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Meeting report

Did Centrioles and Kinetosomes Evolve from Bacterial Symbionts? Report of the Henneguy-Lenhossek Theory Meeting

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A small international conference on the "centriole enigma" was held on June 24–26, 1998, at the University of Massachusetts at Amherst. Funding from the Richard Lounsbery Foundation of New York City permitted us to commemorate the two founders of the field: French histologist Louis-Félix Henneguy (1850–1928) and Mihaly Lenhossek (1863–1937), the Hungarian neurobiologist and relative of conference attendee, Professor Andrew Szent-Györgyi (Brandeis University, Department of Biochemistry).

The centriole, found paired at the mitotic poles in nearly all animal cells, varies in form and function in different eukaryotes. The same [9(3)+0] microtubule structure, the kinetosome (basal body), subtends all undulipodia (eukaryotic flagella and cilia). The organelle, which apparently determines the number, orientation and polarity of mitotic and interphase microtubules, confers cell polarity throughout the cell cycle. Because of the identical nine-fold symmetrical ultrastructure of centriole-kinetosomes in so many taxa, and their proteins (centrin, tubulin), evolutionists believe that these related organelles, called here centriole-kinetosomes (c-ks), originated in the earliest eukaryotes some 2000 million years ago in the Proterozoic eon.

The first session (History and Philosophy), chaired by Michael Dolan, enjoyed Andrew Szent-Györgyi's talk about "My cousin Albert and his uncle" as he traced the history of achievement in the Szent-Györgyi and Lenhossek families over four generations.

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Jan Sapp (York University, Toronto) presented an overview of "History of Henneguy-Lenhossek centriole-kinetosome theory". Sapp indicated the differences between early c-k research (1887–1954), when these structures were iron hematoxylin-staining dots whose visualization was limited by the light microscope, and the second period (1954 to the present), as electron microscopy and molecular genetics enabled new insights (Sapp, 1987). The lack of scientific contact between scientists interested in cell genetics and those knowledgeable about symbiogenesis is remarkable (Sapp, 1994; Khakhina, 1992).

The session on "Protist Genetics", chaired by Dennis Searcy (University of Massachusetts), welcomed contributions by Michael Adams (Eastern Connecticut State University) and John Hall (The Rockefeller University) on both molecular- and transmission-genetics perspectives of the c-ks in the green alga *Chlamydomonas*. The same mitotic centriole moves to the periphery and behaves as a kinetosome in these single cells, admirably justifying the "c-k" appellation. Hall traced structural defects in the undulipodial assembly units and reviewed his DNA fluorescence studies. The uni linkage group-DNA stain he now interprets as chromosomal material inside the nucleus that orients toward the kinetosomes in interphase (Hall, 1995).

Chandler Fulton's (Brandeis University) talk, "*Naegleria* makes new centrioles and counts – but won't tell us how!", showed how, during differentiation, kinetosomes form first as a single unit (in a kinetid), and then two axonemes appear. Using inhibitors, cells can be arrested at the one-kinetosome stage.

Joseph Frankel (University of Iowa), who spoke on "Kinetosomes of ciliates: masters or slaves?", demonstrated how a global control system in *Tetrahymena* cells (independent of the nuclei and their DNA) determines the positions of cortical landmarks in offspring cells.

Commentary followed by John Hall on the ciliate genetic perspective, David Nanney (University of Illinois) on "Ciliate cortical behavior" and Mark McMenamin (Mt. Holyoke College) on "Eukaryote origins and the Proterozoic fossil record" (McMenamin, 1997).

Lynn Margulis showed the power of the symbiosis concept to analyze the levels on which members of different species are partners: behavioral, nutritional, gene product and genic (Margulis, 1993).

Michael Chapman, who reviewed this meeting in more detail (1998), chaired the session on "Development as community ecology". Ricardo Guerrero (University of Barcelona) talked about "Modern microbial communities". Michael Dolan (University of Massachusetts) discussed his research in termite hindgut protists in a talk entitled, "Calonymphid evolution and differential centriole-kinetosome numbers per cell". Termite symbionts such as *Calonympha* and *Snyderella* are superb subjects for c-k research, since they have variable numbers of kinetosomes per cell organized into "karyomastigonts", which

include kinetosomes in kinetids, parabasal bodies (Golgi) and nuclei and other such structures (the "akaryomastigonts") that are the same in all respects (they have the same configuration of kinetosomes, Golgi, etc.), except that they lack nuclei. These anaerobic protists lack mitochondria, too, at all stages. In calonymphids, c-k reproduction occurs and a paradesmose (thin spindle) links offspring nuclei as all the nuclei, up to hundreds, in a single cell divide. Dolan treated calonymphids with various DNA-specific stains. He demonstrated accumulation of DAPI in the Golgi apparatus but no akaryomastigont signal attributable to c-k specific DNA was found. Dolan concludes the genetic determinants of the c-ks are in the nucleus (Dolan, 1999).

Radhey Gupta (McMaster University) presented molecular sequence data against Woese's three-domain model of life (Archaea, Bacteria and Eukarya). Through sequence comparisons of several highly conserved proteins such as Hsp70, glutamine synthase I, asparaginyl tRNA synthase and diaminopimelate epimerase, Gupta showed a close evolutionary relationship between archaebacteria and Gram-positive bacteria. Both of these types of bacteria are bounded by a single membrane. In contrast, all true Gram-negative bacteria, those bounded by two membranes (the inner plasma membrane and the outer that defines an enclosed periplasmic space) form a distinct clade. His new proposal recognizes only two highest taxa ("Domains") of life: Prokarya and Eukarya. The Prokarya he divides into the Monoderm (single-membrane) and the Diderm subdomains (Gupta, 1998). Gupta's scheme, especially the aspects that recognize the chimeric nature of the amitochondriate protists is consistent with Margulis' view of the symbiotic origin of all eukaryotes (Margulis, 1996). Her concept (that c-ks still reproduce with their own timing because they descend from ancient symbiotic bacteria) aids in reconstruction of mammalian chromosomal evolution (Kolnicki, 1999).

Dorion Sagan (*Sciencewriters*) used playing cards to illustrate relationships between parts and the whole. He made analogies between the origin of cells from communities of microbes and the origin of the genetically conglomerate nature of eukaryotes. He explained how we humans individual, with telephone, Internet, satellite and other linked global communication systems unite our bodies into a living phenomenon that transcends life science (Sagan, 1992).

The enthusiastic participants, nearly all of them speakers, are shown here in a photo taken by Michael Zide in the garden of the Durfee Conservatory, a famous 19th century greenhouse on the Amherst campus. Still fascinated by this set of organelles, they concur that the question of the bacterial origin, or any other for that matter, of centriole-kinetosomes remains enigmatic. Indeed, Michael Chapman and his colleagues, in memory of Henneguy-Lenhossek theory, are preparing a detailed review of the current status of the function and origin of centriole-kinetosomes based on recent cognate literature and on

Standing left to right:
Front row: Ben Wise, Grier Sellers, David L. Nanney, Michael Dolan, Michael Adams, Chandler Fulton, Lynn Margulis, Joseph Frankel, John Hall
Back row: Peter Catalano, Annie Thompson, Dorion Sagan, Luis Vidali, Sona Dolan, Lois Brynes

Insets:
Top: Left – Jan Sapp, Right – Michael Chapman
Bottom: Andrew Wier, Dennis Searcy, Andrew Szent Gyorgyi, Radhey Gupta, Ricardo Guerrero, Mark McMenamin

the scientific results of this meeting. The review is expected to be available by Summer 1999.

The fact that questions of function and origin of the centriole-kinetosomes, the foci of intracellular development and motility still manage to draw together differently-trained scientists as they have for so many years since Henneguy and Lenhossek, remains remarkable.

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