

Metazoan deep phylogenies – can the Cambrian explosion be resolved with molecular markers?

Martin Schlegel¹, Guido Fritsch^{1,2} and Peter F. Stadler²

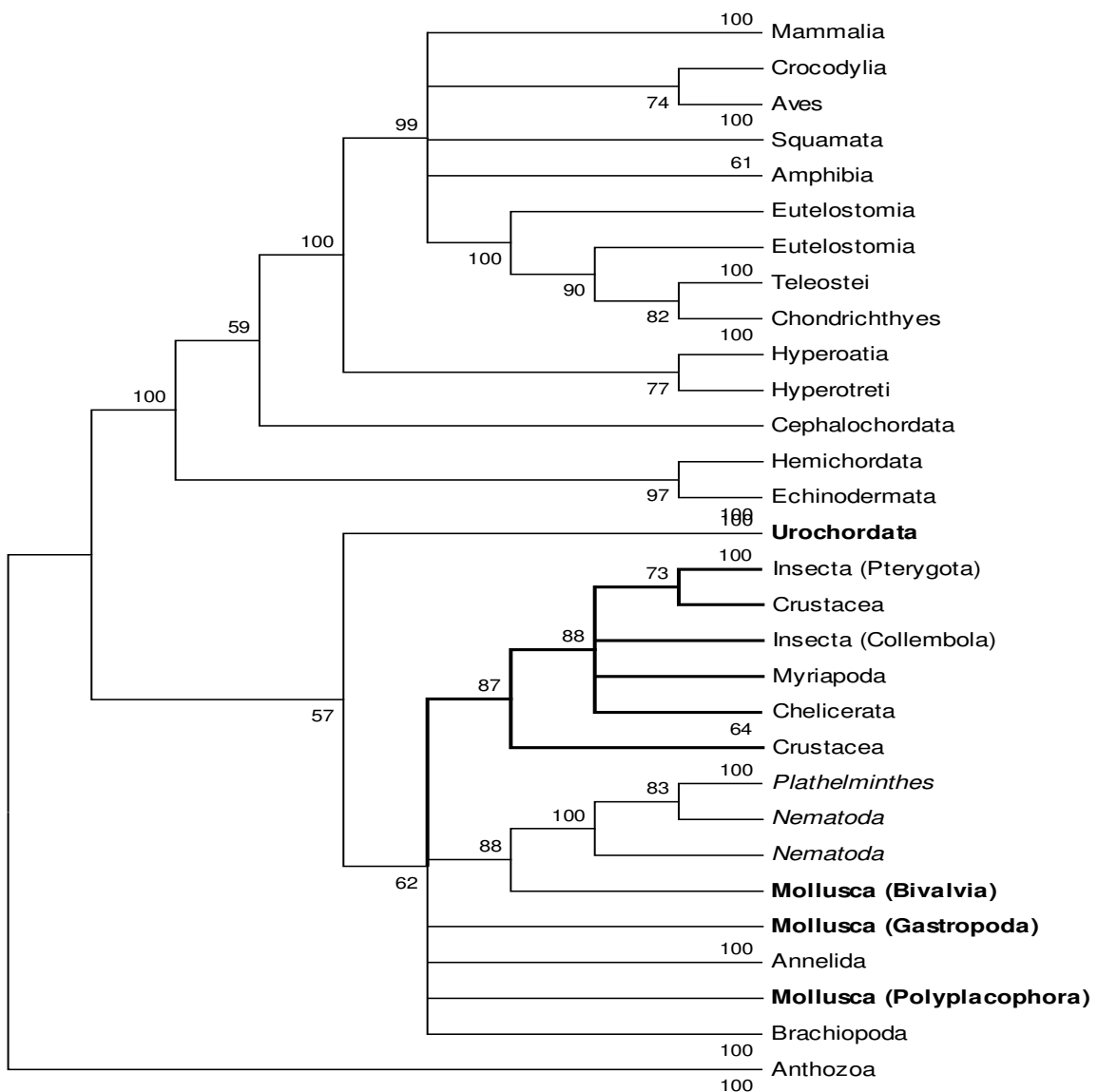
¹Institut für Zoologie
Universität Leipzig
Talstraße 33
04103 Leipzig

²Interdisziplinäres Zentrum für Bioinformatik und
Institut für Informatik
Universität Leipzig
Kreuzstraße 7b
04103 Leipzig

Fossils are our primary window to the history of life. Already Darwin was aware that the abundance of the fossil record dramatically increased in the Cambrian some 530 million years ago. Arthropods, annelids, molluscs, brachiopods, echinoderms, chordates, i.e. representatives of most of the recent animal phyla appeared (and a considerable number of life forms that did not survive and cannot be assigned to recent taxa). The appearance and radiation within ten million years is referred to the Cambrian explosion. To date it remains a problem to resolve the order of ramification within the extant major lineages and thus to understand the evolution of the various metazoan body plans, developmental processes, genome and proteome organisation as well as the phylogenetic position of important model organisms, such as *Caenorhabditis* and *Drosophila*.

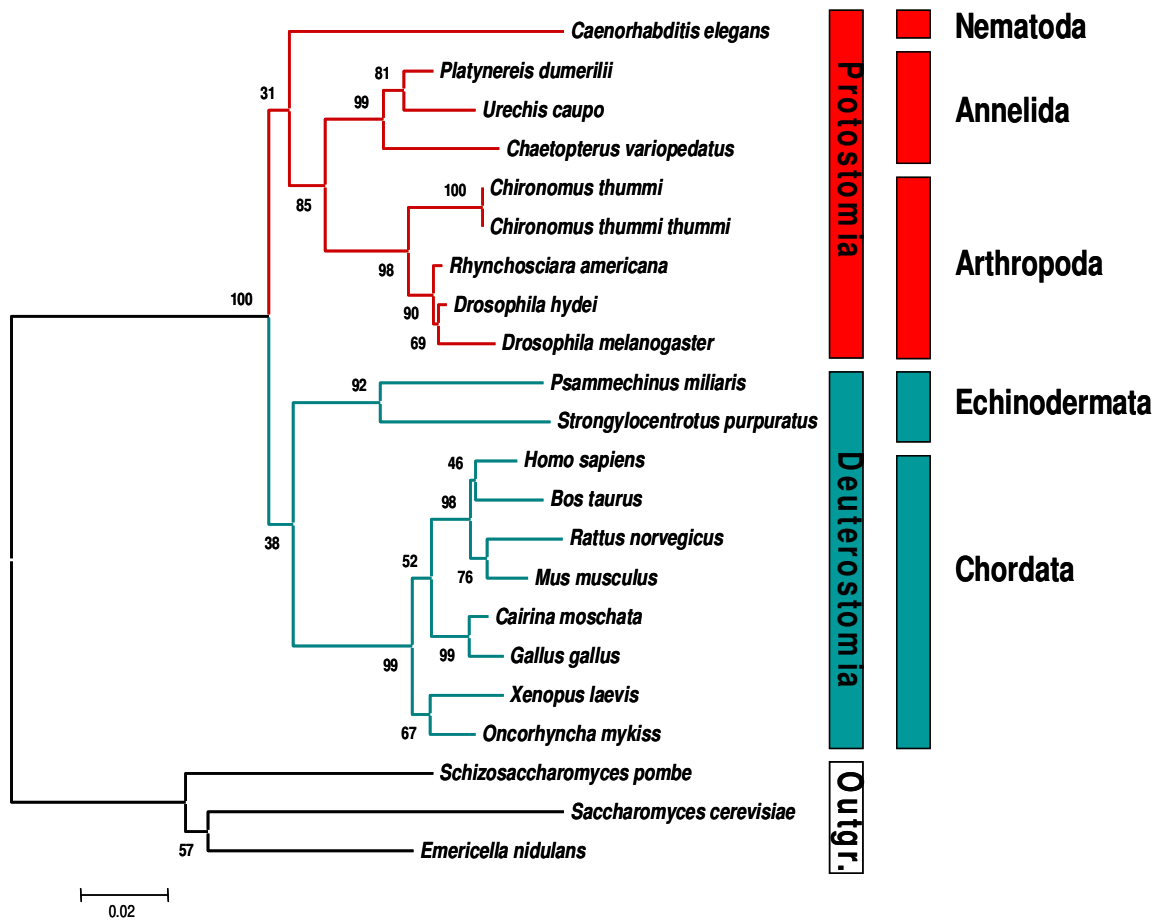
Besides comparative morphology and anatomy molecular data are increasingly applied in reconstruction of phylogenetic relationships. However, a consistent view of Cambrian phylogeny did not yet emerge from molecular investigations, which are mainly based on small ribosomal subunit RNA sequence comparisons. It has been hypothesised that the phylogenetic ramification of the extant animal phyla was so rapid, that no apomorphies evolved between the short branching intervals. Alternatively, the phylogenetic separation of major extant phyla may have already begun long before the Cambrian, but fossilisable material was not evolved before the Cambrian. Hints for such an evolution come from Precambrian fossils of sponges, cnidarians and from traces of bilaterians. Consequently, if ramification occurred considerably before the Cambrian, a more intensive and extensive analysis of gene sequences should provide consistent information on deep metazoan phylogeny and an alternative to the Cambrian "big bang" evolution. In order to test this alternative hypothesis we (and other working groups) started a comprehensive multi-gene sequence analysis in order to contribute to the solution of this outstanding evolutionary phenomenon in metazoan evolution.

Here, we report on our first results of the analyses of mitochondrial genome sequence comparisons and the Histone genes H2a, H2b, H3 and H4.



First results of the analysis of mitochondrial amino acid sequences with the maximum likelihood method. This tree shows a number of implausible features: (1) the placement of the urochordates outside the deuterostomes, (2) the disruption of the mollusca, (3) the placement of the plathelminthes inside the nematoda, (4) the interspersing of insecta and crustacea.

A comprehensive taxon sampling is available from mitochondrial genome sequences. Phylogenetic analyses are congruent with traditional concepts of deuterostome monophyly and support classical subgroup division, with the exception of the position of the Urochordata, which are branching off before the deuterostomes. Within the protostomes mitochondrial analyses did not yield the desired improvement in resolution of branching patterns. Even monophyletic taxa such as the molluscs were not recovered. Thus, this character does not support the alternative hypothesis of phylogenetic ramification significantly before the Cambrian. At present we are analysing whether this is due to the lack of evolution of character differences (which would support the “big bang” hypothesis) or due to saturation effects by multiple substitutions.



First results of the analysis of Histone genes (H2A, H2B, H3, H4). It shows the analysis of amino acid sequences with neighbour-joining method (gamma model)

A more promising result was obtained by analyses of concatenated histone genes. Although data are still lacking from some important lineages, such as the molluscs and the urochordates, clear character differences were detected in the sequences analysed so far which yield a consistent phylogenetic tree. Further sequences from representative samples are therefore urgently requested from histone genes, which were hitherto regarded to be evolutionarily too conserved to contain phylogenetic information.