On the evolutionary age and stability of deep-sea chemosynthetic communities

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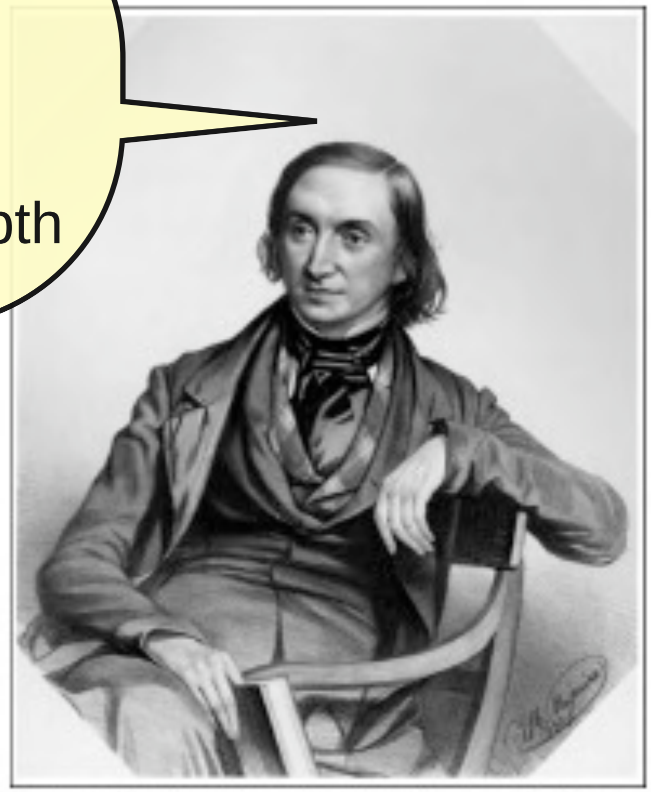
Москва, Россия (18 Apr. 2013)

1850: the azoic hypothesis

The deep ocean basins are:

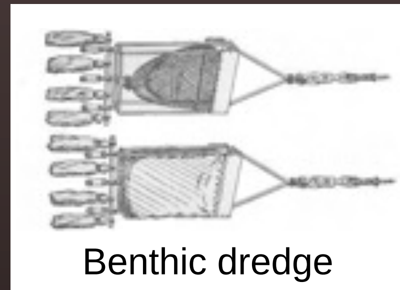
* cold, dark & ~~inhospitable~~
X nourished **only** by marine snow
X uniform globally & constant in time
X biological diversity **decreases** with depth



Edward Forbes, ca. 1850

Ocean floor is not inhospitable

technology



- Deep-sea is home for **living fossils** (to be continued)
- Did life evolve in deep-sea environment?

~~***Urschleim***, the primordial slime from which life originated (Haeckel 1866).~~

~~*Bathybius haecklei* (Huxley 1868)~~

$CaSO_4$ (John Young Buchanan 1877)

1960s: Discovery of hydrothermal vents

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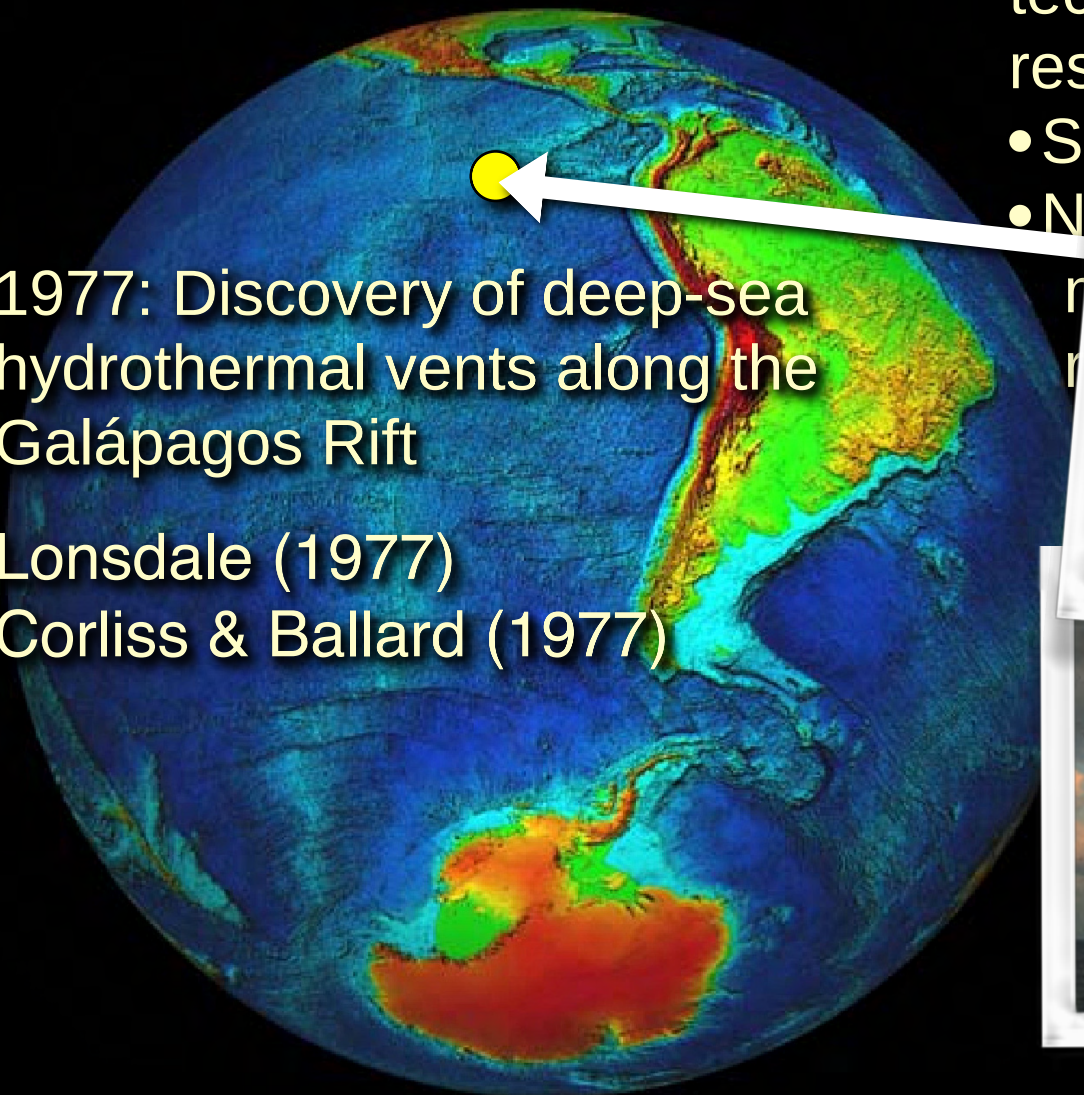
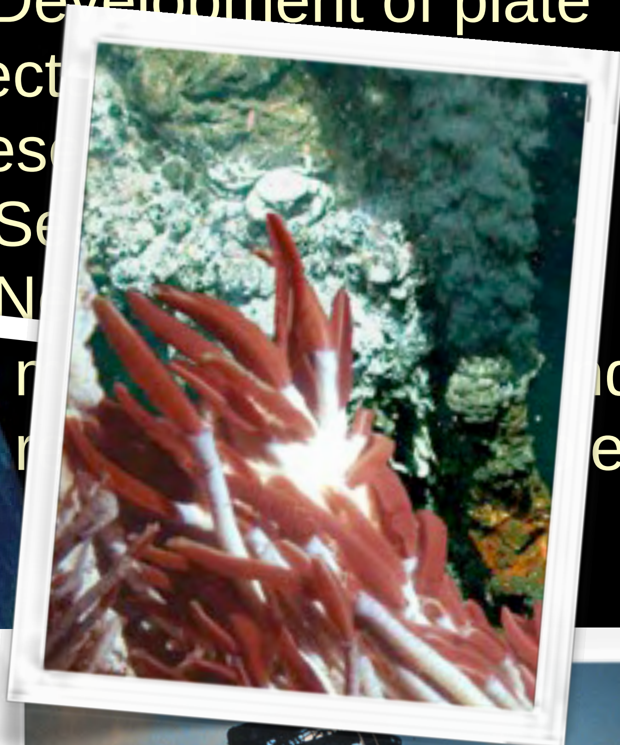


1977: Discovery of deep-sea hydrothermal vents along the Galápagos Rift

Lonsdale (1977)
Corliss & Ballard (1977)



1979: Chemosynthetic habitats

Riftia tubeworms
Calyptogena clams
Bythograeia crabs, *etc.*

"... revealed ... animal communities ... dependent on energy derived from seawater-rock reactions and ***chemosynthesis*** *by bacteria for their primary productivity."*

(Corliss *et al.* 1979 *Science* 203:p. 1080)

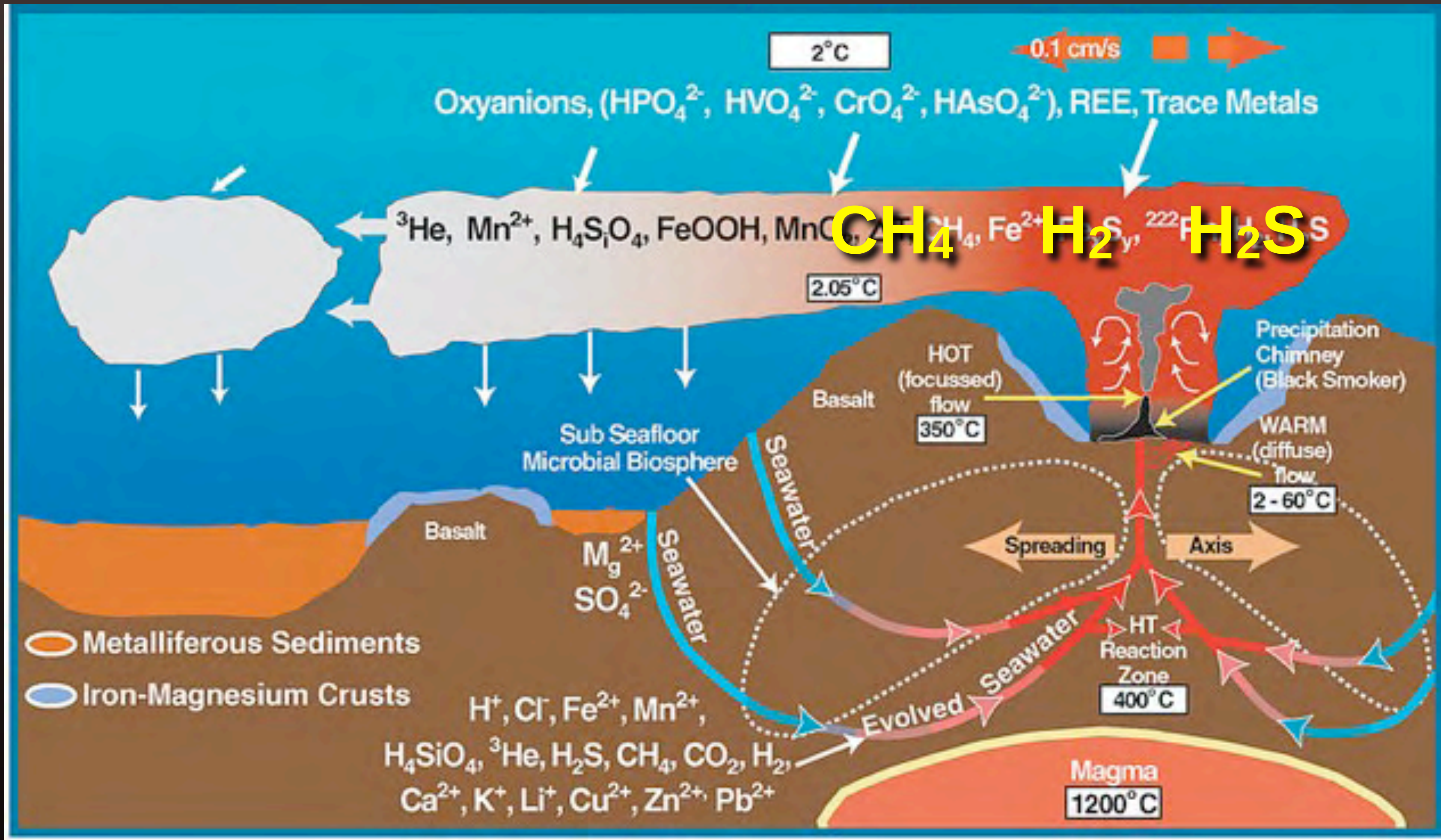
Vent studies led scientists to realize:

- life can flourish without photosynthesis.
- significance of chemoautotrophic symbiosis for deep-sea productivity.
- potential for life under extreme conditions.
- new ideas about the origin of life on Earth.
- possibilities for life elsewhere in (or outside of) our solar system

American Museum of Natural History, New York

Europa ?

Vent geochemistry

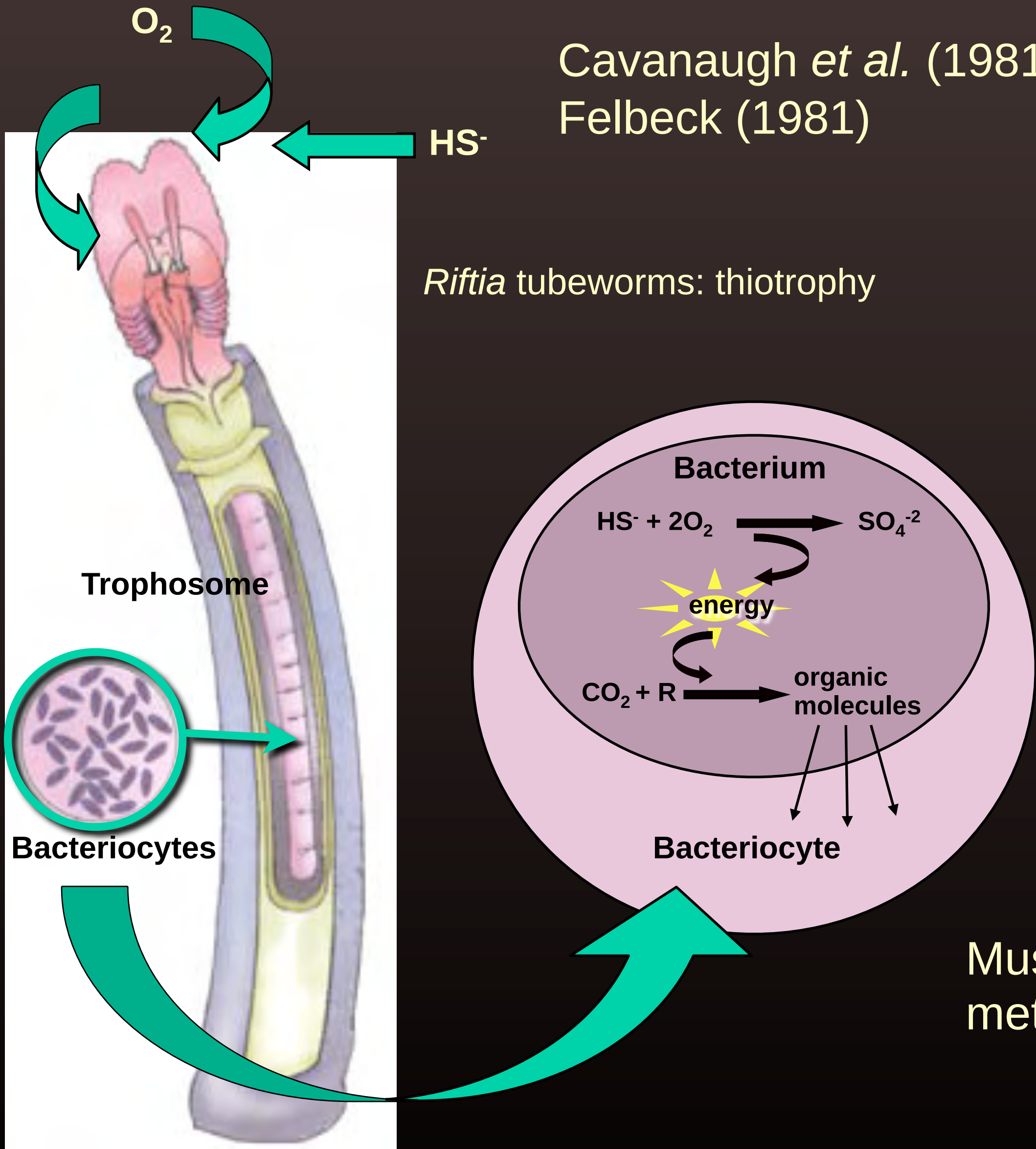


credit: National Oceanic and Atmospheric Administration Vectorization: via Wikimedia Commons

1981: Chemosymbioses

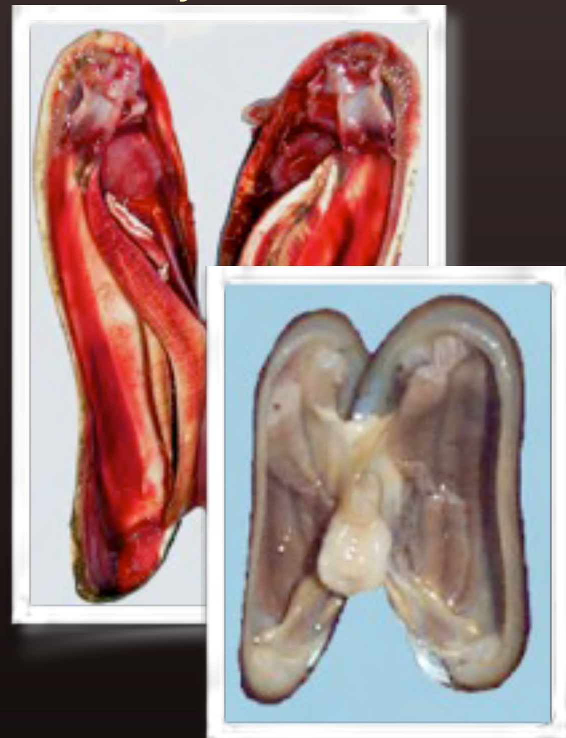
Cavanaugh *et al.* (1981)
Felbeck (1981)

Riftia tubeworms: thiotrophy



credit: Dodson, 2000

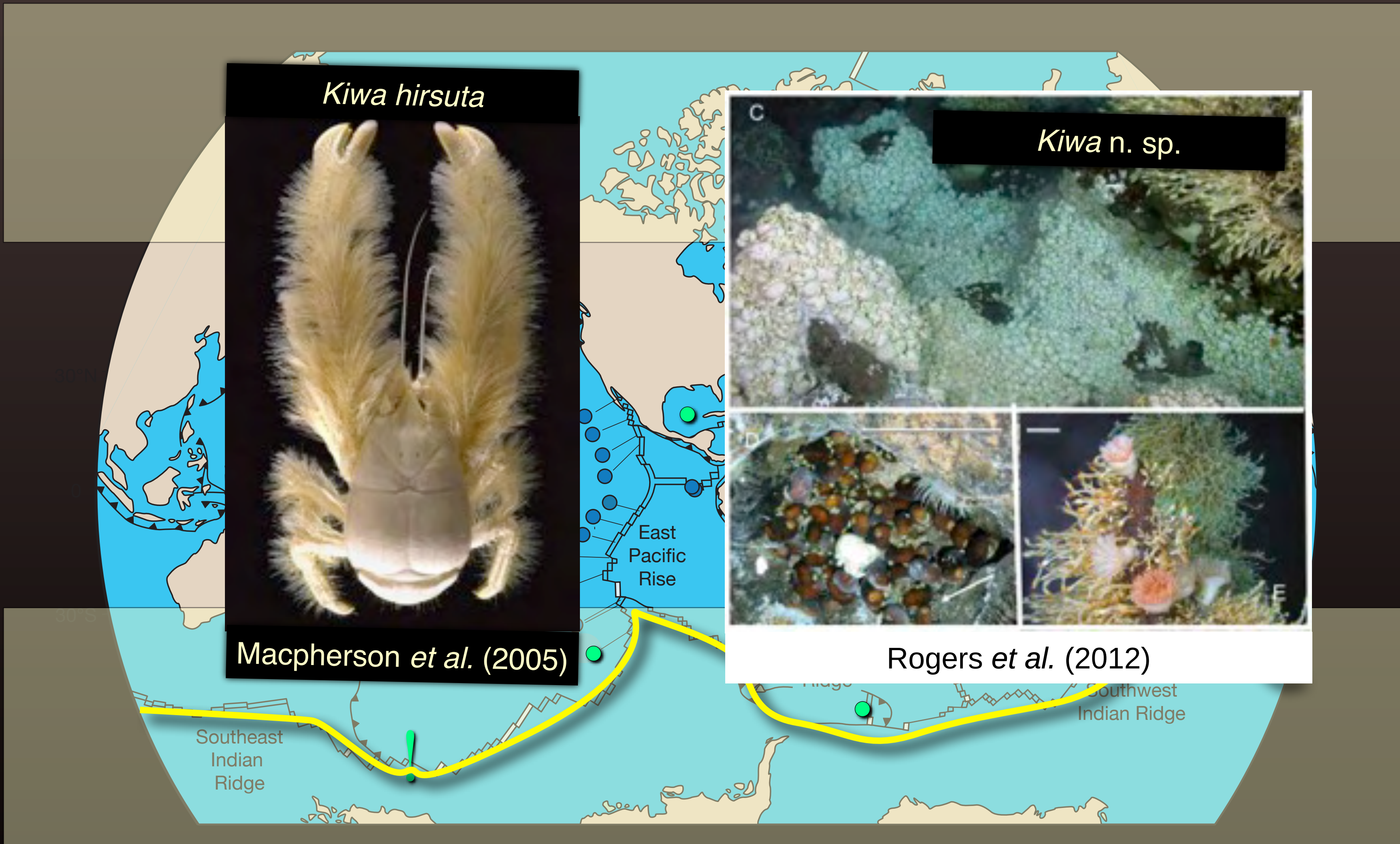
Clams: thiotrophic endosymbionts



Mussels: thiotrophy and/or methanotrophy (Fisher *et al.* 1987)

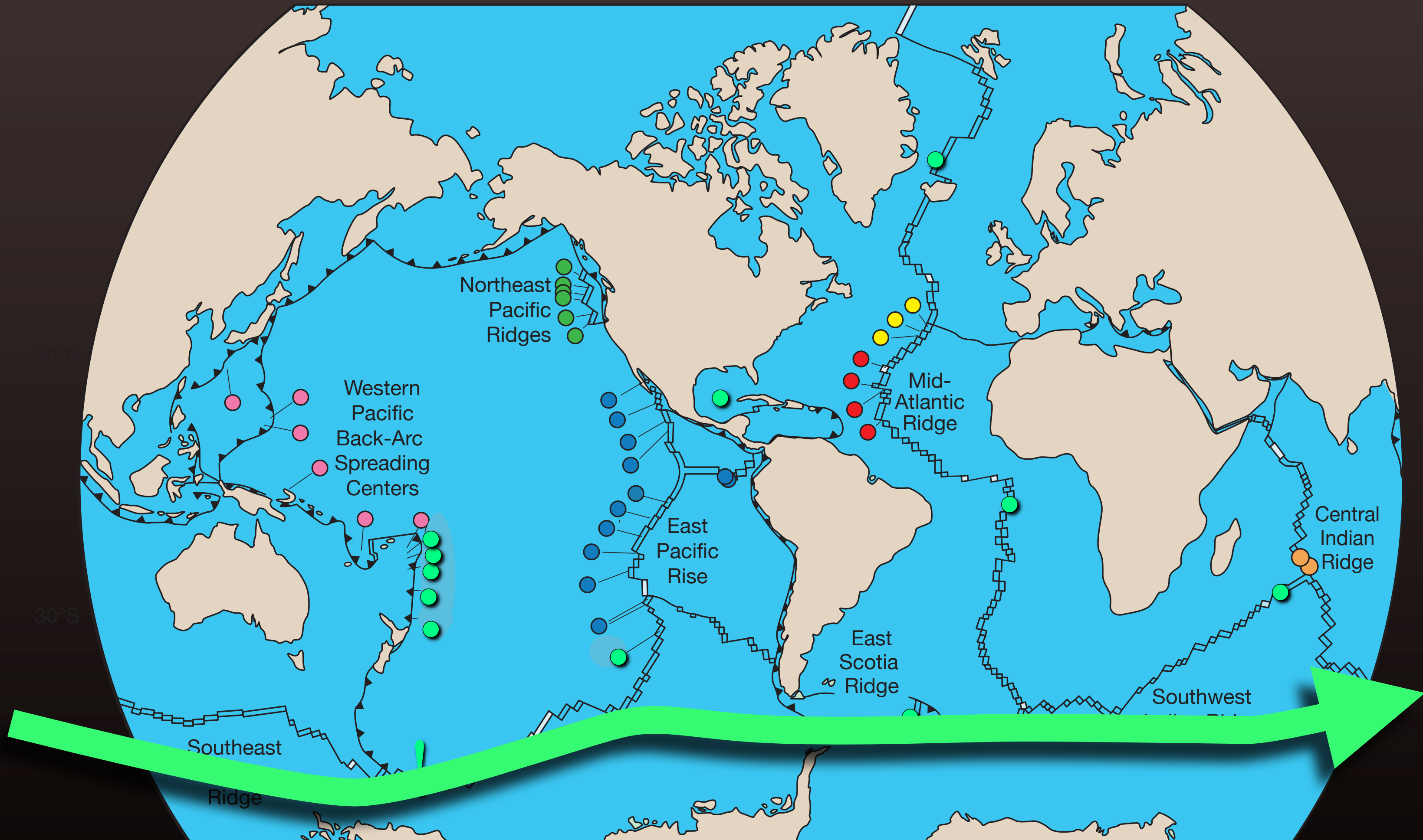
Life is precarious at the oxic/anoxic interface

Vent communities occur globally



Van Dover, German, Speer, Parson, Vrijenhoek (2002) *Science* 295: 1253–1257

Antarctic Circumpolar Current



~ 20 Million years ago

Origin of life ?

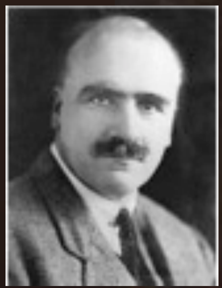
Darwin's warm little pond?

(letter to Joseph Hooker, 1871)

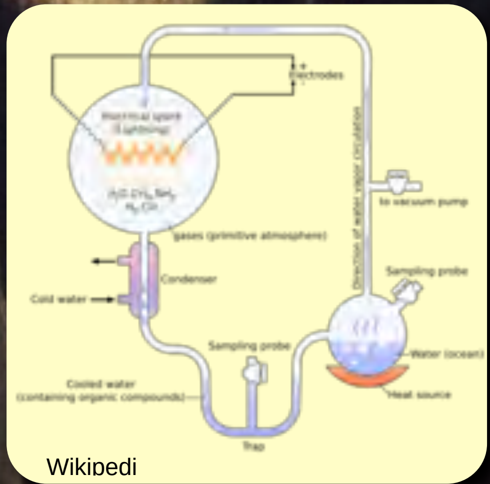
*"But if (and Oh! what a big if!) we could conceive of some **warm little pond**, with all sorts of ammonia and phosphoric salts, light, heat, electricity, etc., ... that a protein compound was chemically formed ready to undergo still more complex changes…"*

Alexander Oparin (1924): reducing atmosphere

JBS Haldane (1929): prebiotic soup



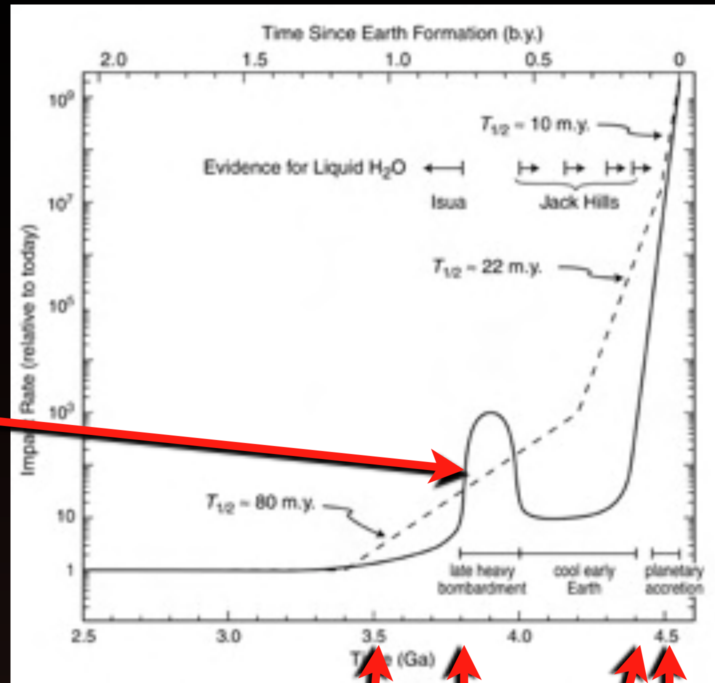
Urey-Miller experiment (1953)



Criticisms of Oparin-Haldane theory

Life at the surface needed protection from:

- UV damage
- Late heavy bombardment, 3.8 to 4.1 billion years ago (Ga)



Stromatolites (Shark Bay, Australia)

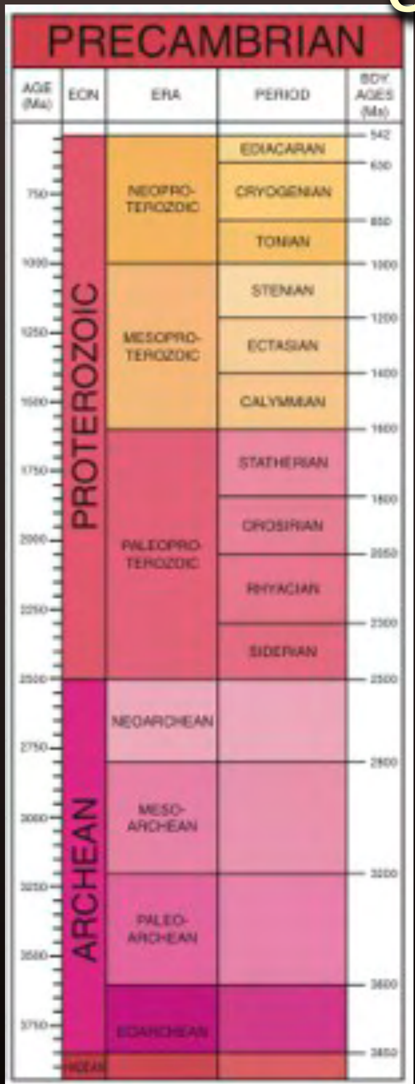
⋆ Stromatolite formation: 3.5 Ga

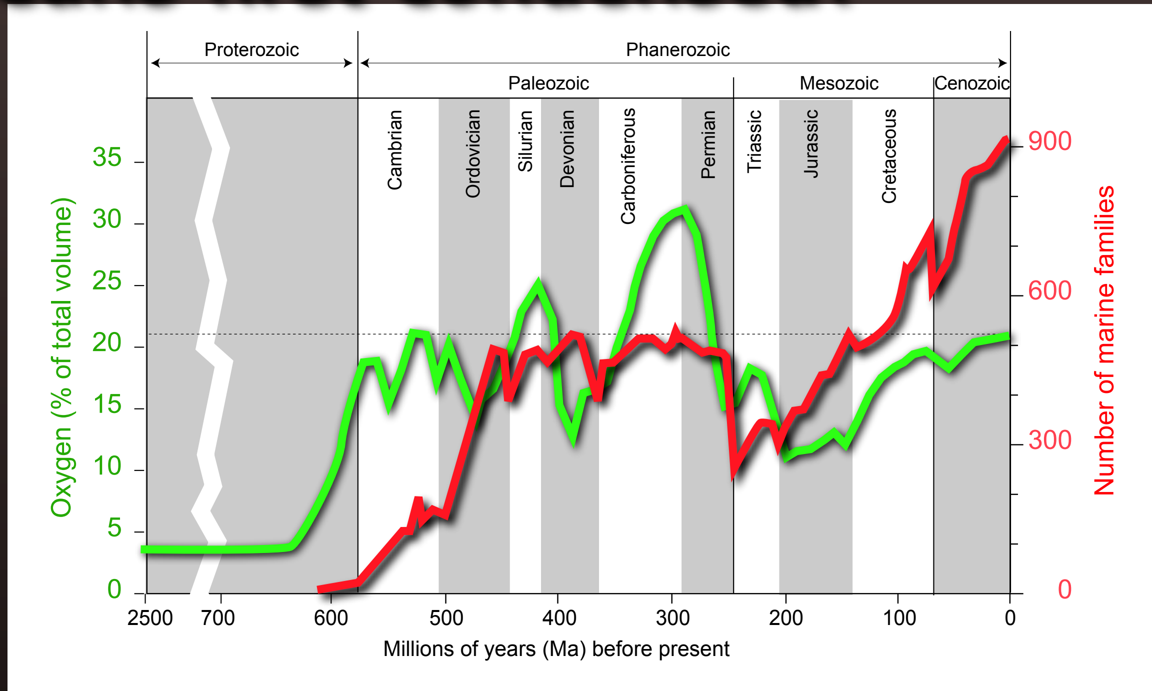
⋆ Evidence for biological carbon fixation: 3.8 Ga

⋆ Oceans condensed: 4.4. Ga

⋆ Age of Earth: 4.5 Ga

Have hydrothermal vents existed since oceans first condensed?





Ward, P.D., 2006. Out of Thin Air: Dinosaurs, Birds, and Earth's Ancient Atmo- sphere. Joseph Henry Press, Washington, DC.

Sepkoski Jr, J.J., 1984. A kinetic model of Phanerozoic taxonomic diversity. III. Post-Paleozoic families and mass extinctions. Paleobiology, 246–267.

Valley et al. 2002. A cool early Earth. Geology 30:351–354 http://www.geology.wisc.edu/zircon/Valley2002Cool_Early_Earth.pdf

Did microbial life arise at vents?

Corliss, Baross & Hoffman (1981); Baross & Hoffman (1985),

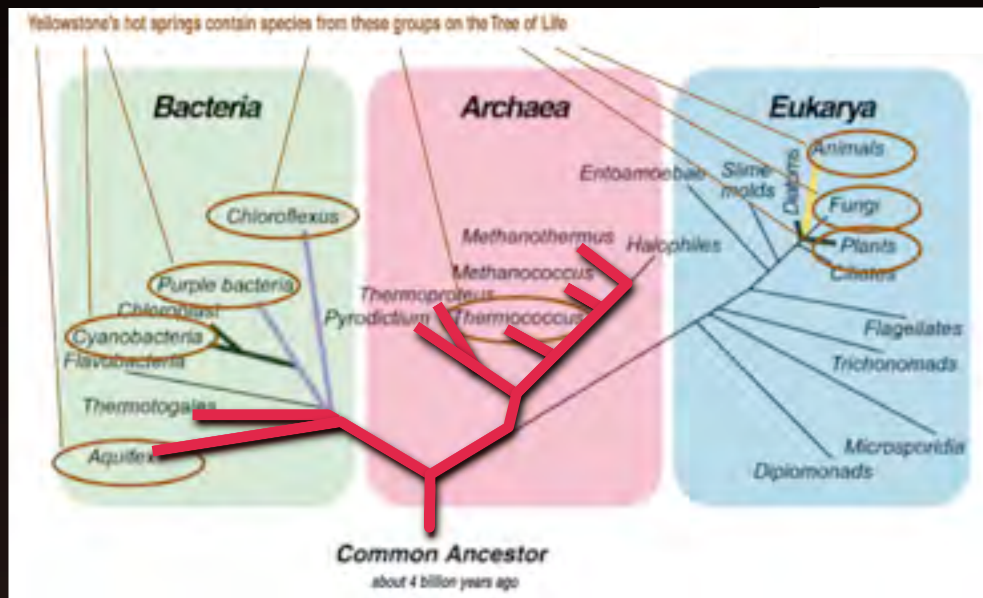
- Catalytic clays and minerals, water rich in H_2, H_2S, CO, CO_2, CH_3, CN^- and NH_3.
- Plenty of energy.
- Protection from UV damage.
- Home to microbes that thrive at 80 to 110° C.

Critics: Miller & Bada (1988)

- Lack of long-term stable environments.
- What is source of organic molecules?

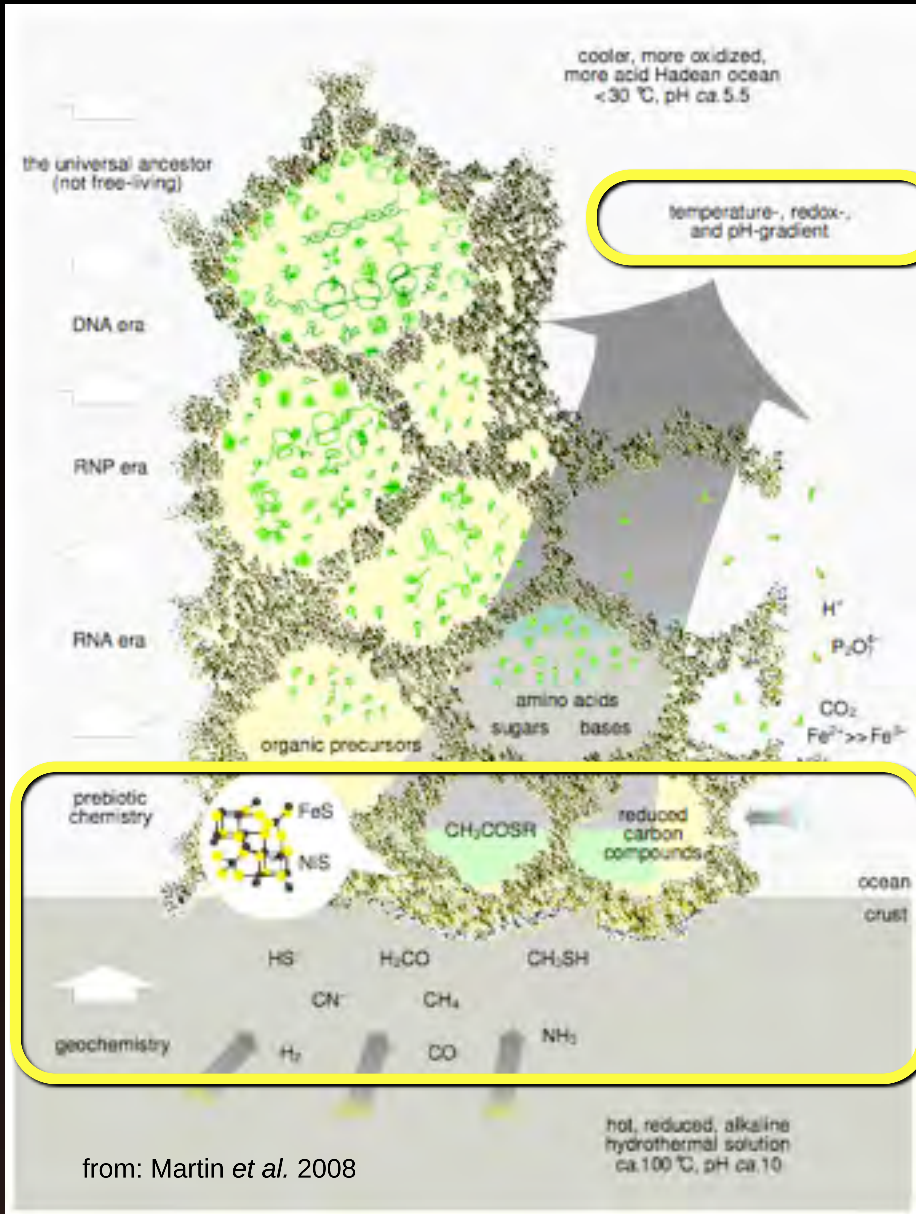
Response: Günther Wächterhäuser (1990)

- Carbon fixation (oxidative formation of pyrite FeS_2 from FeS, H_2S and SH^-)



from: Woese, C. R. (2000) *Proc. Natl. Acad. Sci. USA* 97, 8392–8396.

Did cells arise at vents?



from: Martin *et al.* 2008

Michael Russell et al. (1988)

- addressed criticisms of Miller and Bada

Russell & Hall (1997)

- theory for origin of cells in metalliferous foams

Martin, Baross, Kelley, Russell (2008)

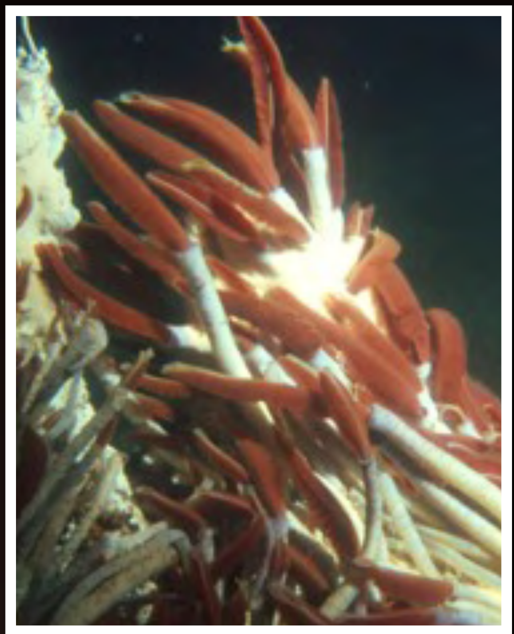
- alkaline vents (Lost City on Mid-Atlantic Ridge)

Tantalizing hypotheses

Are chemosymbiotic taxa ancient?

Bulletin of the Biological Society of Washington 1985

Vents are home to living fossils!



Mesozoic "relics"

Newman (1985): scapellomorph barnacles
McLean (1985): archaeogastropod limpets

Jones (1985): "Vestimentifera" elevated to new Phylum !
suggested *Riftia*-like tubeworms had Cambrian origin !

review: Little & Vrijenhoek (2003) *Trends in Ecology and Evolution* 18: 582-588

Hyperbole: vent taxa escaped global mass extinctions

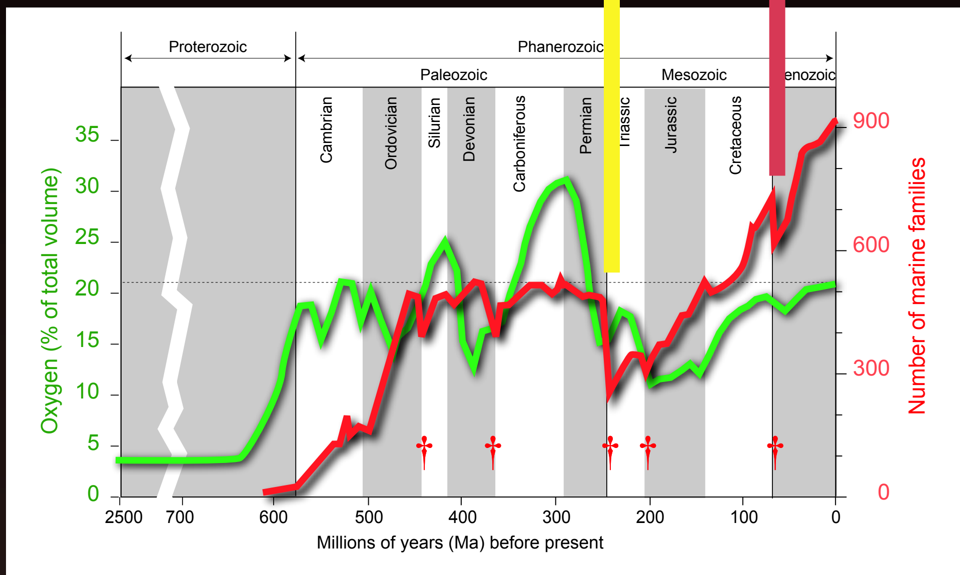
Tunnicliffe, Fowler & McArthur (1996); McArthur & Tunnicliffe V (1998)

High numbers of "endemic" species, genera, families, … phyla that are new to science.

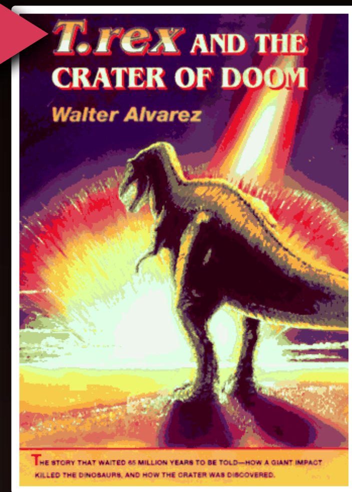
Conclusion: vent taxa **MUST** be ancient

KT boundary (> 46% extinct)

PT boundary (70% extinct)



e.g., Deccan Traps

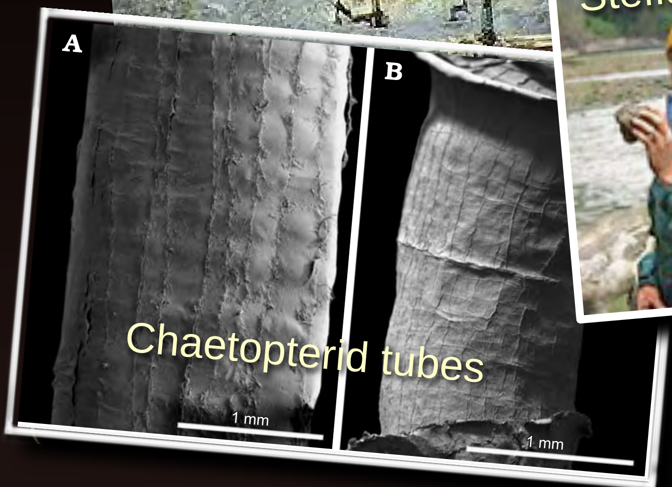


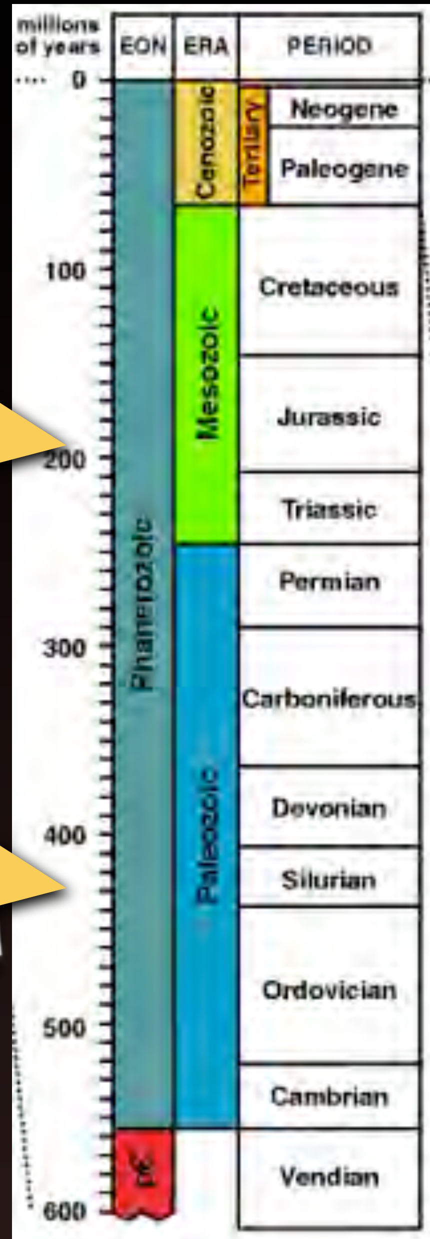
Chicxulub crater

Fossil vent communities

Ancient vestimentiferan tubes?

Yaman Kasy open pit mine, Urals (Early Silurian, 430 Ma)





Kiel & Dando (2009) *Acta Palaeontologica Polonica* **54**, 443-448.

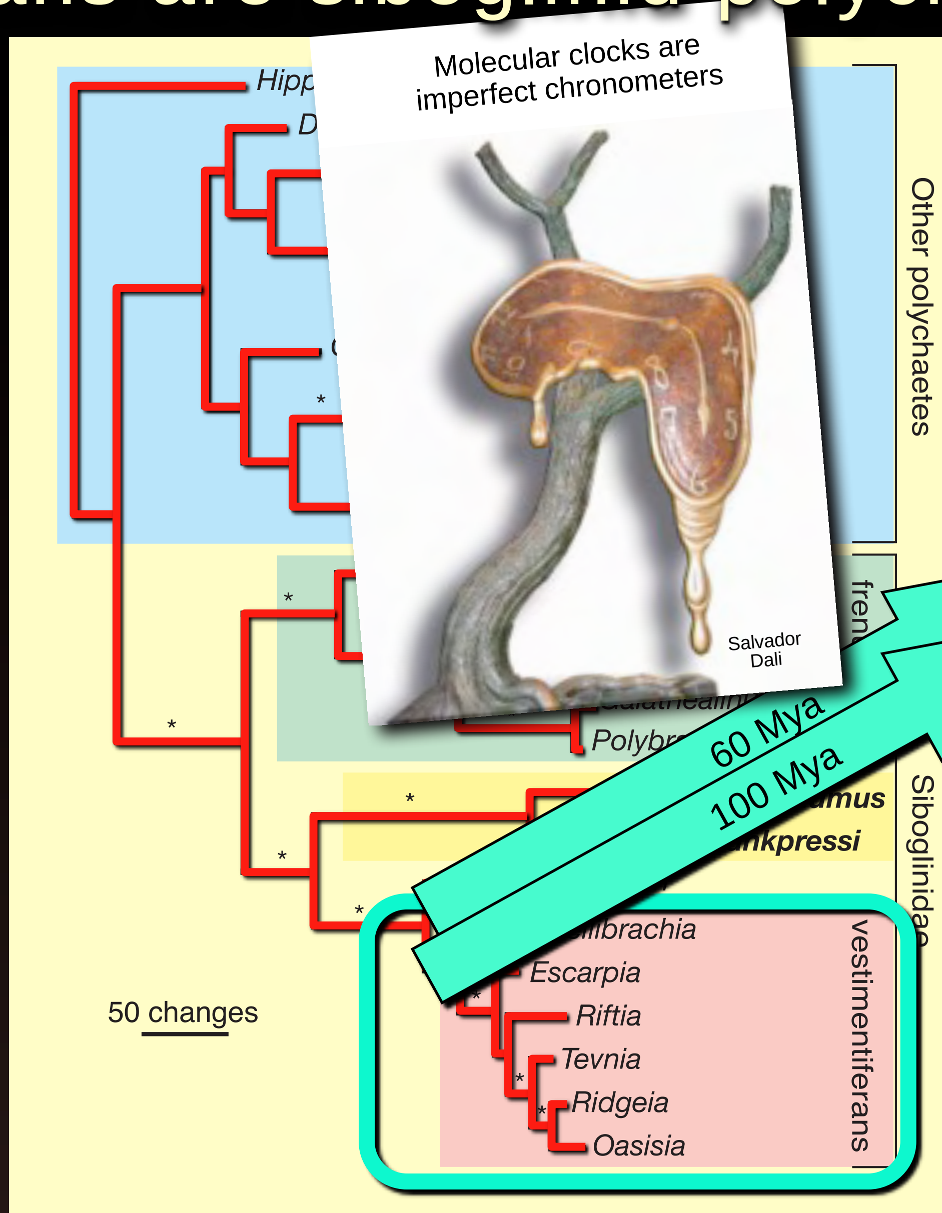
Figueroa sulfide deposit, ca. Santa Barbara, CA (Early Jurassic, 200 Ma) "worm" tubes deposits near Santa Barbara (Little *et al.* 2004)

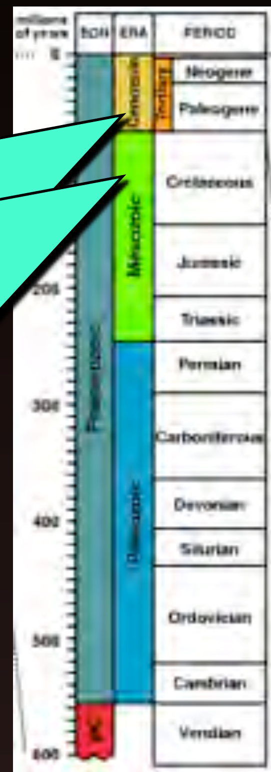
Vestimentiferans are siboglinid polychaetes

mitochondrial COI, 18S rRNA, morphology

Jones' "Phylum Vestimentifera" submerged into polychaete family: Siboglinidae

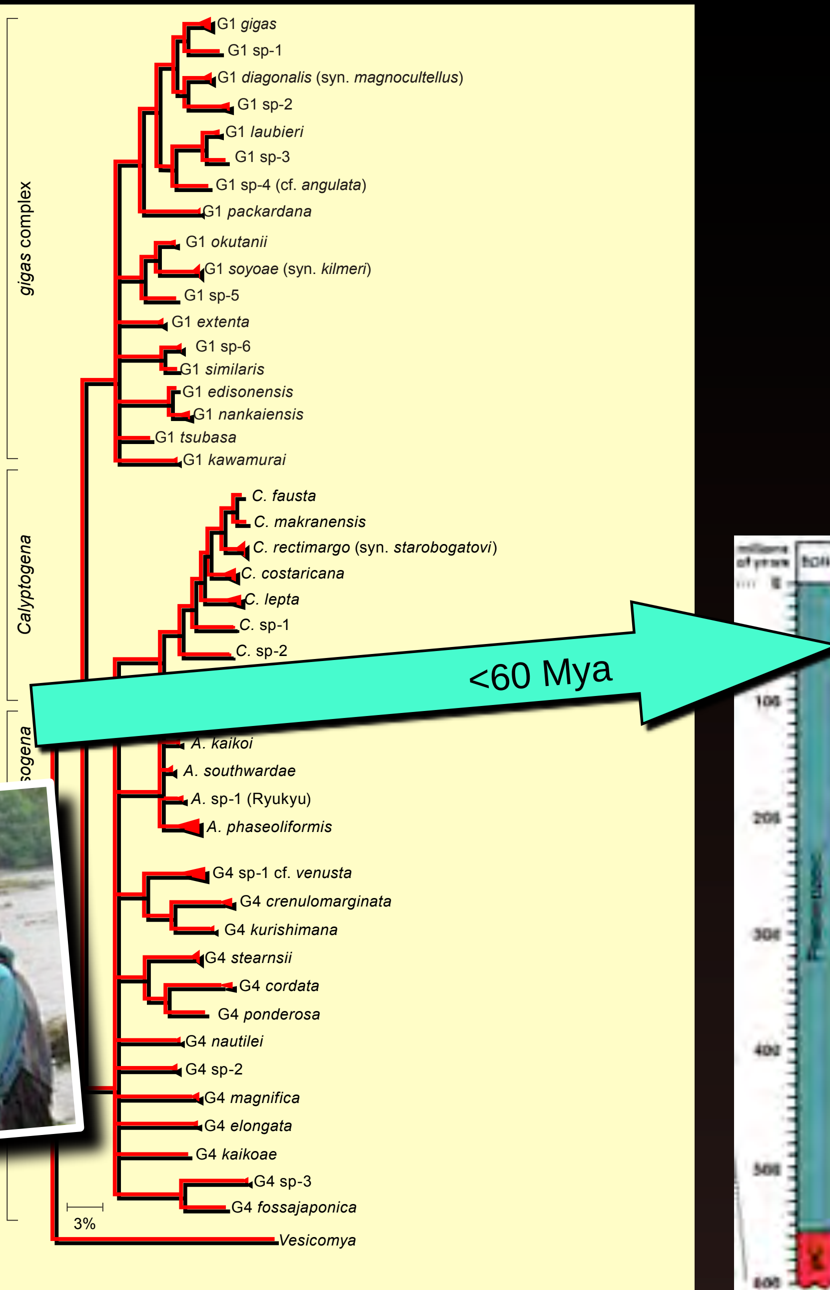
- Black, Halanych, Maas, Hoeh, Hashimoto, Desbruyères, Lutz & Vrijenhoek (1997)
- Rouse (2001)
- Halanych, Feldman & Vrijenhoek (2001)
- Rouse, Goffredi & Vrijenhoek (2004)
- Rouse, Johnson & Vrijenhoek (2008)

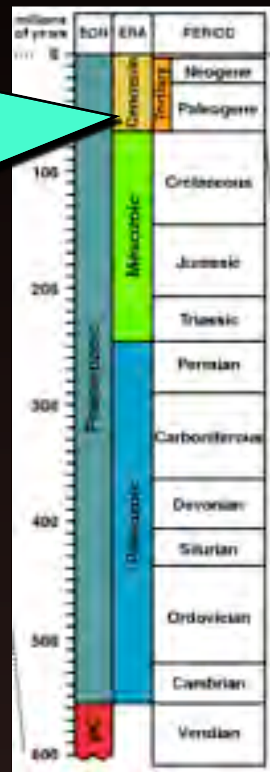




Vesicomyid clams

- Peek et al. (1997, 2000)
- Baco et al. (1999)
- Audzijonyte, Krylova, Sahling & Vrijenhoek (2012) 44 OTUs
- Kiel et al. 2008. Acta Palaeontologica Polonica 53:525-537.
  No credible evidence for any vesicomyids before Cenozoic

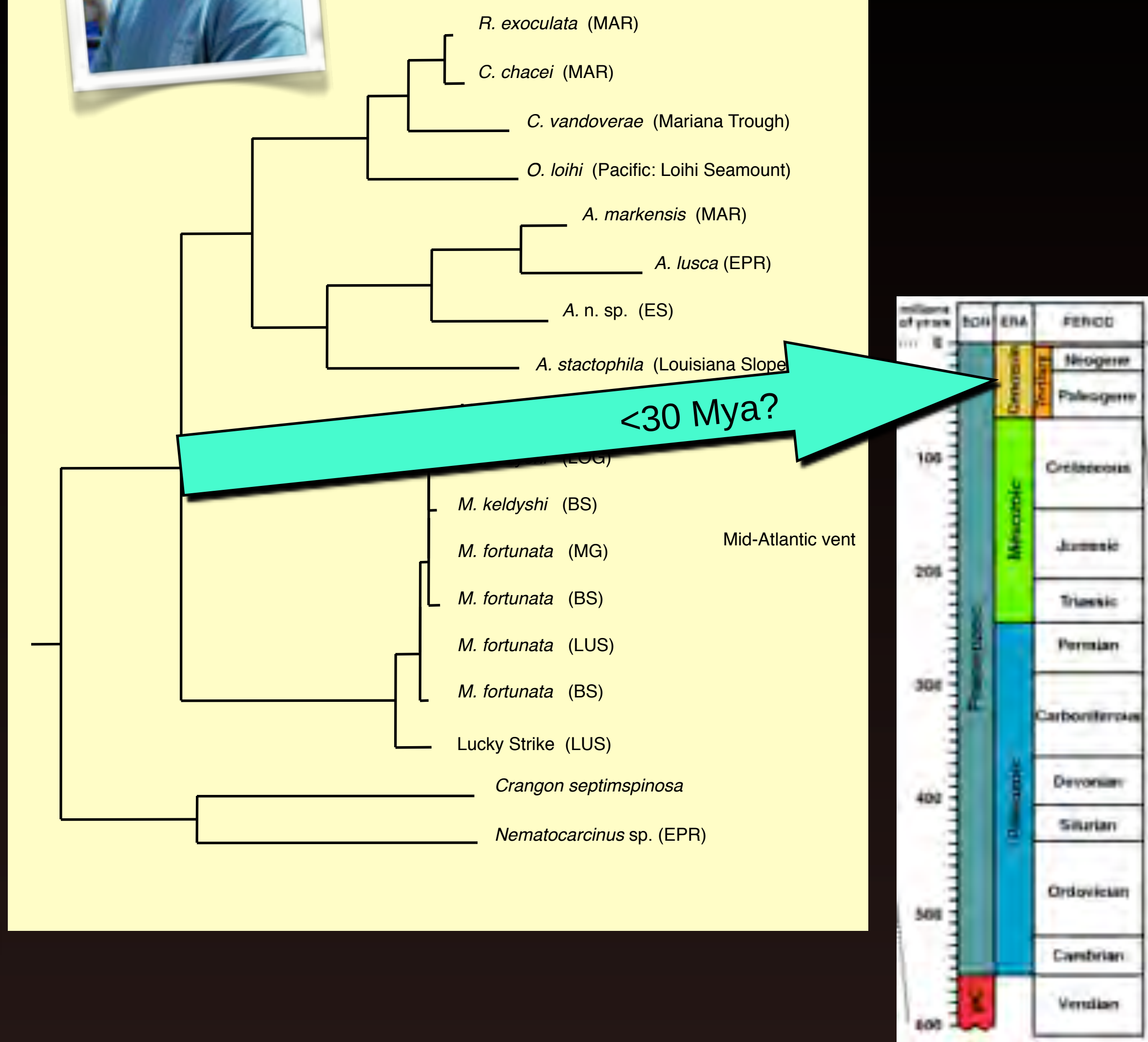




Bresiliid shrimp

Shank, Halanych, Black, Lutz & Vrijenhoek (1999) *Molecular Phylogenetics and Evolution* **12**, 244-254.

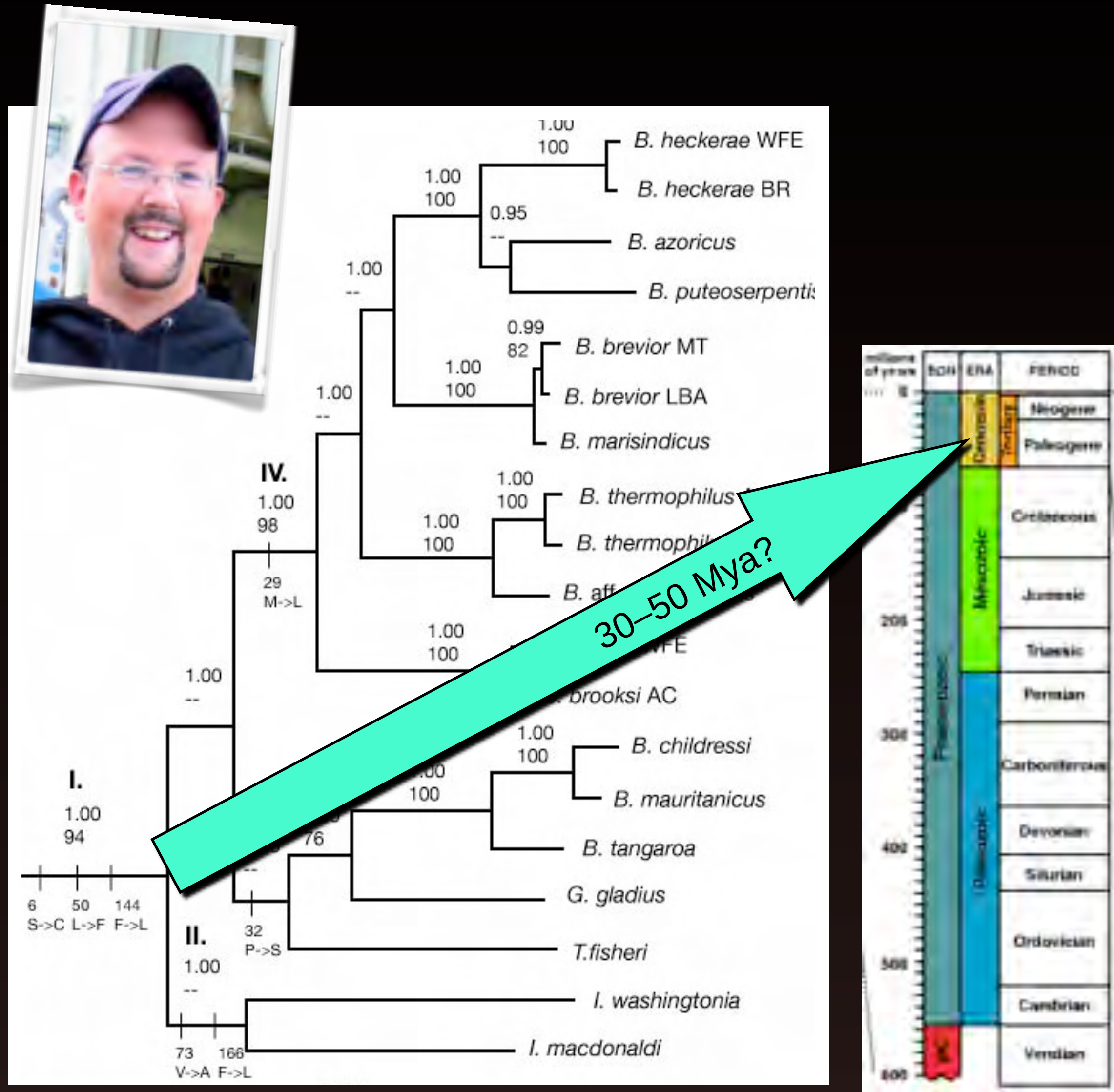
COI



Bathymodiolin mussels

Jones, Won, Maas, Smith, Lutz & Vrijenhoek (2005) *Marine Biology* 148:841-851

combined Bayesian analysis of *COI*, *ND4*, *18S* & *28S* rRNA



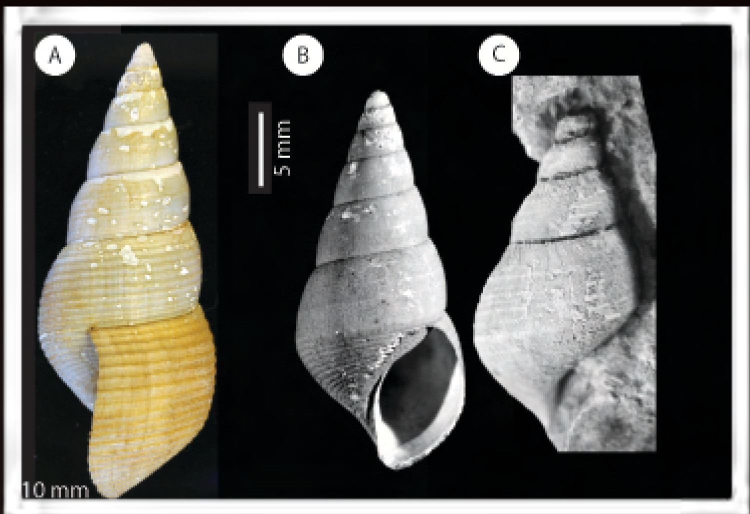
Julien Lorien, Steffen Kiel, et al. *pers. comm.*

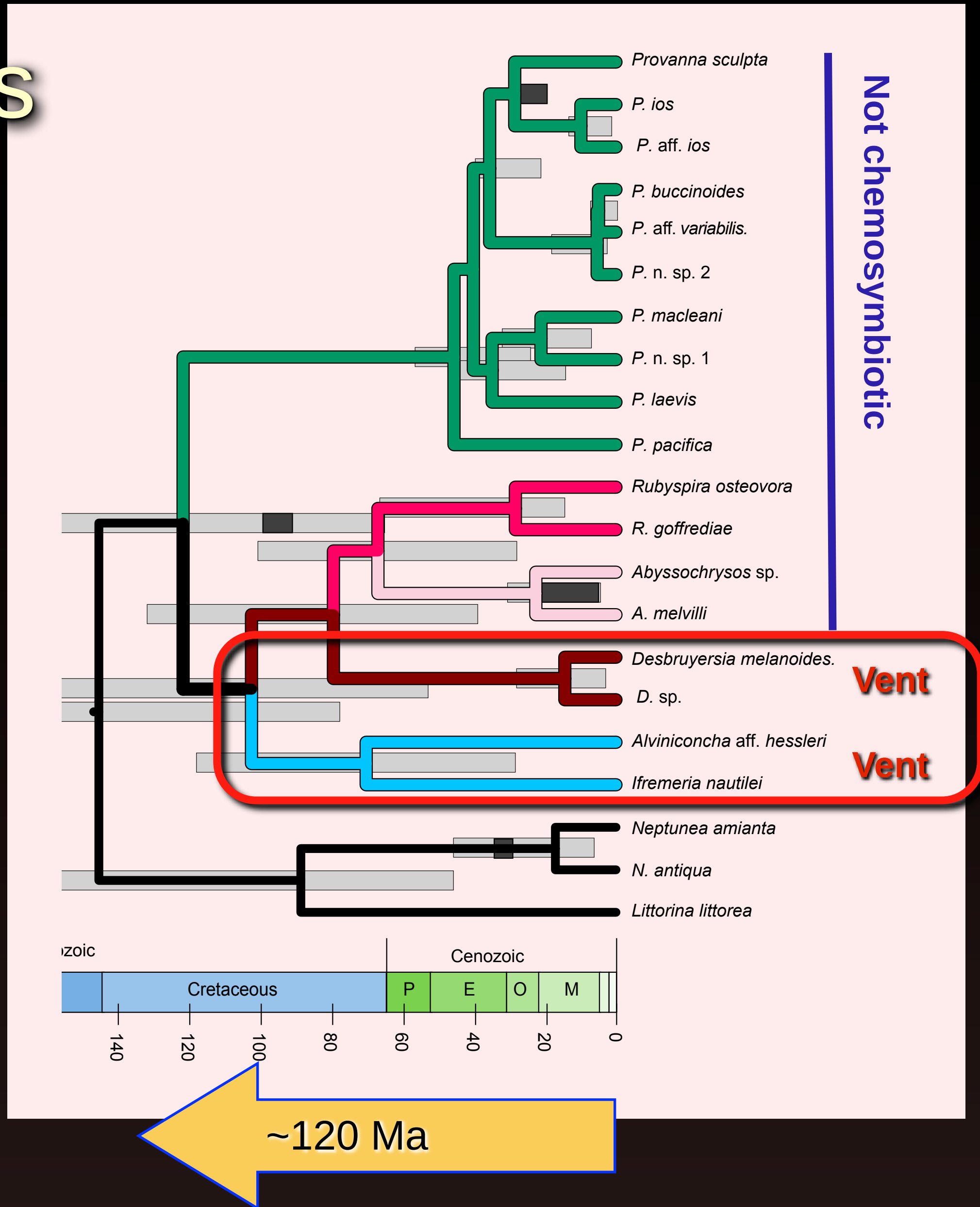
~ 45–50 Mya

“Provanid” snails

- Paraphyletic with Abyssochrysidae
- Not vent restricted: also seeps, wood-falls, whale-falls.
- Mostly non-chemosymbiotic.

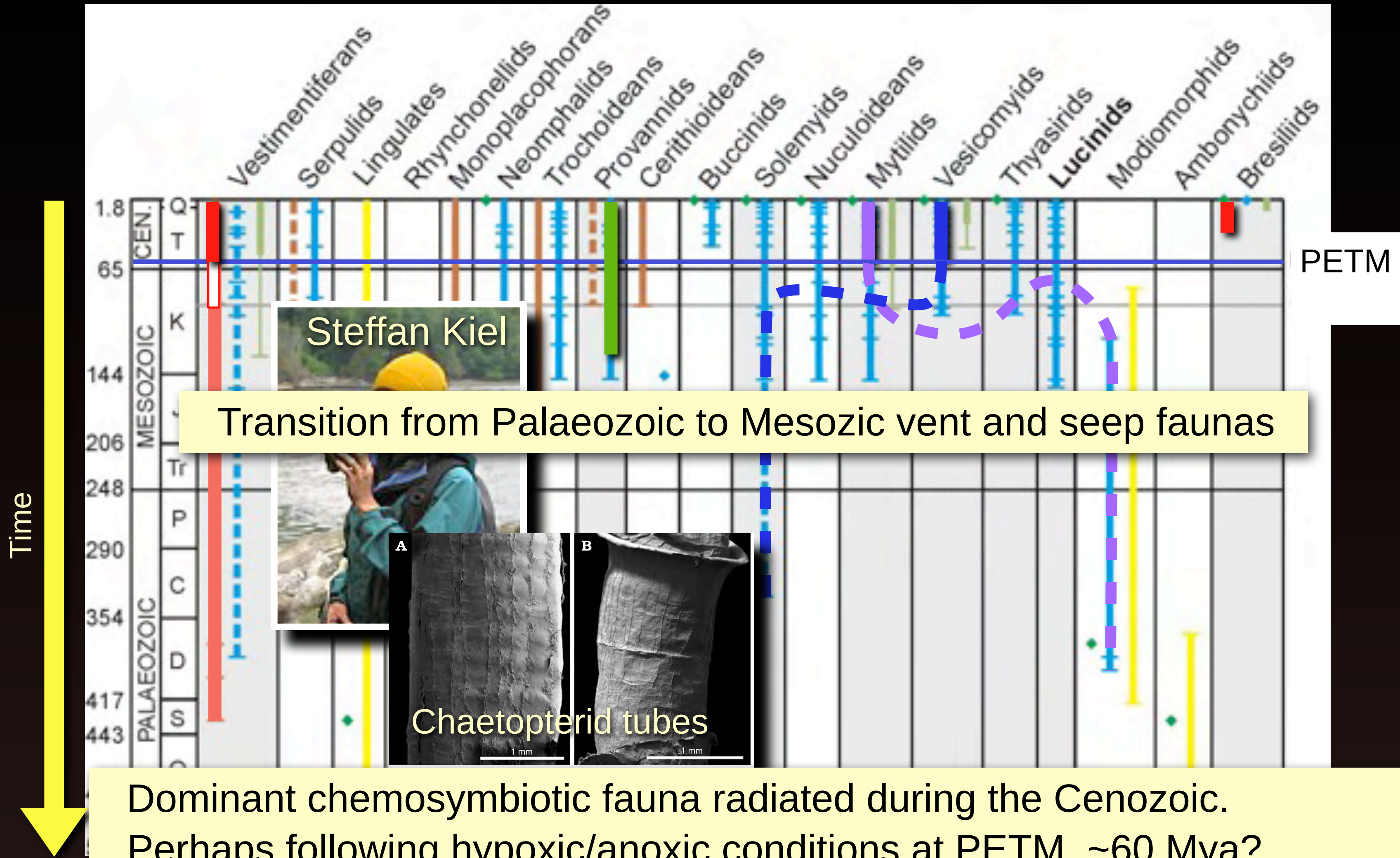
combined Bayesian analysis of *COI*, *16S*, *12S*, *18S*, *28S* rRNA & *Histone-3*





Johnson *et al.* (2010). *Biological Bulletin* **219**, 166-177.

Life at oxic/anonic interface is risky



Transition from Palaeozoic to Mesozic vent and seep faunas

Dominant chemosymbiotic fauna radiated during the Cenozoic.
Perhaps following hypoxic/anoxic conditions at PETM, ~60 Mya?

Little & Vrijenhoek (2003) *Trends in Ecology and Evolution* 18: 582-588

Oxygen and evolutionary patterns in the sea: Onshore/ offshore trends and recent recruitment of deep-sea faunas

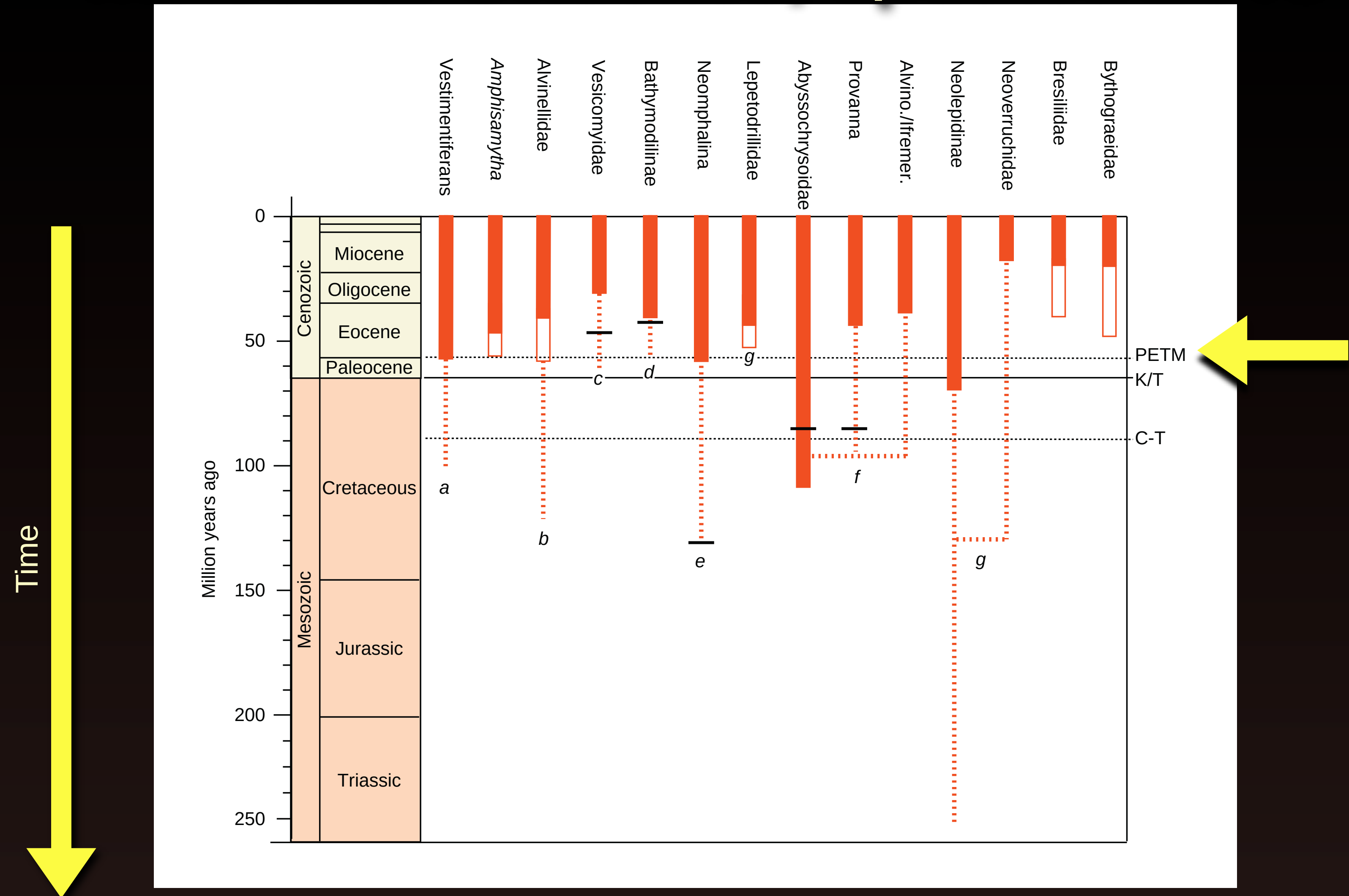
DAVID K. JACOBS & DAVID R. LINDBERG

Proc. Natl. Acad. Sci. USA 95: 9396–9401 (1998)

Given a narrow existence at the oxic/ anoxic interface, vent taxa should be especially susceptible to regional extinctions (Little & Vrijenhoek 2003**)**

	STAGE	AGE	ANOXIC/DYSOXIC EVENTS	OFFSHORE BIOTA		ONSHORE BIOTA	
CENOZOIC	Quat	1.6					Oph
	Plio	5.2					Oph
	Mio3	10.4					Oph
	Mio2	16.3			Oph		Oph
	Mio1	23.3					Oph
	Oli2	29.3					Oph
	Oli1	35.4		30	N		Oph
	Eoc3	38.6				30	Oph
	Eoc2	50.0			Oph	30	Oph
	Eoc1	56.5		30	Oph	30	Oph
	Pal2	60.5	G,I		Oph	30	Oph
	Pal1	65.0				30	Oph
CRETACEOUS	Maa	74.0		30	Oph	30	Oph
	Cmp	83.0		10	Oph	10	Oph
	San	86.6	R	10		10	Oph
	Con	88.5	R			2	Oph
	Tur	90.4				2	Oph
	Cen	97.0	GI		N	2	Oph
	Alb	112.0	GI,GI			1	
	Apt	124.5	G,I	0		1	
	Bar	132.0	R+		N	1	Oph
	Hau	135.0		1	N	1	
	Vlg	140.5	R,I	0		1	Oph
	Ber	145.5				1	Oph
JURASSIC	Tth	152.1		0		1	Oph
	Kim	154.7	R+		N		
	Oxf	157.1					Oph
	Clv	161.3	R				Oph
	Bth	166.1					Oph
	Baj	173.5					Oph
	Aal	178.0					
	Toa	187.0	G,I				
	Plb	194.5	RI		N		Oph
	Sin	203.5	R		N		N
	Het	208.0					N
TRIAS	Rht	210.0					
	Nor	223.0	R?				
	Crn	235.0	R,I				
	Tr2	241.0			N		N
	Tr1	245.0	G?				

Molecular evidence, updated 2013



Vrijenhoek (2013) On the instability and evolutionary age of deep-sea chemosynthetic communities. Deep-Sea Research II Available online 8 December 2012: http://dx.doi.org/10.1016/j.dsr1012.2012.1012.1004.

Part 3: Vent habitats are ephemeral

"... an individual vent area has a finite lifetime. We discovered several dead vent areas along the axial ridge, recognizable by the abundant dead clam shells that were slowly dissolving away..." (Corliss *et al.* 1979 *Science* 203:1073-1083, p. 1079)

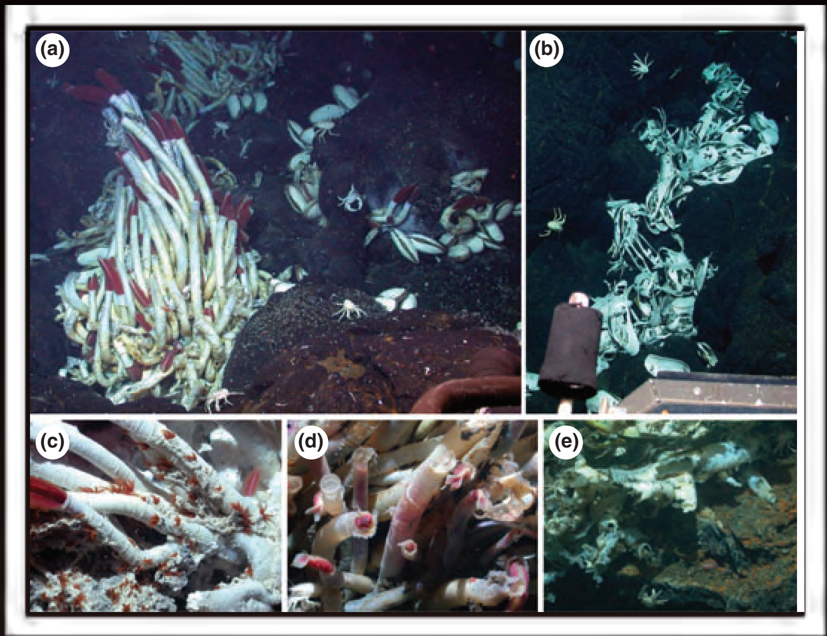
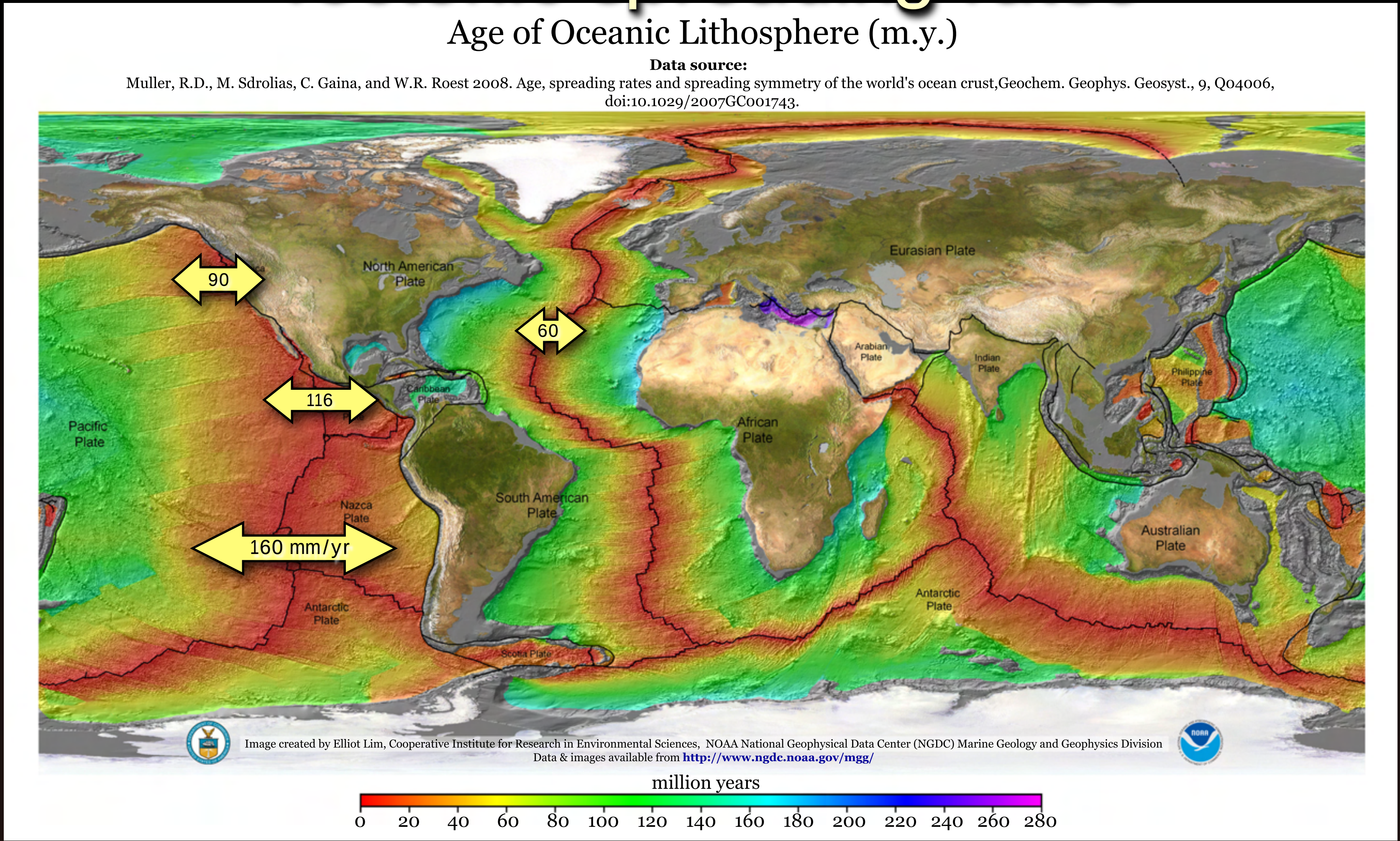


Fig. 1: Vrijenhoek (2010) *Molecular Ecology* **19**, 4391-4422.

Patchy distribution of living and dead vent organisms

Life is short!

Tectonic spreading rates



Habitat turnover varies with spreading rate

Juniper & Tunnicliffe (1997) Crustal accretion and the hot vent ecosystem. *Philosophical Transactions: Mathematical, Physical and Engineering Sciences* **355**, 459-474.

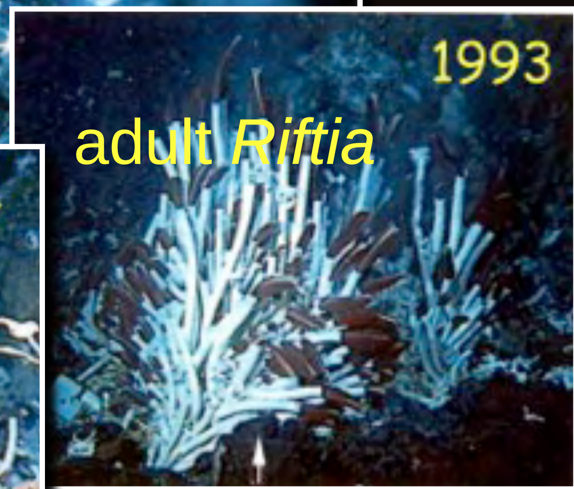
Birth of vents

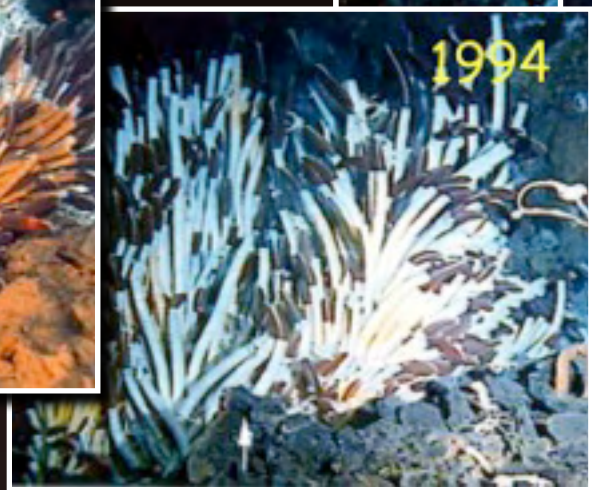
Spreading rate: 116 mm/yr

Shank et al. 1998 *Deep-sea Research* 45: 465-515

9°50' N

April eruption repaves vent field





Death of habitat patches

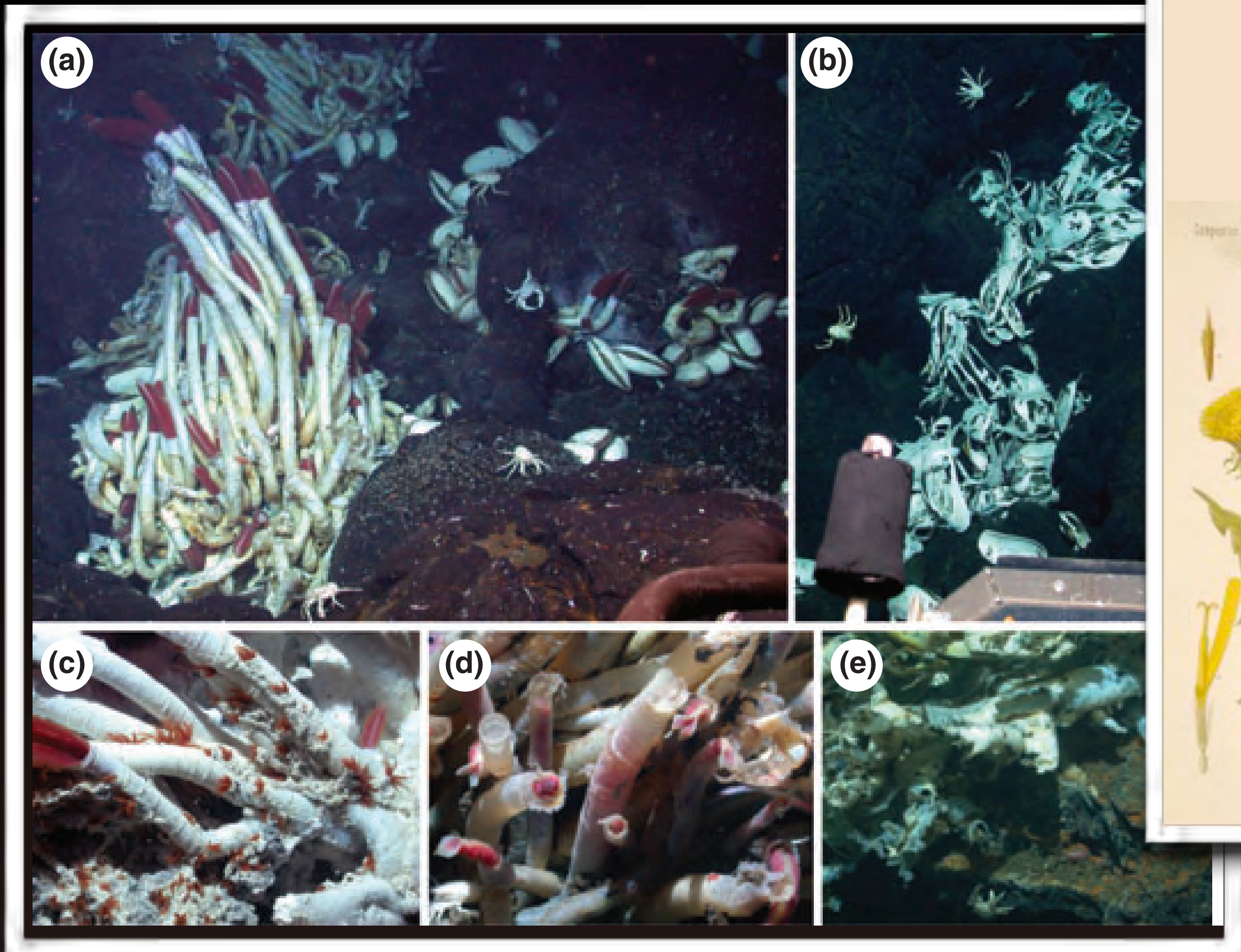


Fig. 1: Vrijenhoek (2010) *Molecular Ecology* **19**, 4391-4422.

Weedy species?

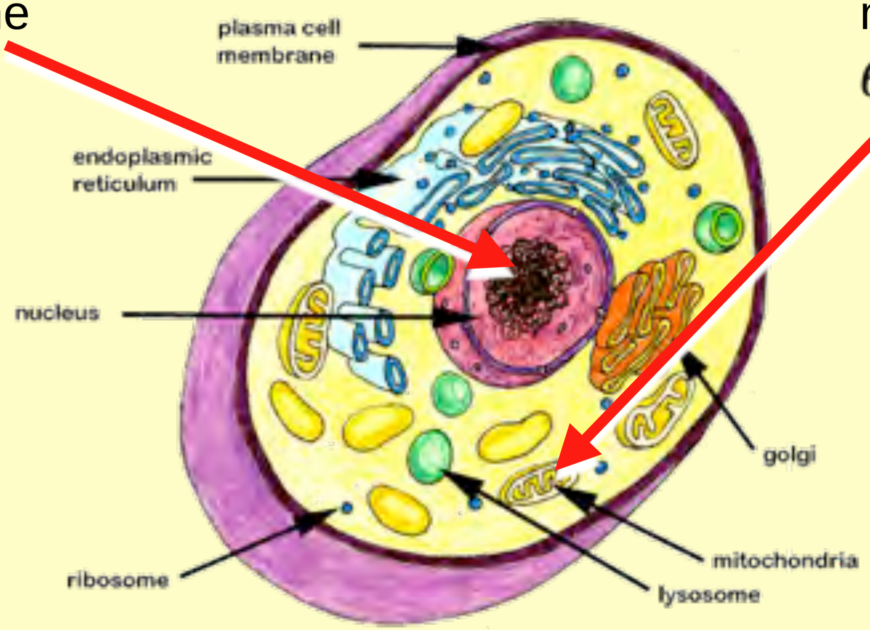
- high fecundity
- rapid growth
- early maturity
- effective dispersal

MOLECULAR DIVERSITY

θ = normalized gene diversity
μ = mutation rate (per nucleotide per generation)
N_e = genetically effective population size

nuclear gene
$\theta = 4N_e\mu$

mitochondrial gene
$\theta = 2N_e\mu$



METAPOPULATION PROCESSES

N_e = genetically effective population size

Harmonic mean of N_t in each generation

$$\tilde{N}_e = \frac{1}{\sum \frac{1}{N_t}}$$

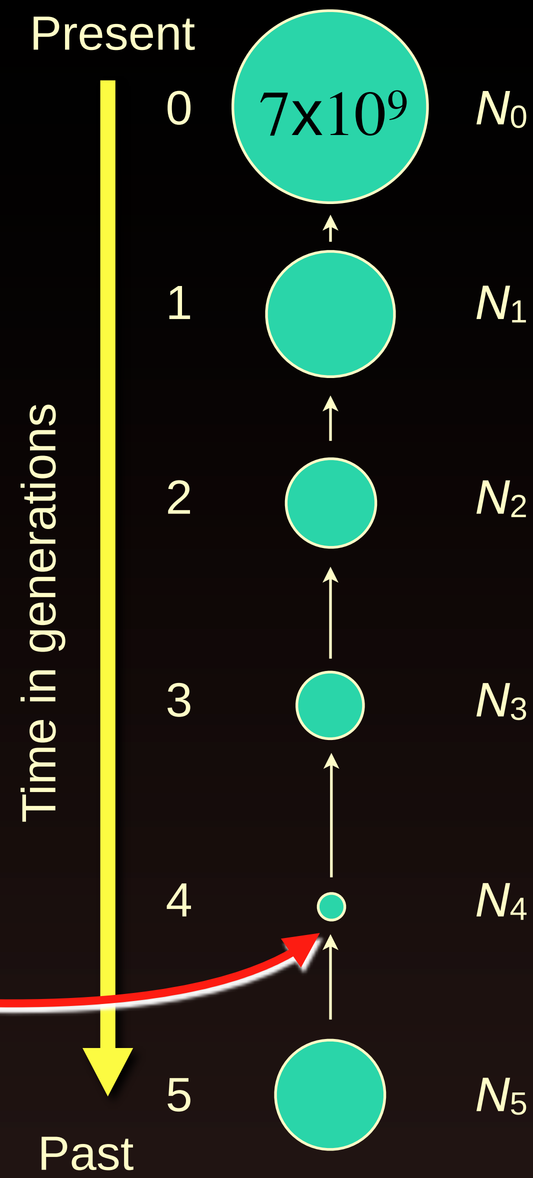
Population bottlenecks greatly influence N_e

Rare alleles are lost

$$\theta = 2N_e\mu$$

long-term N_e for humans ≈ 10,000 females

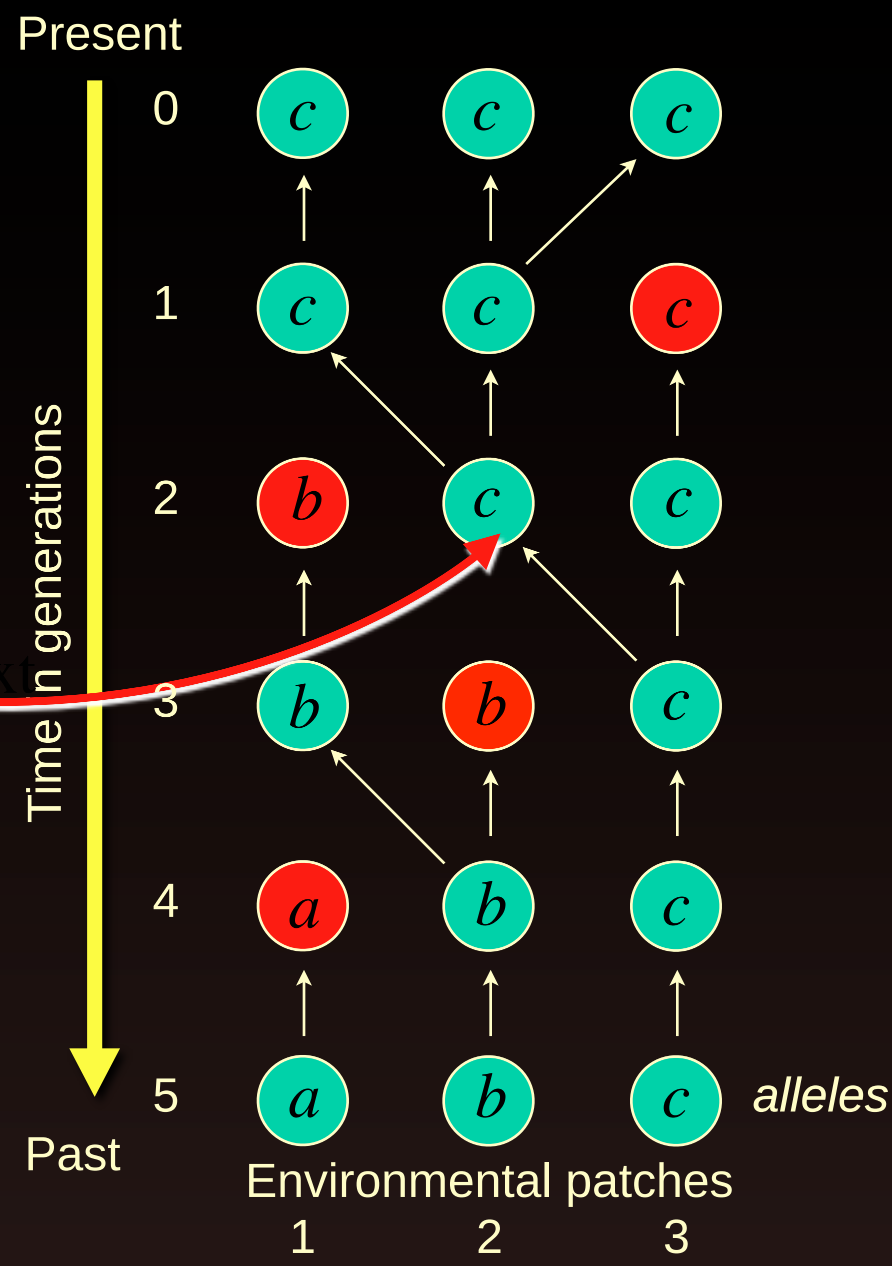
Takahata *et al.* 1995. *Theoretical Population Biology* 48:198-221



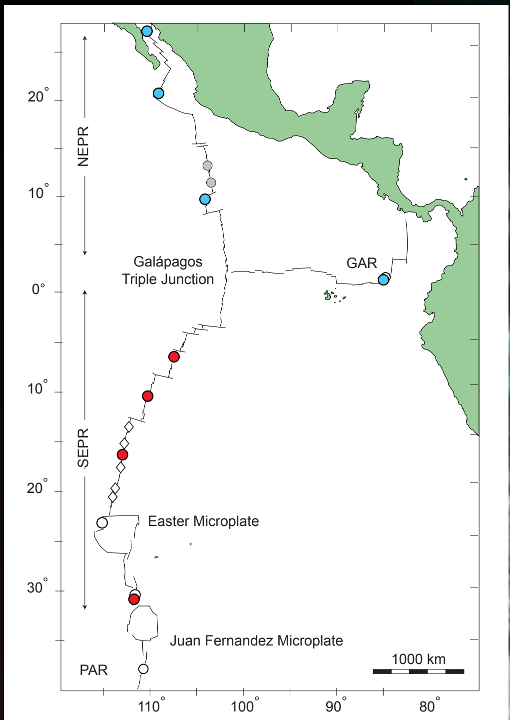
Extinction (λ) & colonization (m)

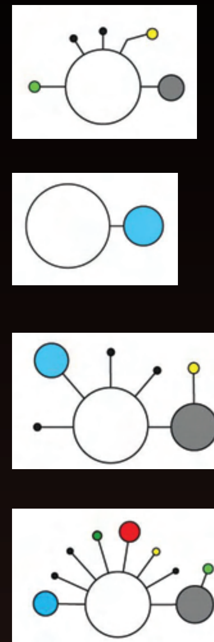
τ = time (in generations) to most recent common ancestor = 2

- As tempos of λ and m increase, τ becomes shorter
- i.e. patches = rapidly coalesce on a single common ancestor.



Demographic instability and genetic diversity in *Riftia* populations



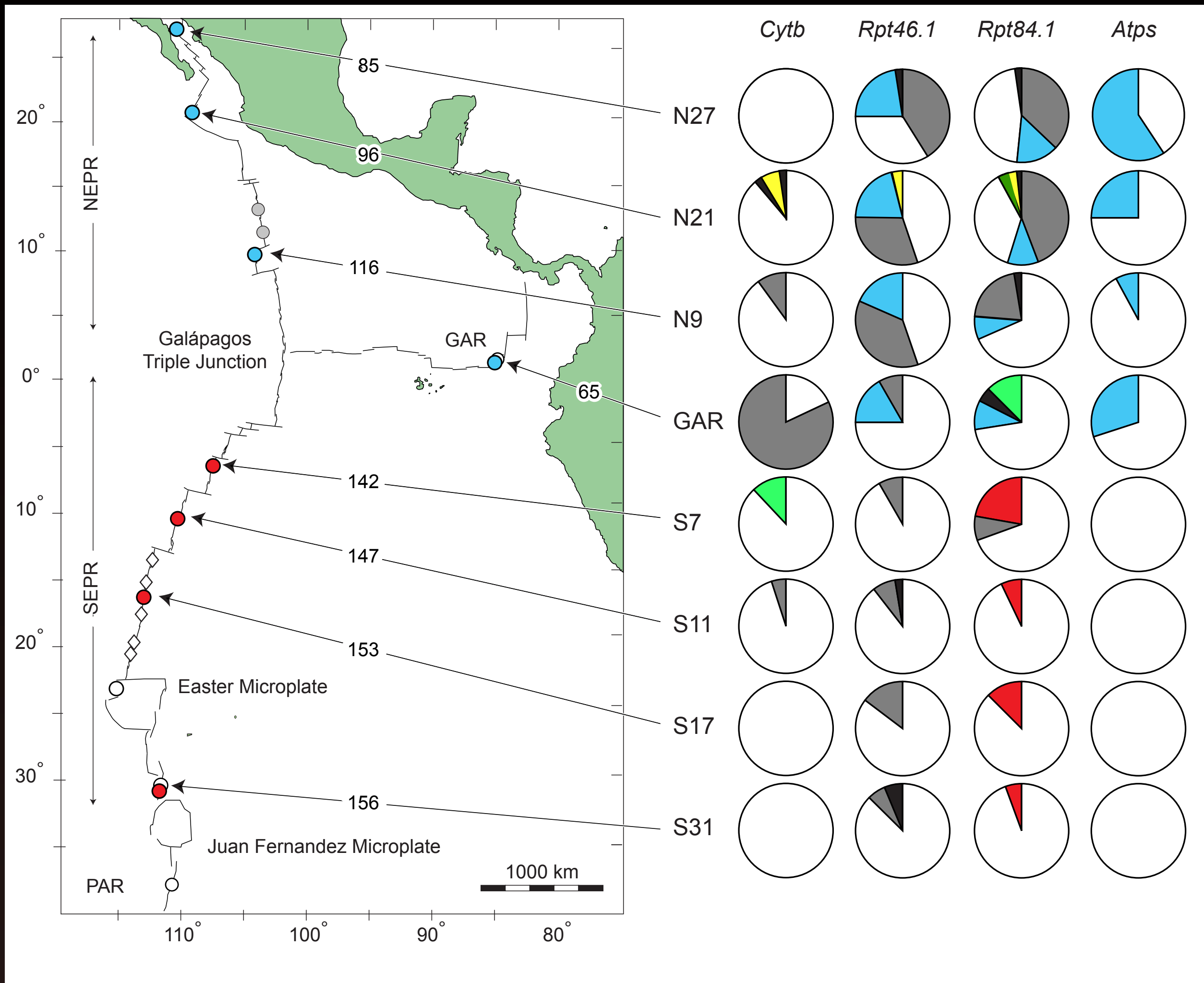


Coykendall, Johnson, Karl, Lutz & Vrijenhoek (2011) *BMC Evolutionary Biology* 11, 98 (11 pp).

- Very simple gene networks.
- Size of ball represents frequency of DNA sequence variant for each gene.

Spreading rates

Spreading rates (mm/yr) Gene frequencies



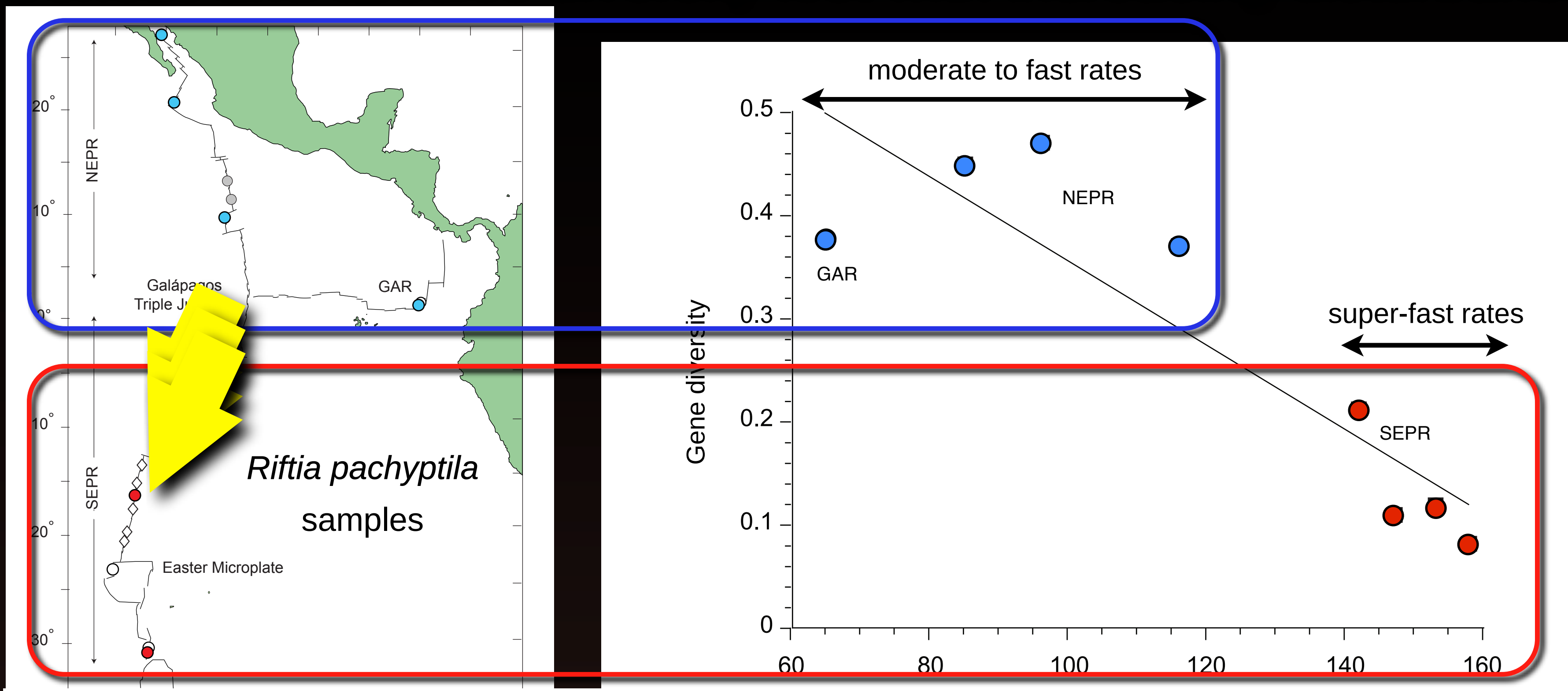
Rare alleles

7

tend to be lost with bottlenecks

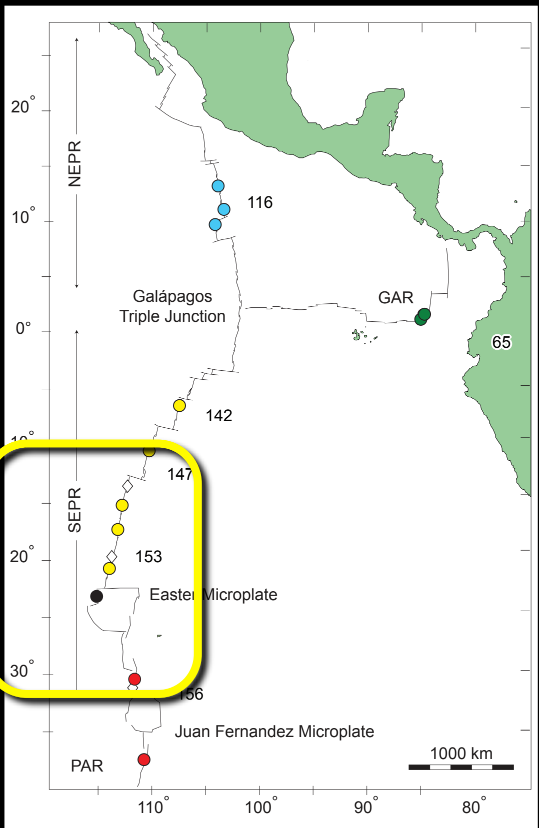
2

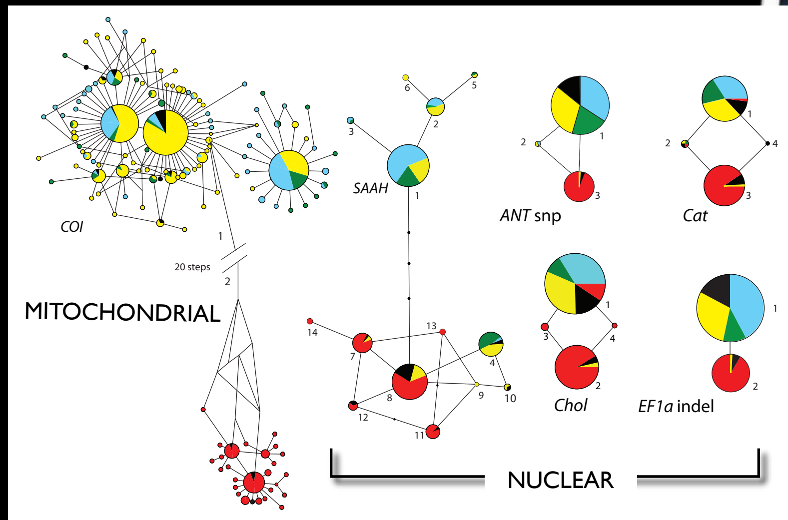
Genetic and species diversity lost with increasing disturbance

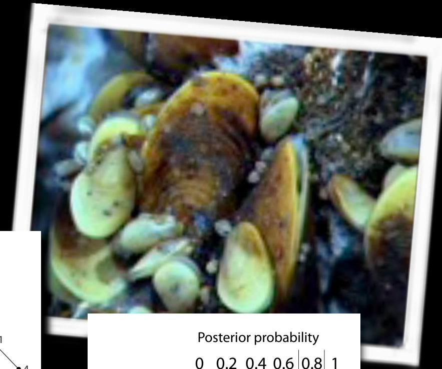


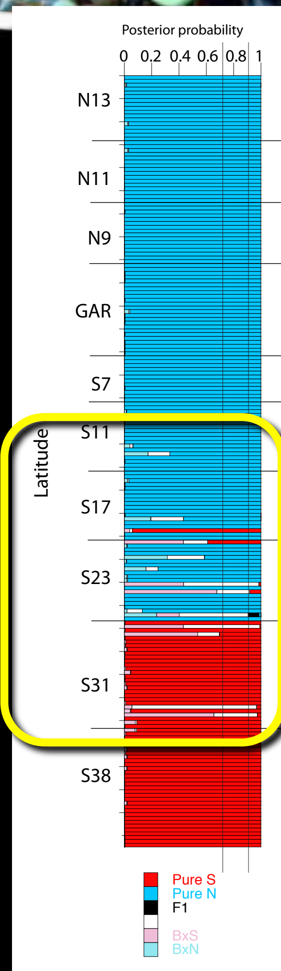
- Genetic diversity also reduced in clams, limpets, and several worms distributed along the southern East Pacific Rise (review: Vrijenhoek 2010, *Molecular Ecology* **19**, 4391-441).
- Species diversity is substantially lower along the SEPR (Bachraty *et al. Deep Sea Research Part I*: **56**, 1371-1378).
- Re-invasions of SEPR from NEPR.

Bathymodiolus thermophilus complex hybrid zone



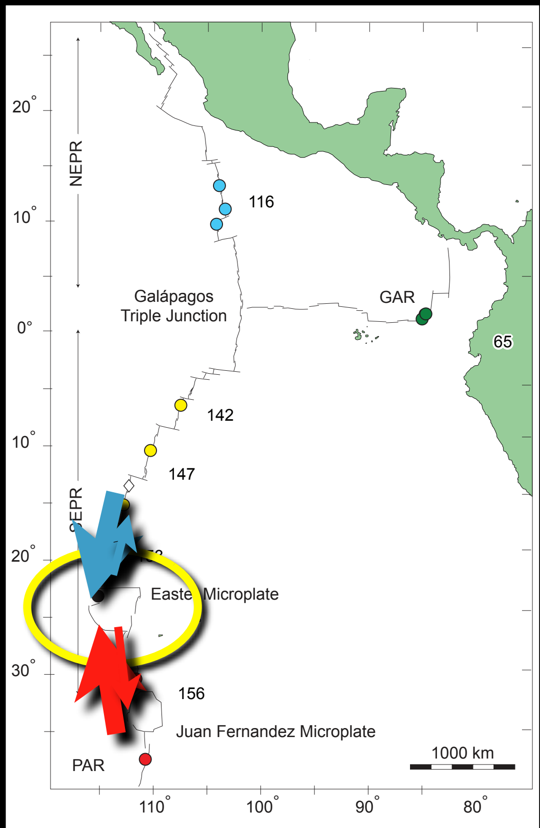


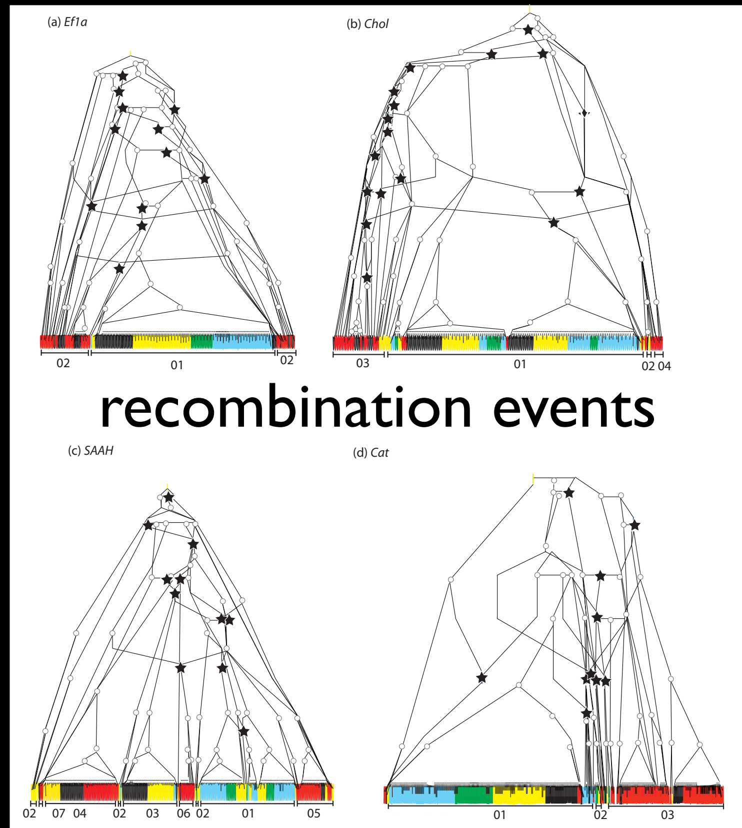




Johnson, Won, Harvey, Vrijenhoek: A hybrid zone between *Bathymodiolus* mussel lineages from eastern Pacific hydrothermal vents. *BMC Evolutionary Biology* 2013, 13:21.

Bathymodiolus thermophilus and *B. antarcticus* new species





History of contact, partial isolation and re-connection

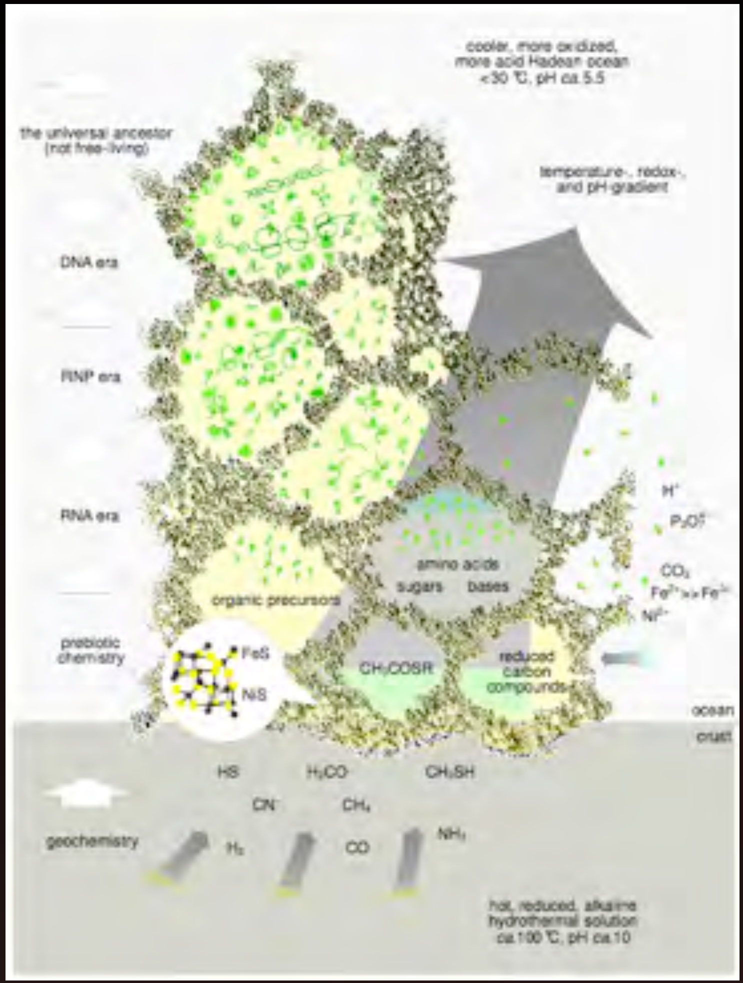
Conclusion: vents unstable on long and short timespans

Does instability of hydrothermal vents preclude origin of life?
e.g., Miller & Bada (1988)

Can alkaline vents (e.g., Lost City on Mid-Atlantic Ridge) provide an alternative?

e.g., Martin, Baross, Kelley, Russell (2008)

More to come on this subject...



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