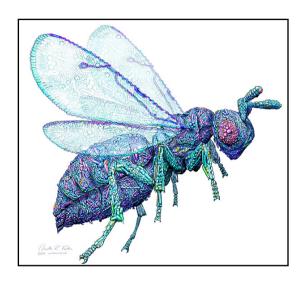


From modern symbioses... to the origin of the eukaryotic cell

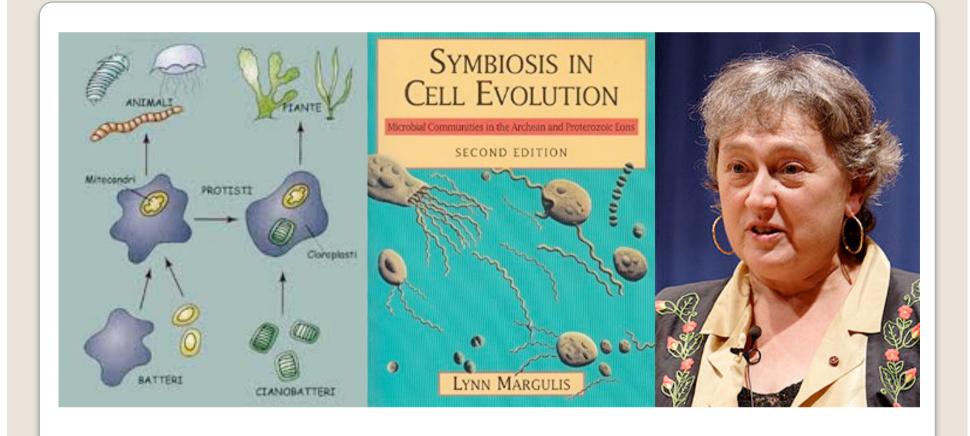
Mauro Mandrioli

Department of Life Sciences University of Modena and Reggio Emilia









"Life did not take over the globe by combat, but by networking"



A SYMBIOTIC VIEW OF LIFE: WE HAVE NEVER BEEN INDIVIDUALS

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KEYWORDS

symbionts, symbiosis, individuality, evolution, holobiont

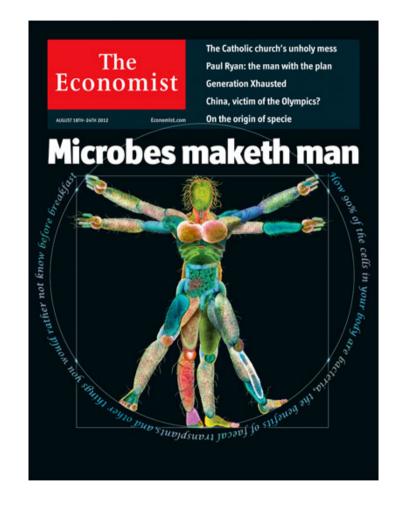
ABSTRACT

The notion of the "biological individual" is crucial to studies of genetics, immunolog, evolution, development, analong, and physiology. Each of these biological subdisciplines has a specific conception of individuality, which has historically provided conceptual contents for integrating manipal acquired data. During the past decade, mulcic acid analysis, especially genomic sequencing and high-throughput ENA techniques, has challenged each of these disciplinary definitions by finding significant interactions of animals and plants with symbiotic microorganisms that disrupt the boundaries that heretofore had characterised the biological individual. Animals cannot be considered individuals by anatomical or physiological criteria because a discretify of symbionts are both present and functional in completing metabolic pathways and serving other physiological functions. Similarly, these new studies have shown that animal development is incomplete without symbionts. Symbionts also constitute a second mode of genetic inheritance, providing selectable genetic variation for natural selection. The immune system also develops, in part, in dialogue with symbionts and

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0033-5770/2012/8704-000\$\$15.00







From bacterial bleaching to the hologenome theory of evolution

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 Open University of Israel, Raanana, Israel 43107

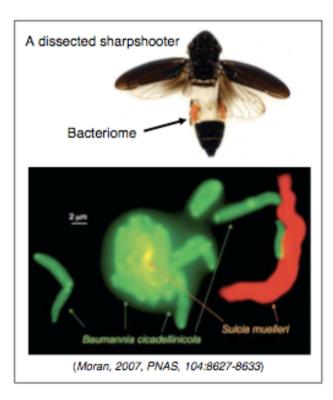
Abstract. Extensive bleaching of the coral *Oculina patagonica* in the eastern Mediterranean Sea occurs every summer when the seawater temperature exceeds 25°C. The infection by *Vibrio shiloi* and subsequent bleaching occurred only above 25°C because several of the bacterial virulence factors, superoxide dismutase, adhesion and toxin P, are only expressed above 25°C. Starting in 2002, the corals developed resistance to *V. shiloi*. Attempts to explain the resistance led to the Coral Probiotic Hypothesis, which posits that corals can adapt to their environment, including resistance to pathogens, by changing their symbiotic bacteria. The hologenome theory considers the holobiont a unit of natural selection. The hologenome is defined as the sum of the genetic information of the host and its microbiota. The theory is based on four well documented generalizations: (1) All animals and plants establish symbiotic relationships with microorganisms. (2) Symbiotic microorganisms are transmitted between generations. (3) The association between host and symbiont affects the fitness of the holobiont. (4) Under environmental stress, the symbiotic microbial community can change rapidly. These points taken together suggest that the genetic wealth of diverse microbial symbionts can play an important role both in adaptation and in evolution of higher organisms.

Keywords: Coral bleaching; Vibrio; holobiont, hologenome, evolution



PRIMARY SYMBIONTS

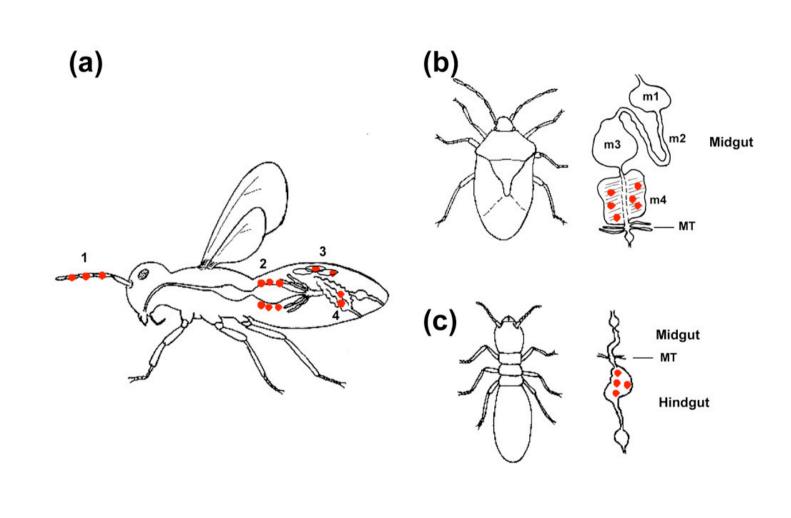
They provide to the host essential factors that are lacking in the natural diet (Dale & Moran 2006, Cell 126:453-465)

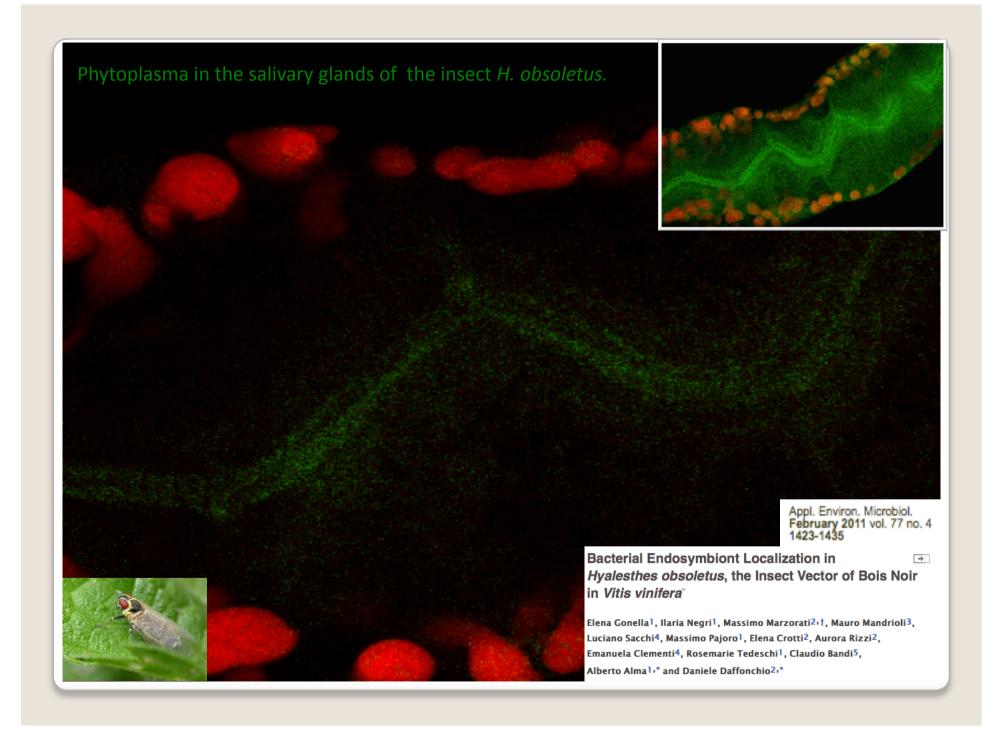


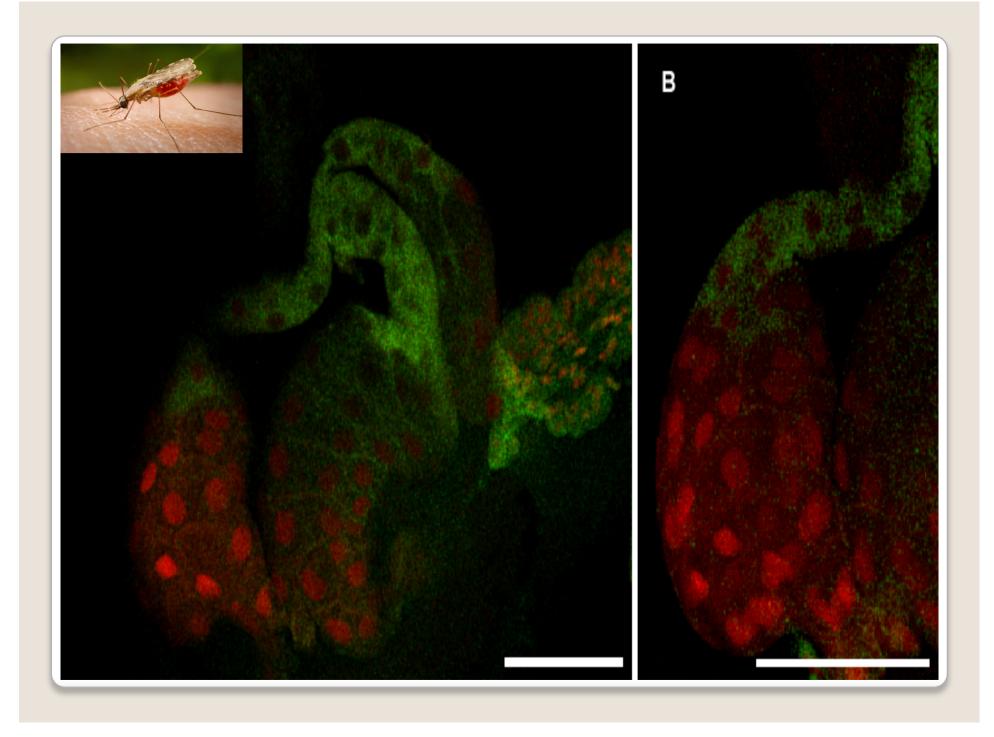
Xylem sap: amino acids, organic acids, and sugars; primarily aspartate, asparagine, glutamate, glutamine, malate, and glucose

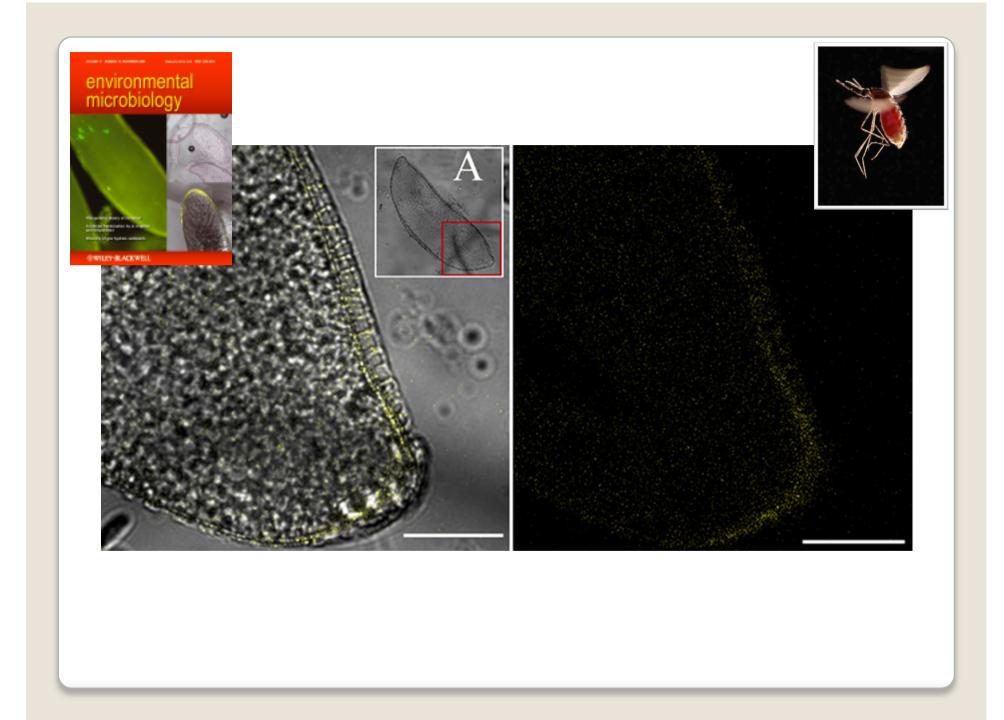


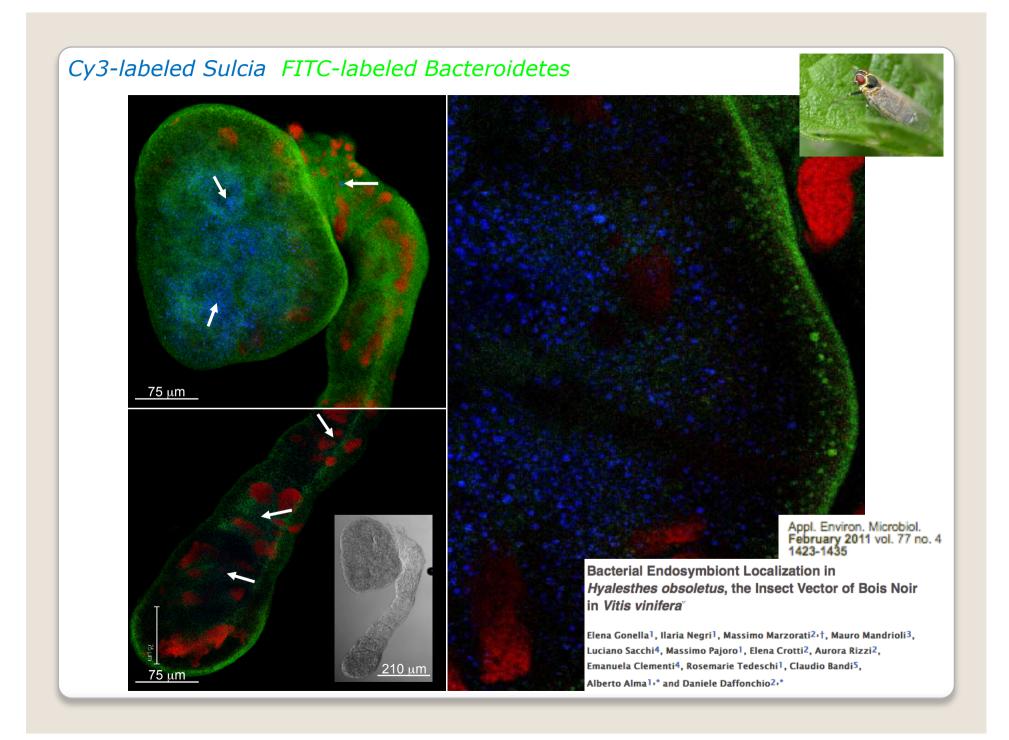
Secondary symbionts



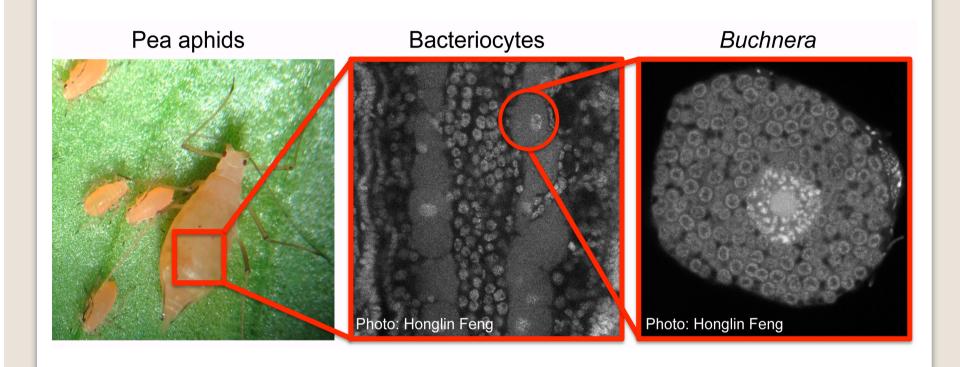


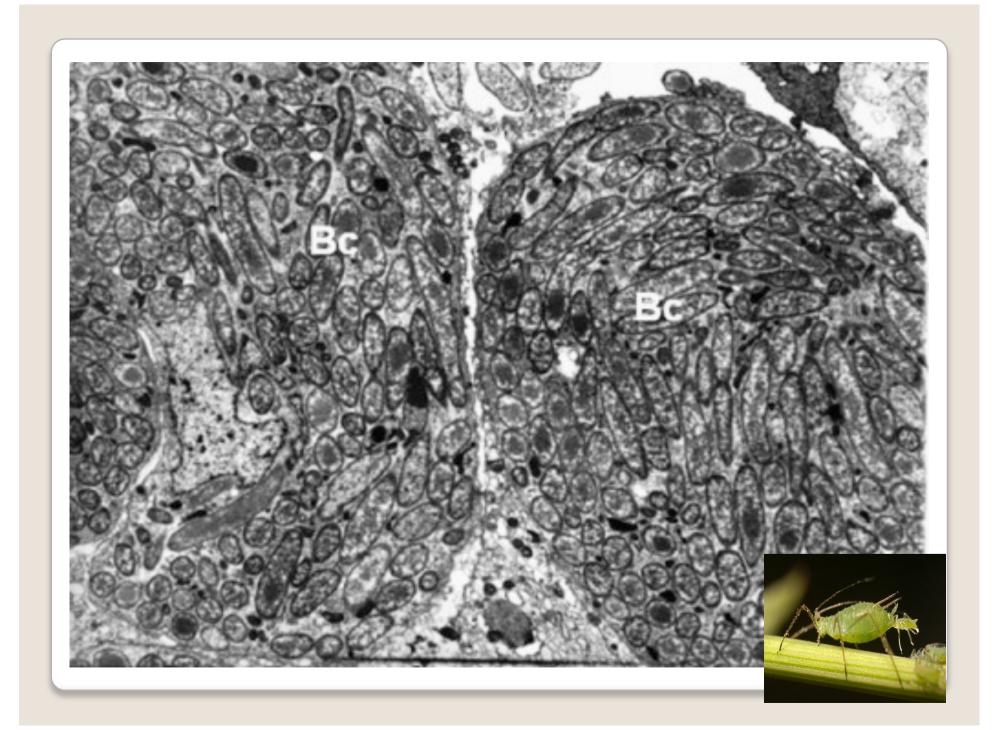


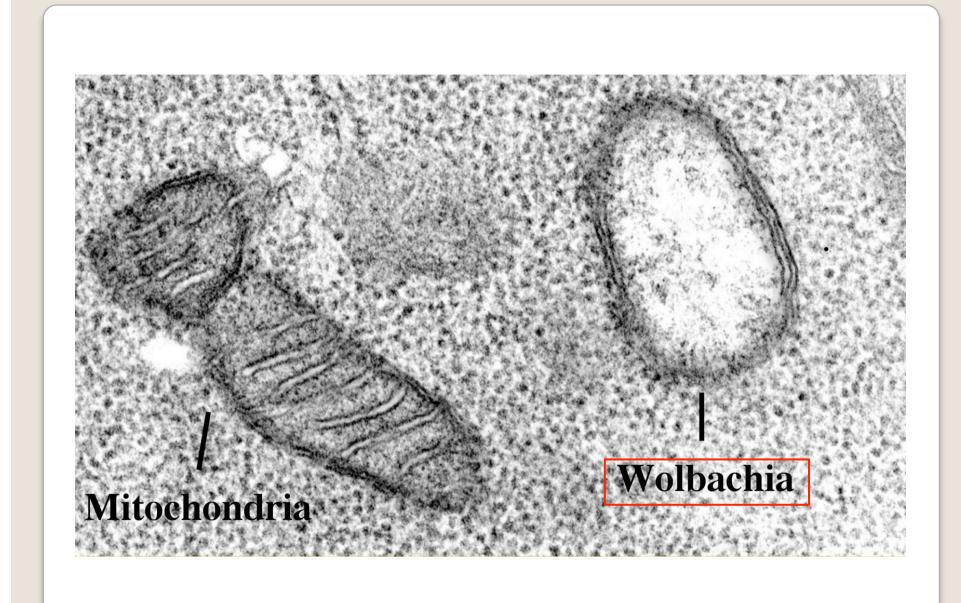


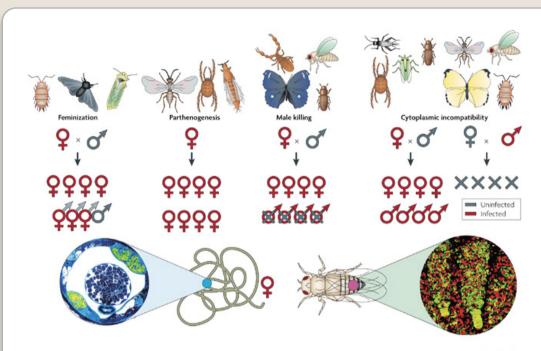


Symbionts (both primary and secondary) may be intracellular...









Nature Reviews | Microbiology

Strain	Host	Supergroup	Phenotype [‡]	Genome size Status (Mb)		Refs or project leaders	
wMel	Drosophila melanogaster	Α	Cytoplasmic incompatibility	1.27	Complete	94	
wBm [§]	Brugia malayi	D	Mutualist	1.08	Complete	<u>18</u>	
wMelPop	D. melanogaster	Α	Cytoplasmic incompatibility	1.3	Assembled	S. O'Neill	
wPip	Culex pipiens	В	Cytoplasmic incompatibility	1.48	Assembled	J. Parkhill and S. Sinkins	
wRi	Drosophila simulans	Α	Cytoplasmic incompatibility	1.44	Assembled	S. Andersson, R. Garrett and K. Bourtzis	
wAna	Drosophila ananassae	A	Cytoplasmic incompatibility	Unknown	Unfinished	<u>19</u>	
wSim	D. simulans	Α	Cytoplasmic incompatibility presumed	Unknown	Unfinished	<u>19</u>	
wAu	D. simulans	A	Not cytoplasmic incompatibility	Unknown	Unfinished	S. O'Neili	
wWil	Drosophila willistoni	Α	Unknown	Unknown	Unfinished	J. Craig Venter Institute	
wVitA	Nasonia vitripennis	Α	Cytoplasmic incompatibility	Unknown	In progress	J. Werren and S. Richards	
wUni	Muscidifurax uniraptor	A	Parthogenesis	Unknown	In progress	S. Anderson and K. Bourtzis	
wBol1	Hypolimnas bolina	В	Male killing	~1.6	In progress	A. Duplouy and S. O'Neill	
wVul	Armadillidium vulgare	В	Feminization	~1.7	In progress	R. Garrett, P. Greve, D. Bouchon and K. Bourtzis	
None designated	Diaphorina citri	В	Unknown	Unknown	In progress	W. Hunter, Y. Ping Duan, R. Shatters and D. Hall	
wDim	Dirofilaria immitis	С	Mutualist	~1.0	In progress	C. Bandi and B. Slatko	
wOv	Onchocerca volvulus	С	Mutualist	~1.1	In progress	M. Taylor, M. Blaxter and B. Slatko	



Molecular Ecology (2004) 13, 2009-2016

doi: 10.1046/j.1365-294X.2004.02203.x

Distribution of the bacterial symbiont *Cardinium* in arthropods

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A Cardinium-like symbiont in the proturan Acerella muscorum (Hexapoda)

R. Dallai*, D. Mercati, F. Giusti, M. Gottardo, A. Carapelli

Department of Evolutionary Biology, University of Siena, I-53100 Siena, Italy

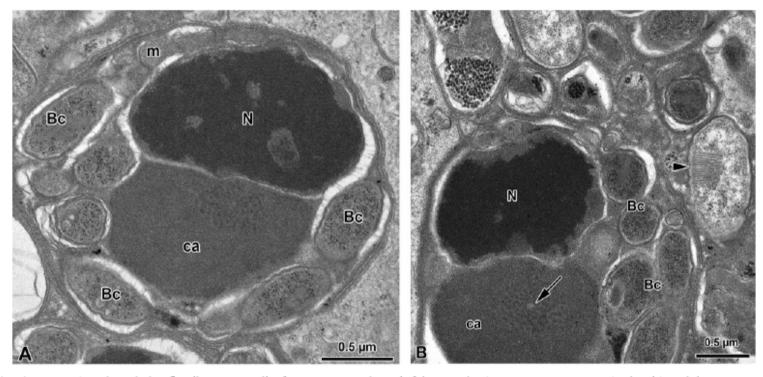


Fig. 3. (A–B) Cross sections through the aflagellate sperm cells of *A. muscorum* at the end of the reproductive process. Note some mitochondria and the numerous bacteria (Bc) in the narrow space between the nucleus (N) and the centriole adjunct material (ca); a bacterium provided with the characteristic microtubule-like complex (MLC) (arrowhead). Centriole: arrow.

Phylogenomic Evidence for the Presence of a Flagellum and cbb₃ Oxidase in the Free-Living Mitochondrial Ancestor

Davide Sassera,† ¹ Nathan Lo,† ² Sara Epis, ¹ Giuseppe D'Auria, ³ Matteo Montagna, ¹ Francesco Comandatore, ¹ David Horner, ⁴ Juli Peretó, ^{3.5,6} Alberto Maria Luciano, ⁷ Federica Franciosi, ⁷ Emanuele Ferri, Elena Crotti, Chiara Bazzocchi, Daniele Daffonchio, Luciano Sacchi, Daniele Daffonchio, Luciano Sacchi, Daniele Daffonchio, Daniele Daffonchio, Chiara Bazzocchi, Daniele Daffonchio, Daniele Andres Moya, 3.5,11 Amparo Latorre, 3.5,11 and Claudio Bandi 1.*

Mol. Biol. Evol. 28(12):3285-3296. 2011



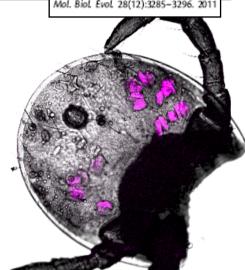


Evolution of Mitochondria Reconstructed from the **Energy Metabolism of Living Bacteria**



Mauro Degli Esposti¹*, Bessem Chouaia², Francesco Comandatore³, Elena Crotti², Davide Sassera^{3 na}, Patricia Marie-Jeanne Lievens^{1nb}, Daniele Daffonchio², Claudio Bandi³

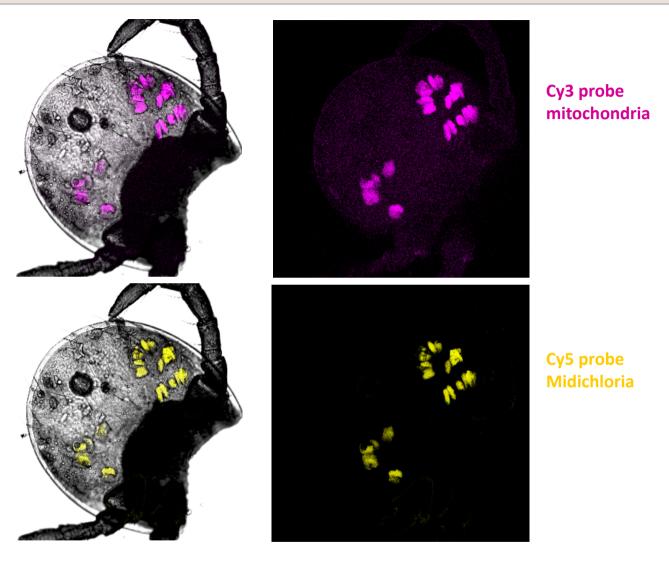
1 Italian institute of Technology, Genoa, Italy, 2 Department of Food, Environmental and Byolutionary Sciences, University of Milan, Milan, Italy, 3 Dipartment of ISdenze Veterinarie e Sanită Pubblica, University of Milan, Milan, Italy



S. Epis et al. / Ticks and Tick-borne Diseases 4 (2013) 39-45

Localization of the bacterial symbiont Candidatus Midichloria mitochondrii within the hard tick *Ixodes ricinus* by whole-mount FISH staining

Sara Epis^{a,d}, Mauro Mandrioli^b, Marco Genchi^c, Matteo Montagna^a, Luciano Sacchi^c, Dario Pistonea. Davide Sasseraa,*



Localization of the bacterial symbiont *Candidatus* Midichloria mitochondrii within the hard tick *Ixodes ricinus* by whole-mount FISH staining

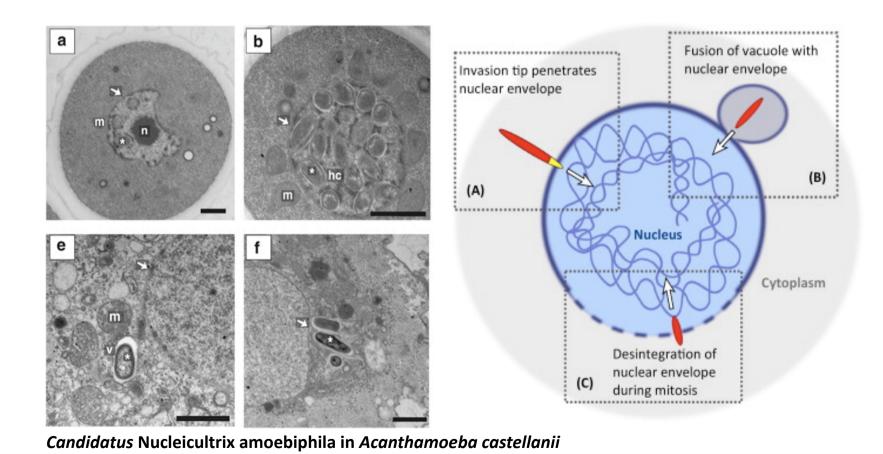
Sara Epis ^{a,d}, Mauro Mandrioli ^b, Marco Genchi ^c, Matteo Montagna ^a, Luciano Sacchi ^c, Dario Pistone ^a, Davide Sassera ^{a,*}

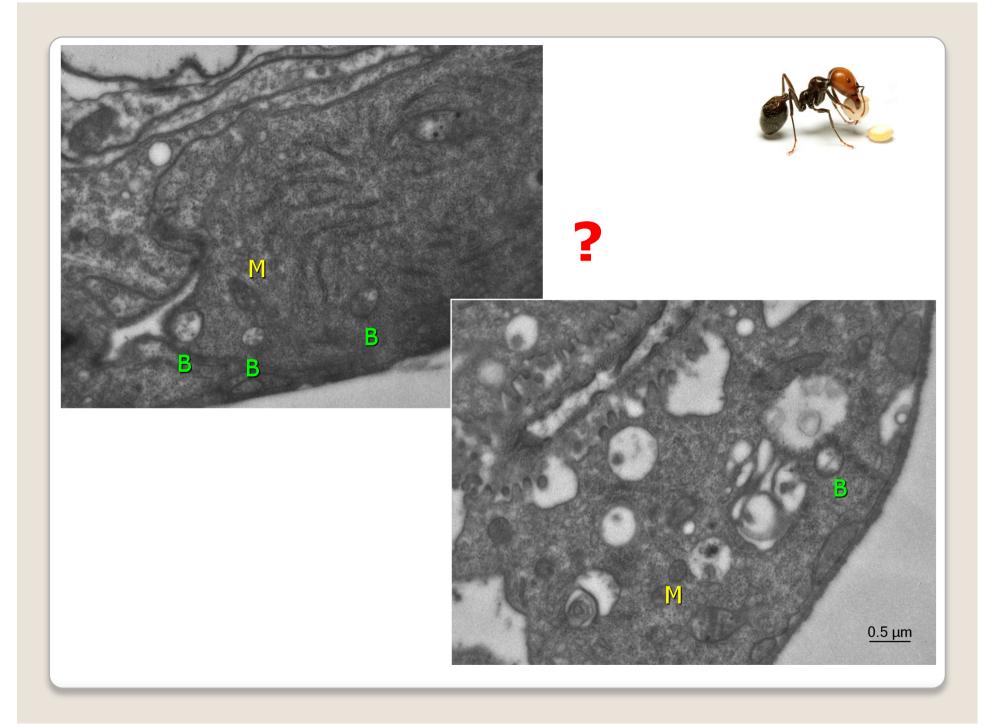
The ISME Journal (2014) 8, 1634-1644; doi:10.1038/ismej.2014.5; published online 6 February 2014

Life in an unusual intracellular niche: a bacterial symbiont infecting the nucleus of amoebae

OPEN

Frederik Schulz 1 , Ilias Lagkouvardos 1 , Florian Wascher 1 , Karin Aistleitner 1 , Rok Kostanjšek 2 and Matthias Horn 1





Bacterial endosymbionts in animals

Nancy A Moran* and Paul Baumann†

Molecular phylogenetic studies reveal that many endosymbioses between bacteria and invertebrate hosts result from ancient infections followed by strict vertical transmission within host lineages. Endosymbionts display a distinctive constellation of genetic properties including AT-biased base composition, accelerated sequence evolution, and, at least sometimes, small genome size; these features suggest increased genetic drift. Molecular genetic characterization also has revealed adaptive, host-beneficial traits such as amplification of genes underlying nutrient provision.

Addresses

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Current Opinion in Microbiology 2000, 3:270-275

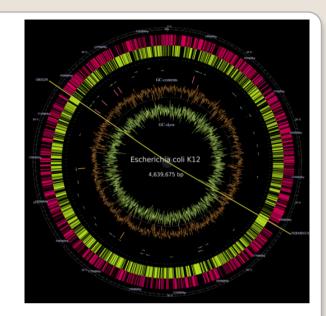


Table 1. Genomic features of primary bacteriocyte endosymbionts of insects

	Blochmannia floridanus	Blochmannia pennsylvanicus	Wigglesworthia glossinidius	Buchnera aphidicola Aps	Buchnera aphidicola BCc	Buchnera aphidicola Bp	Buchnera aphidicola Sg
Phylum	γ-Proteobacteria	y-Proteobacteria	γ-Proteobacteria	y-Proteobacteria	y-Proteobacteria	γ-Proteobacteria	γ-Proteobacteria
Host	Camponotus floridanus	Camponotus pennsylvanicus	Glossina morsitans	Acyrthosiphon pisum	Cinara cedri	Baizongia pistacea	Schizaphis graminum
Genome size (bp)	705,557	791,654	697,724	640,681	422,434	615,980	641,454
GC content (%)	27.4	29.6	22.5	26.2	20.1	25.3	25.3
Plasmids (total size in bp)	0	0	1 (5280)	2 (11,434)	1 (6054)	1 (2399)	2 (11,547)
Predicted protein coding sequences (number on plasmids)	583	610	617 (6)	562 (9)	357 (5)	504 (3)	550 (9)
rRNAs	3	3	6	3	3	3	3
tRNAs	37	39	34	32	31	32	32
Small RNA genes	2	2	2	2	2	2	2
Pseudogenes	4	4	14	13	3	9	33
ORF average length (bp)	1006	995	990	990	994	990	983
Host nutrition	Omnivorous	Omnivorous	Blood	Phloem	Phloem	Phloem	Phloem
Reference	Gil et al. (2003)	Degnan et al. (2005)	Akman et al. (2002)	Shigenobu et al. (2000)	Perez-Brocal et al. (2006)	van Ham et al. (2003)	Tamas et al. (2002)

Horizontal transfer of genes in bacteria

Paul H. Roy

Symbiont Genes in Host Genomes: Fragments with a Future?

Mark Blaxter1,*

¹Institute of Evolutionary Biology, School of Biological Sciences, Ashworth Laboratories, King's Buildings, University of Edinburgh, West Mains Road, Edinburgh, Scotland EH9 3JT, UK

*Correspondence: mark.blaxter@ed.ac.uk DOI 10.1016/j.chom.2007.09.008

While lateral transfer is the rule in the evolutionary history of bacterial and archaeal genes, events of transfer from prokaryotes to eukaryotes are rare. Germline-transmitted animal symbionts, such as *Wolbachia pipientis*, are well placed to participate in such transfers. In a recent issue of *Science*, Dunning Hotopp et al. identified instances of transfer of *Wolbachia* DNA to host genomes. It is unknown whether these transfers represent innovation in animal evolution.

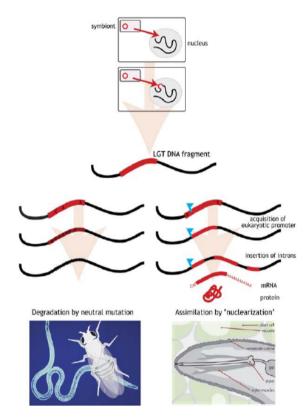
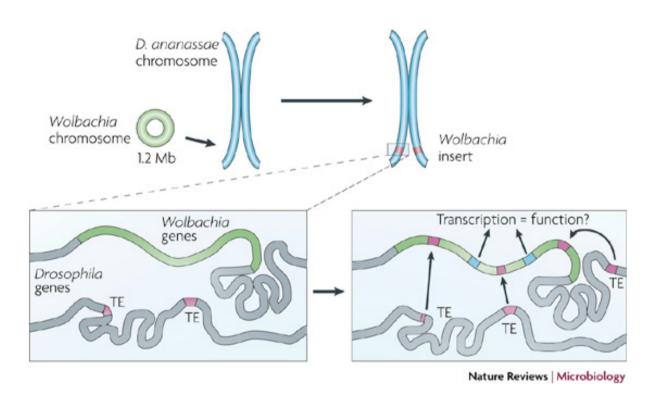


Figure 1. The Fate of Laterally Transferred Genes

A DNA fragment laterally transferred from an intracellular germline symbiont to the nucleus of an eukaryotic cell (lob) can either be degraded by neutral mutation, and play no significant part in the evolution of the eukaryotic host genome ne (left), or become integrated into the host genome and provide a novel function (right) by acquiring eukaryotic promoter elements and RNA processing signals. The Wolbach'a insertions thus far described fit the left-hand model, while the rhizosphere bacterial genes acquired by plant parasitic mematodes fit the right-hand model. The images below represent Drosophila melanogaster, the filarial nematode Brugia melayi, and a cartoon of a transmission electron micrograph of a Meloidogyne sp. nematode within a root showing the feedings stylet (in the center) used to penetrate oell walls with the aid of laterally transferred gene product

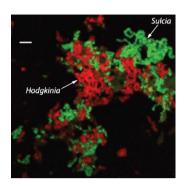


Almost the entire *Wolbachia* genome (green) has been transferred into the second chromosome of *Drosophila ananassae* (blue). Following this lateral gene transfer, Drosophila ananassae transposable elements (TEs) have become inserted within Wolbachia genes. At least 28 Wolbachia genes are transcribed from within the D. ananassae genome, although the functional significance of this is unknown.

Origin of an Alternative Genetic Code in the Extremely Small and GC-Rich Genome of a Bacterial Symbiont

John P. McCutcheon^{1,2+}, Bradon R. McDonald², Nancy A. Moran²

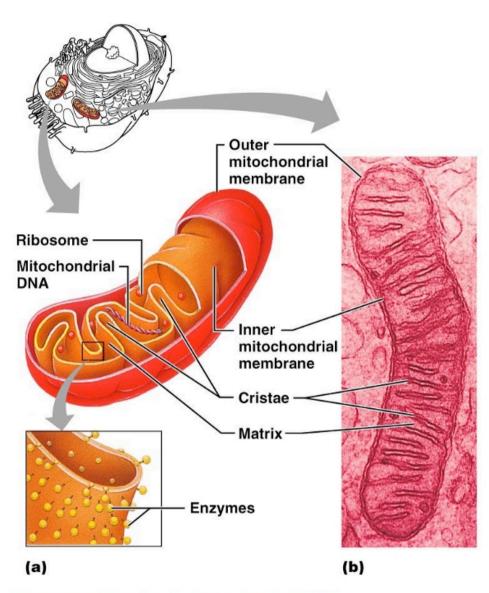
1 Center for Insect Science, University of Arbona, Tucson, Arizona, United States of America, 2 Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona, United States of America



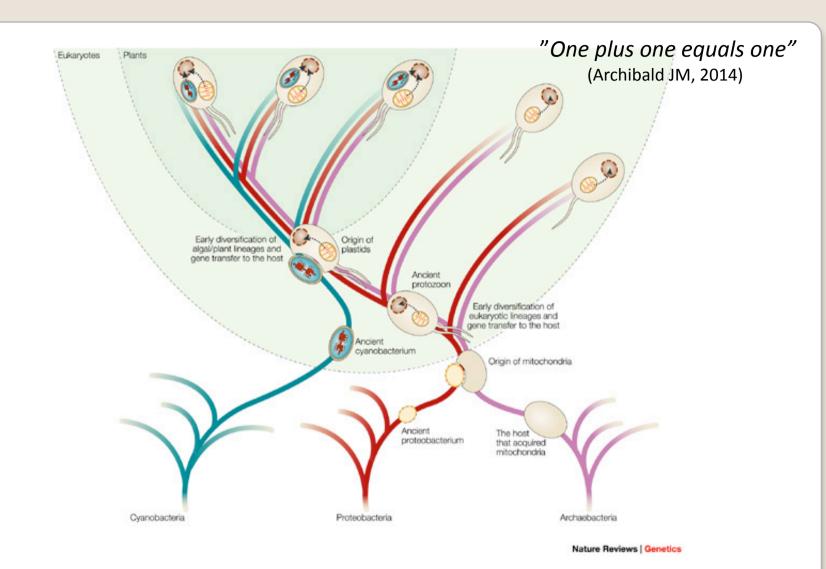
UGA stop codon to Tryptophan (StopRTrp) recoding in the α -proteobacterial symbiont *Candidatus* Hodgkinia cicadicola from the cicada *Diceroprocta semicincta*



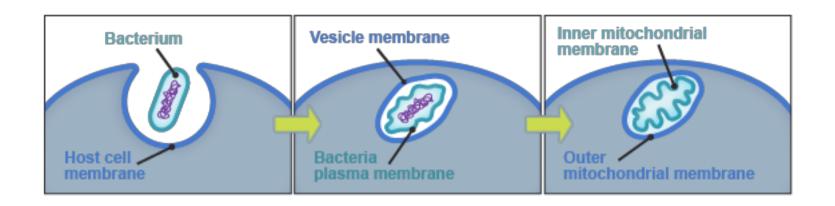
	tRNA-Trp anticodon	release factors	UGA encodes
initial state	CCA	RF1 RF2	STOP
1 mutation of tRNA-Trp gene			
some readthrough of UGA	*CCA	RF1 RF2	STOP Trp
2 loss of Release Factor 2 (RF2)			
only UAA and UAG read as stop	*CCA	RF1	Trp
mutation of tRNA-Trp anticodon			
UGA, UGG both read by wobble rules	UCA	RF1	Trp
4 genomic codon adaptation			
new UAA and UAG stops generated; some UGG codons changed to UGA	UCA	RF1	Trp

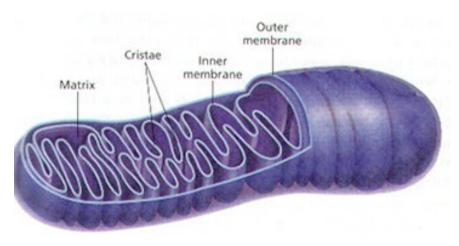


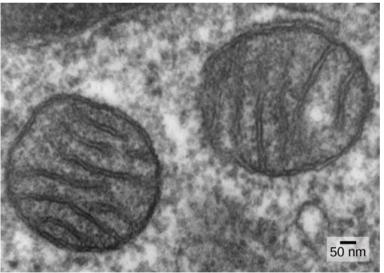
Copyright © 2008 Pearson Education, Inc., publishing as Benjamin Cummings.

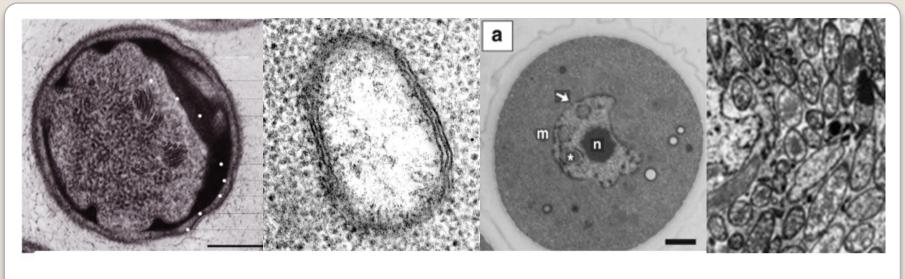


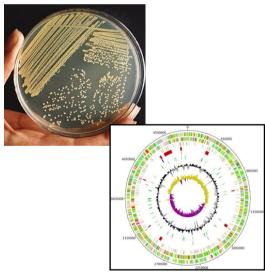
Timmis, J. N. et al. Endosymbiotic gene transfer: organelle genomes forge eukaryotic chromosomes. Nature Reviews Genetics 5, 123–135 (2004).



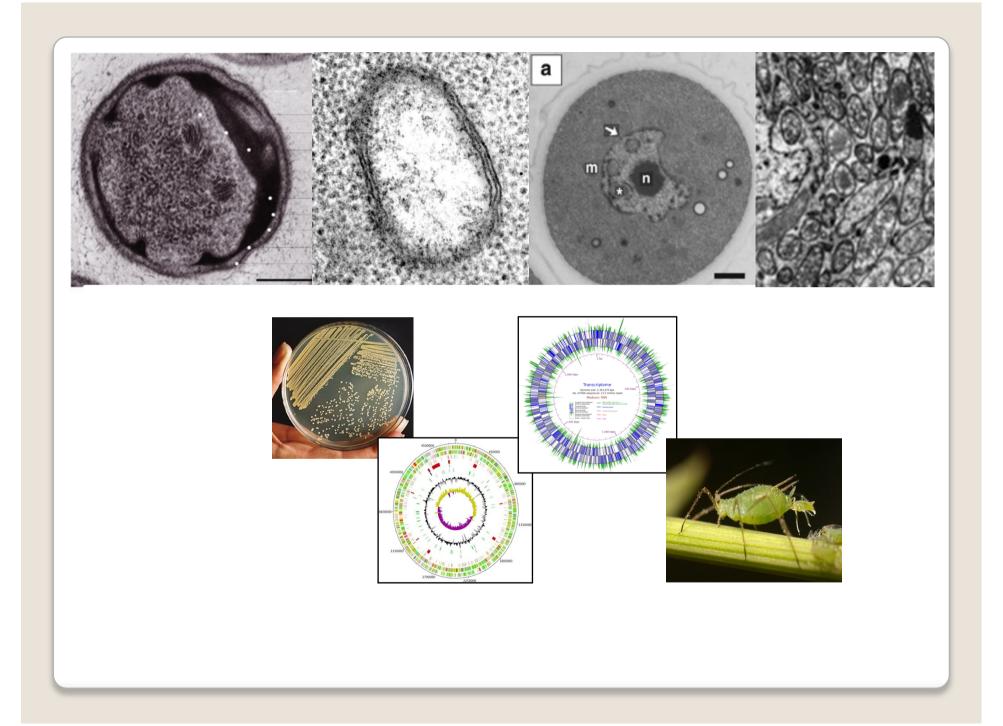


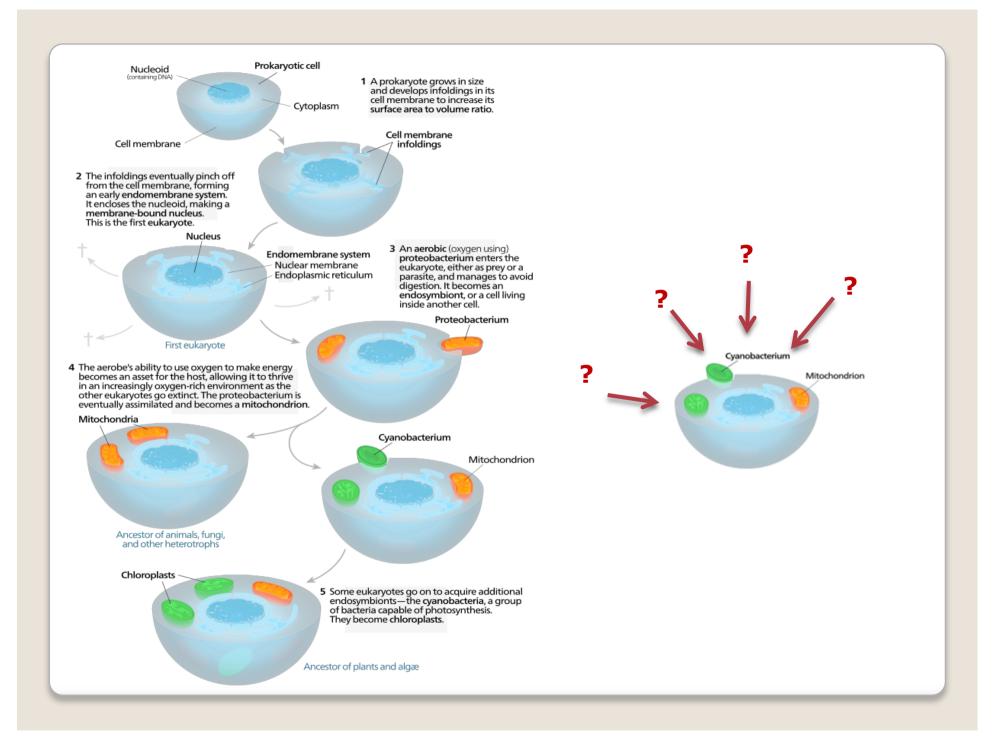






Epis S, Luciano AM, Franciosi F, Bazzocchi C, Crotti E, Pistone D, Bandi C, Sassera D (2010) A novel method for the isolation of DNA from intracellular bacteria, suitable for genomic studies. Annals of Microbiology. 60:455-460







The Major Antigenic Membrane Protein of "Candidatus Phytoplasma asteris" Selectively Interacts with ATP Synthase and Actin of Leafhopper Vectors

Luciana Galetto¹, Domenico Bosco², Raffaella Balestrini³, Andrea Genre⁴, Jacqueline Fletcher⁵, Cristina Marzachi¹*

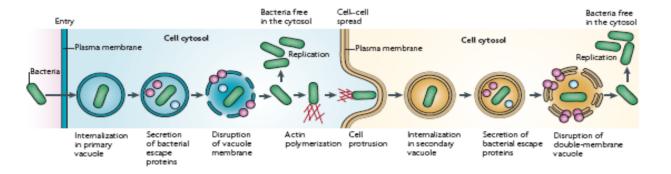
Life on the inside: the intracellular lifestyle of cytosolic bacteria

Katrina Ray*, Benoit Marteyn**, Philippe J. Sansonetti* and Christoph M. Tang*

Abstract | Bacterial pathogens exploit a huge range of niches within their hosts. Many pathogens can invade non-phagocytic cells and survive within a membrane-bound compartment. However, only a small number of bacteria, including Listeria monocytogenes, Shigelia flexneri, Burkholderia pseudomailei, Francisella tularensis and Rickettsia spp., can gain access to and proliferate within the host cell cytosol. Here, we discuss the mechanisms by which these cytosolic pathogens escape into the cytosol, obtain nutrients to replicate and subvert host immune responses.

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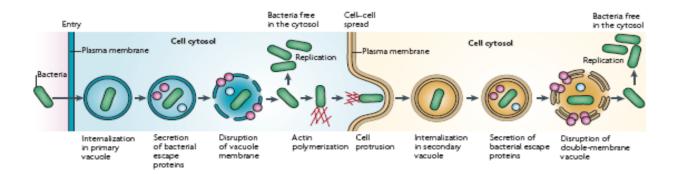
Considering that bacteria frequently hijack the host endocytic and secretory pathway...

Invasion between prokaryotes and the origin of eukaryotes

Yaacov Davidov and Edouard Jurkevitch*

Department of Plant Pathology and Microbiology, The Hebrew University of Jerusalem, Rehovot, Israel

BioEssays 31:748-757, © 2009 Wiley Periodicals, Inc.





Proc. R. Soc. B doi:10.1098/rspb.2009.0324

Unravelling the *Wolbachia* evolutionary role: the reprogramming of the host genomic imprinting

Ilaria Negri^{1,*}, Antonella Franchini², Elena Gonella¹, Daniele Daffonchio³, Peter John Mazzoglio¹, Mauro Mandrioli² and Alberto Alma^{1,*}

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Environmental factors can induce significant epigenetic changes that may also be inherited by future generations. The maternally inherited symbiont of arthropods Wolbachia pipientis is an excellent candidate as an 'environmental' factor promoting trans-generational epigenetic changes: by establishing intimate relationships with germ line cells, epigenetic effects of Wolbachia symbiosis would be manifested as a 'maternal effect', in which infection of the mother modulates the offspring phenotype. In the leafhopper Zyginidia pullula, Wolbachia feminizes genetic males, leaving them as intersexes. With the exception of male chitinous structures that are present in the last abdominal segment, feminized males display phenotypic features that are typical of females. These include ovaries that range from a typical histological architecture to an altered structure. Methylation-sensitive random amplification of polymorphic DNA profiles show that they possess a female genomic imprint. On the other hand, some rare feminized males bear testes instead of ovaries. These specimens possess a Wolbachia density approximately four orders of magnitude lower than feminized males with ovaries and maintain a male genome-methylation pattern. Our results indicate that Wolbachia infection disrupts male imprinting, which dramatically influences the expression of genes involved in sex differentiation and development, and the alteration occurs only if Wolbachia exceeds a density threshold. Thus, a new Wolbachia's role as an environmental evolutionary force, inducing epigenetic trans-generational changes, should now be considered.

PeerJ

The relative importance of DNA methylation and *Dnmt2*-mediated epigenetic regulation on *Wolbachia* densities and cytoplasmic incompatibility

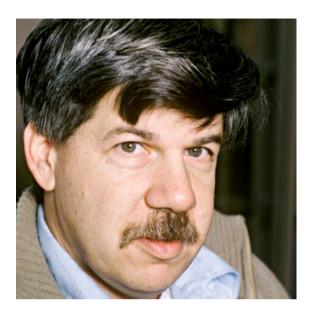
Daniel P. LePage¹, Kristin K. Jernigan^{1,2} and Seth R. Bordenstein^{1,3}

LePage et al. (2014), PeerJ, DOI 10.7717/peerj.678

Transposable element proliferation as a possible side effect of endosymbiont manipulations

Ken Kraaijeveld1,* and Jens Bast2

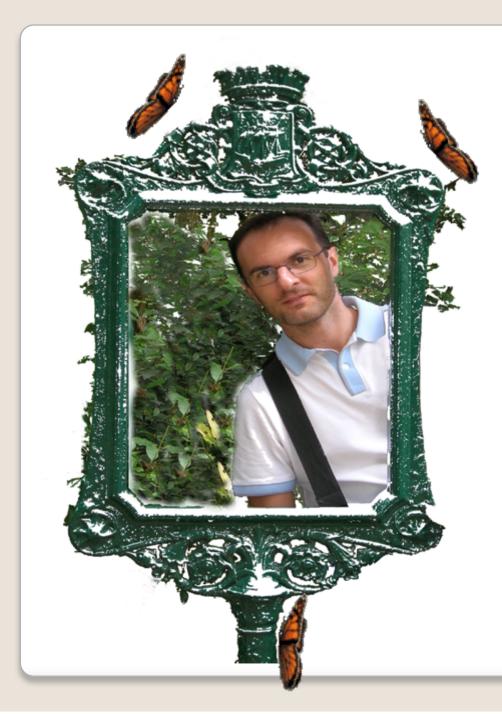
Mobile Genetic Elements 2:5, 253-256; September/October 2012; © 2012 Landes Bioscience



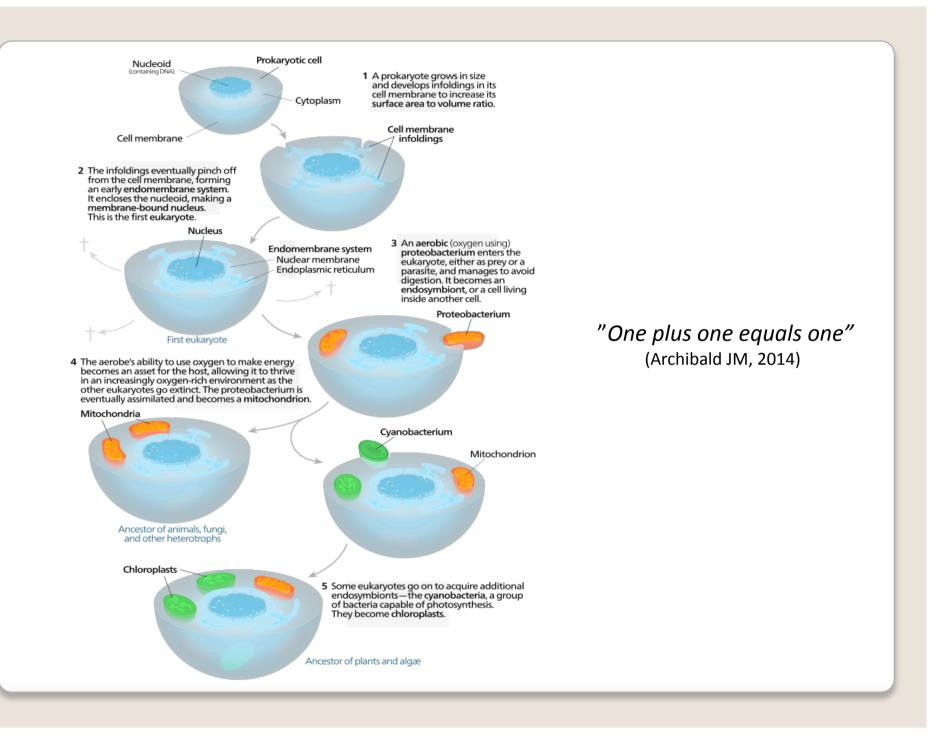
"If you could rewind the tape of life, erasing what actually happened and let it run again, you'd get a different set of ten each time".



«In perspective, our work provides new means for selecting bacterial organisms that are most suitable for **experimentally reevolving proto-mitochondria with mitochondria-depleted eukaryotic cells**». (Degli Esposti et al. 2014)



Thank you for your attention!

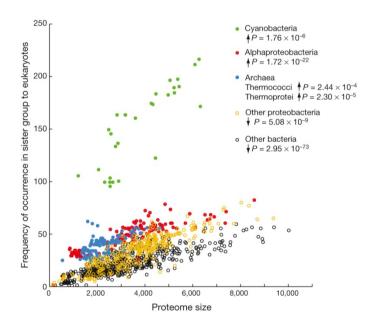


Endosymbiotic origin and differential loss of eukaryotic genes

nature

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The cyanobacterial signal for plastids, the alphaproteobacterial signal for mitochondria, and the archaeal signal for the host bear out the predictions of endosymbiotic theory. But beyond those three signals, no significant contributions are detected from other prokaryotes that are discussed in various formulations of endosymbiotic theory

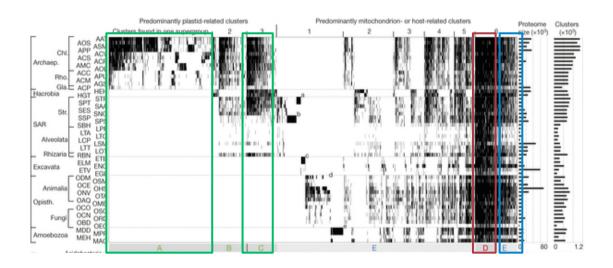
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"We clustered 956,053 protein sequences from 55 eukaryotes from six supergroups and 6,103,025 sequences from prokaryotes (5,793,897 from 1,847 bacteria and 309,128 from 134 archaea)"



Blocks A and C are densely distributed in cyanobacteria in accordance to the endosymbiotic theory Block E encompasses genes present in the eukaryotic common ancestor Block D mitochondrion gain

