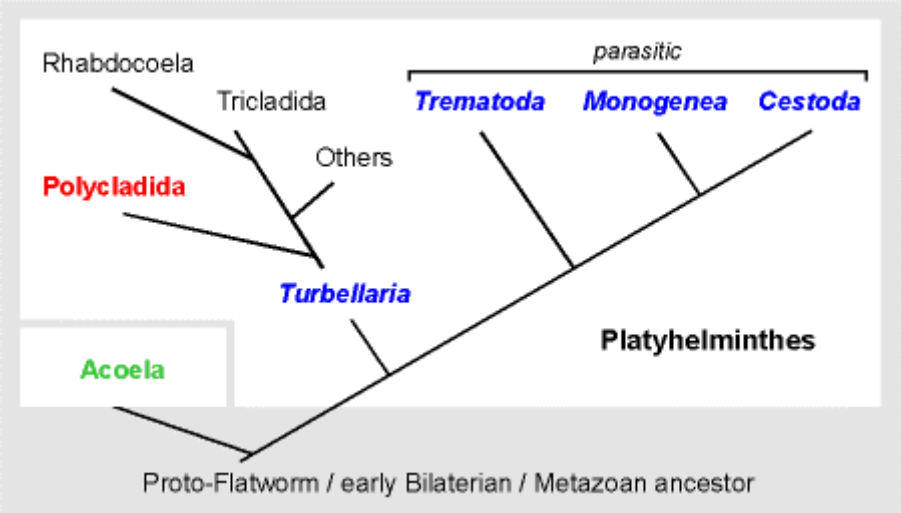
Phylogeny

Since the first Metazoa were almost certainly radial animals, animals with bilateral symmetry (Bilateria) must have sprung from a radial ancestor, and there must have been an alteration from radial to bilateral symmetry. This change still constitutes a most difficult gap for phylogeneticists to bridge, and various highly speculative conjectures have been made (Brusca & Brusca, 1995). Paleontological and molecular data indicate that most bilaterian phyla appeared and diversified during the Cambrian explosion, which occurred between 560 and 520 Mio years ago (Wang et al., 1999).



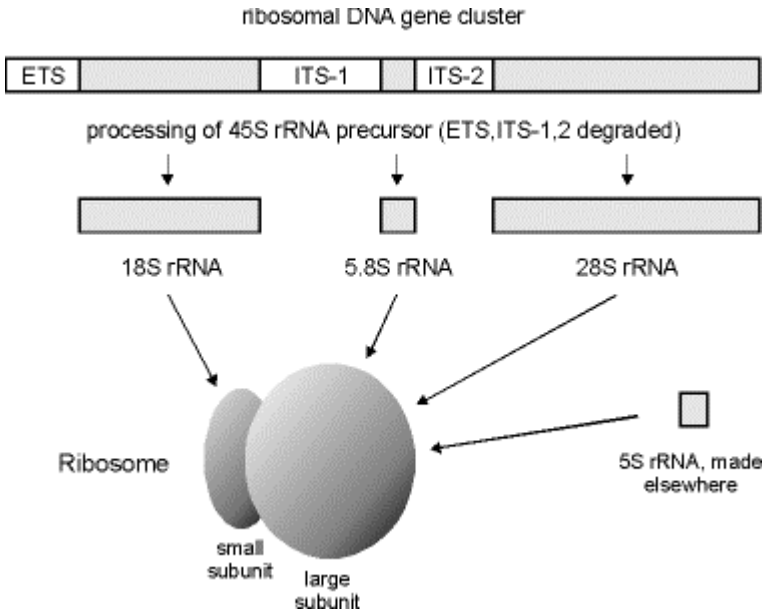
The phylum Platyhelminthes represents a diverse group of early Metazoa which are thought to be the key to understanding the origin and evolution of Metazoa. In most zoological textbooks, they are described as an early-emerging clade forming the likely sister group of all other animals with bilateral symmetry (Bilateria). Other authors see them either as the sister group of most of the Protostomia or as a group derived from protostome coelomate ancestors. The main difficulty in the correct phylogenetic placing is the lack of convincing synapomorphies for all Platyhelminthes. This indicates that they are polyphyletic. In a simplified taxonomic scheme, the phylum Platyhelminthes holds four classes: **Trematoda** (flukes), **Monogenea** and **Cestoda** (tapeworms), which represent endo/ectoparasites of vertebrates, some with complex life cycles, and the class **Turbellaria**, which represents primarily free-living flatworm species. The class Turbellaria consists of nine orders (Nemertodermatida, Catenulida, Macrostomida, Lecithoepitheliata, Rhabdocoela, Prolecithophora, Proseriata, Tricladida, **Polycladida**). The most relevant orders are depicted in this scheme.

The acoel flatworms (**Acoela**) have been classified as an order of the Turbellaria for a long time. They were considered the most primitive turbellarian order and have been viewed as either basal metazoans that evolved from ciliate protozoans (= syncytial or ciliate-acoel theory) or a direct link between diploblasts and triploblasts (= planuloid-acoeloid theory). Their simple organization has been interpreted as a secondary loss of derived features of more complex ancestors (regressive evolution). Today, several lines of evidence support the theory that the acoels branched before the Cambrian radiation from unknown bilaterian ancestors. For example, the structure of the nervous system indicates that the acoels are not related to other platyhelminths. Most Platyhelminthes have a bilobed brain with neuropile surrounded by nerve cells and two main longitudinal nerve cords with traverse commissures making an orthogon (see section: Polyclads and Neurobiology). In contrast, the nervous system of acoels comprises a simple brain formed by clusters of nerve cells that lack a neuropile, and a variable number of longitudinal nerve cords that do not make an orthogon (Ruisz-Trillo et al., 1999).

Recently, molecular techniques as DNA (desoxyribonucleic acid) and protein sequencing have been used successfully to construct a phylogenetic tree of life that allows assessment of phylogenetic relationships among animal taxa. Most common, DNA sequence data of highly conserved genes, for example genes coding for ribosomal RNA (rRNA), are used in such studies. Comparison of the sequence data of 18S ribosomal DNA genes of acoels and other Metazoa confirm that the Acoela do not belong to the Platyhelminthes but represent the extant members of the earliest divergent Bilateria. These findings suggest that the Acoela are a missing link between the first simple radially symmetric organisms like jellyfish and the more complex bilaterally symmetric organisms like arthropods and vertebrates. They should be placed in their own phylum (Ruisz-Trillo et al., 1999).

DNA sequence data can also help to discriminate even morphologically similar organisms.This has been demonstrated by Goggin & Newman (1996) for pseudocerotid turbellarians. Nucleotide sequence data from the internal transcribed spacer-1 (ITS-1) in the ribosomal RNA (rRNA) gene cluster were used to discriminate species (*Pseudoceros jebborum*,*Pseudoceros paralaticlavus*) and genera (*Ps. jebborum* and *paralaticlavus* versus *Pseudobiceros gratus*) of pseudocerotid polyclads. The nucleotide sequence of the ITS-1 of *Ps. jebborum* differed from that of *Ps. paralaticlavus* by 6% and from that of *Pseudobiceros gratus* be 36%. As expected these results confirm that species of the same genus are phylogenetically closer related than species derived from different genera. Therefore, sequence data from the ITS-1 will be a useful taxonomic tool to discriminate pseudocerotid flatworms.

The ribosomal DNA gene cluster: A growing eukaryotic cell contains about 10 Mio ribosomes, cellular machines for protein production (translation of mRNA into protein). Since ribosomal RNA is the essential structural component of ribosomes 10 Mio copies of each type of ribosomal RNA molecule (5S, 5.8S, 18S, 28S rRNA) have to be synthesized in each cell generation to meet the cells requirements for protein synthesis. For production of adequate quantities of ribosomal RNAs eukaryotic cells contain multiple copies of the genes coding for ribosomal RNA (rRNA genes = rDNA). Human cells contain about 200 rRNA gene copies per haploid genome, spread out in small clusters on five different chromosomes (chromosomes 13, 14, 15, 21, 22), while cells of the frog *Xenopus laevis* contain about 600 rRNA gene copies in a single cluster on one chromosome. However, the general pattern of rRNA gene organization and rRNA synthesis is identical in all eukaryotes. The multiple copies of the highly conserved rRNA genes on a given chromosome are located in a tandemly arranged series in which each gene is separated from the next by regions known as spacer DNA, which varies in length and sequence among species. A single cluster consists of the rRNA genes for 18S, 5.8S, and 28S rRNA molecules which are separated by internal



transcribed spacers (ITS-1 and ITS-2). Adjacent clusters which have a length of about 10,000 nucleotides each are separated by external transcribed spacer regions (ETS).

The rRNA genes are transcribed by RNA polymerase I, and each set of genes produces the same primary RNA transcript, known as 45S precursor rRNA (pre-rRNA). Before it leaves the nucleus in assembled ribosomal particles, the 45S pre-rRNA is cleaved to give one copy each of the 28S rRNA (about 5000 nucleotides), the 18S rRNA (about 2000 nucleotides), and the 5.8S rRNA (about 160 nucleotides) of the final ribosome. The remaining parts of each primary transcript (ETS, ITS-1 and ITS-2) are degraded. Together with about 200 different cellular proteins and a 5S rRNA derived from another chromosomal locus, the newly synthesized rRNA is packaged to generate the ribosomes. This packaging takes place in the nucleus, in a large, diffuse structure called nucleolus.

Since intact rRNA molecules are essential for ribosome generation, protein synthesis, and cell function, a strong selective pressure (evolution) to maintain functional rDNA exists. Thus, ribosomal genes belong to the most conserved genes in eukaryotic cells showing an extreme sequence similarity even between distant phylogenetic taxa. However, far less homology is found in the internal spacer regions (ITS-1 and ITS-2) because these DNA regions do not contribute to structural RNA. Therefore, less selective pressure applies and DNA sequence differences (point mutations), even between species of the same genus, can be found in these regions. Due to these features molecular rDNA data are very useful for determination of phylogenetic relationships (tree of life) or for discrimination of closely related species.

| main | back | photo galleries! |

Last update: *April 26, 2002*