

The Hologenome Theory of Evolution

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You are not just yourself

- Colonised by trillions of microbes
- Microorganisms outnumber human cells by **10 to 1**
- Required in vital functions

Animals and plants as ‘holobionts’

- All plants and animals have some degree of symbiotic associations with microbes
- Existence sans microbial symbionts in nature- virtually impossible
- Co-existence at the genetic level- certain microbial genes essential for vital functions
- Plants and animals- no longer viewed as ‘autonomous’ individuals

Holobiont: “a unit of biological organization composed of a host and its microbiota”(Bordenstein *et al.* 2015)

Hologenome: “the complete genetic content of the host genome, its organelles’ genomes, and its microbiome” (Bordenstein *et al.* 2015)

Evolution

Darwinism:

- Theory of evolution: Evolution by natural selection.
- Favourable traits were ‘selected for’
- *Variation*- occurs in the genes. Organisms most suited to the environment survive, reproduce and pass on these to the next generation.

Lamarckism:

- *Acquisition of characteristics*
- Changes in organisms are induced by the environment
- Acquired characteristics are then passed on

The hologenome and evolution

- An organism cannot be viewed as being separate from its microbiome
- Microbiome perform useful functions, critical role in some key processes
- Darwinism- variation in nuclear genome
- Variation in the ‘total repertoire of genetic information that make up eukaryotic function’– i.e. the hologenome

***Hologenome theory of evolution:* “holobiont and its hologenome act in consortium and thus should be considered a single unit of selection in evolution” (Zilber-Rosenberg and Rosenberg, 2008)**

The hologenome theory of evolution- early studies

The role of microorganisms in coral health, disease and evolution

*Eugene Rosenberg**, *Omry Koren**, *Leah Reshef**, *Rotem Efrony** and *Ilana Zilber-Rosenberg**

Abstract | Coral microbiology is an emerging field, driven largely by a desire to understand, and ultimately prevent, the worldwide destruction of coral reefs. The mucus layer, skeleton and tissues of healthy corals all contain large populations of eukaryotic algae, bacteria and archaea. These microorganisms confer benefits to their host by various mechanisms, including photosynthesis, nitrogen fixation, the provision of nutrients and infection prevention. Conversely, in conditions of environmental stress, certain microorganisms cause coral bleaching and other diseases. Recent research indicates that corals can develop resistance to specific pathogens and adapt to higher environmental temperatures. To explain these findings the coral probiotic hypothesis proposes the occurrence of a dynamic relationship between symbiotic microorganisms and corals that selects for the coral holobiont that is best suited for the prevailing environmental conditions. Generalization of the coral probiotic hypothesis has led us to propose the hologenome theory of evolution.

Microbiome and coral adaptation

- Thousands of genetically identical polyps- secrete calcium carbonate exoskeleton.
- Coral reefs- contain an abundant and complex microbiome- bacteria, archaea, eukarya and some viruses.
- Possess an innate immune system- barriers, phagocytic cells + symbiotic bacteria (antimicrobials)
- Coral bleaching: loss of photosynthetic zooxanthellae
- Koch's postulates: *Vibrio shiloi* responsible for death of zooxanthellae

Microbiome and coral adaptation (contd.)

- 90s-early 2000s – Bleaching of *Oculina patagonica* occurred every summer (*V.shiloi*) in eastern Mediterranean
- 2003- Resistant to *V.shiloi*
- No change in corals or the pathogen
- **“Coral probiotic hypothesis”**
 - Dynamic relationship between coral and its microbiota
 - Undergo changes with changes in the environment
 - Environment selects for the most advantageous holobiont
- Basis for ‘hologenome theory of evolution’

Hologenome theory of evolution: The proposal

1. All animals and plants establish symbiotic relationships with microorganisms.

Hologenome theory of evolution: The proposal

1. All animals and plants establish symbiotic relationships with microorganisms.
2. Transmission of symbionts between holobiont generations
 - Vertically (direct) or closely from the environment (indirect)

Hologenome theory of evolution: The proposal

1. All animals and plants establish symbiotic relationships with microorganisms.
2. Transmission of symbionts between holobiont generations
3. Cooperation between the host and the microbiota contributes to the fitness of the holobiont

Importance of gut microbiota in mice

- Microbiota introduced to sterile newborns via environment (close contact with parents)
- Significant differences in gut development and function in ‘germ-free’ mice vs. conventionally grown mice
 - ‘germ-free mice: longer digested food transit time, larger caloric intake, altered epithelial turnover kinetics and increased susceptibility to disease

Abrams GD & Bishop JE (1967) Effect of normal microbial flora on gastrointestinal motility. *Proc Soc Exp Biol Med* 126: 301–304.

Savage DC, Siegel JD, Snellen JE & Whitt DD (1981) Transit time of epithelial cells in the small intestines of germfree mice and ex-germfree mice associated with indigenous microorganisms. *Appl Environ Microbiol* 42: 996–1001.

Silva AM, Barbosa FHF, Duarte R, Vieira LQ, Arantes RME & Nicoli JR (2004) Effect of *Bifidobacterium longum* ingestion on experimental salmonellosis in mice. *J Appl Microbiol* 97: 29–37.

Wostmann BS (1981) The germ-free animal in nutritional studies. *Ann Rev Nutr* 1: 257–297

Hologenome theory of evolution: The proposal

1. All animals and plants establish symbiotic relationships with microorganisms.
2. Transmission of symbionts between holobiont generations
3. Cooperation between the host and the microbiota contributes to the fitness of the holobiont
4. Genetic variation can arise from changes in either the host or the symbiotic microbiota genomes

Genetic variation in holobionts

- Variation in host genomes
 - sexual reproduction, chromosome rearrangements and mutation
- Microbiome: haploid bacteria
 - mutation, conjugation, transduction and DNA transformation within same species
- Additional mechanisms of variation in holobionts
 1. **Microbial amplification/reduction:** change in relative number of associated microorganisms. *Causes: Temperature change, nutrient availability, antimicrobials etc.*
 2. **Acquisition of new symbionts:** Acquired organism finds a niches and gets established. Introduces new genes into the holobiont.
 3. **Interspecies horizontal gene transfer**

ESSAY

Host Biology in Light of the Microbiome: Ten Principles of Holobionts and Hologenomes

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Darwinian principle with an essence of Lamarckism

- Holobiont with the most favourable hologenome selected for (Darwinism)
- Acquisition of microbial symbionts from the environment- if favourable, long term symbiotic relationship may be established. (Lamarckism)
- Potentially passed on to the offspring-directly/indirectly
- Offspring would continue acquiring microbial symbionts from the environment

Commensal bacteria play a role in mating preference of *Drosophila melanogaster*

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Authors' conclusions*

- (i) Diet-induced mating preference occurred in *D. melanogaster*
- (ii) Fly-associated commensal bacteria were responsible for the mating preference
- (iii) *L. plantarum* was responsible, at least in part, for the mating preference
- (iv) The source of *L. plantarum* was the commensal microbiota of the CMY-bred flies, which were amplified in starch medium

*Sharon, Segal, Ringo, Hefetz, Zilber-Rosenberg, Rosenberg. Commensal bacteria play a role in mating preference of drosophila melanogaster. *Proceedings of the National Academy of Sciences*. 2010;107(46):20051-20056.

ESSAY

The Hologenome Concept: Helpful or Hollow?

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Criticism

- Consideration of the hologenome as a single unit of selection may be an oversimplified approach
- Microbiome may have its own fitness interest
 - *Wolbachia* and *Spiroplasma*: protection vs favoring female progeny
- Symbiont fitness may depend on host fitness- selection on hologenome may be insignificant compared to individual genome
- Hosts and symbionts may have coadapted, but a degree of antagonism may still exist due to difference in fitness interests of genomes
- Validity of the theory is case dependant

Summary

- Microbiota are a necessity- existence without microbial symbionts is virtually impossible
- Host and its symbionts may be seen as a polygenomic entity (holobiont represented by its hologenome)
- Hologenome theory of evolution: Hologenome single unit for natural selection
- Parallel with Darwinism with elements of Lamarckism
- Still subjected to criticism
- May be a way of explaining rapid adaptive changes
- Needs to be supported by a larger set of empirical data- for mainstream acceptance.

Thank you!