European Journal of Cell Biology 94 (2015) 249–256

Contents lists available at ScienceDirect

European Journal of Cell Biology

journal homepage: www.elsevier.com/locate/ejcb

Evolution of centrosomes and the nuclear lamina: Amoebozoan assets

Ralph Gräf*, Petros Batsios, Irene Meyer

Universität Potsdam, Institut für Biochemie und Biologie, Karl-Liebknecht-Strasse 24-25, Ha. . ., 14476 Potsdam-Golm, Germany

ARTICLE INFO

Article history:
Received 28 January 2015
Received in revised form 21 April 2015
Accepted 21 April 2015

Keywords:
LINC complex
Sun1
Nuclear lamina
Lamin
Nuclear envelope
Centrosome
Basal body
Centriole
LEM-domain

ABSTRACT

The current eukaryotic tree of life groups most eukaryotes into one of five supergroups, the Opisthokonta, Amoebozoa, Archaeplastida, Excavata and SAR (Stramenopile, Alveolata, Rhizaria). Molecular and comparative morphological analyses revealed that the last eukaryotic common ancestor (LECA) already contained a rather sophisticated equipment of organelles including a mitochondrion, an endomembrane system, a nucleus with a lamina, a microtubule-organizing center (MTOC), and a flagellar apparatus. Recent studies of MTOCs, basal bodies/centrioles, and nuclear envelope organization of organisms in different supergroups have clarified our picture of how the nucleus and MTOCs co-evolved from LECA to extant eukaryotes. In this review we summarize these findings with special emphasis on valuable contributions of research on a lamin-like protein, nuclear envelope proteins, and the MTOC in the amoebozoan model organism *Dictyostelium discoideum.*

Introduction

In the last decade molecular data, mostly rRNA sequences, have revolutionized our view of the tree of life. Today, all organisms are grouped into three domains, Bacteria, Archaea and Eukaryota (Eukarya). There is still a debate whether the latter two are sister groups descending from a common ancestor (Fig. 1A) (Woese et al., 1990) or whether Eukarya root within the Archaea (Williams et al., 2013). Other models, where the origin of diversified life traces back to the early history of Archaea were put forward as well (Caetano-Anolles et al., 2014). The last eukaryotic common ancestor, called LECA, gave rise to five supergroups, the Excavata, SAR (Stramenopile, Alveolata, Rhizaria), Archaeplastida, Amoebozoa, and Opisthokonta. These five form the domain of Eukaryota, together with a few taxonomic groups of *incertae sedis*, i.e. yet undefined relationship (Adl et al., 2012) (Fig. 1B). Some authors subsume the latter ones collectively as the sixth supergroup, under the acronym CCTH (cryptophytes, centrohelids, telonemids, haptophytes) (Walker et al., 2011). Among these supergroups, Amoebozoa and Opisthokonta (the latter encompassing Metazoa and Fungi) are considered sister groups collectively called Amorphea (formerly called Unikonta). LECA most probably possessed a nucleus, nuclear transport, an intron-splicing machinery, meiosis, an endosymbiont-derived mitochondrion, an elaborate endomembrane system, an actin/tubulin cytoskeleton, the capability to form pseudopodia, and at least one cilium with a basal body also involved in microtubule organization and a further MTOC associated with the nucleus (Cavalier-Smith, 2010).

In many extant eukaryotes, microtubule organization is achieved by centrosomes, tiny non-membranous organelles harboring several functions, most of which somehow involve microtubules. Mononucleated cells generally contain only one centrosome. After its duplication, it contributes to the organization of the mitotic spindle, whereby each of the duplicated centrosomes organizes microtubules at each of the two spindle poles. In most eukaryotes, microtubule organization centers are tightly associated with the nuclear envelope (NE). The nuclear envelope consists of an outer and inner membrane. The outer nuclear membrane is directly connected both to the endoplasmic reticulum and, at the nuclear pore complexes, to the inner nuclear membrane. The perinuclear space separates the inner and outer nuclear membrane, and forms a continuum with the lumen of the ER. In metazoans, the inner nuclear membrane is associated with the nuclear lamina, mainly consisting of specialized intermediate filaments (IF) called lamins (Herrmann et al., 2007). The lamin-based nuclear lamina is indirectly connected with all cytoplasmic cytoskeletal elements through so-called LINC complexes (linker of nucleoskeleton and cytoskeleton) (Crisp et al., 2006). These complexes consist of a SUN protein in the inner nuclear membrane, and a KASH-domain protein in the outer nuclear membrane. Their respective SUN and KASH

* Corresponding author. Tel.: +49 03319775520.
E-mail address: rgraef@uni-potsdam.de (R. Gräf).

http://dx.doi.org/10.1016/j.ejcb.2015.04.004
0171-9335/

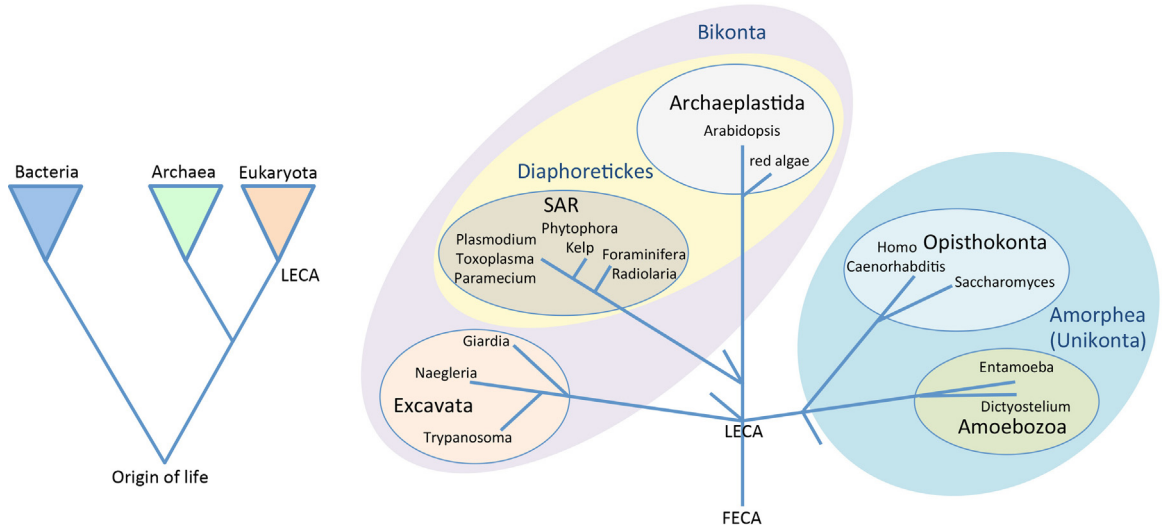

Fig. 1. Tree of life and phylogenetic tree of eukaryotes. (A) Common model of the three-domain-tree of life based on rRNA sequences; adapted from Pace (2006). (B) Current view of eukaryotic evolution (Adl et al., 2012). FECA/LECA = first/last eukaryotic common ancestor; SAR-CCTH = Stramenopile, Alveolata, Rhizaria + Cryptophyta, Centrohelida, Telonemia, Haptophyta. Loose ends indicate putative branching points of *incertae sedis*, i.e. taxonomic groups of yet undefined relationship.

domains interact within the perinuclear space. At the nuclear face, Sun proteins, lamins and nuclear pore complexes interact mutually with each other (Al-Haboubi et al., 2011; Starr and Fridolfsson, 2010). In addition, lamins associate with chromatin, whereby they also regulate gene expression and differentiation (Van Bortle and Corces, 2013). Due to the many binding activities of lamins, in particular to cytoskeletal elements, the nucleus also serves as an abutment against mechanical forces for the whole cell (Dahl et al., 2004). Such mechanical forces also employ the nuclear lamina as a transducer affecting the expression of certain genes (Fedorchak et al., 2014; Swift and Discher, 2014). While centrosomal structures are found in most eukaryotes, until recently little was known about the molecular basis of the nuclear lamina in organisms other than metazoans. Meanwhile, comparative cell biology and database analyses of centrosomal structures and the nuclear lamina have provided novel insights into early events in eukaryotic evolution (Fig. 1).

Centrosomes in different eukaryotes

Centrosomes generally consist of a central, highly organized structure embedded in a matrix serving as a scaffold for microtubule nucleation complexes. If present, centrosomes serve as the main microtubule-organizing centers (MTOCs), and thus they are essential for the whole cell architecture in all organisms using the microtubule system to position their organelles in the right place. In vegetative cells, centrosomes generally duplicate once per cell cycle, are physically attached to the nucleus, and keep themselves close to the centroid of the cell, due to their microtubule-organizing activity and the interaction of microtubules with motor proteins at the cell cortex (Azimzadeh, 2014). Since these features are shared by all organisms containing an MTOC as a clearly discernable single organelle, we use the term “centrosome” for all these kinds of organelles, independent of their structural organization.

Eukaryotic evolution has engendered different types of centrosomes. The most common type is found among the Opisthokonta in animals, but also in some Amoebozoa and bikonts such as lower plants (within the SAR group). It is characterized by centrioles consisting of a nine-fold symmetrical, cylindrical arrangement of short microtubules and associated proteins (Fig. 2A). In G1 centriolar centrosomes contain two centrioles, and after duplication, usually in S-phase, each centriole (now called mother centriole) has given rise to one immature daughter centriole in a perpendicular orientation at its side. Thus, centrioles are the duplicating units of the centrosome. They are embedded in a pericentriolar matrix (PCM) mainly consisting of scaffolding proteins which bind microtubule nucleation complexes and regulators of microtubule dynamics. The presence of centrioles is inevitably coupled to the occurrence of cilia or flagellae in at least one differentiated cell type or developmental stage of an organism. This is because the mother centriole also serves as the basal body of the primary cilium, which has signaling and sensory functions (Pedersen et al., 2012). Besides these non-motile primary cilia, there are also cells using single or several cilia for cell locomotion or transport of fluids. Cells containing more than one cilium employ a specialized structure, so-called deuterosomes, to allow biogenesis of multiple centrioles. Only most recently Al Jord et al. (2014) could show in multiciliated mouse epithelial cells that these deuterosomes do not arise *de novo* as previously thought, but are formed by multiple rounds of procentriole seeding at the daughter centriole of the preexisting centrosome.

Opposed to centriolar centrosomes are acentriolar centrosomes, sometimes also called nucleus associated bodies (NABs) or spindle pole bodies (SPBs), found among the Amorphea in fungi and many amoebozoans. Instead of centrioles, these bodies often possess layered, electron-dense structures, and are best characterized in yeasts and *Dictyostelium* amoebae (Fig. 2B). In budding yeast the SPB mainly consists of a stack of three plaques, and is permanently inserted into the nuclear envelope. It organizes a very simple intra-nuclear and extra-nuclear microtubule cytoskeleton, which is required for nuclear positioning and chromosome segregation during mitosis. In the amoebozoan *Dictyostelium*, the centrosome (NAB) also contains a three-layered core structure, which in addition is surrounded by a corona reminiscent of a PCM (Fig. 2B). Although being attached to the nuclear envelope, this centrosome is entirely located in the cytosol during interphase, by contrast to the budding yeast SPB. It enters the nuclear envelope only upon centrosome duplication during mitosis, in a manner reminiscent of the SPB behavior in fission yeast (Ding et al., 1997; Ueda et al., 1999). The time point of *Dictyostelium* centrosome duplication starting at the G2/M transition may appear unusual, because unlike in many other species, it is not synchronized with S-phase. Yet, there is no general rule. The acentriolar centrosome of fission yeast for instance starts to duplicate only in G2 (Ding et al., 1997), and there are examples also among centriolar centrosomes duplicating late in