of the animal tree of life are still far from being resolved. Participants of the Berlin conference agreed that it will not be sufficient to publish ever more (conflicting) trees or simply increase the amount of raw data, but to work towards a new synthesis of several scientific disciplines to answer the open questions. 'From the Origin of Species to Deep Metazoan Phylogeny' made a first step in that direction. Novel mathematical algorithms and new molecular markers were suggested that will help to fish out informative genes. Finally, this meeting signified a revival of classical morphological approaches to test proposed phylogenies and to envision evolutionary pathways. For this is what phylogenetic studies in the end try to

achieve. We do not just want to present dichotomous branching patterns of an abstract tree, but draw a lively picture of what has happened in the past, because, as Claus Nielsen phrased it, 'molecular phylogenies without morphological data are like deciduous trees in winter time'.

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