Cambridge University Press & Assessment 978-1-009-63377-2 — The Origin and Nature of Life on Earth Eric Smith , Harold J. Morowitz Table of Contents <u>More Information</u>

Contents

	Preface						
	Acknowledgments						
1	The planetary scope of biogenesis: the biosphere is the fourth geosphere						
	1.1 A new way of being organized			1			
		1.1.1	Life is a planetary process	2			
		1.1.2	Drawing from many streams of science	5			
	1.2 The organizing concept of geospheres						
		7					
		1.2.2	The interfaces between geospheres	8			
		1.2.3	The biosphere is the fourth geosphere	10			
	1.3	Summ	ary of main arguments of the book	12			
	1.3.1 An approach to theory that starts in the phenomenology of th						
			biosphere	13			
		1.3.2	Placing evolution in context	16			
		1.3.3	Chance and necessity understood within the larger framework				
			of phase transitions	22			
		1.3.4	The emergence of the fourth geosphere and the opening of				
			organic chemistry on Earth	28			
	1.4	The or	rigin of life and the organization of the biosphere	31			
2	The o	organiza	ation of life on Earth today	35			
	2.1	Many	forms of order are fundamental in the biosphere	35			
		2.1.1	Three conceptions of essentiality	37			
		2.1.2	The major patterns that order the biosphere	37			
	2.2	Ecosy	stems must become first-class citizens in biology	40			
		2.2.1	No adequate concept of ecosystem identity in current biology	40			
		2.2.2	Ecosystems are not super-organisms	41			
		2.2.3	Ecological patterns can transcend the distinction between				
	individual and community dynamics						

v

vi			Contents			
	2.3	 2.3 Bioenergetic and trophic classification of organism-level and ecosystem-level metabolisms 2.3.1 Divergence and convergence: phylogenetic and typological classification 				
		schemes				
		2.3.2	The leading typological distinctions among organisms	45		
		2.3.3	Anabolism and catabolism: the fundamental dichotomy			
			corresponding to the biochemical and ecological partitions	50		
		2.3.4	Ecosystems, in aggregate function, are simpler and more			
		universal than organisms				
		2.3.5	Universality of the chart of intermediary metabolism	56		
	2.4	Bioch	emical pathways are among the oldest fossils on Earth	58		
		2.4.1	Evidence that currently bounds the oldest cellular life	58		
		2.4.2	Disappearance of the rock record across the Hadean horizon	58		
		2.4.3	Metabolism: fossil or Platonic form?	59		
	2.5 The scales of living processes			60		
		2.5.1	Scales of biochemistry	60		
		2.5.2	Scales of physical organization	64		
		2.5.3	Scales of information and control	64		
	2.6	Divers	sity within the order that defines life: the spectrum from			
		necess	sity to chance	66		
		2.6.1				
			evolution to origins	67		
			Natural selection for change and for conservation	68		
			Different degrees of necessity for different layers	68		
	2.7	.7 Common patterns recapitulated at many levels		70		
3	The g	eochen	nical context and embedding of the biosphere	73		
	3.1	Order	in the abiotic context for life	73		
		3.1.1	Many points of contact between living and non-living			
			energetics and order	74		
		3.1.2	Barriers, timescales, and structure	75		
	3.2	Activa	ation energy and relaxation temperature regimes in abiotic			
	chemistry and metabolism		stry and metabolism	75		
	3.3	Stella	r and planetary systems operate in a cascade of disequilibria	77		
		3.3.1	The once young and now middle-aged Sun	77		
		3.3.2	Disequilibria in the Earth are gated by a hierarchy of phases			
			and associated diffusion timescales	82		
	3.4	The re	estless chemical Earth	106		
		3.4.1	Mafic and felsic: ocean basins and continental rafts	107		
		3.4.2	Three origins of magmas	108		

4

		Contents	vii
3.5	The d	ynamics of crust formation at submarine spreading centers	115
0.10	3.5.1	Melt formation and delivery at mid-ocean ridges	116
	3.5.2	Tension, pressure, brittleness, and continual fracturing	117
	3.5.3	Fractures, water invasion, buoyancy, and the structure of	
		hydrothermal circulation systems	119
	3.5.4	Chemical changes of rock and water in basalt-hosted systems	126
	3.5.5	Serpentinization in peridotite-hosted hydrothermal systems	131
	3.5.6	Principles and parameters of hydrothermal alteration: a summary	138
3.6	The pa	arallel biosphere of chemotrophy on Earth	140
	3.6.1	The discovery of ecosystems on Earth that do not depend on	
		photosynthetically fixed carbon	140
	3.6.2	The evidence for a deep (or at least subsurface), hot (or at least	
		warm) biosphere	142
	3.6.3	The complex associations of temperature, chemistry, and	
		microbial metabolisms	148
	3.6.4	Major classes of redox couples that power chemotrophic	
		ecosystems today	150
	3.6.5	Why the chemotrophic biosphere has been proposed as a	
		model for early life	155
	3.6.6	Differences between hydrothermal systems today and those in	
		the Archean	157
	3.6.7	1 25	167
3.7	Expec	stations about the nature of life	168
The a	architec	ture and evolution of the metabolic substrate	170
4.1	Metab	oolism between geochemistry and history	170
4.2	Modu	larity in metabolism, and implications for the origin of life	173
	4.2.1	Modules and layers in metabolic architecture and function	173
	4.2.2	Reading through the evolutionary palimpsest	174
	4.2.3	Support for a progressive emergence of metabolism	175
	4.2.4	Feedbacks, and bringing geochemistry under organic control	175
	4.2.5	The direction of propagation of constraints: upward from	
		metabolism to higher-level aggregate structures	176
4.3	The co	ore network of small metabolites	178
	4.3.1	The core in relation to anabolism and catabolism	180
	4.3.2	The core of the core	182
	4.3.3	Precursors in the citric acid cycle and the primary biosynthetic	
		pathways	183
	4.3.4	One-carbon metabolism in relation to TCA and anabolism	192
	4.3.5	The universal covering network of autotrophic carbon fixation	196
	4.3.6	Description of the six fixation pathways	200

viii		Contents				
	4.3.7	Pathway alignments and redundant chemistry	214			
	4.3.8	Distinctive initial reactions and conserved metal-center enzymes	216			
	4.3.9	The striking lack of innovation in carbon fixation	217			
4.4	A reco	onstructed history of carbon fixation, and the role of innovation				
	constr	aints in history	219			
	4.4.1	Three reasons evolutionary reconstruction enters the problem				
		of finding good models for early metabolism	219			
	4.4.2	Phylogenetic reconstruction of functional networks	221			
	4.4.3	Functional and comparative assignment of biosynthetic				
		pathways in modern clades	224			
	4.4.4	A maximum-parsimony tree of autotrophic carbon-fixation				
		networks	230			
	4.4.5	A reconstruction of Aquifex aeolicus and evidence for broad				
		patterns of evolutionary directionality	241			
	4.4.6	The rise of oxygen and the attending change in metabolism				
		and evolutionary dynamics	244			
	4.4.7	Chance and necessity for oxidative versus reductive TCA	248			
4.5	Cofac	tors and the first layer of molecular-organic control	249			
	4.5.1	The intermediate position of cofactors, feedback, and the				
		emergence of metabolic control	249			
	4.5.2	Key cofactor classes for the earliest elaboration of				
		metabolism	253			
	4.5.3	The complex amino acids as cofactors	261			
	4.5.4	Situating cofactors within the elaboration of the				
		small-molecule metabolic substrate network	262			
	4.5.5	Roles of the elements and evolutionary convergences	264			
4.6	Long-	loop versus short-loop autocatalysis	268			
4.7	Summ	nary: continuities and gaps	269			
4.8	Graph	ical appendix: definition of notations for chemical reaction				
	netwo	rks	270			
	4.8.1	Definition of graphic elements	271			
5 Hig	gher-level	structures and the recapitulation of metabolic order	273			
5.1		ed subsystems and shared patterns	273			
	5.1.1	Shared boundaries: correlation is not causation	274			
	5.1.2	Different kinds of modularity have changed in different				
		directions under evolution	275			
5.2	Metab	oolic order recapitulated in higher-level aggregate structures	277			
5.3						
	5.3.1	Context for the code: the watershed of the emergence of	278			
		translation	283			
	5.3.2	The modern translation system could be a firewall	285			

			Contents	ix
		5.3.3	What kinds of information does a pattern contain, and	
			how much?	287
		5.3.4	Part of the order in the code is order in the amino acid inventory	290
		5.3.5	Four major forms of metabolic order in the code	291
		5.3.6	Rule combinations	302
		5.3.7	Accounting for order	306
		5.3.8	A proposal for three phases in the emergence of translation	319
	5.4	The es	ssential role of bioenergetics in both emergence and control	322
		5.4.1	Energy conservation, energy carriers, and entropy	323
		5.4.2	Three energy buses: reductants, phosphates, and protons	325
		5.4.3	The cellular energy triangle	328
		5.4.4	Geochemical context for emergence of redox and phosphate	
			energy systems	330
	5.5	The th	ree problems solved by cellularization	331
		5.5.1	Distinct functions performed by distinct subsystems	332
		5.5.2	An exercise in transversality	333
	5.6	The pa	artial integration of molecular replication with cellular metabolism	337
	5.7	Cellul	ar life is a confederacy	338
5	The e	mergen	ce of a biosphere from geochemistry	340
	6.1	-	universals to a path of biogenesis	340
		6.1.1	On empiricism and theory: evaluating highly incomplete	
			scenarios	341
		6.1.2		344
		6.1.3	An emergent identity for metabolism or the emergence of a	
			control paradigm?	349
	6.2	Planet	ary disequilibria and the departure toward biochemistry	355
		6.2.1		356
		6.2.2	Species that bridge geosphere boundaries to form the great	
			arcs of planetary chemical disequilibrium	359
		6.2.3	Mineral-hosted hydrothermal systems are pivotal in the sense	
			that they are key <i>focusing centers</i> for chemical disequilibria	366
		6.2.4	The alkaline hydrothermal vents model	368
	6.3	Stages	s in the emergence of the small-molecule network	370
		6.3.1	Carbon reduction and the first $C-C$ bonds	371
		6.3.2	rTCA: the potential for self-amplification realized and the first	
			strong selection of the metabolic precursors	384
		6.3.3	Reductive amination of α -ketones and the path to amino acids	387
		6.3.4	A network of sugar phosphates and aldol reactions	388
	6.4		arly organic feedbacks	389
		6.4.1	C–N heterocycles	391
		6.4.2	Cyclohydrolase reactions: purine nucleotides and folates	396

х		Contents		
		6.4.3 Thiamin-like chemistry: lifting rTCA off the rocks	398	
		6.4.4 Biotin: uses in rTCA and in fatty acid synthesis	399	
		6.4.5 Alkyl thiols	399	
	6.5	Selection of monomers for chirality	400	
		6.5.1 Degree of enantiomeric selection at different scales	400	
		6.5.2 Mechanisms and contexts for stereoselectivity	401	
		6.5.3 The redundancy of biochemical processes simplifies the		
		problem of chiral selection	402	
	6.6	The oligomer world and molecular replication	403	
		6.6.1 Increased need for dehydrating ligation reactions	404	
		6.6.2 Coupling of surfaces and polymerization	405	
		6.6.3 Distinguishing the source of selection from the emergence of		
		memory in a ribozyme-catalyzed era	407	
	6.7	Transitions to cellular encapsulation in lipids	409	
		6.7.1 Contexts that separate the aggregate transformation into		
		independent steps	412	
	6.8	The advent of the ribosome	413	
		6.8.1 The core and evolution of catalysis	414	
		6.8.2 Catalytic RNA and iron	416	
		6.8.3 The origin of translation and the three-base reading frame	417	
	6.0	6.8.4 Reliable translation and the birth of phylogeny	419	
	6.9	The major biogeochemical transitions in the evolutionary era	420	
	6.10	Tentative conclusions: the limits of narrative and the way forward	421	
7	The p	phase transition paradigm for emergence	424	
	7.1	Theory in the origin of life	424	
		7.1.1 What does a phase transition framing add to the search for		
		relevant environments and relevant chemistry?	426	
	7.2	Arriving at the need for a phase transition paradigm	427	
		7.2.1 Why there is something instead of nothing	428	
		7.2.2 Selecting pattern from chaos in organosynthesis	430	
		7.2.3 The phase transition paradigm	431	
		7.2.4 Developing the stability perspective	432	
		7.2.5 A chapter of primers	435	
	7.3	Large deviations and the nature of thermodynamic limits	436	
		7.3.1 The combinatorics of large numbers and simplified		
		fluctuation-probability distributions	437	
		7.3.2 Interacting systems and classical thermodynamics	439	
		7.3.3 Statistical roles of state variables	446 451	
	L			
	7.4	Phase transitions in equilibrium systems	452	
		7.4.1 Worked example: the Curie–Weiss phase transition	452	

			Contents	xi
		7.4.2	Reduction, emergence, and prediction	466
		7.4.3	Unpredictability and long-range order	468
		7.4.4	The hierarchy of matter	471
		7.4.5	Parallels in matter and life: the product space of chemical	
			reactions	479
		7.4.6	Oil and water	481
	7.5	The (I	large-deviations!) theory of asymptotically reliable error	
		correc	ction	486
		7.5.1	Information theory as a mirror on thermodynamics	487
		7.5.2	The large-deviations theory of optimal error correction	488
		7.5.3	Transmission channel models	489
		7.5.4	Capacity and error probability	491
		7.5.5	Error correction and molecular recognition in an energetic	
			system	496
		7.5.6	The theory of optimal error correction is thermodynamic	499
		7.5.7	One signal or many?	500
	7.6	Phase	transitions in non-equilibrium systems	501
		7.6.1	On the equilibrium entropy and living systems	502
		7.6.2	Ensembles of processes and of histories	509
		7.6.3	Phase transfer catalysis	510
		7.6.4	A first-order, non-equilibrium, phase transition in the context	
			of autocatalysis	511
			The lightning strike analogy	520
		7.6.6	Conclusion: the frontier in the study of collective and	
			cooperative effects	524
	7.7	Techn	ical appendix: non-equilibrium large-deviations formulae	525
		7.7.1	1	526
		7.7.2	Ordinary power-series generating function and Liouville	
			equation	527
		7.7.3	Escape trajectories and effective potential for non-equilibrium	
			phases	531
		7.7.4	Gaussian fluctuations about stationary-path backgrounds	534
8	Recor	nceptua	lizing the nature of the living state	539
	8.1	Bring	ing the phase transition paradigm to life	539
		8.1.1	Necessary order in the face of pervasive disturbance	542
		8.1.2	The role of phase transitions in hierarchical complex systems	544
		8.1.3	How uniqueness becomes a foundation for diversity	549
		8.1.4	Beyond origins to the nature of the living state	552
	8.2	Metab	polic layering as a form of modular architecture	554
		8.2.1	Herbert Simon's arguments that modularity is prerequisite to	
			hierarchical complexity	554

xii		Contents	
	8.2.2	The modularity argument in a dynamical setting	558
	8.2.3	Error correction from regression to ordered thermal states	558
	8.2.4	The universal metabolic chart as an order parameter	559
	8.2.5	The use of order parameters in induction	561
	8.2.6	Control systems and requisite variety	566
	8.2.7	Biology designs using order parameters	568
8.3	The en	mergence of individuality	569
	8.3.1	Darwinian evolution is predicated on individuality	570
	8.3.2	How unique solutions give rise to conditions that	
		support diversity	572
	8.3.3	The nature of individual identity	575
	8.3.4	Individuality within the structure of evolutionary theory	580
	8.3.5	The ecosystem as community and as entity	584
	8.3.6	Why material simplicity precedes complexity in the phase	
		transition paradigm	586
8.4	The na	ature of the living state	587
	8.4.1	Replicators: a distinction but not a definition	589
	8.4.2	Life is defined by participation in the biosphere	591
	8.4.3	Covalent chemistry flux and other order parameters	591
	8.4.4	The importance of being chemical	593
8.5	The en	rror-correcting hierarchy of the biosphere	597
	8.5.1	The main relation: a general trade-off among stability,	
		complexity, and correlation length	597
	8.5.2	Simple and complex phase transitions	598
	8.5.3	Living matter as active data	601
	8.5.4	Patterns and entities in the biosphere	606
Epilogue			608
Refere	ences		611
Index			660