Patterns in genomic chaos: bacterial cells as vehicles of war in genetic struggle for existence

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Motivation: oftentimes, it is not obvious what the things we call bacteria (or archaea) really are

BGI Sequencing news: German EHEC strain is a chimera created by horizontal gene transfer

by David Tribe on 2 June 2011

Molecular genetics in China is providing answers in the frantic effort to solve the urgent food safety crisis in EU.

Rapid work in China has applied third generation DNA decoding technologies to decode the German outbreak disease bacterium genome. It has revealed the germ to be a hybrid (which can be described alternatively as a chimera, a true natural GMO). But before readers get excited about what this implies, they need to consider that all *E. coli* strains are chimeras.

The novel germ has some virulence abilities of a class of pathogenic *E. coli bacteria* called entero-aggregative *E. coli* (#EAEC). It has similarities to a bacterial strain called EAEC 55989 , which was isolated in the Central African Republic and is known to cause serious diarrhea. EAEC typically carry extra mini-chromosomes called plasmids. The German outbreak strain has the typical plasmid genes of EAEC bacteria as well as shigatoxin genes seen in EHEC (sometimes called STEC, or VTEC) germs.

Microbes

Bacteria have been here for four billion years

..replicating
..adapting
..evolving

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Research Article

Vehicles, Replicators, and Intercellular Movement of Genetic Information: Evolutionary Dissection of a Bacterial Cell

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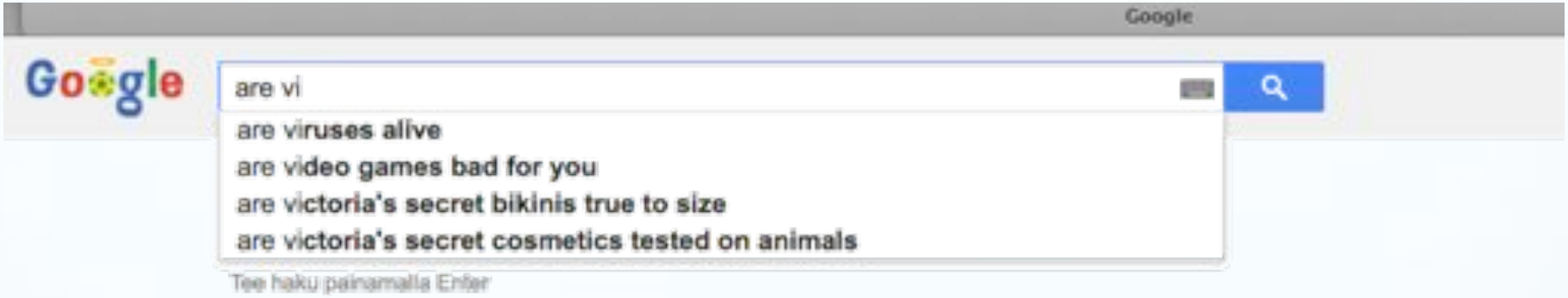
Prokaryotic biosphere is vastly diverse in many respects. Any given bacterial cell may harbor in different combinations viruses, plasmids, transposons, and other genetic elements along with their chromosome(s). These agents interact in complex environments in various ways causing multitude of phenotypic effects on their hosting cells. In this discussion I perform a dissection for a bacterial cell in order to simplify the diversity into components that may help approach the ocean of details in evolving microbial worlds. The cell itself is separated from all the genetic replicators that use the cell vehicle for preservation and propagation. I introduce a classification that groups different replicators according to their horizontal movement potential between cells and according to their effects on the fitness of their present host cells. The classification is used to discuss and improve the means by which we approach general evolutionary tendencies in microbial communities. Moreover, the classification is utilized as a tool to help formulating evolutionary hypotheses and to discuss emerging bacterial pathogens as well as to promote understanding on the average phenotypes of different replicators in general. It is also discussed that any given biosphere comprising prokaryotic cell vehicles and genetic replicators may naturally evolve to have horizontally moving replicators of various types.

1. Introduction

Viruses that infect prokaryotic cells are known to be enormously diverse in terms of genetic information [1, 2]. Most novel viral isolates are likely to have at least some genes that have no homologues among any of the previously known genes, including those in the genomes of related viruses [3]. Yet, there has been a dispute whether or not new genes may actually emerge in viruses [3]. Viruses are dependent so that their common ancestry with the host genes can no longer be derived? Or perhaps, is it indeed possible that new genes actually emerge in viruses themselves?

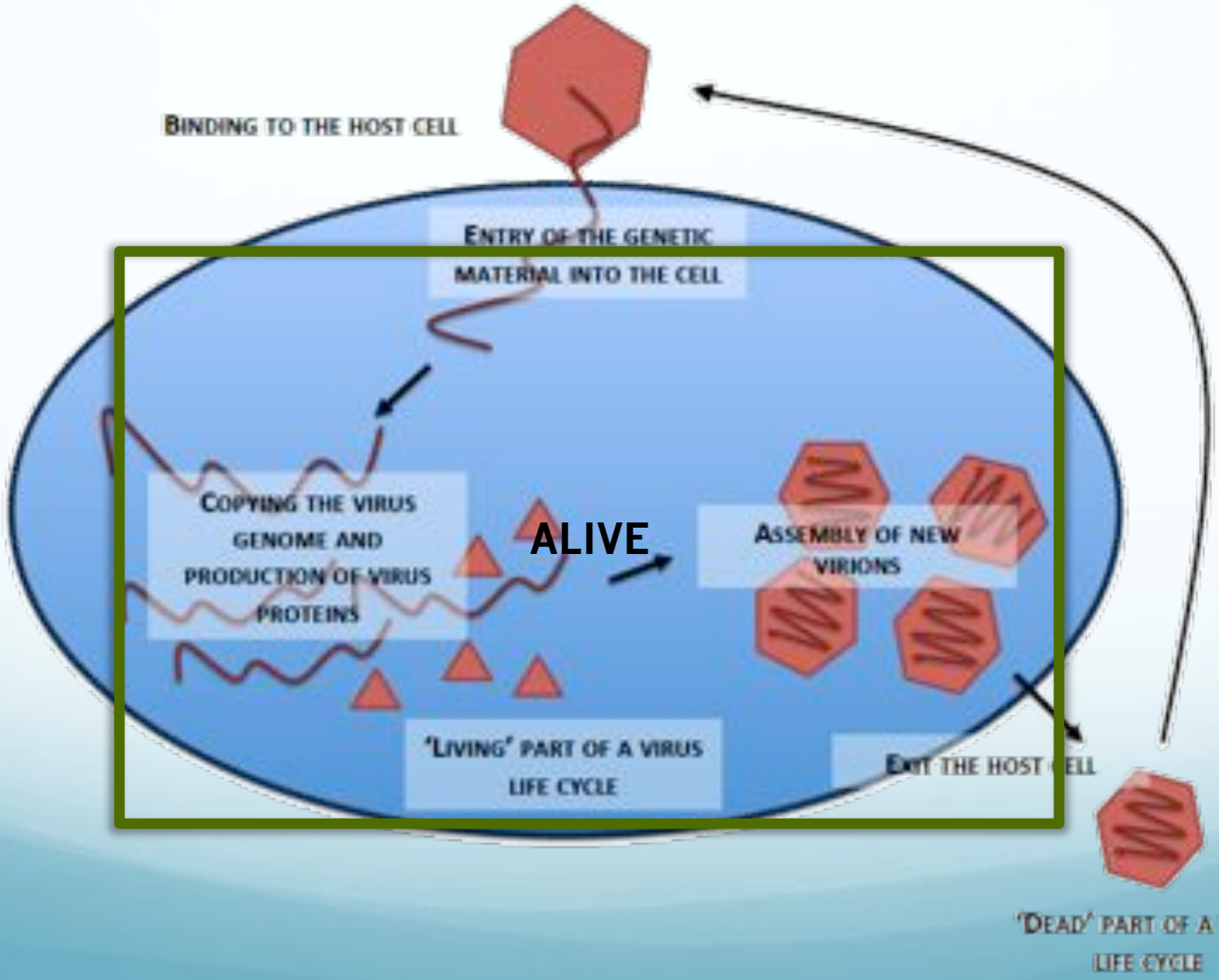
Forterre and Prangishvili from Pasteur Institute argued that the core of the dispute appears to be in the notion that viruses are often considered to be just their protein-encapsulated extracellular forms [4] that are only stealing cellular resources (including genes) for their own purposes [3, 5, 6]. Take any textbook on viruses and majority of

Are viruses alive?

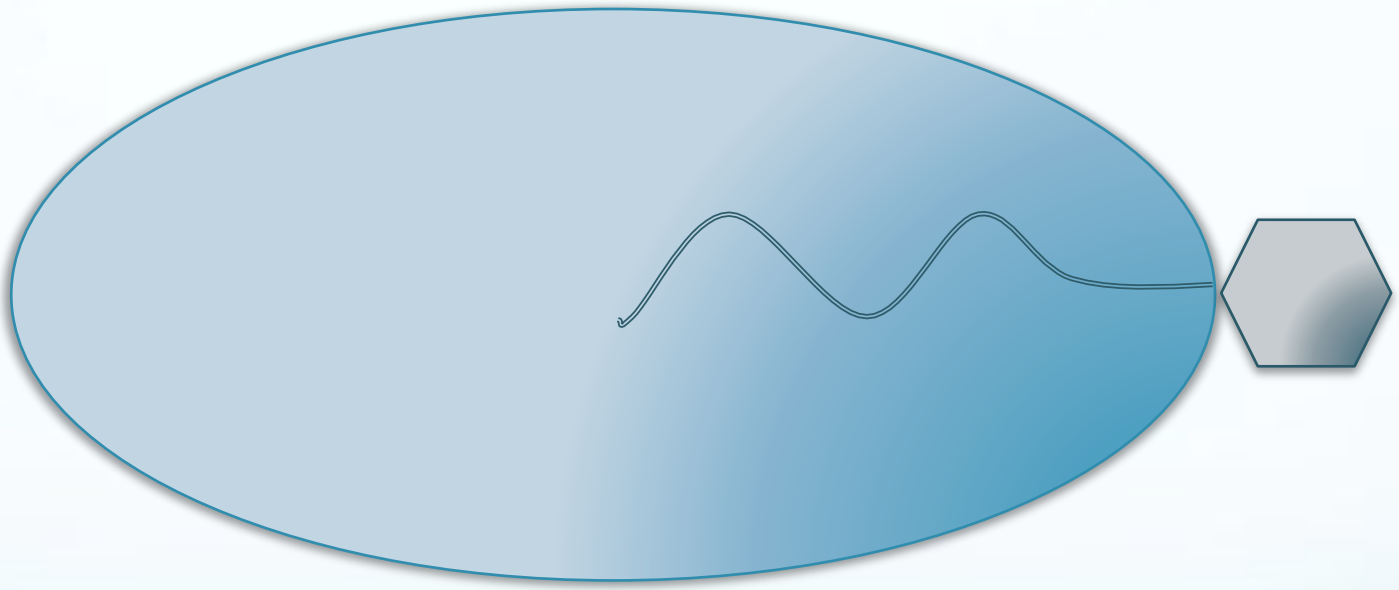


- Viruses reproduce genetically
- Viruses can go extinct
- Viruses evolve

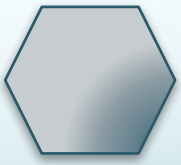
Are viruses alive?



Life constitutes of cells: Virocell concept by Patrick Forterre



Cell + virus = virocell

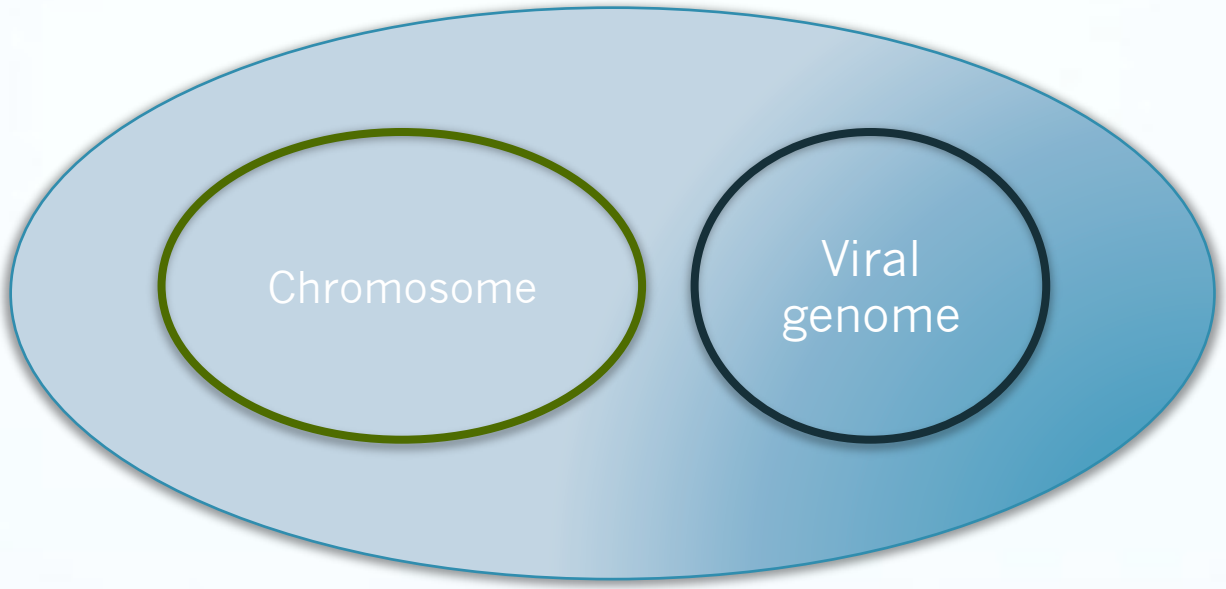


Virus (virion)

Chromosome encodes for ribosomes = Ribocell

Virus encodes for virions = Virocell

Phenotype and genotype of the virocell depends on both the virus and the cell



Both the chromosome and the virus utilizes the cell-vehicle for replication

Benefits of virocell concept

- Easier to understand how viruses come up with new genes (viruses are not just pickpocketing genes)
- We notice why viruses are often considered dead: we fail to acknowledge the most important stage in the life of a virus, the virocell
- We don't consider bacterial spores dead just because they are dormant: in a way, virion is the dormant state of a virus

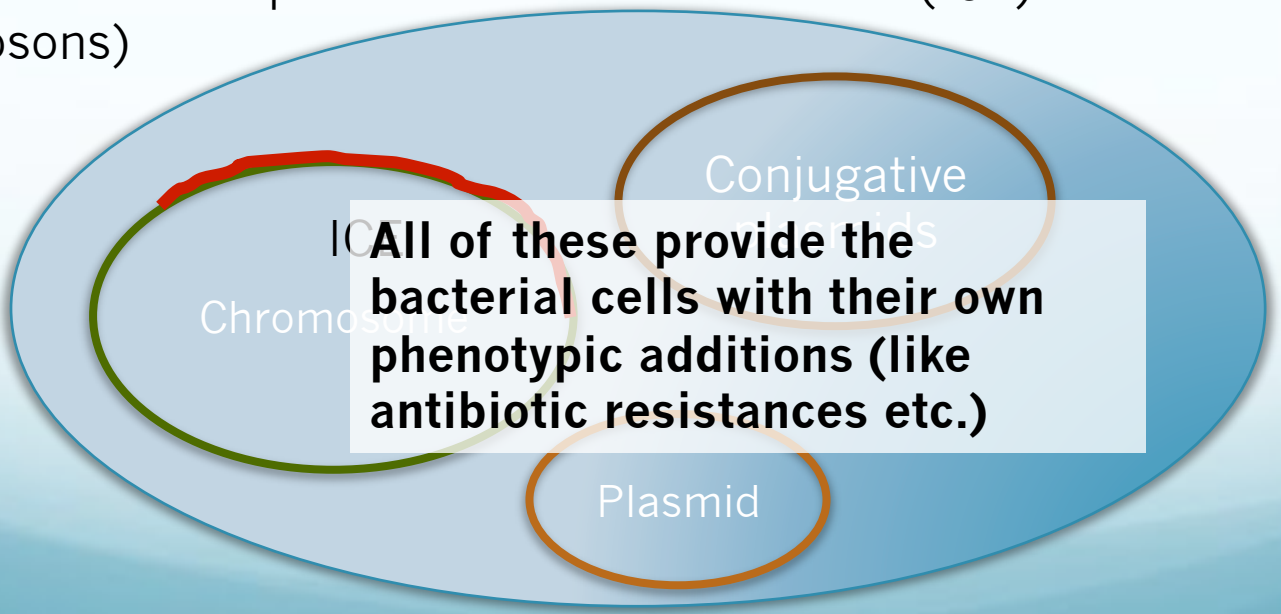
However

...viruses are not the only genetic elements that exploit (bacterial) cells as hosts

Plasmids (and transposons)

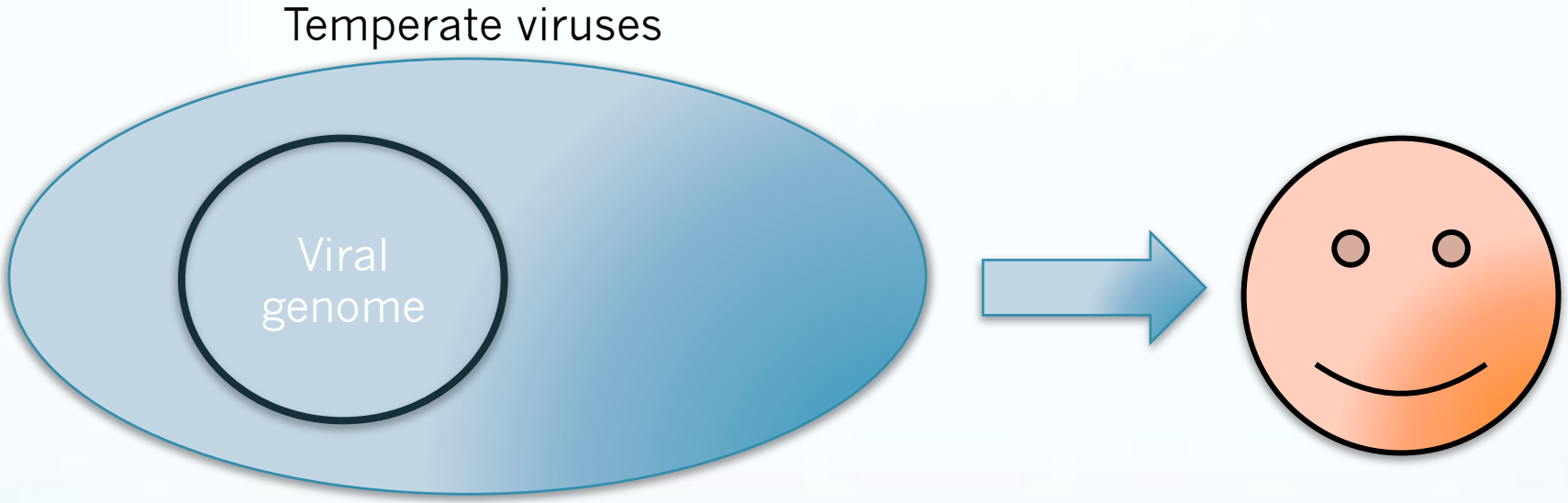
Conjugative plasmids

Integrating and conjugative elements (ICE)



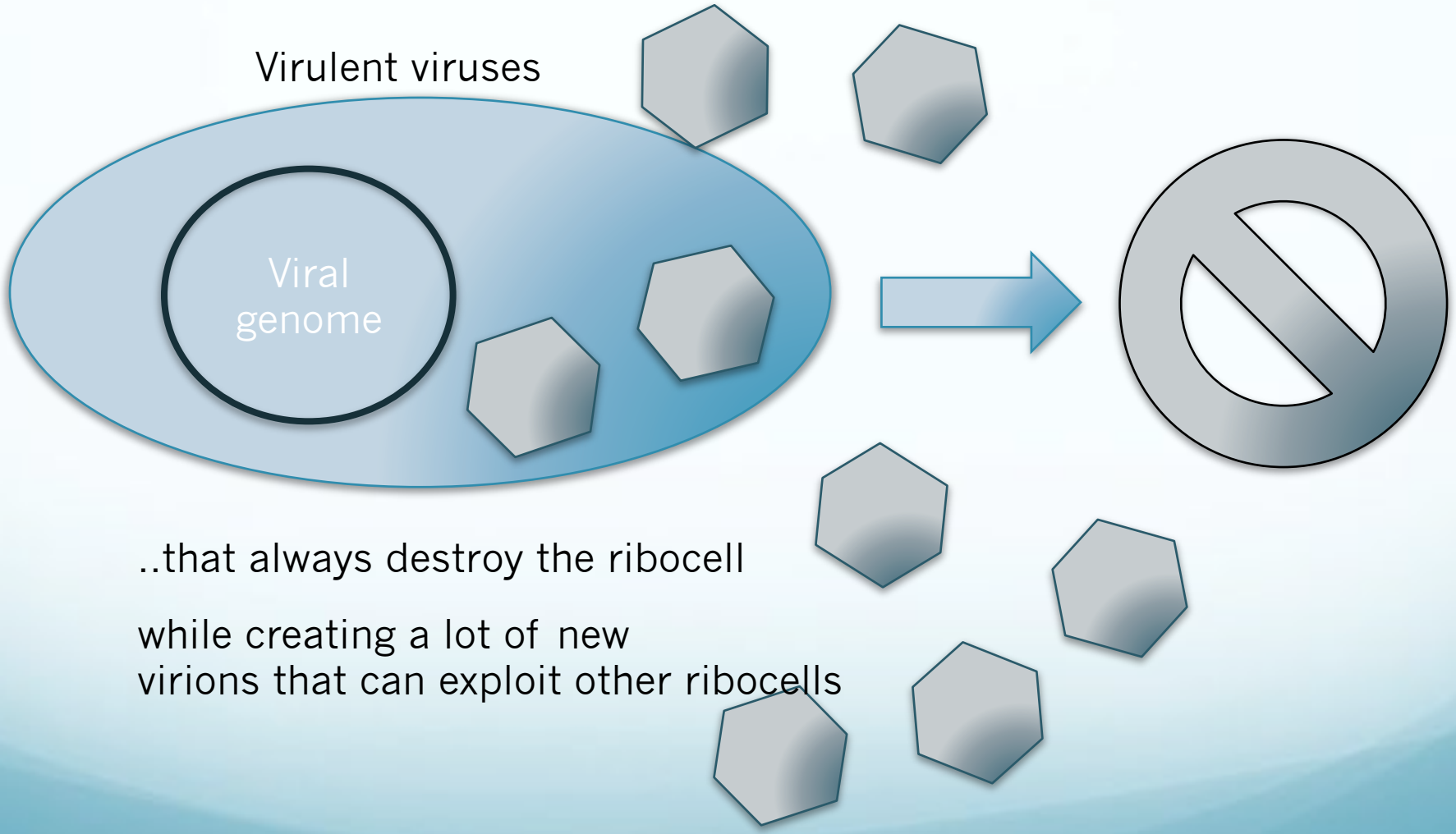
All of these provide the bacterial cells with their own phenotypic additions (like antibiotic resistances etc.)

There are also different types of viruses



..that can co-exist with the ribocell

There are also different types of viruses

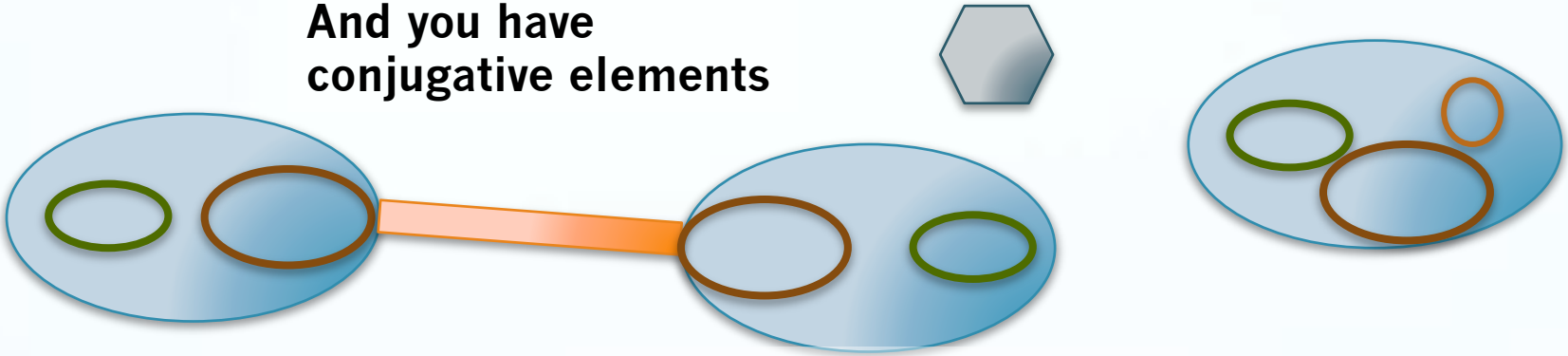


..that always destroy the ribocell

while creating a lot of new virions that can exploit other ribocells

A normal Monday in a bacterial world

And you have conjugative elements



You have bacteria competing for resources

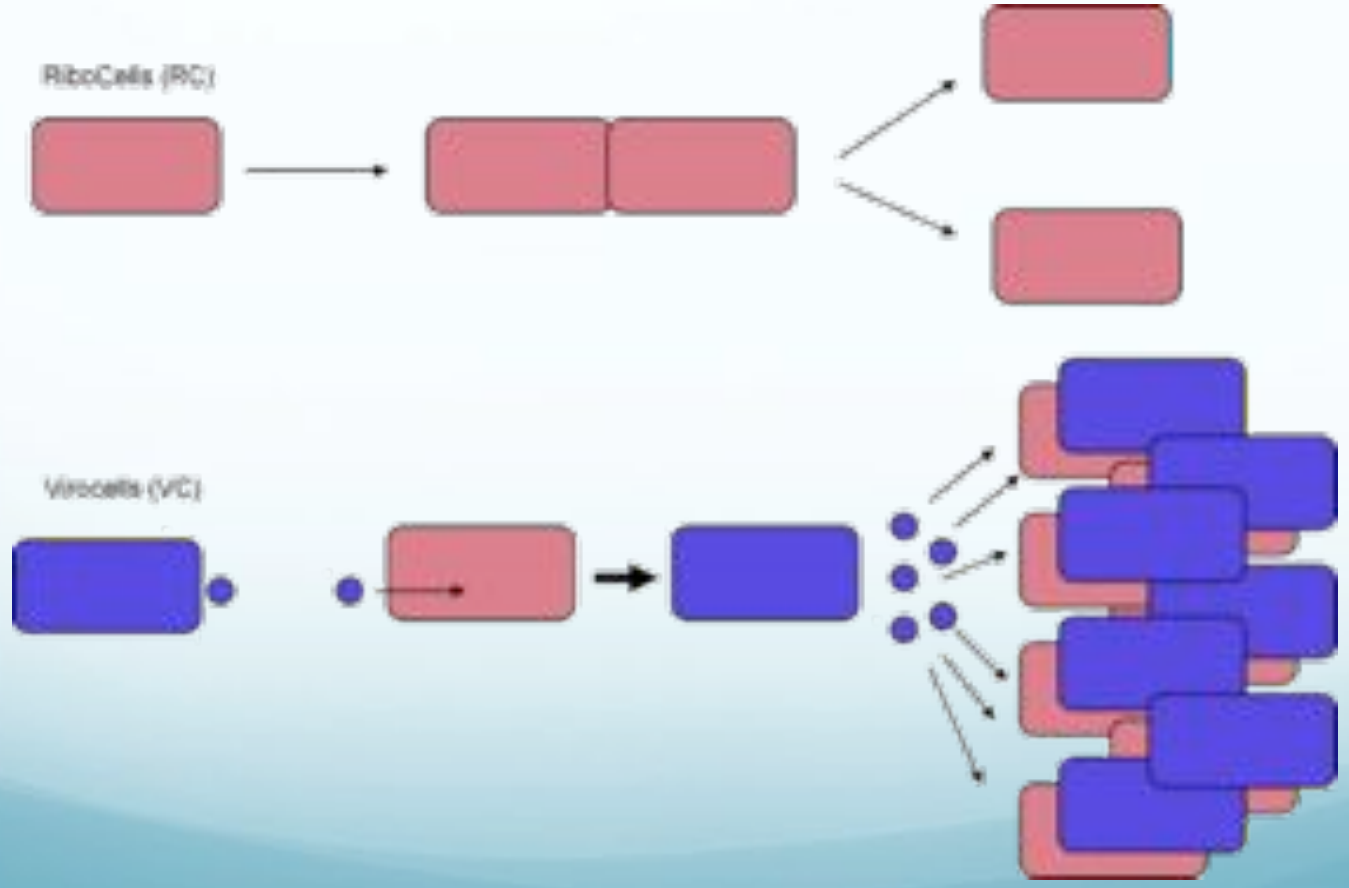
..but you also have viruses competing for bacterial cells and for the resources therein

Then you have plasmids also competing for cells and resources

..so, in a way, it is a world of tanks, where everyone is fighting who is going to drive which vehicle

Virocell-concept

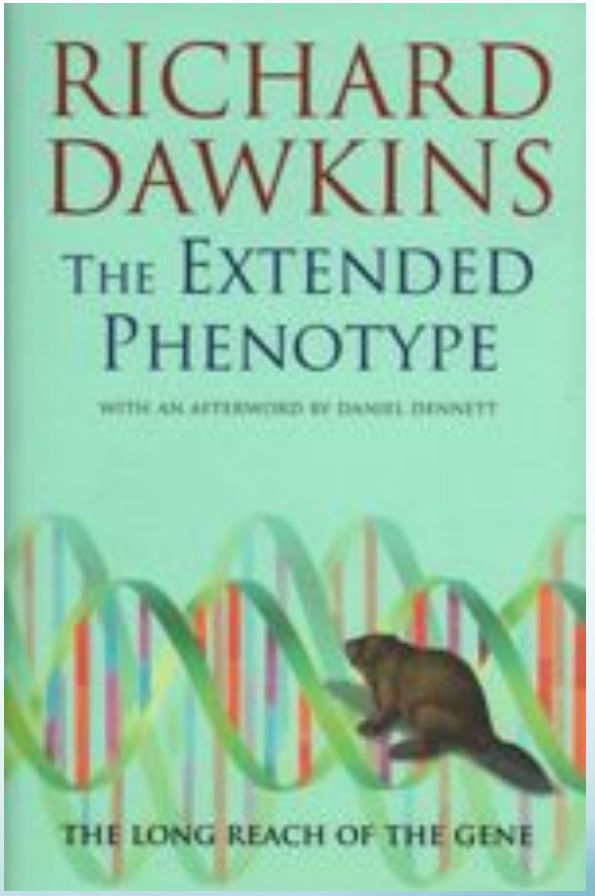
- ...can help realize what viruses really are



Order to the chaos: Dawkinsian approach

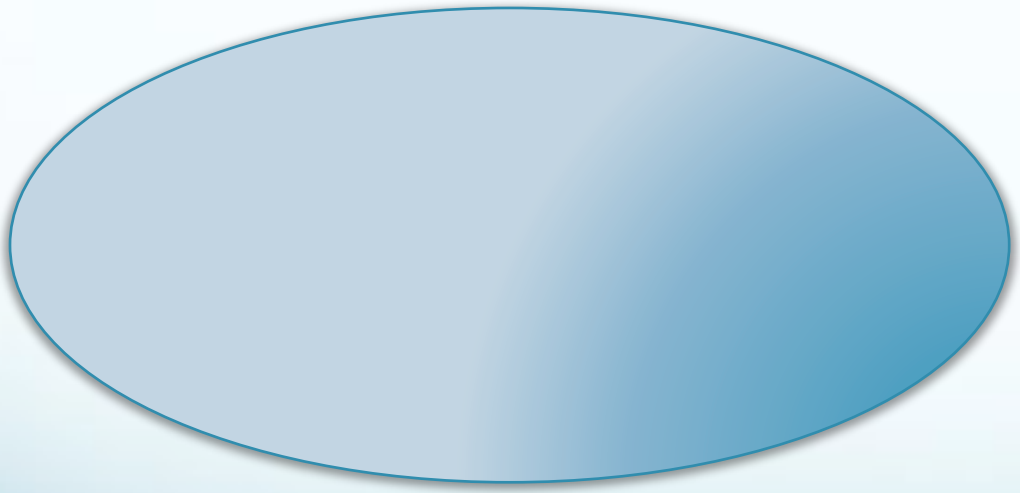
- **"A vehicle is any unit, discrete enough to seem worth naming, which houses a collection of replicators and which works as a unit for the preservation and propagation of those replicators"**

Richard Dawkins, Extended Phenotype.

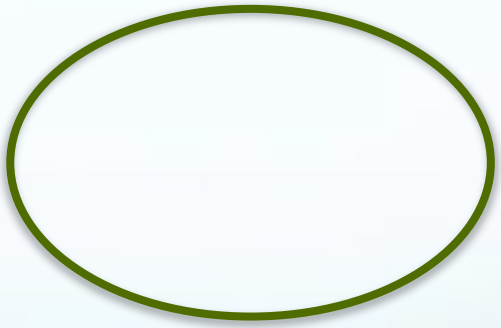


Order to the chaos: Dawkinsian approach

- Let's completely separate the vehicle and replicators from each other



Cell-vehicle



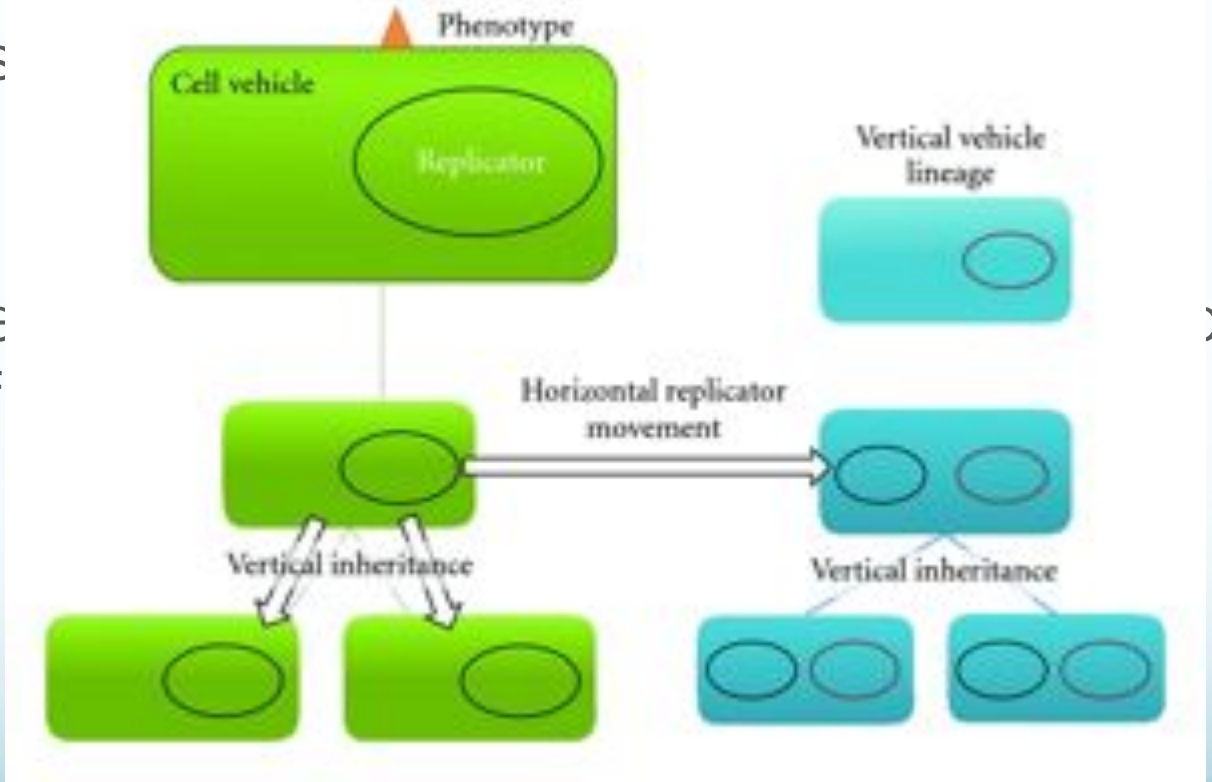
Replicator
(like bacterial chromosme)

Replicators are any genetic entities that utilizes the cell-vehicle for "replicating and maintaining" the replicator

In other words

- Cell-structures are ”vehicles” in which genetic inform
thems

- The re
transf
ome



Classification of replicators

- Genetic elements can be separated by their dependencies on the vertical survival of the particular cell they are currently in
- For example, bacterial chromsomes are completely dependent on their cell whereas a lytic virus requires the cell only transiently and will survive even if the cell dies (and it often does)
- The dependence reflects their general phenotypic effect on the host cell: lytic virus destroys its host

Horizontal movement can be either passive or active

- **Passive:**
- for example: a capsid-less virus; or a plasmid that does not encode conjugation channel and thus relies on other replicators for getting transferred between cell-vehicles
- **Active:**
- a plasmid that encodes conjugation channel: it is able to facilitate its own movement between vehicle-lineages

Replicators can have an extracellular form, or not

- Virus has an extracellular stage

- Conjugative plasmid does not have an extracellular stage

CHROMOSOMES VS CONJUGATIVE PLASMIDS VS VIRULENT VIRUSES

PLASMIDS TEMPERATE VIRUSES

Table 1: Classification of replicators.

Class	Example replicators	Vertical dependency	Horizontal movement potential	Description of average phenotypes
I	Prokaryotic chromosomes	*Completely dependent*	*No potential*	Encodes the main functional units of all cell vehicles. Required for the binary fission of the cell vehicle.
II	Plasmids, transposons	*Highly dependent*	*Passive*	Low reproductive cost to host cell vehicle. Can encode opportunistically useful phenotypic traits.
III	Conjugative plasmids, integrative and conjugative elements (ICEs)	*Moderately dependent* (always requires a cell vehicle)	*Active* without an extracellular stage	Moderate or low reproductive cost to host cell vehicle. Usually encode opportunistically useful phenotypic traits.
IV	Temperate viruses	*Somewhat dependent* (can survive even if the cell-vehicle terminates)	*Active* with an extracellular stage	Moderate or low reproductive cost to host cell vehicle. Sometimes encode opportunistically useful phenotypic traits.
V	Virulent viruses	*Not dependent*	*Active* with an extracellular stage	Insurmountable reproductive cost that terminates the host cell vehicle. Does not encode cell-vehicle benefitting traits.

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Rocell

RiboPlasmidCell

RiboConjugative-elementCell

RiboViroCell

Virocell

..various combinations are constantly forming in the nature

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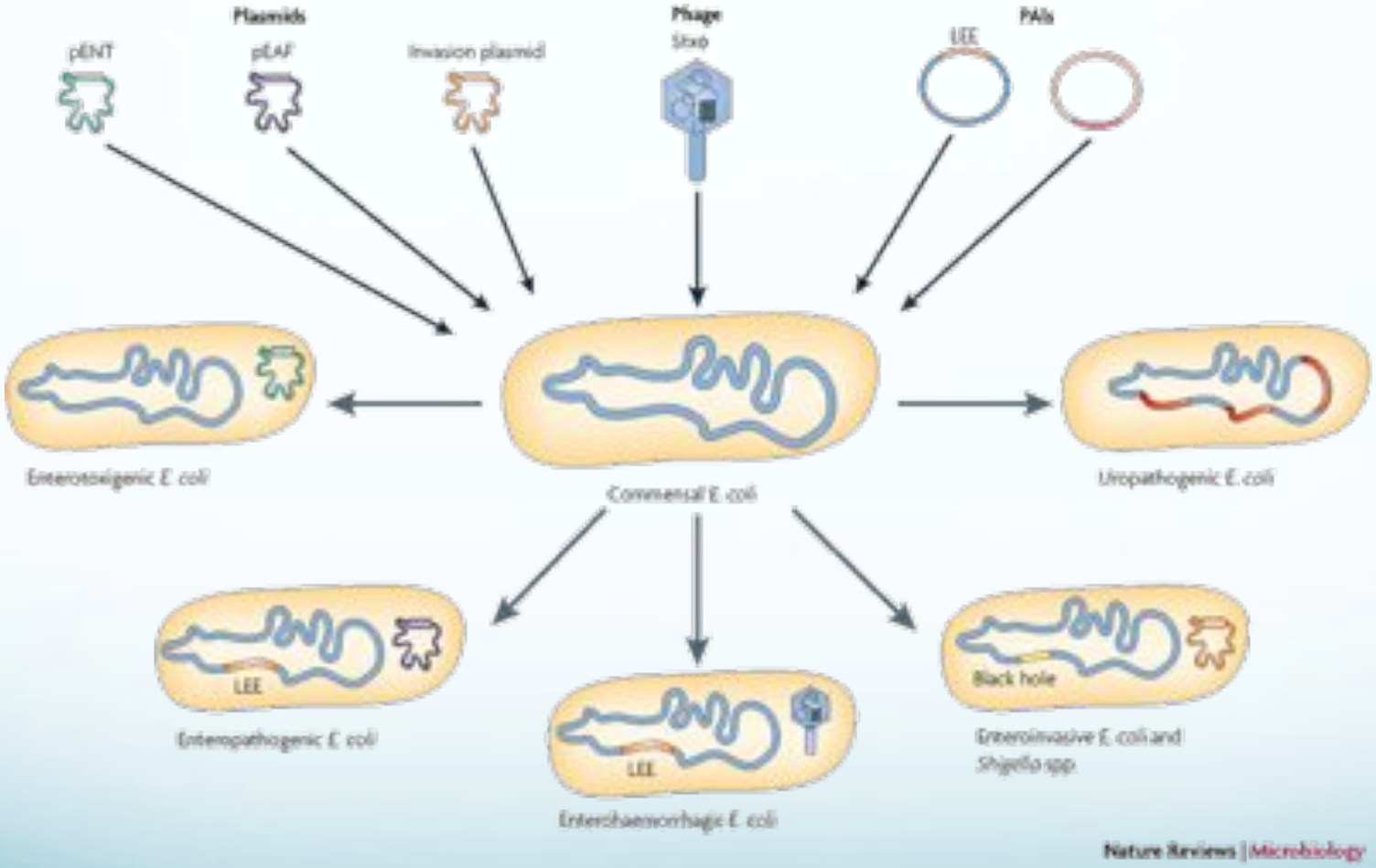
RiboViroPlasmidICECell ..etc



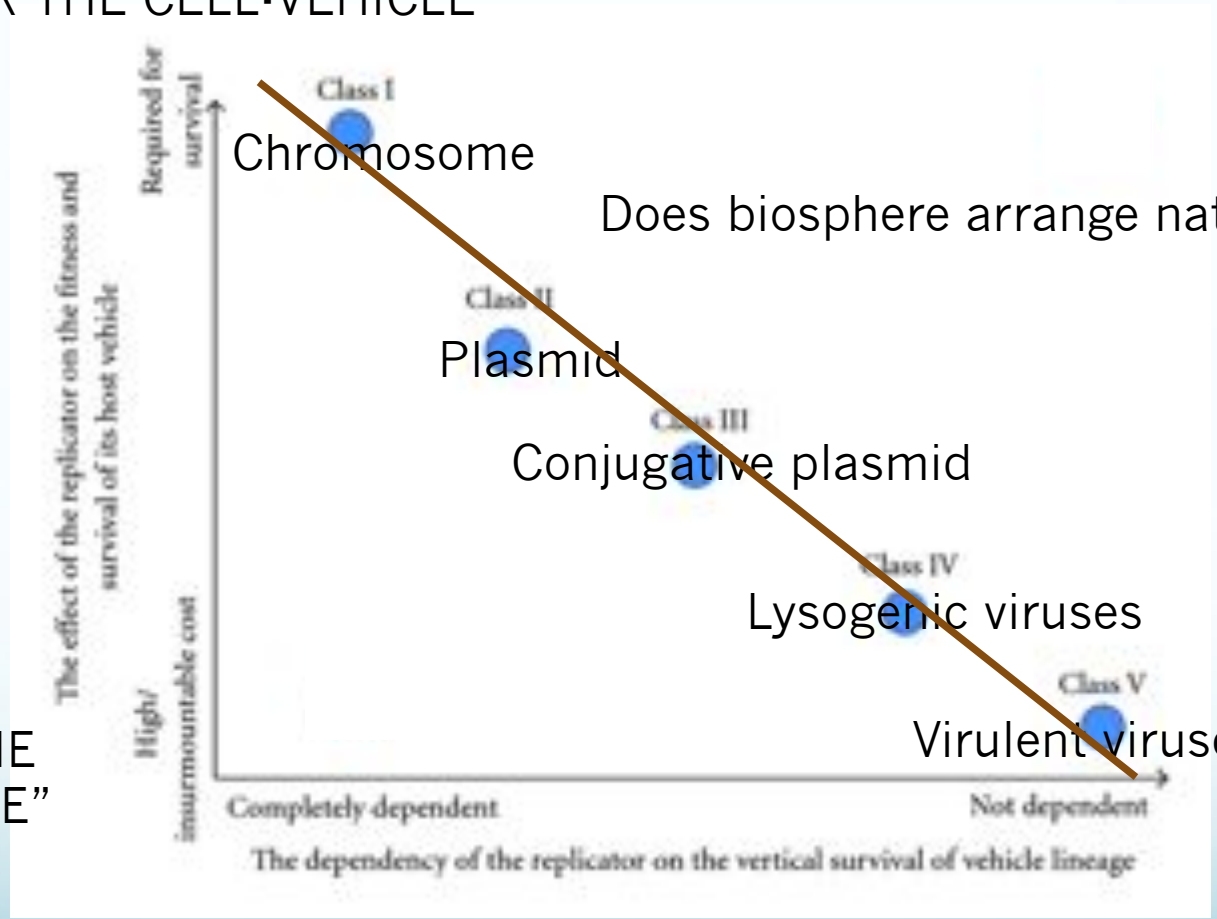
Ahmed et al., 2008. Nat Rev Microbiol.

It appears possible to classify the replicators: is nature trying to tell us something?

- What if the presence of these various classes is not just a mere coincidence but **a direction towards which any biosphere formed of cells and genetic information tends to evolve into?**

The average phenotype of a replicator

"GOOD FOR THE CELL-VEHICLE"

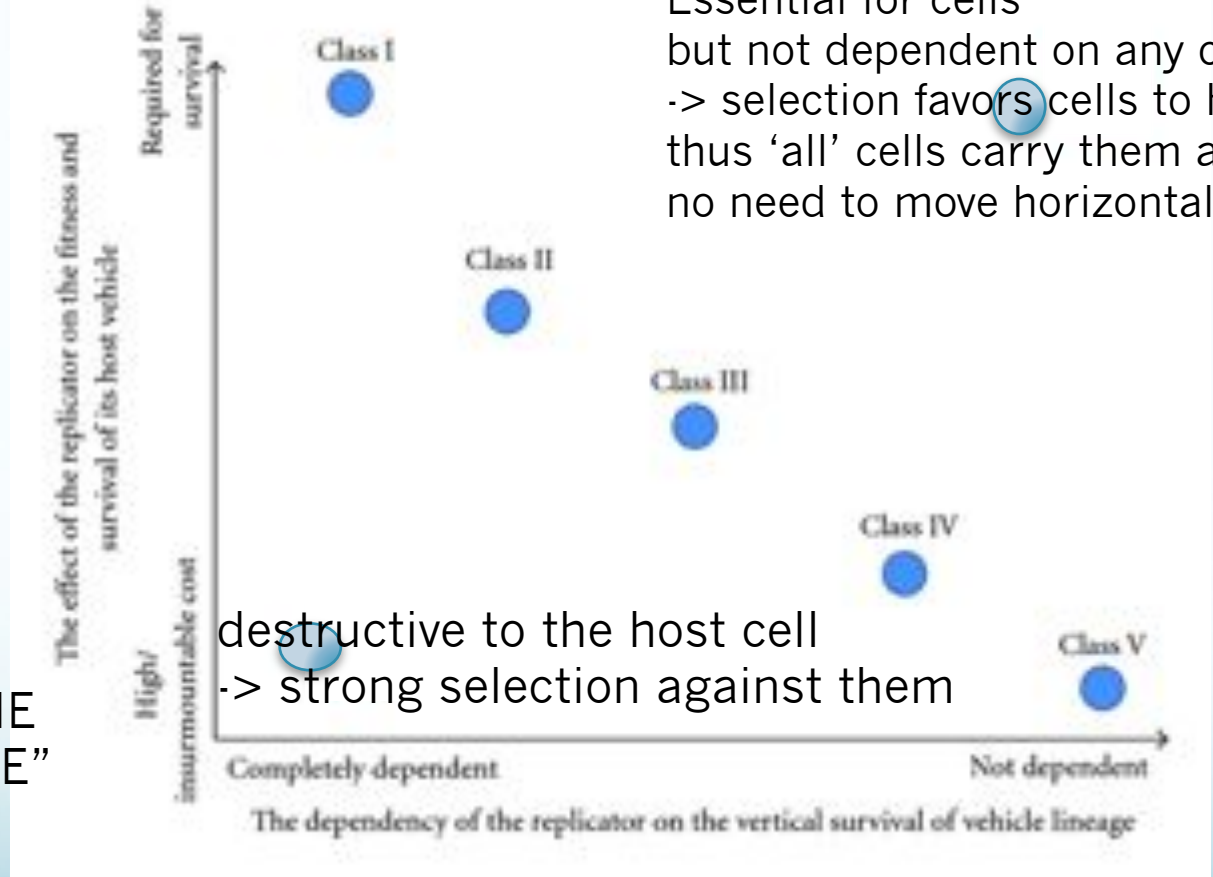


Does biosphere arrange naturally like this?

"BAD FOR THE CELL-VEHICLE"

Unstable ”paradoxical” replicators

“GOOD FOR THE CELL-VEHICLE”

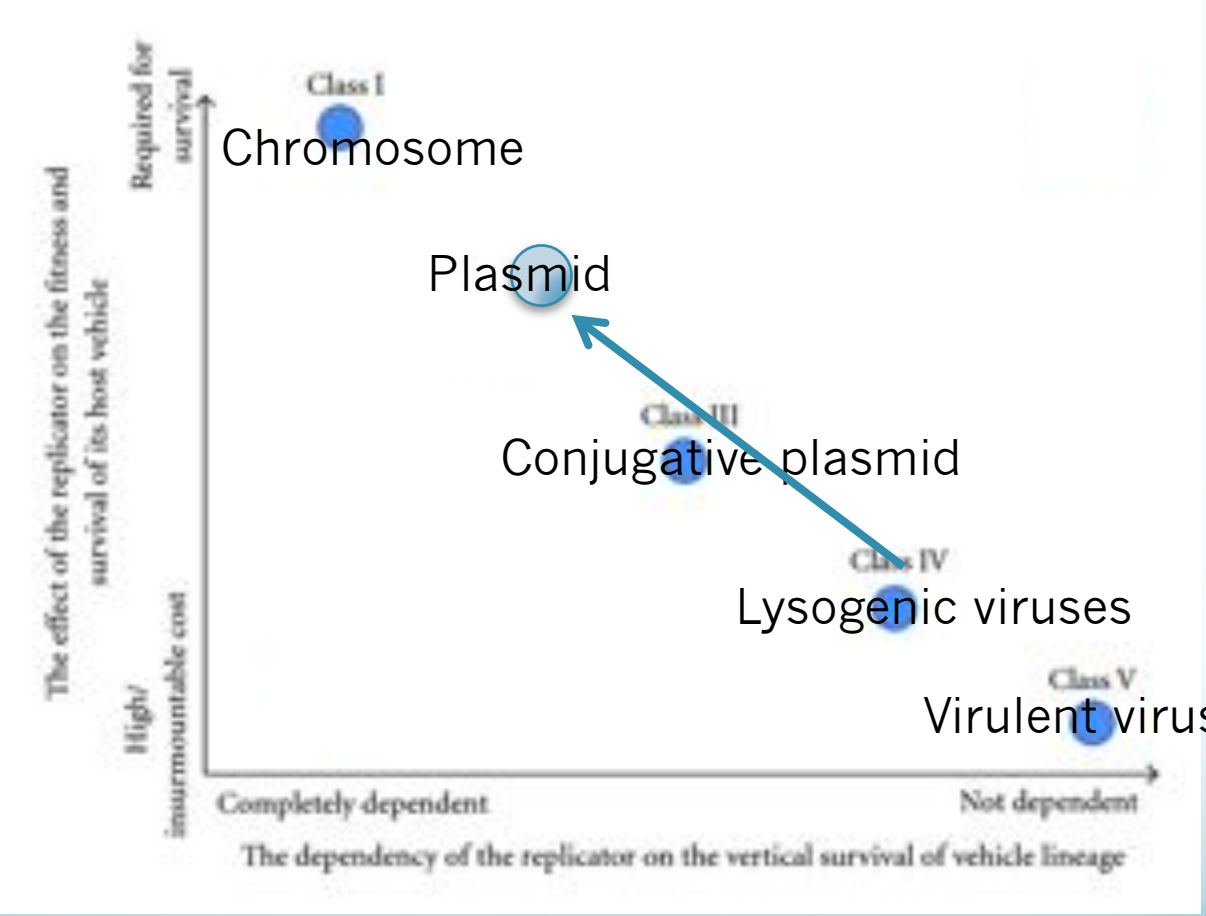


Essential for cells
but not dependent on any cell
-> selection favors cells to have them,
thus ‘all’ cells carry them and there is
no need to move horizontally between cells

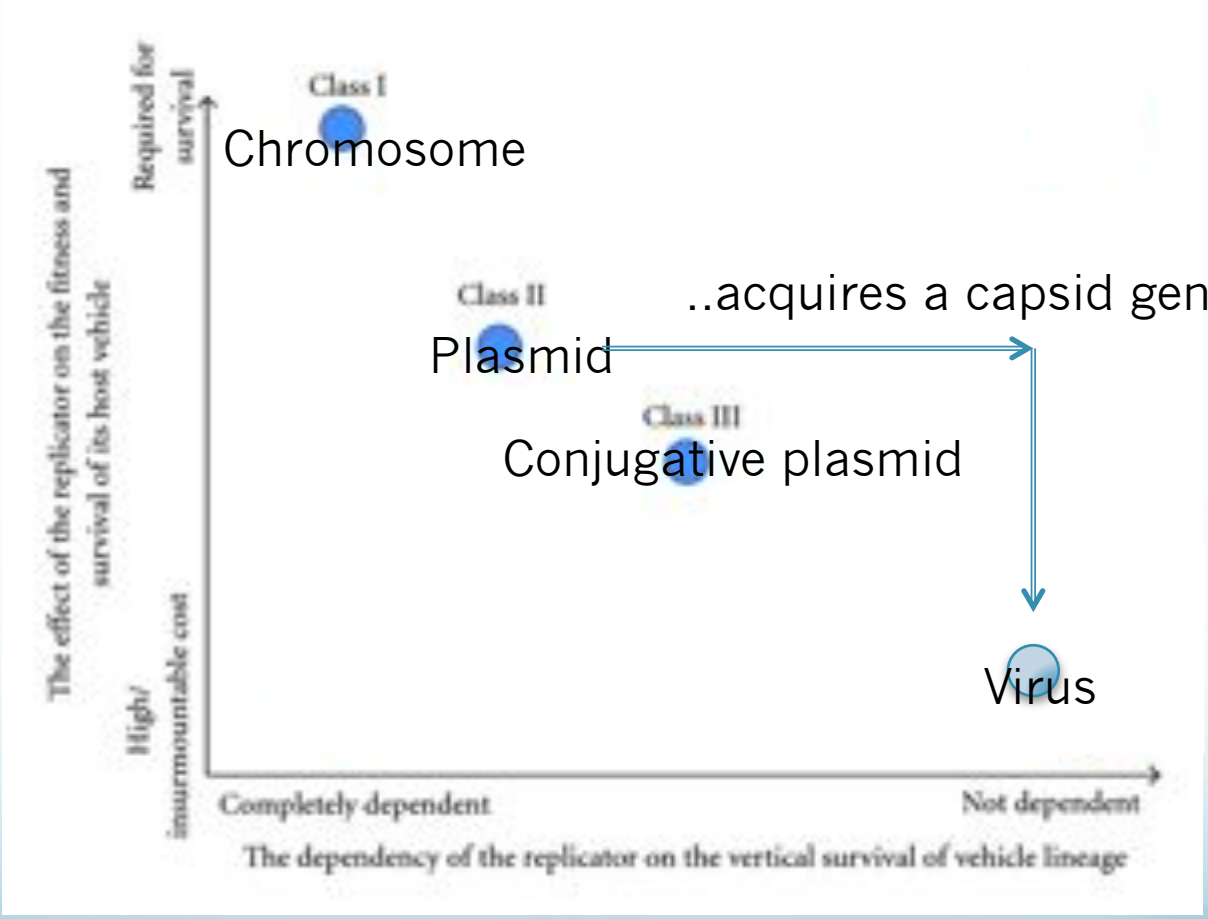
destructive to the host cell
-> strong selection against them

“BAD FOR THE CELL-VEHICLE”

If the biosphere lacked, for example, plasmids, would some other replicator eventually take their place?

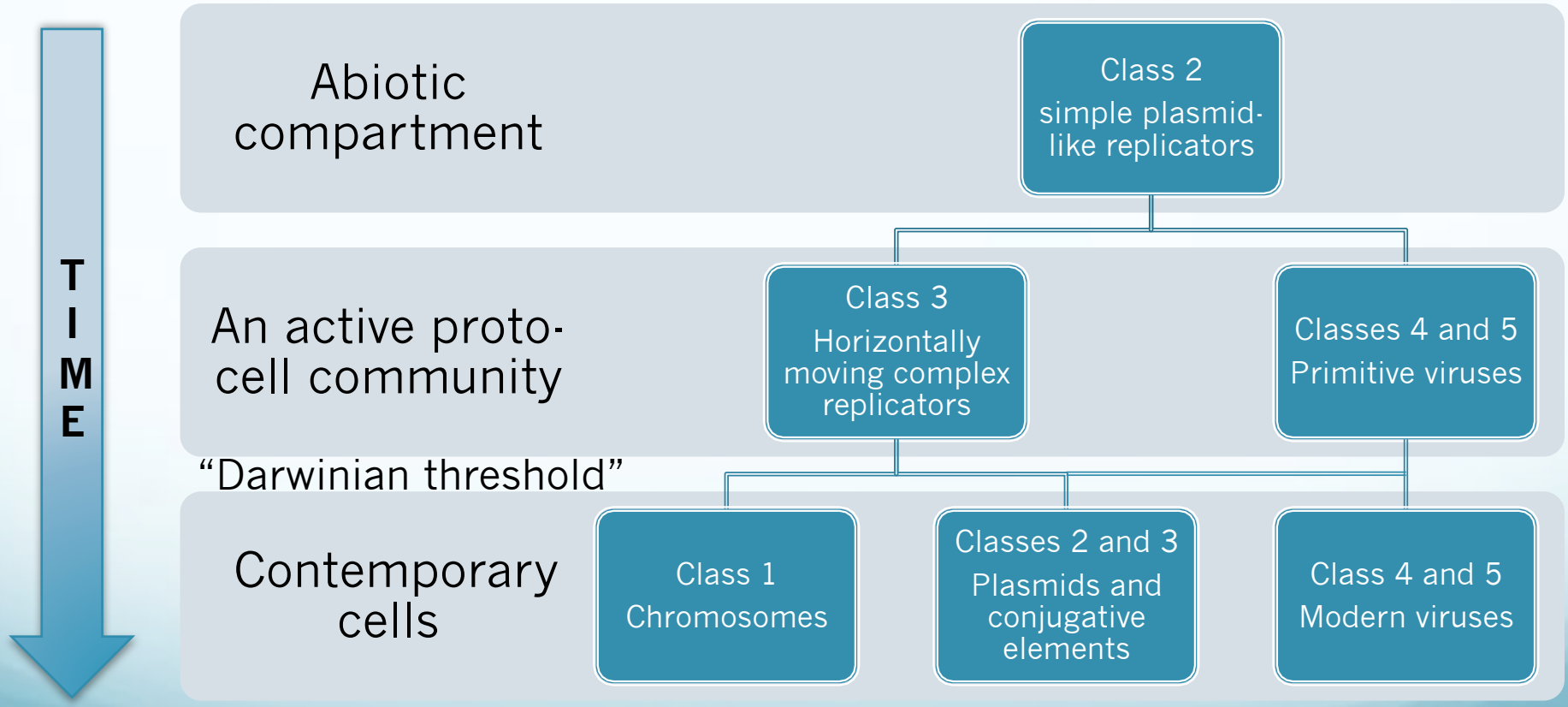


Or if viruses were absent altogether?



- Maybe biospheres naturally organize to have these different replicator types

The origin of different classes occurred during different stages in the early evolution of life



Independent cells emerged as a result of evolutionary competition and co-operation between replicators

Summary: the classification

- May help grasp a more “realistic” picture of the prokaryotic biosphere
- No need to ask “why bacteria exchange genetic material if it is not evolutionarily favorable for them” (i.e. EHEC epidemic in Germany 2011)
- Viruses are as alive and as dead as every other genetic entity
- Naturally includes entities like capsid-less viruses
- Provides a general framework for the current “ribocells”, “virocells” and “ribovirocells”

Acknowledgements

Thank you