New trends in the megasystems of Eukaryote (Review)

Nové trendy v systematice Eukaryot

Tomáš K a l i n a

Department of Botany, Charles University, Benátská 2, CZ-12801 Prague, Czech Republic

Contemporary biology attempts to develop an advanced tree of life based on mutually related monophyletic units, which are usually called kingdoms. The cladistic term "monophyletic" means that all beings included in such a group are offspring of a common ancestor. In the last two decades various models of the multikingdom tree were introduced (MARGULIS & SCHWARZ 1980, CAVALIER-SMITH 1998, etc.). The more typical approach used the morphological (ultrastuctural) and biochemical characters, while later authors used composite characters, including the results of molecular phylogeny. As documented in the recent publication, the potential of older methods using one gene comparison (SSU r RNA) is largely exhausted. Many authors offer advanced solutions, based on extensive comparison of RNA samples complemented with the amino acid position in various sets of selected proteins (tubulins, elongation factors, heat shock proteins, etc.)

New trees differ significantly in the position from the main root of the tree. The root is defined as the oldest point in the tree and corresponds with the theoretical last common ancestor of everything in the tree. The root gives directionality of the evolution within the tree, and the relative order of branching events (BALDAUF 2003).

The recent trees assigned the eukaryotes to one of six or eight kingdoms. Two recent megasystems are shown in the following table.

	Kingdoms	Groups included		Kingdoms	Groups included
BALDAUF (2003)	**Opistokonta**	choanoflagellates, **animals**, microsporidia, **fungi**, choanozoa	SIMPSON & ROGER (2004)	**Opistokonta**	**Animalia**, Choanoflagellata, Ichthyosporea, nucleariid amoebae, **Fungi** + Microsporidia)
	Amoebozoa	lobose amoebae, dictyostelid slime molds, plasmodial slime molds, protostelid slime molds, pelobionts		**Amoebozoa**	lobose amoebae, Mycetozoa (= Myxomycota), Pelobionta, Entamoebae.
	Plants	glaucophyte algae, red algae, chlorophyte algae, "prasinophyte algae", land plants,		**Plants**	Glaucophyta, Rhodophyta Chlorophyta Embryophyta.
	Cercozoa	Euglyphid amoebas, Foraminiferans, Cercomonads, Chlorarachniophytes, Radiolarians		**Rhizaria**	Radiolaria, Cercozoa, (incl. Foraminifera).
	Alveolates	Marine groups I, Apicomplexans, Dinoflagellates, marine group II, ciliata		**Chromalveolata**	Alveolata (Ciliata, Dinophyta, Apicomplexa), Stramenopiles, Haptophytes, Cryptophytes.
	Heterokonts	bicosoecids, oomycetes, diatoms, brown algae, more chloroplast a+c algae, labyrinthulids, opalinids			
	Discicristates	acrasid slime molds, vahlkampfid amoebas, euglenoids, trypanosomes, leishmanias			
	Excavates	diplomonads, parabasalids, retortamonads, oxymonads		**Excavata**	Euglenozoa, Heterolobosea, Jakobida, Oxymonada, Diplomonada, Retortomonada, Parabasala.

Notes: The names of the groups are identical to the original publication. The names of groups previously recognized as kingdoms are in bold letters.

Both the compared surveys show some similarity in the elimination of ”crown radiation”, which in CAVALIER-SMITH (1998) resulted in five eukaryote kingdoms: Animalia, Fungi, Plantae, Chromista and Protozoa. The kingdom Protozoa has been subdivided recently. The former protozoan groups have been spread into almost all kingdoms. Plants represent the only kingdom that remains without any change. The kingdom Chromista was reclassified as a subkingdom of a new unit, Chromalveolata

Short characteristic of the kingdoms

Opistokonta

The reproductive cells have a single posterior flagellum (if present) with only one kinetosome and a flat mitochondrial cristae). Flagellate cells of most other kingdoms are bikont, having two kinetosoms. Mitochondrial cristae are tubular, or discoid. BALDAUF (2003) placed the initial eukaryote roots between Opistokonta and the other kingdoms.

Amoebozoa

Most species included in this kingdom use pseudopodia for movement and feed via phagotrophy. Some species lost mitochondria secondarily.

Plantae

All plants contain plastids, which are considered as the ”primary endosymbionts”. They originated from the cyanobacterial unicel. In general, the symbiogenesis integrates the disparate genomes and different membranes into a more complex cell. CAVALIER-SMITH (2000) argued that plants evolved the transit mechanism for plastid protein import. The symbiotic act occurred only once. In subsequent evolution, the cyanobacterial genome was reduced; some of its functions were transferred into nuclear genome of the host cell. The trees based on elongation factor 2 (EF 2) suggested close relationships between red algae and green plants. Glaucophytes are probably the sister group of this lineage. Plantae is the only kingdom whose interpretation and position has not changed in contemporary trees.

Alveolata and Heterokonta or Chromalveolata

Chloroplast containing groups resulted in the ”secondary endosymbiosis”, which means that the host cell engulfed the chloroplast-containing eukaryote.

The rhodophyte unicell serves as the donor of a chloroplast (with some exclusion in dinophytes). The secondary endosymbiosis occurs repeatedly in evolution. In cryptophytes the chloroplast contains phycobilins and nucleomorph as the remnant of endosymbiont nucleus. Such plastid containing groups are called ”secondary algae”, ”meta-algae” or ”photosynthetic chimeras”. Independent of Chromalveolata, the secondary endosymbiosis occurs in chlorarachniophytes and euglenids. The heterotrophic groups are primarily without plastids and are considered primitive (CAVALIER-SMITH 1998). Dick (2000) prefers the name Straminipila (often written as Stramenopila) as an alternative name for Chromista, established formerly by CAVALIER-SMITH (1998). The only difference between Chromista and Straminipila is in DICK'S (2002) interpretation. The name Straminipila highlights the presence of tubular tripartite mastigonems, which cover the flagella in all groups (stramina, *lat.*= straw, pilus, *lat.*= hair). The only exception is haptophytes, where the flagellar hairs are soft, without tripartite structure. DICK considered heterotroph groups as ancestral. Cavalier-Smith (2002) established the name Chromalveolata. As the reason for the merging of Alveolata and Heterokonta in Chromalveolata he considers the common plastid donor in dinoflagellates and heterokonts. CHRISTENSEN (1980) proposed such a union when he established the division Chromophyta.

Rhizaria

This kingdom was established as the result of advanced RNA analysis. It comprises free living and parasitic species, such as a plant parasite *Plasmodiophora* and a group of animal parasites Haplosporidia. The extant free-living groups are classified in Cercozoa (Radiolaria and Foraminifera.). *Chlorarachnion* also belongs to the same group. A green alga was found as the chloroplast donor in *Chlorarachnion* (as well as in euglenids). The plastid of *Chlorarachnion* contains nucleomorph.. The localization of plastid in the above mentioned species differs from Chromalveolata. In *Chlorarachnion* and in euglenids the symbiont is deposited in a dictyosome-derived vesicle. In Chromalvelata the plastid is located in an ER-derived vesicle.

Discicristata and Excavata

These are unicellular, mostly heterotroph eukaryotes. Cavalier-Smith (1998) established the name Discicristata.. The mitochondria containing discoid cristae are considered an important feature. Discicristata united free-living and parasitic forms; some of them contain kinetosomes (modified mitochondria), which do not serve in oxidative phosphorylation. Some forms inhabit animal guts, thus live in almost anoxic conditions. The conception of Excavata differs in both compared systems. BALDAUF (2003) introduces both kingdoms as distinct units. SIMPSON & ROGER (2004) recognized only Excavata, including all groups of Discicristata. As they suggest, this kingdom is the most questionable of all kingdoms.

The transfer and position of some groups in the proposed systems

CAVALIER-SMITH (1998)	New position	Authors
PROTOZOA – Acrasiomycota	DISCICRISTATA – Acrasea EXCAVATA – “Acrasids”	BALDAUF et al. (2000) SIMPSON & ROGER (2004)
PROTOZOA – Myxomycota	AMOEBOZOA – Mycetozoa	BALDAUF et al. (2000), SIMPSON & ROGER (2004)
PROTOZOA – Plasmodiophoromycota	RHIZARIA – *Plasmodiophora*	SIMPSON & ROGER (2004)
PROTOZOA – Chlorarachniophyta	RHIZARIA – “Chlorarachniophytes”	SIMPSON & ROGER (2004)
PROTOZOA – Euglenophyta	DISCICRISTATA – Euglenozoa EXCAVATA – Euglenozoa	BALDAUF et al. (2000) SIMPSON & ROGER (2004)
PROTOZOA – Dinophyta	CHROMALVEOLATA Alveolata	BALDAUF et al.(2000), SIMPSON & ROGER (2004)
CHROMISTA	Heterokonta	BALDAUF et al. (2000),
CHROMISTA	Chromalveolata – Stramenopiles	SIMPSON & ROGER (2004)
FUNGI	Opistoconta – FUNGI (incl. Microsporidia)	BALDAUF et al. (2000), SIMPSON & ROGER (2004)

Conclusion

The never-ending challenge to explain the complicated history of life on the Earth requires new power and improved methods. One of the new findings demonstrates a greater biodiversity of eukaryote lineages than we expected. These unknown lineages form the parallel world to the phylogenetic tree, based on well-known cultured species. New, so far unrecognized eukaryotes, emerge in RNA trees, which are based on samples collected in nature.

Phycological research focuses on a photosynthetic groups, which are gradually elucidated in context with contemporary proposed megasystems of eukaryotes. Some ideas are encouraging or unexpected, others limit the optimistic expectations. SIMPSON & ROGER confirm the growing suspicion: the molecular data do not contain the information about the age of the divergences. Such information has been completely lost.

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